Bulletin OF THE Museum of Comparative Zoology

Volume 143
1972

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138 U.S.A.

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Museum of
Comparative
Zoology

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VOLUME 143, NUMBER 1
18 FEBRUARY 1972

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN 1863–
BREVIORA 1952–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
OCCASIONAL PAPERS ON MOLLUSKS, 1945–

Other Publications.

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THE ANOLES (SAURIA, IGUANIDAE) OF THE LESSER ANTILLES

JAMES D. LAZELL, JR.[1]

CONTENTS

FOREWORD

This work goes to print somewhat modified from the doctoral dissertation submitted to the University of Rhode Island in May, 1968. The principal modifications have been deletions. Originally written as "the iguanid lizards of the Lesser Antilles," the entire section on *Iguana*—the only other living genus—has been removed and will be published elsewhere. A scathing critique of mathematical approaches to island biogeography has been cut, simply because my emotional involvement against that nefarious pseudoscience precluded a report that was not vindictive and vitriolic.

Most important to me, what now follows seems dry, dull, and stultifying. I tried not to write it that way, for I firmly believe that unless scientists can make their work interesting, or even entertaining, it will not be read, even by their colleagues and fellow specialists. As I read over these pages now, I find scant allusion to what it was like to spend a decade—in the field and in the lab—getting to know this remarkable fauna. Gone from these pages are the perils of caclin bush and huge vipers; nothing remains of giant boas and Cicero parrots; there is no more the taste of salt and blood on the rocks in the surf at Pelikan Cay or Kick-'em-Jenny. Counting subdigital lamellae, or arguing over the best possible species definition, is dull work indeed. Sadly, that is about all that now remains.

It has been over two years since the last revision of this work was done for the University of Rhode Island. I have long moved on to a study of the herpetology and ecology of our coastal islands from Cape Cod to Cape Fear, and have not now time to rewrite this as I did the original. Publi-

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[1] Massachusetts Audubon Society, Lincoln, Mass. 01773.

cation of this work is overdue, in any form, and these are hard times: the cost of a printed page is high indeed. So, to make up for all that what follows lacks, I recommend to you the Lesser Antilles: the sea, the islands, the people, and, of course, the iguanid lizards. In reality, they are very far from dull.

James D. Lazell, Jr.

ABSTRACT. The iguanid lizards of the genus *Anolis* from all islands from the St. Croix Bank southward to the Grenada Bank are reviewed systematically. Two major groups are recognized; the *bimaculatus* group, from the northern islands (St. Croix to Dominica), has three parasternal chevrons attached to dorsal ribs; the *roquet* group, from the southern islands (Martinique to Grenada), has four chevrons attached to ribs.

Nine species of *bimaculatus* group *Anolis* are recognized: *acutus*, *wattsi* (with four subspecies: *wattsi*, *forresti*, and two newly described), *sabanus*, *gingivinus*, *bimaculatus* (with two subspecies: *bimaculatus* and *leachi*), *nubilus*, *lividus*, *marmoratus* (with twelve subspecies: *marmoratus*, *alliaceus*, *girafus*, *setosus*, *kahouannensis*, *speciosus*, *inornatus*, *desiradei*, *chrysops*, *ferreus*, *terraealtae* and *caryae*), and *oculatus* (with four subspecies: *oculatus*, *cabritensis*, *montanus*, and *winstoni*). Morphological, karyotypic, and geographic considerations lead to an opinion that *Anolis acutus* is the primitive member of this group, and that evolution has been in some five stages of radiation; the most recently evolved full species is thought to be *Anolis nubilus*.

The *roquet* group is divided into seven species: *luciae*, *griseus*, *richardi*, *trinitatis*, *aeneus*, *extremus*, and *roquet* (the latter divided into five subspecies: *roquet*, and four newly described). Morphological, karyotypic, and behavioral evidence argues strongly that *Anolis luciae* is the most primitive member of this group, and that *Anolis roquet*, and its subspecies on Martinique, is the most recently evolved. Five stages of invasion and differentiation are envisioned for this group, too.

The theory of species group level taxonomy on oceanic islands is given especial consideration; it is suggested that the "biological" species concept is neither logically nor theoretically applicable in many cases, and that the inclusive evolutionary species concept of Simpson (1961) is required. The geology and climatology of the Lesser Antilles are discussed in detail, and reconstructions of the evolution of the lizards are developed in that context.

THE LESSER ANTILLES: AN INTRODUCTION

> In no other regime on earth do the winds blow so steadily. Life has adjusted to this uniform wind stream in numerous ways.
>
> —Herbert Riehl (1954)

The basin of the Caribbean is the great cul-de-sac of the western North Atlantic. Separated in the north from the Gulf of Mexico by Yucatan and the Greater Antilles, this sea is bounded on the west and south by solid land long known simply as the "Spanish Main," but today composed of the Mexican State of Quintana Roo, the Crown Colony of British Honduras, and the Republics of Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, and Venezuela. The equatorial surface waters of the Atlantic are swept unceasingly into the Caribbean cul-de-sac; to quote Slocum (1900): "the trade winds . . . , produce this current which, in its course . . . , is governed by the coastline of Brazil, Guiana, Venezuela, and, as some would say, by the Monroe Doctrine." This great current of surface water, pouring into the Caribbean cul-de-sac from the southeast, must change direction to get out again in the northeast: it is strained between Cuba and Yucatan into the Gulf of Mexico, fended off by the vast, shallow banks of the Bahamas, and sent ripping through the Straits of Florida to form the Gulf Stream.

The Trade Winds are best regarded as a vector quantity; air, heated in the equatorial area, rises to great elevations, cools, and descends towards the temperate latitudes of the earth; pushing back across the surface, it completes its cycle. At the surface of the earth, convection currents provide a north-to-south Trade Wind component in the northern hemisphere, and an opposite, south-to-north Trade Wind component in the southern hemisphere. The residual inertia of the air mass surrounding a rotating earth provides a continuous east-to-west Trade Wind component. Thus, surface water in the southern Atlantic is literally blown northwestward against the continental mass of South America, whence it is swept into the Caribbean. The Trade Winds themselves sweep into the Caribbean basin from the north and east, unimpeded by any continental barrier.

This simple picture has but one major complication: the earth is tilted on its axis. As the earth orbits the sun, the shortest distance from earth to sun is caused to move from the equator northward and southward, producing the alternating pattern we call seasons. The effects of the seasons are different in tropical regions such as the Caribbean than they are in temperate climes; the sun is always comparatively close, and temperature variations at the earth's surface are therefore comparatively minor. The small fluctuations that do occur, however, may be antecedent to storms whose violence and destructive potential are unmatched by other phenomena of man or nature.

When the shortest distance from the earth to the sun has reached its northernmost limit, the Tropic of Cancer, the summer solstice is reached; as the earth orbits, the shortest distance from the earth to the sun again coincides with the equator, and the autumnal equinox has been attained. From about the summer solstice until after the autumnal equinox the tropical North Atlantic is slightly warmer, on the average, than is the tropical South Atlantic; the northern equatorial air mass is usually somewhat warmer in correspondence, and the upward beginning of the convection currents is, as a result, comparatively strong. Cooler, southern air may sometimes be pushed by the Trade Winds across the equator. The resulting clash of temperatures and pressures can create a sudden "bulge" of rising, warm air in a local field of descending, cool air; this bulge, with its concomitant suction of updraft, may, under the influence of Coriolis effect, begin to swirl: a cyclonic storm may be born. This beginning may occur anywhere in the north equatorial Atlantic from Africa to the Caribbean. Often, there is a tendency for these cyclonic storms to be carried westward by the wind and current; they may be swept into the basin of the Caribbean and, gaining tremendous velocity of rotation, become West Indian Hurricanes. For sheer force, the West Indian Hurricane may be compared only to its sister storm, the Pacific Typhoon.

Across the mouth of the Caribbean cul-de-sac extends an arc of small massifs. Rising independently from the bottom of the sea, these massifs form submarine banks which, in most cases, are today topped by islands: The Lesser Antilles. These islands rake the air and sea pouring into the Caribbean cul-de-sac like the teeth of a gigantic comb. Hurricanes, when their paths are averaged, may show a tendency to approximate the current flow and leave the cul-de-sac in the north and east; but individually they are often deflected southward by the push of the Trade Winds, and the comb of the Lesser Antilles may thus strain out detritus borne across the sea from the west and north. No method for accurately predicting the path of any hurricane has ever been devised.

The Lesser Antilles are truly oceanic islands. Although cycles of glaciation have caused sea level fluctuations probably uniting most of the islands on a given Lesser Antillean submarine bank (see Flint, 1957: 258–271), there is no evidence that any connection has occurred between islands on different banks or from any Lesser Antillean bank to any other land area. Matthew (1915, 1918, and 1930) progressively built the case against continental connections to the Antilles until it was unassailable. The entire polemic and the views of Matthew's principal antagonist, Thomas Barbour, are available under one cover (Matthew, 1939).

The causal zoogeography of oceanic islands, such as the Lesser Antilles, is simplicity itself. Aside from the recent introductions of man (which have had but scant effect on Lesser Antillean iguanid lizards), the land animals of the Lesser Antilles are descendants of what Dunn (1934) aptly called "waifs"; these usually reached the islands by passive "waif dispersal" across the sea rather than by any active intentions of their own. There can be no genuinely predictable patterns of land animal distribution on oceanic islands. Land animal distribution here has been controlled by two major factors: the whimsy of the wind, and the caprice of the sea.

Davis (1926) provided the most detailed account of the physiography of the islands and their geological composition. Following this, two principal subdivisions may be recognized:

The *first cycle islands* form a continuous inner (western) chain, beginning with Saba in the northwest and extending to the southernmost cay, Glover Island on the Grenada Bank. These islands are of igneous, extrusive strata, and many are still actively volcanic.

The *second cycle islands,* beginning at the extreme northern end of the arc with Sombrero, and extending southward only as far as Marie Galante, are older; their igneous strata are largely eroded away, and they have been submerged and capped over with oceanic limestone, a sedimentary stratum. Many of them still have old basalt spires protruding from the limestone, but all are low in elevation (under 1400 feet).

Barbados lies on a continental base. On the same ridge as Tobago, Trinidad, and the Coastal Andes, this island has, like those of the second cycle, been submerged and capped with limestone.

St. Croix also resembles the islands of the second cycle, though its base (and protruding highest hills) are of sedimentary rocks: slates and shales. Although St. Croix is distinct from the eroded plutonic rock islands of the Puerto Rico Bank, including all the other Virgin Islands, it is distinct from its Lesser Antillean neighbors also in not being of volcanic origin.

The tiny atoll of *Aves* lies far at sea, west of Dominica and south of Saba. It lacks iguanid lizards, and need not concern us here (see Lazell, 1967a). The banks and major islands are shown in Figure 1.

The only historical geology of these islands is that of Schuchert (1935). Schuchert was a bridge-builder; he erected land bridges across wide areas to explain the presence of a single form on a particular island. The distribution of animal life in the Lesser Antilles fails to support any such hypothetical land bridges, either between the Lesser Antillean banks, or from them to either the Greater Antilles or South America.

Two major meteorological generalizations are evident in the Lesser Antilles: (1) the wind blows from the northeast, (2) clouds (cumulus) lie at 2000 feet.

The first of these, wind direction, is subject to change only at times of imminent storm: the hurricane season from June to November. In this period the wind may shift temporarily from its usual direction.

The second generalization, that clouds lie at 2000 feet, is subject to greater inaccuracies. As a generalization, however, it is excellent. I kept notes on the lower limit of cloud line on La Guadeloupe for six weeks in August and September of 1961; never did the cloud line lie below 650 meters, and there were always at least some clouds at 700 meters along the mountain range. (The 2000-foot line is between these two elevations.) In nine years of collecting in these islands, from three to four months per year, I never saw cloud lines below 1300 feet, and some clouds (even on the clearest days) were always present below 3000 feet. The only cloud formations of immediate concern are those which bring rain: cumulus and strato-cumulus. Cumulus is produced directly by evaporation off the tropical Atlantic, and strato-cumulus results from cumulus backing up against a mountain range and

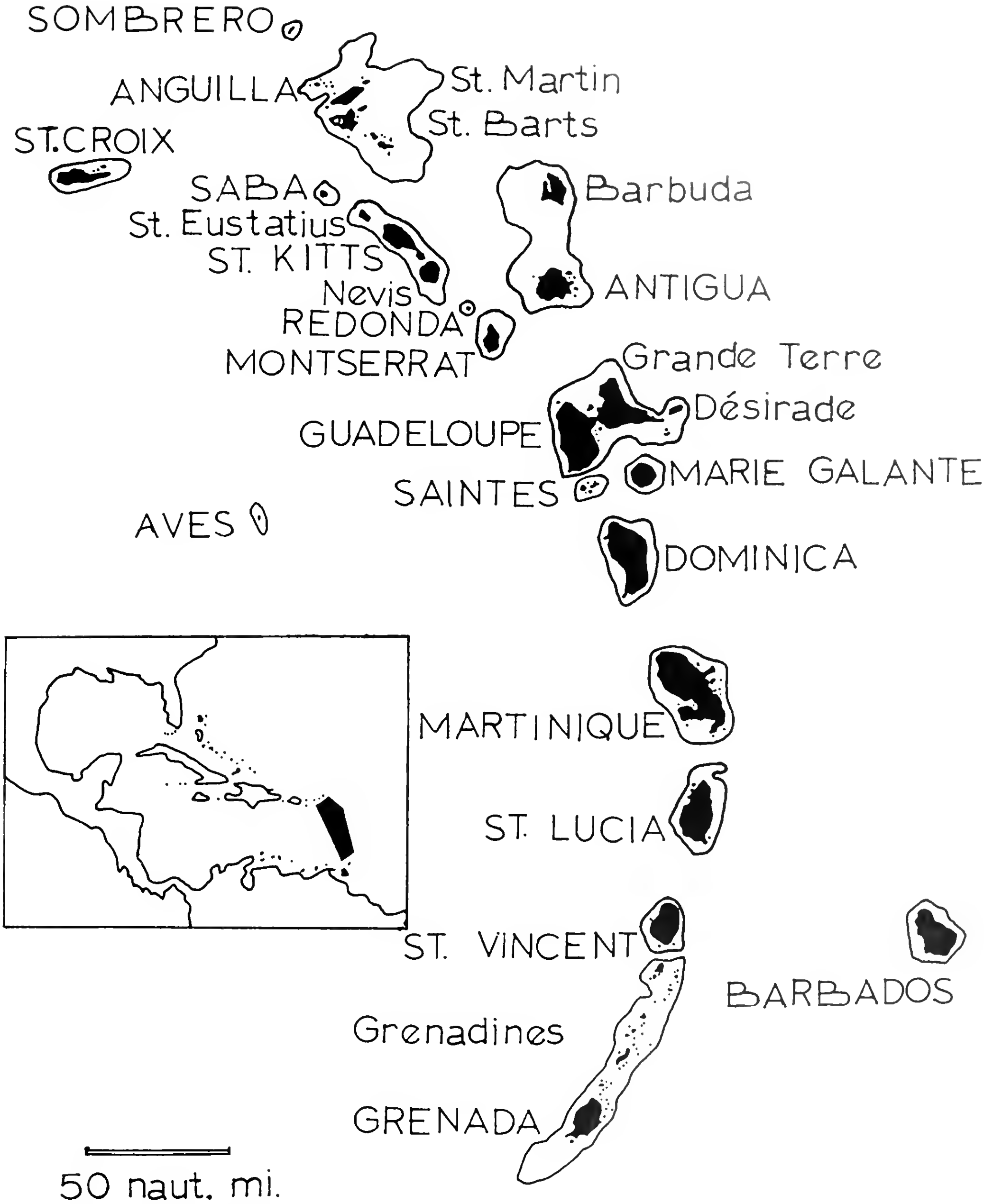

Figure 1. The Lesser Antilles. Approximate bank borders are indicated; banks are named for their largest island (capitalized). The inset shows the position of the Lesser Antilles (black) relative to the other land areas of the Caribbean Basin. (From various sources.)

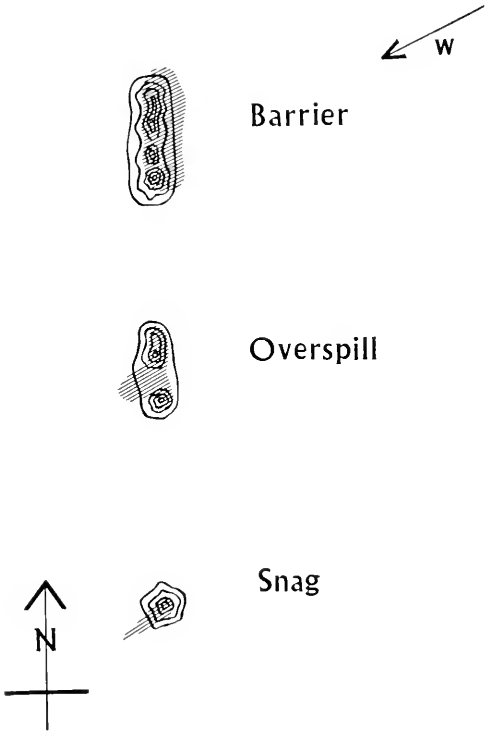

Figure 2. The three kinds of first cycle islands that affect precipitation by their land forms, and the general pattern of cloud cover they induce (hatching). Compass direction is indicated lower left, wind direction upper right. See text.

combining with water evaporated from the land and vegetation.

The second cycle islands, Barbados and St. Croix, are nowhere sufficiently high to stop or hold any quantity of clouds. With the single exception of southwestern Grande Terre, which lies close enough to windward of La Guadeloupe to be well watered lowland, all of these islands are dry. They receive 35–75 inches of rain, on the average, per year. The open ocean receives 35–45 inches. Rainfall data for these areas may be found in U. S. Navy Hydrographic Office Publication 22 (1963).

Some first cycle islands are sufficiently high in elevation to receive great quantities of rain. On the northern leeward coast of Dominica, rainfall averages about 45 inches per year; six miles inland, amid peaks rising to nearly 5000 feet, from 350 to 450 inches of rain fall per year (Beard, 1949; Hodge, 1954). The spectacular differences between localities separated by short distances in the first cycle islands, and their implications for the flora, have been discussed by the authors cited immediately above, as well as by Stehle in numerous papers (see especially 1936), and Stoffers (1956). Lazell (1962, 1964a) discussed the implications of these changes for some elements of the fauna.

Thus the initial, and major, causal factor in rendering land areas wet or dry is elevation. Beard (1949: 15) has mistaken the secondary causal effects—those which result in wet lowlands—as proximity of the mountains to the coast. As is evident from Lazell (1964a), Stehle (1936), and reason, the height and spacing of the mountain peaks is far more important in producing wet lowlands than is their relative distance from the coast.

To clarify this, Figure 2 shows the three sorts of mountain arrangements possible in these islands.

"*Snag*" islands have a single high peak (over 2000 feet) that catches a small bit of cloud and is able to hold it, largely through evaporation from the island; their lowlands are quite dry. Such islands are Saba, St. Eustatius, and Nevis.

"*Overspill*" islands have two or more high peaks, or massifs, that are either too low or too separated to effectively halt the clouds in their southwestward traverse, and therefore, for the most part, only slow them down. In these cases the clouds are usually strung out to leeward of the mountains; the leeward coast may be as wet as the windward coast, or even wetter. Examples of "overspill" islands are St. Kitts, Montserrat, St. Lucia, St. Vincent, and Grenada.

"*Barrier*" islands are those on which the mountains are sufficiently high and close enough together so that they effectively stop the clouds. Clouds, therefore, pile up to windward, forming a wet region for some distance, and rarely overlie the leeward coastal areas, which are, therefore, exceedingly dry. The leeward slopes of barrier island mountains are clothed in rain forest to as low as 2000 feet; then an abrupt shift to arid lowlands occurs. This is explained by the fact that precipitation is "whipped over" the peaks from the windward, as described by Geiger (1959). Examples of "barrier" islands are La Guadeloupe, Dominica, and Martinique, the largest and highest islands of the arc.

Of the banks of islands in the first cycle, only two, Redonda and Les Iles des Saintes (both tiny), are too low to have rain forest or montane plant associations. All three islands on the St. Kitts bank have them (all of these islands are small in comparison with La Guadeloupe, Dominica, or Martinique). Each of the remaining banks contains a single island with rain forest. The three largest islands, La Guadeloupe, Dominica, and Martinique, have by far the most extensive rain forest areas and the greatest complexities of montane plant associations in the Lesser Antilles.

In attempting a synthesis of ecological information, the political diversity of the islands has been a handicap. Stoffers (1956) is my sole reference to land plant ecology in the Dutch Islands. The French Islands are perhaps the best known of the entire chain. For information on general distribution, zonation, and succession, Stehle (1936, 1937a, 1937b, and 1941) provides accounts as detailed as could be desired. Stehle's (1945–46) attempt at a synthesis of plant ecology for all the Caribbean islands is poor, owing to his lack of information on those islands not part of France; the map provided there is, however, very useful in ascertaining the general distribution of floral ecological zones.

Dominica has been treated exhaustively with respect to floral zonation and succession by Hodge (1943, 1954), and taxonomically by the Conservator of Forests, Trinidad and Tobago (1944), and Beard (1949). All of the islands south of Martinique are British, and the two latter references have supplied the bulk of my information on them, augmented by Sands (1912), for ecological succession, and Grisebach (1864).

I use the general term "rain forest" to combine both "lower rain forest" and "montane rain forest" (*sensu stricto*) with the three montane formations represented —montane thicket, palm brake, and elfin woodland—all *sensu* Beard (1949). In Saba and St. Eustatius the very depauperate and tiny areas of "rain forest" are an admixture of all the types mentioned above except lower rain forest. In St. Kitts, Nevis, and Montserrat the floras are richer and zonation more apparent; lower rain forest is, however, absent from these islands, too. St. Lucia, St. Vincent, and Grenada have small areas of lower rain forest; St. Vincent, however, apparently lacks elfin woodland.

Only the "barrier" islands, La Guadeloupe, Dominica, and Martinique, have all five associations well developed. In these islands the highest peaks are often covered by *Clusia mangle*, referred to as "*caclin*"; this nearly impenetrable tangle of large trunks may form a continuous covering over exceedingly broken terrain, and is often deceptively dangerous to travel through. It might be best regarded as a separate consociation, rather than as a type of elfin woodland.

Exhaustive information has been available for the typical "overspill" island of Grenada. This includes Knight (1960), G. W. Smith (1961), and the manuscripts of Cromwell (1960a, 1960b, 1961); the clearest and most detailed pictures of ecology on an "overspill" island may be seen in Regional Research Centre of the British Caribbean Publication 9 (1959). The complex integration and blending of rainfall distributions, land humidity, and topographic relief distort ecological zonation on "overspill" islands far beyond the relatively simple picture presented by Hodge (1943,

1954) for Dominica, a typical barrier island.

The island of Martinique, largest in the chain, is the most complex. It forms a typical barrier in the north, but overspills and has snags in the central and southern regions; the extreme eastern end of the Presqu'île de la Caravelle and most of the southeast extremity, Pointe des Salines, are so far removed from the rest of the land mass, and so low in elevation, as to be climatically similar to second cycle islands: arid and xeric. Stehle (1937b, 1941) has discussed this complexity from a floral viewpoint, and I will here give it further consideration under *Anolis roquet*.

King (1962), after an excellent discussion of waif dispersal (pp. 38–40) is guilty of an over-generalization: that propagules should be expected to infiltrate the Lesser Antilles along the course of the averaged storm tracks: "If the lizards are dispersing southward in the Lesser Antilles, they are being carried against the ocean currents, against the prevailing winds, and against the direction taken by cyclonic storms" (p. 40). He concludes that for the geckos of the genus *Sphaerodactylus*, at least, it is far more likely that they have come north and west, from South America. It seems clear, however, that the nine species of *bimaculatus* group *Anolis* must have come south and east from the Greater Antilles (see below). The writer agrees with Darlington (1938) that windstorms are of major importance in transporting small lizards, like *Anolis*. The answer to this apparent dilemma is in avoiding a generality about storm tracks: averaging storm tracks in the Caribbean is no more valid or useful than averaging the direction of long distance 'phone calls leaving Boston; it tells us nothing about the direction of a particular storm (or 'phone call) in the past, and provides no predictive information about the direction of any future storm (or 'phone call) that does not absolutely require to be checked by empirical observation. U. S. Navy Hydrographic Office Publication 22 (1963) gives speed and directional data for tropical storms and hurricanes in the eastern Caribbean region; especial attention is called to figure 15 (p. 49) of that volume, which shows an individual storm proceeding directly from the eastern Greater Antilles into the northern Lesser Antilles at 16 knots, as well as numerous other storms not going in the average direction.

Tannehill (1952), the authority on the subject of hurricanes, sums up (p. 55): "Much has been written about average storm tracks but they are of little value. . . . While a large percentage of these tracks are described as 'parabolic,' there are numerous exceptions." Average storm tracks have no place in serious zoogeography.

Underwood (1962) provided a historical essay on reptilian systematics of the Lesser Antilles; he stated of Linnaeus (p. 7) that "he probably did not have any specimens from any of the islands and presumably knew nothing of their fauna." That is not quite true: Linnaeus (1758) described the largest known Lesser Antillean snake, *Constrictor c. orophias* (see Lazell, 1964b), although he did not know where it had been collected. Also, he described the largest lizard, *Iguana iguana*, although he knew merely that his specimen came from "the Indies." With that correction, the nomenclatural history of Lesser Antillean iguanid lizards may stand as amply reviewed by Underwood (1959, 1962).

The Lesser Antilles are a fascinating chain of islands; to quote Vandercook (1938), perhaps their most sympathetic chronicler, "within sail, and often within sight, of each other are the colonies and cultures of more nations than one may find . . . so close together anywhere else on earth. . . . Nowhere else is so much variety so accessible." He also notes: "Men of all nations drifted to the islands." I did myself. "They found peril, strangeness and beauty—all they had come for."

MATERIALS, METHODS, TERMS, AND CONCEPTS

> 'When I use a word,' Humpty replied, in a scornful tone, 'it means just what I choose it to mean—nothing more nor less.' 'The question is,' said Alice, 'whether you can make a word mean so many different things.' 'The question is,' said Humpty, 'who is to be master, that's all.'
>
> —Lewis Carroll (1866)

The present revision is based on the examination of about 10,000 specimens in the following institutions: Museum of Comparative Zoology (MCZ), Muséum National d'Histoire Naturelle, Paris (MNHN) Albert Schwartz Field Series (ASFS); and my own collection (JDL).* Of these specimens, I collected about 8,000 between June, 1958 and April, 1966. With the exception of a few collected in 1958, all specimens collected were carefully annotated in life with respect to coloration, habits, habitat, and general behavior. Field sketches, in color, augment the catalogued notes. My field catalogues contain information on the lizards, snakes, frogs, and other animals of the islands, as well as observations on their plant life, topography, climate, and people. The information relevant to particular species or places is available on request.

COLLECTING

The best general description of herpetological collecting technique is that of Mayer (1967); the methodology there depicted corresponds to that frequently used with Lesser Antillean iguanid lizards, though some sophistications have proved valuable. In general, lizards are best caught with a noose. This method does not normally damage the specimen in any way, and delivers it live into the collector's hand. I prefer, for *Anolis* and lizards of similar size, a monofilament (fishing leader) noose extending from the tip of a fiberglass, three-piece fishing pole. I prepare the noose as follows: tie monofilament of 6- to 15-pounds test weight in a hard square knot on a wooden match stick; break the match stick at the point of the knot, thus freeing the monofilament; cut off the monofilament about 18 inches from the knot (and its now-present, small loop—previously encircling the match stick), and pass the cut end through the small loop; masking-tape the monofilament to the pole tip about one inch from the noose now formed, after closing the noose to a suitable size; spiral the monofilament down the pole and tape it again; tying it to the pole after the second taping is a good idea. A noose carefully made in this manner may catch 300 lizards. Catching a lizard is simplicity itself: place noose around lizard's neck and pull. Anybody can catch a lizard, and in the West Indies, at one time in life or another, almost everybody does. It is catching the particular lizard you want that may be difficult. High up on a sodden, windy peak, with a thunderstorm visibly and rapidly approaching to windward, a magnificent specimen of some montane rain forest form, squirrelling farther and farther out on the caclin trunks over a great abyss, can lead to intemperance in a man. I have shot my share of lizards.

Locality Data

I have tried to keep my locality data on specimens as vernacular as is consistent with some readily available map. Translating the English place names used on Saba, St. Eustatius, or St. Martin into Dutch, merely because the islands belong to the Netherlands, is sheer affectation; no one there speaks Dutch under normal circumstances. The Lesser Antilles boast a plethora of Mornes Rouges, Marigots, St. John's, and Green Islands; whenever collecting at one of these localities I have been careful to specify which, even if I had to improve on the map in so doing. Thus, "Morne Rouge (du Nord), La Guadeloupe" delimits which of the two places on the island

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* Now all deposited in the MCZ.

is meant, even though the parenthetic statement is my own addition. Small islands tend to have simple, rather charming place names: it might be uncomfortable to spend a night on sandy ground, but at Sandy Ground (Anguilla) things aren't so bad. You can easily go from The Level to The Bottom (on Saba), and Behind the Mountain is precise, not relative (on St. Eustatius). Malendure (La Guadeloupe) and Porte d'Enfer (Grande Terre) speak for themselves. A number of the Grenadines have already become well known in ornithology as great nesting cays: the Battowi' Bullet, All-a-Wash, and Kick-'em-Jenny. The spelling of other Grenadine names has been a problem for me. The terminal "a" in Bequia and Battowia is not pronounced, but all the maps retain it, so I have, too, in catalogue entries. Many of the cays have names now much modified from their original French: Ile-à-Quatre of some maps is just called "Cot" by people in the Grenadines; I have compromised at "Quatre." Petite Tobago is called "Patty Taback," and "Petite" is always called "Patty" there; I have retained French spellings for lack of a real alternative. In the case of the Ile-à-Ronde, the Ile-à-Caille, and some others, I have improved on the map; their mapped names are usually given as Isle Ronde or Isle-o-Ronde, but those are neither French, English, or the way the names are said: I have deemed Isle-a-Ronde, Isle-a-Caille, etc., as colloquially acceptable spellings, since they fulfill at least the last criterion. Many people deplore the use of St. Kitts for St. Christopher and St. Barts for St. Bartelemy, but those older, cumbersome, official names are simply colloquially incorrect: they are not even used on official documents. I may, perhaps, be taken to task at this point for insisting on La Guadeloupe for the island so often called "Basse Terre"; in this case, however, the official name is preferred because it eliminates confusion between the island (La Guadeloupe) and the capitol city (Basse Terre), and calling a spectacularly mountainous island "Basse Terre" strikes me as inappropriate.

Elevations and distances are given in the relevant local system: feet and miles on American and British islands, meters and kilometers on French and Dutch. I prefer the metric system, but consistency must here be sacrificed to sanity: giving elevations in meters for Dominica would hardly be useful; no map of the island uses them. For those not fully accustomed to thinking in both systems, this work may provide valuable practice.

The two best general maps of the Lesser Antilles are U. S. Navy Hydrographic Office (USNHO) 5487 and the National Geographic Society map of the West Indies issued in March, 1954 (and not to be confused with the abomination published by the same Society in December, 1962, as Atlas Plate 23). The Sombrero Bank is included in USNHO 1834, and the Aves Bank in USNHO 1011. For St. Croix I recommend U. S. Geological Survey MR 6849, 2445, and 5306. For the Anguilla Bank use the following: Directorate of Overseas Surveys (DOS) 343 (Series E848), Sheet 1 (Anguilla and Cays), Netherlands Antilles Cadastrial Survey Department (CSD) Topografische Kaart St. Maarten (St. Martin and Cays), and L'Institut Géographique National (IGN) No. 36, 1952 (St. Barts and Cays). For Saba the best map is CSD Topografische Kaart Saba. The St. Kitts Bank is excellently covered by CSD Topografische Kaart St. Eustatius, and DOS 343 (Series E848), Sheets 2 and 3, for St. Kitts and Nevis. For the remaining banks I list my preferences: Antigua Bank: U. S. Army Map Service E741 (Antigua and Cays), and the locally available British Survey Map (1848) of Barbuda; Montserrat Bank and Redonda Bank: DOS 359 (Series E803); Guadeloupe Bank, Marie Galante Bank, and Saintes Bank: IGN Guadeloupe (1958); Dominica Bank: DOS 451 (Series E703); Martinique Bank: IGN Martinique (1957); St. Lucia Bank: DOS

345 (Series E849); St. Vincent Bank: DOS 417 (Series E743); Grenada Bank: USNHO 1640, 1316, and DOS 342 (Series E844); Barbados Bank: DOS 418 (Series E749).

Preservation

Iguanid lizards should be fixed in strong (85–95 per cent) ethanol; methanol or isopropanol may be used as substitutes, but ethanol, in the common form of "cask rhum" is locally available almost everywhere. Formalin is very destructive to these specimens (Williams, 1962a: 455); I cannot repeat the facts too strongly: formalin usually alters the colors and patterns of these lizards to a dark, muddy condition unlike anything the animal was able to do itself; formaldehyde in solution (formalin) tends to go to formic acid (Lillie, 1954) and actually breaks down the epidermal (and other) structures: the scales become mealy and crumble away; bones decalcify and etch. The alcohols are far from perfect preservatives, and colors do, of course, fade; greens tend to become blue, reds tend to yellow, and yellow itself may completely disappear. The basic pattern, however, is usually very well preserved, at least in ethanol.

Specimens should be fixed in a flat tray, bodies straight, toes separated, tails brought parallel to the bodies. Specimens prepared in this manner are readily measured and examined.

Measurements and Meristics

The length of a lizard is measured from the tip of the snout to the anterior edge of the vent (= cloaca); it is vital to measure this length "over the curves" of the ventral surface: a straight line distance will be dependent on the position in which the animal was fixed.

Relative head width may be measured by numerous indices; I have used the distance across the supraorbitals at the narrowest point, as measured with vernier calipers, and divided this into the standard distance (see below). There are important differences and distinctions among many Lesser Antillean *Anolis* with respect to scale size; some method of quantifying scale size, therefore, requires codification. My preferred method has been the "standard distance count."

The standard distance is the straight line distance from the center of the eye to the tip of the snout. It is measured with vernier calipers accurate to a tenth of a millimeter. The accuracy of the calipers exceeds the possible accuracy of the measurer, for several reasons: the center of the eye (functionally, the center of the pupil) is in practice located visually, not quantitatively; the position of the animal's eye at time of fixation may affect the location of the center; the tip of the snout (premaxillaries) is clothed by layers of soft tissues, that, though shallow, may yield variably to the pressure of the caliper point at different times or for different measurers. Standard distance measurements and middorsal counts were made on several hundred specimens of *Anolis wattsi* in March and April, 1966. In August, 1966, I repeated measurements and counts on one hundred randomly selected individuals of this species without consulting previous data. When I compared the August data with the original, I found that my standard distance measurements were off as much as 0.2 mm (or about two per cent) in a few cases, but that every scale count was identical to that originally made. This is less remarkable, perhaps, than it seems, for *Anolis wattsi* have large, neatly aligned middorsal scales, and miscounts are hard to make. During June and July, 1966, I made counts of the middorsals contained in the standard distance at midbody on about 1,000 *Anolis marmoratus*. Most of these had been examined in 1962 and 1963, prior to publication of my work on the races of this species (Lazell, 1964a); some had been collected subsequently. While making the 1966 counts, I recounted dorsals contained in the standard distance on 200 specimens

Table 1. A table of shrinkage times and percentages for some Lesser Antillean *Anolis* specimens fixed and stored in ethanol. See text.

Species	Specimen	Date 1	Snout-vent (mm)	Date 2	Snout-vent (mm)	Time Lapse (Months)	Per Cent Shrinkage
OCULATUS	JDL 260	24.ii.66	90	3.vii.66	87	4	3.3
MARMORATUS	JDL 282	28.ii.66	85	13.vii.66	82	4.5	3.5
BIMACULATUS	JDL 230	15.ii.66	114	29. vi .66	110	4.5	3.5
GRISEUS	MCZ 82926	4.vi.64	135	1.vii.66	127	26	5.9
MARMORATUS	MCZ 71068	14.ix.61	80	1.viii.66	73	58.5	8.8
MARMORATUS	MZC 70769	11.ix.61	119	1.viii.66	102	58.5	15.5
BIMACULATUS	MCZ 75779	6.v.63	122	20. iii .65	113	22.5	7.4

included in the 1962–63 data (as well as on all fresh material). When I compared this new data to the original data, I found nowhere an error of more than five per cent; it must be remembered that dorsal scales are always much smaller than middorsals, and are not longitudinally aligned. I believe these examples demonstrate the repeatability of the method.

Of course, there are a large number of other methods for quantifying scale size that could be used. In the course of making standard distance counts on *Anolis richardi* and its close relative, *A. griseus*, I found a strong average difference: *A. griseus* had lower counts (= larger scales). When I calculated standard distance as per cent of snout-vent length, I discovered that *griseus* also had, on the average, a longer snout. What had seemed to be an average difference might be a sharp distinction, but for the proportional difference between the two forms. I therefore counted middorsals contained in ten per cent of the snout-vent length at midbody, and did find a distinction between the forms.

The scales of *Anolis,* in particular, are quite small, and may vary in size considerably on different parts of the body; around-the-body counts of *ca.* 250 may be obtained from species that are obviously distinct in various aspects of scale size: large middorsals may be combined with small ventrals in one species, the reverse true of another. Similarly, longitudinal counts will confound some forms with large nape scales and small middorsals with some other form that has large middorsals but undistinguished nape scales. It is, therefore, imperative that, whatever standard one uses, the distance in which scales are counted be short, or the quantification may be meaningless.

Shrinkage affects all preserved specimens. In Table 1 shrinkage is tabulated for a number of specimens that, because of their large size, were measured when fresh dead by the method of merely stretching them out on a page of my field catalogue and marking the positions of snout and vent; the distance between marks can then be measured anytime subsequently. Naturally, shrinkage will affect scale counts; I have not, however, had it do so to the extent that identification was compromised: even a 16 per cent shrinkage will affect a dorsal count a maximum of five scales, which will not put the average specimen outside the normal range of variation (Lazell, 1964a: 390). It is to be expected that if all fresh-dead, unpreserved specimens were used, the counts I give for fixed specimens would be consistently high: the head (and standard distance) presumably shrinks less than the body, owing to the relative rigidity of the skull.

Maturity

Sexual maturity is easily determined for female *Anolis* merely by the presence or absence of eggs in the oviducts; of course, some mature specimens may lack an egg, but it is certain that no immature specimen will have one. Male *Anolis* are more difficult to assess; in most *bimaculatus*-group species, the testes appear much larger in larger specimens and show clear internal development as a reticulate pattern on the surface: specimens with these features are regarded as mature. In some *roquet*-group *Anolis* (especially *A. griseus* and *A. richardi*) even the tiniest males may have large, reticulated testes; because all of these specimens have been fixed in such a way as to preclude good histological assays, I have, therefore, resorted to a subjective assessment based on the appearance of the testes, development of the hemipenes and throat fan, and general appearance of the individual.

Population

As the term is generally used (e. g., Slobodkin, 1963; Mayr, 1963; etc.) it is ambiguous. This ambiguity is useful and intentional. At its lowest level a population is what is called a "deme"—"the community of potentially interbreeding individuals at a given locality" (Mayr, 1963: 136); this is the panmictic unit. As well, a "population" may be used for a group of demes not taxonomically different from each other, like the population of *Bothrops lanceolatus* on Martinique. For the purpose of this paper, the term will never be used for a collection of more than one taxon. The term may thus mean anything from the deme to the species, but implies that all members of the population in question could interbreed, granted the obvious stipulations given by Mayr.

Form

This term is likewise intentionally ambiguous and is used, for example, by Smith and Taylor (1945) or Underwood and Williams (1959) to mean a taxon at the species group level: a species or a subspecies. Infrasubspecific assemblages (e. g., morphs, taxonomically indistinguishable populations, etc.) are not referred to as forms. Similarly, a "group" is a collection of similar, presumably closely related, forms, as used by the authors cited immediately above.

"Different" versus "Distinct"

All populations of West Indian reptiles exhibit *differences* from other populations. These differences may be minor, even statistically insignificant, or they may serve to distinguish all members of one population from all members of other populations. In the latter case, where no individuals of one population can be confused with individuals of other populations, the animals in question have reached that level of difference that constitutes being *distinct*. Populations that differ on averages, but where some individuals are equivocal in characteristics, are simply not distinct.

Similarity and Relationship

These two terms have caused great practical and philosophical difficulties in biology, but have virtually escaped notice as the causal agents of these difficulties by remaining etymologically buried in the vast poundage of printed matter that has accrued from essentially semantic arguments. Let us consider first of all "similarity." No organism (or anything else) possesses any similarity; a robin has eyes, wings, legs, feathers, haemoglobins, esterases, and so on, but it has no similarity. You can not weigh, measure, count, or in any other way quantify similarity. Similarity is an abstract, comparative concept that exists only in the mind of the observer (and, obviously, then only when the observer compares two or more objects or quantities). Mayr, Linsley, and Usinger (1953) go to great lengths to aid the systematist in quantifying "similarity," but they never succeed in this impossible task. What has been quantified are characteristics (real ones, that an organism actually has), and similarity has then been *inferred*.

Consider a hypothetical case involving three groups of organisms, A, B, and C. The members of each group possess a meristic character, N, which, let us say, is the number of scales between the nares. It is found by one investigator that the values for N are consistently A = 1, B = 4, and C = 5; the inference that B and C are more similar to each other than either is to A is immediate (with respect to the character N only, of course). Subsequently, however, another investigator discovers that A and C belong to a single, polymorphic species and that the counts of 1 and 5, respectively, for these morphs are controlled by a single pair of alleles, one of which displays complete dominance; there are no intermediates, all specimens of this species are either A morph or C morph. This same investigator discovers that B, on the other hand, is a distinct species, and that the count of 4 is polygenic in origin, and that the pleiotropic effects of the genes involved are of such great adaptive value that the character N (which counts as 4) is quite invariable. From the viewpoint of the second investigator, who considers quantity of genetic material involved, the loci of the genes, and the adaptive significance of N, the similarity of A and C (1 and 5) is vastly greater than that of either of them to B (4) with respect to character N.

The example is, of course, hypothetical and simplified. As a real example, is the dorsal stripe of a striped-morph California kingsnake (*Lampropeltis*) really "more similar" to the stripe of a ribbon snake (*Thamnophis*) than it is to blotches of its litter-mate kingsnake? A stripe is obviously more similar to stripe, one might say, than it is to a bunch of spots; but what if it is considered (still as a stripe) from a point of view other than color and position on the body? From the point of view of the genetic material that produced it, or its adaptive significance in the environment?

The point I have tried to make about "similarity" applies with equal force to that other abstract, comparative concept that also exists only in the mind of the observer: "relationship." This concept is even more difficult, however, because not even a systematic biologist can ever be quite certain just what it is that he means by it. Do we mean "propinquity of common ancestry?" If so, then the crocodilians must be regarded as more closely related to birds than they are to squamate reptiles: crocodilians and birds are the living members of the once great thecodont radiation, while squamates branched off the reptilian stock at an altogether different time and place; crocodilians and birds have a closer common ancestor, in time, than either has with the squamates. Propinquity of common ancestry is certainly a perfectly valid indication of relationship, but it does not cause us to group the crocodiles with the birds, and separate them from other reptiles. Is relationship "morphological similarity?" If so, then our placement of the crocodiles in the Reptilia appears justified, for we infer on the basis of many characteristics that crocodilians are more similar to other reptiles than they are to birds. We infer further that morphological similarities imply genetic similarities, and these also are a valid indication of relationship. In the future we may infer genetic similarities directly for many groups, but as yet we are able to do so only within a few small groups, such as the genus *Drosophila*, and then only partially. Ethology, physiology, and ecology also provide food for inference of relationship, but note that the phylogenetic taxonomist increasingly selects those sorts of relationship he regards as valuable, and discards others; no phylogenetic taxonomist, for example, allows himself to believe that the dietary correspondence of crocodilians to sharks implies a relevant propinquity of common ancestry or a relevant quantity of genetic material in common. This selection of characteristics, or, properly, narrowing of viewpoint, is the process of character "weighting." This process introduces a whole new dimension of subjectivity into phylogenetic taxonomy, and only further emphasizes the fact that similarity and relationship are assessments of the observer, not things with an objective reality of their own.

The relationships of taxa at higher categorical levels (above the species level) must always be inferred on the basis of similarity (or difference); there exist no other possible lines of evidence. This is, then, a process of compound inference: similarity is inferred on the basis of objective facts; relationship is inferred on the basis of similarity. It has been repeatedly shown, however, that in the categories species and subspecies (the only defined categories) the inferred similarities are not invariably a valid basis for the inference of relationship. (Examples relevant to Lesser Antillean iguanid lizards are cited in Lazell, 1964a.) This unfortunate fact leads directly to the problem of how we go about ranking indisputably real taxa in the categories of species and subspecies. As a solution to the problem, I recommend using definitions of the categories that are both practically applicable and theoretically sound.

Species

The definition here used is that of Simpson (1961): "An evolutionary species is a lineage (ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies."

The following assumptions are corollary to the concept of evolutionary species:

1. Evolutionary role is both expressed in and controlled by the characteristics of the organisms in question. That is, the characteristics of a population of organisms are to some extent a function of its evolutionary role, and its evolutionary role is to a complementary extent a function of its characteristics. This means that, while natural selection may alter the evolutionary role of a population (and thus alter its characteristics), the characteristics at any given time A directly specify the range of possibilities for natural selection to have modified by time B.

2. "Unity" is here taken to mean bound into an overall oneness—even if diversity exists within it—by progressive alterations in particular characters acted on by evolutionary processes, in such a way that continuity exists between the extremes of diversity, if the steps of a set of stairs may be said to exhibit continuity (they certainly may be said to exhibit unity).

3. Populations, but not individuals, may possess evolutionary roles.

The "biological" species concept of Mayr (e. g., 1942) is not applicable—either logically or practically—to the problem of classifying insular forms. It is certainly true that the finest possible evidence for evolutionary unity is interbreeding in nature; however, we cannot observe it, and it may not occur, between isolated, insular populations of the same species: other criteria must be used, and the concept of evolutionary role provides them (see *Subspecies*, below). Further, the fact that members of two separate species may, and sometimes do, interbreed and produce fertile offspring has one overwhelming taxonomic implication: neither actual nor potential interbreeding can be logically used as the sole criterion of conspecificity.

Subspecies

A subspecies is a population or group of populations occupying a part of the overall range of a species, that *combines diagnostic consistency with geographic continuity.* It is united to the other subspecies within the species in one of three ways: (1) actual intergradation (gene flow), (2) character clines through a series of isolated forms, or (3) tenable evidence that the differences between two isolates are the result of a founder effect in which one isolate appears to be directly derived from the other. (For details see Lazell, 1964a and, especially for geographically isolated forms, 1964b.) In many respects I agree with Wilson and Brown (1953): I do not recognize polytopic "subspecies" or subspecies in animals whose geographic variation is otherwise largely discordant; I do not recognize subspecies in cases where the zone of intergradation is large compared to the subspecies range (gradual clines); I do not recognize isolates that differ on averages, but are not distinct, as subspecies unless more than 75 per cent of the individuals involved can be identified correctly without recourse to locality data; finally, I do not consider distinct isolates to be subspecies of the same species unless it can be plausibly argued that they show a collectively unitary, or continuous, evolutionary role (i. e., comparative similarity is not sufficient evidence). Also, I do not consider a monotypic species to be a species with only one subspecies, but, rather, to be a species with no subspecies whatever: a subspecies is a special sort of geographical variant of which the monotypic species simply has no examples.

Many people take exception to these qualifications for subspecies. For example, Mayr (1963) defends polytopic "subspecies" on the grounds that they too have a geographic range. Polytopy is a case where animals having characters in common are not continuously distributed, but rather separated from each other by conspecific individuals that have different characters; so, however, are morphs, color phases, and the like. In reptiles, at least, it is usually easy to explain polytopy in terms of the independent development, in several separated populations of a species, of similar characters in response to some similar ecological condition; the resultant group of similar populations is convergent and polyphyletic with respect to the characters that they have in common. (For a discussion of what constitutes "monophyletic," as opposed to "polyphyletic," see Simpson, 1961.)

The subspecies concept is extremely useful in some cases of geographic variation, when large segments of a species conform in characteristics and geographic range. In other cases, however, the subspecific names may be far more confusing than useful. A great deal of geographic variation, some of it even spectacular in degree, simply does not produce the sort of pattern usefully regarded as subspeciation.

Sympatry, Dichopatry, and Parapatry

There are three possible geographic situations that may obtain between taxa: they may occur together in the same geographic area (sympatry), they may be separated from each other by a gap occupied by neither (dichopatry), or they may border on each other without either a gap or an overlap (parapatry). Examples of sympatry are obvious, and do not require recounting here. Similarly, dichopatric forms are common; e. g., forms confined respectively to islands separated by water inhabited by neither. Parapatric forms are exemplified by actually intergrading subspecies that abut along a zone of intergradation or hybrid belt; in some cases it is at least possible that full species may be parapatric, though usually only on a very temporary basis. In the use of these terms I follow H. M. Smith (1965), though "parapatric" was initially coined, as here defined, by Smith (1955). The adoption of the term "dichopatric" I regard as an unfortunate necessity. The older term, "allopatric," since it includes two very different biological situations, is no longer useful.

Clines

Strictly speaking, a cline is any sequential change in a condition or characteristic. In dealing with geographic variation in terrestrial vertebrates, it is useful to distinguish a variety of kinds of clines that may appear in the characters of the animals. When a given character changes sequentially in a particular direction over all or most of the geographic range of a taxon, it is regarded as a *gradual cline*. When the geographic area in which sequential change in a given character takes place is small compared to the areas in which no such sequential change takes place, the situation may be referred to as a *stepped cline*.

Previously (Lazell, 1964a) I used the term "stepped cline" for a situation where isolated, or dichopatric populations showed sequential change in one or more characters in such a way that the second population was intermediate in characters between the first and third, the third intermediate in characters between the second and fourth, and so on. This should properly be regarded as a *dichopatric stepped cline*, so as to differentiate it from the situation obtaining when two taxa abut along a stepped cline and animals of intermediate characters fill the gap. In the case of two taxa abutting along a stepped cline the biological situation is quite different (contact) than in the dichopatric stepped cline (no contact), and this situation should be referred to as a *parapatric stepped cline*.

Levins (1962, 1963) provides a very carefully worked out model for conditions that could lead to parapatric stepped clines without a blatantly ostensible ecological correspondence. Although the details of his model are too complex to discuss here (especially since no case of this seems to occur in the Lesser Antillean iguanids), they should be carefully considered when analyzing the etiology of stepped clines in, for example, widespread continental species.

Concordance and Discordance

As can be seen from the preceding comments, geographic variation of the stepped cline sort tends to produce a pattern where large areas of the animals' range show homogeneity of characters, and comparatively small areas show sequential change. Of course, it is possible that animals that display stepped clines in a number of different characters might have their clines so arranged geographically that the majority of the entire range was part of some cline or another. Such a case would be one of striking discordance in geographic variation, but (probably owing to the ecological basis of many stepped clines) I know of no such case in terrestrial vertebrates. When several stepped clines occur, they usually are more or less superimposed, or completely isolated from each other. Frequently, this pattern leaves large areas of homogeneity between the small border zones of sequential change, and permits the useful recognition of subspecies (providing the differences in characters are sufficiently great between animals in the areas of homogeneity).

Highton (1962) described just such a case of compounded stepped clines in the geographic variation of the North American salamander *Plethodon jordani*. Because he synonymized the subspecies in this case, one is left to assume that he regarded geographic variation in *P. jordani* as what he referred to as "nonconcordant"; the term "nonconcordant" does not appear in the English dictionaries available to me, but by tracing the stepped clines in each character onto transparent maps, and then superimposing the maps, one sees that the range of *P. jordani* is really divided into large areas occupied by diagnostically homogeneous populations, with rather narrow zones of sequential change, in one or sometimes several characters, between them. This pattern is concordant.

I can only interpret Highton's synonymization of the apparently well-defined subspecies of *P. jordani* as resting on a belief that "concordance" requires that every character change at every point that any changes. This is to say that every subspecies must differ from every other subspecies in every character that any subspecies differs from any other subspecies. Such a viewpoint is implicit, to some degree, in the argument advanced by Wilson and Brown (1953). Inger (1961), however, has pointed out the logical fallacy of such a viewpoint; to make this requirement strikes at the very heart of animal classification, for animals need to be, and in fact almost always are, classified as much on the basis of their characters in common with related animals as on the basis of their differences and distinctions from their relatives.

When more than one gradual cline occurs in the geographic variation of a species, and where one cline runs in a different direction from one or more others, discordance results. Edgren (1961) provides a magnificent example of just such a situation in the North American snake *Heterodon platyrhinos.* Examples of this may be fairly common, for the selection pressures resulting in gradual clines are clearly not very strong in any particular, confined portion of the species range, and ecologically based, weak selection pressures (like average temperature or humidity in the eastern United States) may themselves vary in ways directionally unrelated to each other.

In the cases of parapatric (actually intergrading) subspecies in the Lesser Antilles, the shift from one form to another is always clinal. It has been my policy to include within each subspecies only those populations in which I could find no intermediate individuals, or evidence of any intergradation. If I adopted the policy of Underwood and Williams (1959), and assigned populations to subspecies on "the balance of characters," the ranges of the various subspecies would be considerably larger and the zones of intergradation correspondingly narrower. Such a policy, however, compromises the integrity of what is, by intention, a presentation of the actual biological situation, and has not been followed.

Synonymies

The synonymies provided here are as complete as I can make them in the sense that I have located every available name I could, and cited it and its author; the references, of course, are cited in the bibliography at the end of the work. These synonymies are not "complete" in the classical sense that every usage of every name, and every combination of available names ever employed, is cited. Underwood (1959) and the lists of Barbour (1930a, 1930b, 1935, and 1937) will provide amusement for those intrigued by all the various combinations of names that are possible.

Keys

The keys given below have been idealistically conceived; they nowhere utilize references to the geographic provenance of specimens, or any characters discernible in only one sex, or one stage in life. They attempt to provide, by the standard series of alternative choices, a means of identifying species belonging to extremely close-knit groups. Further, in framing the keys I have attempted as far as possible to steer clear of color characters. *Anolis* colors fade in all preservatives known to date, even if they are not completely annihilated; in some cases I have been forced to resort to them, but they are of a sort that most preserved specimens should still show. Assuredly, the *Anolis* would (and do) identify each other on the basis of color: all of them differ sharply from each other both in hues and patterns. Certainly, the biology of interspecies relationships does not depend on the correct assessment of the posterodorsal terminus of the prenasal with respect to the naris, or the correct counting of the number of midventrals in the standard distance, by living lizards in the field. In addition, such characters as throat fan size (notable in males only) or the manner in which sexual dimorphism is expressed (scales, or size, or color) are of major evolutionary and biological importance, but they are disbarred here on the grounds that the user of the key may not have both sexes in hand. Lastly, even seemingly insignificant damage to specimens, such as nose rubbing so common in captives, or twisting in preservative, may render some of the characters undeterminable.

These keys will not aways work. Fortunately, perhaps, they do seem to work best when separating geographically proximate species. As an example, the shape of the prenasal scale, which neatly separates all races of *A. oculatus* collectively from all races of its closest neighbor, *A. marmoratus*, collectively, can be confusing in geographically distant forms like *A. acutus* and *A. wattsi*, simply because the sutures in the prenasal area may be incomplete; I can only recommend that every lizard has two sides: if the character fits neither description in a couplet on one side of the animal, try the other side before giving up. Some old specimens were twisted so effectively by their original bottlers that the ear opening on one side may be stretched all out of original shape; on the other side it may be nearly squashed shut. I recommend that the height/width ratios of both sides be averaged.

Keys are not provided for subspecies, but the diagnoses written for them are directly comparable within the particular species in question; that is, within a particular, polytypic species I cite, in the diagnosis of each subspecies, the condition of each character that is diagnostic of any subspecies of that species. The subspecies diagnosis, therefore, gives the condition of all identifying features within the species, even if not a unique character of the subspecies in question; this makes identification merely a matter of finding the particular description (= diagnosis) that fits.

SYSTEMATICS

> *Anolis* must be known intimately—anatomically, ecologically, ethologically—in all its relationships within and between species, if the many puzzles the genus poses are to be solved.
>
> —E. E. Williams (1959)

A plethora of *Anolis* forms inhabits the Lesser Antilles; many are very geographically restricted, but all are abundant where found. There are tiny, geckolike rock anoles; medium-sized anoles of generalized habits and ubiquitous habitat; brilliantly colored forms of the dense jungles that rival birds in hues; dull, somber forms ideally camouflaged on a dung hill; and there are grand giants. The standard criterion for what constitutes a "giant" anole has usually been the existence of individuals exceeding 100 mm snout-vent length. This is an arbitrary criterion, but in the Lesser Antilles, it seems to provide a distinction that is almost uncanny. Thus, in the forms named *bimaculatus*, *leachi*, *ferreus*, *griseus*, and *richardi*, the populations seem composed of two size classes: females and juveniles below about 80 mm in average snout-vent length, and old adult males exceeding 100 mm snout-vent length. This existence of a distinctly bimodal distribution of sizes was what led Etheridge (1964) to postulate the existence of three species in the late Pleistocene of Barbuda: the smallest class was apparently *A. wattsi forresti*, the two larger classes represented female and juvenile *leachi* and old adult male *leachi*, separated by an apparent gap. This bimodal size distribution in species where some individuals exceed 100 mm snout-vent is probably explained by a combination of two factors: (1) a strong sexual dimorphism with respect to size, and (2) predators.

The first factor is quite apparent in *bimaculatus* and *leachi*, but less so in the others—i. e., in most of the "giant" forms occasional females get large, thus demonstrating the potentiality for large size in both sexes (females never get quite as large as males, of course).

With respect to the second factor, *Falco sparverius* is the most commonly observed predator on Lesser Antillean anoles. South of St. Lucia the effect of this bird may be somewhat usurped by the common snake, *Mastigodryas boddaerti*; sparrow hawks are not so common in St. Vincent, the Grenadines, or Grenada as elsewhere. In any case, neither the falcon nor the snake is large enough to tackle very large anoles, and thus, once over a certain size, an individual anole may be relatively free from predation. This supposition agrees with the observation that some forms (*A. luciae, A. roquet, A. extremus, A. nubilus, A. oculatus,* and some of the *A. marmoratus* races other than *ferreus*) that exceed 80 mm but not 100 mm snout-vent, fail to show a striking bimodality with respect to size.

It would appear then, that once an anole got beyond the *ca.* 100 mm snout-vent threshold it would be quite likely to survive for a long time; contrarily, individuals approaching the 100 mm mark might be more prone to predation (big enough to be obvious, but still small enough for predators to cope with). Therefore, in species where there exists individual potentiality for size exceeding 100 mm snout-vent, there seem to be many more individuals, at a given time, beyond that mark than there are immediately (80–99 mm) below it.

The 100 mm standard for the class of "giant" anoles may thus have some real biological significance in Lesser Antillean forms, and may be less arbitrary as a measure than has been previously thought.

Underwood (1959) recognized three groups of Lesser Antillean *Anolis:* the *bimaculatus* group, the *roquet* group, and the *wattsi* group. Etheridge (1959) put *wattsi* into his *bimaculatus* series, and put the entire *roquet* group in with their close South American relatives of his *latifrons* series. That arrangement agrees with subsequent work done by Gorman and Atkins (1968a and b, and papers therein cited) on chromosomes, Gorman and Dessauer (1966) on blood proteins, and Gorman (1968) on behavior. The Etheridge arrangement is the one followed here. None of the scale characters cited by Underwood (1959) as separating his groups holds up when large numbers of specimens are considered, and I find no others that will separate the *bimaculatus* and *roquet* groups as entities. This is inconvenient, perhaps, for the museum curator, but not really a serious problem. Members of the *roquet* group of *Anolis* do not look like those of the *bimaculatus* group; as indicated by Duméril and Bibron (1837) with the name "*Anolis alligator*" (a synonym for *A. roquet*), they have a distinctly crocodilian look. Even the short-nosed species, such as *A. richardi* or *A. griseus,* conform, and look like some of the caimans.

Unfortunately, a considerable familiarity with Lesser Antillean anoles is required before one can separate members of the two groups on the basis of general appearance. The next simplest method of separation is geographic: the *bimaculatus* group occupies the islands from St. Croix southward to Dominica; the *roquet* group occupies the islands from Grenada northward to Martinique. The sole case of geographic overlap results from the tiny, and obviously introduced, colony of *Anolis wattsi* (*bimaculatus* group) in Castries, St. Lucia (a *roquet* group island).

For those who lack both familiarity with the lizards and geographic data, distinguishing definitions may be devised. Etheridge (1959) separated all members of the *bimaculatus* series (both Greater and Lesser Antillean) from all members of his *latifrons* series (Lesser Antillean *roquet* group and South American relatives) by the single character of number of parasternal chevrons attached to dorsal ribs. Gorman's (1968) chromosome data provide a method of separating Lesser Antillean *bimaculatus* group members from one of their Greater Antillean relatives, and head proportions will eliminate the remainder.

Similarly, autotomy septa in the caudal vertebrae separate the Lesser Antillean members of the *roquet* group from most other members of the *latifrons* series. Unfortunately, there are extralimital *latifrons* series *Anolis* that are either members of the *roquet* group itself (*bonairensis, blanquillanus*) or are so poorly known osteologically at the present time (*agassizi*) that a geographic clause must remain in my definition of the group. In short, then:

Lesser Antillean *Anolis* of the *bimaculatus* group have: (1) three parasternal chevrons attached to dorsal ribs, (2) an $X_1X_1X_2X_2$ (female) and X_1X_2Y (male) trivalent sex inheritance system, and (3) a moderately long snout: the standard distance is greater than 125 per cent of the distance from the center of the eye to anterior edge of the ear. The *roquet* group (and all *latifrons* series anoles) are eliminated by character (1). *Anolis evermanni*, of Puerto Rico, lacks character (2). All the remaining *bimaculatus* group members (the *stratulus-distichus* complex) are short-headed and eliminated by character (3).

The Lesser Antillean *Anolis* of the *roquet* group have as follows: (1) four parasternal chevrons attached to dorsal ribs, (2) no karyotypic sexual heteromorphism, (3) functional autotomy septa in the caudal vertebrae, and (4) they occur east of 63° W longitude.

As noted above, three extralimital *Anolis* of the *latifrons* series agree with members of the *roquet* group in having functional caudal autotomy septa: *A. agassizi*, of Malpelo Island, eastern Pacific; *A. bonairensis*, of Bonaire, and *A. blanquillanus* of Blanquilla, both off the coast of Venezuela west of 64° W longitude. I have seen none of these forms in life. Etheridge (personal communication) reports that *agassizi* is osteologically distinct, and under study. Gorman and Dessauer (1966) and Gorman and Atkins (1967) show *bonairensis* to be distinct in karyotype and blood proteins from its close relatives in the Lesser Antilles. *A. blanquillanus* was described by Hummelinck (1940) as a subspecies of *A. bonairensis.* Gorman and Atkins suggest that *blanquillanus* "is the living intermediate between *luciae* and *bonairensis*"; but there is no karyotypic or biochemical evidence on this point. Removal of the geographic clause in the above definition must await the collection of further information.

Underwood (1959) recognized thirteen forms of Lesser Antillean *bimaculatus* group anoles, and divided them among six species (one unnamed). Of these, one (*bimaculatus*) was credited with six subspecies, another (*speciosus*) with two; the remainder were considered monotypic.

Anolis wattsi was placed in a group by itself on the grounds that it possessed a double row of enlarged middorsals, keeled ventrals, and narrow digital dilations. Actually, all Lesser Antillean members of the *bimaculatus* group possess a double row of enlarged middorsals (including *sabanus*, noted by Williams, 1962a, as not having such scales). Underwood did not regard *Anolis acutus* as being Lesser Antillean, but keeled ventrals are widely distributed among such *bimaculatus* group forms as *lividus* (listed as a subspecies of *bimaculatus* by Underwood, 1959), *marmoratus*, and *oculatus*. *Anolis acutus* and *A. sabanus* bridge the gap in digital dilation width between *A. wattsi* and the other Lesser Antillean members of the group. Gorman and Atkins (1968) have shown that *wattsi* is karyotypically similar to *bimaculatus*, *gingivinus*, *sabanus*, *marmoratus*, and *lividus*, but different from either *acutus* or *oculatus*—which are very different from each other karyotypically; both, though, may show very heavy ventral keeling. A large amount of fresh material, with color notes and field sketches made from life, has been accumulated, principally by me, since Underwood's (1959) paper.

I have restored *A. wattsi* to the *bimaculatus* group. *Anolis oculatus* has been subdivided into four races (Lazell, 1962); *Anolis marmoratus* now includes six forms listed by Underwood as members of different species, and six additional forms as well (Lazell, 1964a). *Anolis nubilus* Garman (1887) was resurrected from provisional synonymy to subspecies status under *bimaculatus* by Williams (1962a), and is here reinstated as a full species. *A. gingivinus* was returned to species status (Lazell, 1964c). *A. sabanus* Garman (1887) is here returned to species level. *A. acutus* of St. Croix is included in this account.

In synthesis, then, the *bimaculatus* group of *Anolis* in the Lesser Antilles consists of a complex of forms distinct from their Greater Antillean relatives. Most of them are dichopatric, and no more than three full species have ever been collected together on the same island; however, twenty-six are arranged below in nine full species. Only *Anolis bimaculatus leachi* has remained unaffected by nomenclatorial changes since the last revision of these forms (Underwood, 1959).

In the Lesser Antillean members of the *bimaculatus* group, the males possess conspicuously enlarged postanal plates; these are absent in females. Remarks made below on sexual dimorphism in squamation do not include this universal feature of the group.

The Lesser Antillean members of the *roquet* group have been reviewed extensively with respect to display behavior (Gorman, 1968), karyotypes (Gorman and Atkins, 1967), and blood proteins (Gorman and Dessauer, 1966). The general aspects of the zoogeography of the best known forms are reviewed by Gorman and Atkins (1968b). None of these works is taxonomic in nature or intent, and none resorts to anatomical features at a level higher than karyotype. The last revision of these forms is that of Underwood (1959). He recognized nine forms in three full species: *roquet* (with three subspecies), *trinitatis* (with four subspecies), and *richardi* (with two subspecies). Gorman and Atkins (1968b, and works cited therein and above) regard Underwood's *roquet* as confounding three distinct forms (*roquet, extremus*, and *aeneus*) and including a fourth (*cinereus*) not separable from *aeneus*. They regard *trinitatis* of Underwood as confounding two very distinct forms (*trinitatis* and *luciae*), each of which they consider monotypic (i. e., *vincenti* equals *trinitatis; procuratoris* equals *luciae*). They regard *richardi* and *griseus* as distinct. My work substantiates the views of Gorman and Atkins as a skeletal arrangement; five new parapatric races of *Anolis roquet* are described, so not even *Anolis roquet roquet* of Underwood remains as in his usage.

All *Anolis* seem to be basically insectivorous; dietary niche segregation between sympatric species must, therefore, depend on the habitat in which prey is hunted, or the size of the prey, or both. Both Gosse and Barbour reported *Anolis garmani* eating vegetable matter, and Grant implied disbelief (all in Lynn and Grant, 1940: 84–85). I have observed that many species of *Anolis* commonly eat vegetable matter, and have watched *A. garmani* (in Jamaica) eating green leaves, *A. bimaculatus* biting pieces out of *Opuntia* fruits, and *A. griseus, A. richardi*, and *A. aeneus* eating berries (the latter two together); details for all but the first mentioned are given in the species accounts.

A Key to Lesser Antillean *Anolis* of the *bimaculatus* Group

1. a. Prenasal subrectangular, not extending to the level of the naris .... *oculatus*
   b. Prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris 2
2. a. Midventrals smooth or weakly keeled 4
   b. Midventrals strongly keeled 3
3. a. Interparietal in contact with supraorbital semicircles, or, if separated by one scale, then more than 23 midventrals in standard distance, or, if separated by two scales, then more than 28 midventrals in standard distance .... *acutus*
   b. Not as above .... *wattsi*
4. a. Width of ear opening contained in height 2.3 or more times 7
   b. Width of ear opening, at middle of ear, contained in height of ear opening 2.2 or less times 5
5. a. 26 or more subdigital lamellae under the second and third phalanges of the fourth toe 6
   b. 25 or less subdigital lamellae .... *gingivinus*

6\. a. Male with large plain white fan; female with white spots or streak over hind limb .... *nubilus*
   b. Male with small marked or colored fan; female without white spots or streak over hind limb .... *bimaculatus*
7\. a. Males with very large, very dark spots covering dorsal surfaces; females with smaller, more mottled, but very definite dark spots laterally .... *sabanus*
   b. Not spotted as above 8
8\. a. Eyelids yellow to red, but no dark vermiculations or speckles on nape .... *lividus*
   b. Any combination not covered by 7 or 8a (that is, males with dark spots confined to sides or anterior body; or females without large, dark, mottled, lateral spots; or with yellow to red eyelids *and* nape speckling; do not despair, there are only 12 races) .... *marmoratus*

KEY TO THE *ANOLIS* OF THE *ROQUET* GROUP

1\. a. Enlarged sublabials extend posteriorly beyond the posterior level of the orbit .... *luciae*
   b. Enlarged sublabials terminate below eye 2
2\. a. Scales of the supraorbital semicircles arranged so that four or fewer abut, or, if more, then interparietal separated from supraorbital semicircles 3
   b. Not as above 4
3\. a. Middorsals in ten per cent of the snout-vent length 11 or less (8–11) .... *griseus*
   b. Middorsals in ten per cent of the snout-vent length 12 or more (12–15) .... *richardi*
4\. a. Dorsals in standard distance 37 or more .... *trinitatis*
   b. Dorsals in standard distance 35 or less 5
5\. a. Axilla without dark pigment .... *aeneus*
   b. Axilla with dark pigment 6
6\. a. Head relatively broad: width between eyes across supraorbitals at narrowest point contained in standard distance less than four times .... *extremus*
   b. Head relatively narrow: width between eyes contained in standard distance four or more times .... *roquet*

Anolis acutus Hallowell

Anolis acutus Hallowell (1856: 228)
Anolis newtoni Günther (1859: 212)

Type. None designated. Apparently none of Hallowell's original material is still in existence: I personally searched both the collection and the catalogues of the Academy of Natural Sciences of Philadelphia; Edmond Malnate (personal communication) is of the opinion that if no specimen can be found on the shelves, or in the catalogues, none is there. The description given by Hallowell would fit any Lesser Antillean *Anolis* of the *bimaculatus* group with keeled ventrals, and certainly fits *acutus*. Because the name is in standard usage for the St. Croix anole (e.g., Gorman, 1968, and works cited therein; Maldonado and Oritz, 1966), I feel that no neotypic designation is presently required.

Type locality. Unknown (Hallowell gives "Cuba?"). Here restricted to Christiansted, St. Croix, where this species is abundant and easily obtained.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals sharply keeled; interparietal in contact with supraorbital semicircles, or, if separated by one scale, then more than 23 midventrals contained in the standard distance, or, if separated by two scales, then more than 28 midventrals contained in the standard distance. (See relationships, below.)

Squamation. One hundred seventeen specimens (76 males, 37 females, and 4 juveniles) are similar to other Lesser Antillean *bimaculatus* group anoles, except in the following features: the prenasal is posterodorsally elongate and frequently constitutes the entire dorsal border of the naris. The midventrals are sharply keeled and average smaller than the middorsals; from 23–35 (average 30) are contained in the standard distance at midbody. The middorsals are keeled or tectiform and imbricate or subimbricate in males, though sometimes quite inimbricate in females; there are 18–25 (average 21) middorsals in the standard distance at midbody. The scales lateral to the middorsals show a graded but rapid decrease in size; there are 38–48 (average 43) dorsals in the standard distance six scale rows lateral to the dorsal midline at midbody. The subdigital pads are of the "raised" type of Boulenger (1885). There are 19–26 (average 23) subdigital lamellae beneath the second and third phalanges of the fourth toe.

Coloration. Males are basically brown, but vary from ash or pale olive-green to chocolate, frequently in the same individual. Color change to darker tends to bring out an irregular pattern of slatey, transverse mottlings; concomittantly, fine ashy-white frosting or speckles usually develop. The orbital skin may be undistinguished, or vary from dull yellowish to faintly reddish. The ventral surfaces, from chin to tail, are pale and variably suffused with yellow; dark mottling usually appears along the lateral belly, at least, though it may be highly inconspicuous in the pale color phase. The throat fan varies from virtually white to dull grey-green, and has a yellow to orange-red blotch near (but not at) the anterodistal edge. The fan scales tend to correspond to the ground color of the fan, and thus contrast to the brighter color in the blotch area.

Females are usually brown with a variably bold ladder or striped middorsal pattern and a variable flank stripe; they can turn virtually patternless green-brown or grey-brown. The ventral yellow tends to be more extensive and brighter in females than in males; this situation also occurs in *Anolis gingivinus* (see below).

There is something of a geographic element in color variation. Some individuals from Green Cay and Buck Island appeared dingier or duller than those from Christiansted; the same was true of some specimens from the interior, e. g., Creque Dam. The reddest fan blotches were noted on Buck Island, the reddest orbital skin on an individual from Creque Dam (JDL 77). Buck Island specimens sometimes have bold, light flank stripes, even apparent in males. Some specimens of both sexes in the northwestern part of St. Croix (e. g., Hams Bluff Coast Guard Station and Creque Dam) show a yellowish dorsal wash. Specimens from xeric, coastal areas (e.g., East Point or Sandy Point, opposite extremes of St. Croix) tend to be paler than those from more mesic areas. A male from East Point (JDL 61) turned "a very pretty ashen-grey with a decidedly pinkish tinge" when handled; it had previously been olive-drab.

Adult *Anolis acutus* are shown on Plate 1.

Size and sexual dimorphism. Males of *Anolis acutus* attain 65 mm snout-vent length (JDL 51; S shore, Buck Island); females attain 48 mm (JDL 49, Green Cay, and JDL 62, East Point). Males as small as 48 mm (JDL 61, East Point) appear to be sexually mature; the presence of eggs in the oviducts demonstrates the maturity of females as small as 38 mm (JDL 74, Hams Bluff Coast Guard Station).

The standard distance is 18–22 (average 19) per cent of the snout-vent length in males, and 18–20 (average 19) per cent of the snout-vent length in females. Although there is not an average difference in significant figures, more accurate measurements (e. g., snout-vent to tenths of a millimeter), or larger samples, might show a faint dimorphism.

Sexual dimorphism is well developed in both coloration and average adult size. It is not, however, nearly so striking in either respect as in some other Lesser Antillean forms. This is in keeping with the postulated position of *Anolis acutus* in *bimaculatus* group phylogeny (see below).

Population structure and ecology. This is a genuinely ubiquitous anole. Most foraging, in both sexes, is done on the ground, and perches are selected from just above ground level to at least ten feet; females and juveniles tend to perch closer to the ground than do adult males.

Retreat behavior may be either up, with the intention of escaping out of reach of the collector, or down into cavities and crevices. In a wooded, fairly rugged area, like that around Creque Dam, *Anolis acutus* can be maddeningly effective at both techniques.

Two eggs (MCZ 46238; no precise locality) measure 10.5 × 7.0 mm and 11.0 × 7.6 mm.

The sex ratio appears to be balanced, although there is a bias for male captures on the part of collectors (including myself). I have observed copulation in June and February, and assume breeding behavior occurs through the year. Judging from the fact that females characteristically contain one large egg in one oviduct and one small one in the other, it is reasonable to assume that eggs are laid singly at intervals of a few weeks. In all of these respects, *Anolis acutus* seems typical of Lesser Antillean *Anolis* as a whole.

Distribution. Anolis acutus is confined to the St. Croix Bank, where it is abundant and infradispersed throughout St. Croix itself and on the coastal cays. MCZ 10339(5), collected by G. K. Noble and labelled "St. Claude, Guadeloupe" are a simple case of label switching: MCZ 10428–37, also collected by Noble, bear the locality datum "St. Croix," but are *Anolis marmoratus* typical of the St. Claude population.

Relationships. Anolis acutus, like all other Lesser Antillean *bimaculatus* group anoles, shows male chromosomal heteromorphism (Gorman, 1965; Gorman and Atkins, 1966, 1967, 1968a and 1968b). Characteristically, in this group, $2n = 29$ in males, $2n = 30$ in females. *Anolis oculatus* is an exception where $2n = 31$ and 32. *Anolis acutus* resembles *oculatus* in having $2n = 31$ and 32, for males and females respectively, but the morphology of the karyotype is very different: "There are six large pairs of metacentric macrochromosomes, and then a small seventh pair somewhat intermediate in size between the macro- and microchromosomes." (Gorman and Atkins, 1968b). This contrasts to the situation in *oculatus* and all other Lesser Antillean members of the *bimaculatus* group, which have at least nine pairs of macrochromosomes. It is, however, similar to that of *Anolis stratulus* of the Puerto Rico Bank, and not far different from other Greater Antillean members of the group. The work of Gorman and Atkins thus argues for the phylogenetic intermediacy of *acutus* between the two geographic subgroups: it has the sex chromosome heteromorphism of its Lesser Antillean relatives, but resembles its Greater Antillean relatives in other aspects of karyotype morphology. It is, of course, geographically intermediate as well. Usually, Greater Antillean *bimaculatus* group anoles have a throat fan with a bright, central blotch color contrasted to a border color; Lesser Antillean forms do not. *A. acutus*, with its yellow to orange-red blotch, resembles its western relatives in this respect.

Despite karyotype and color distinctions, *A. acutus* is strikingly similar in morphology to *A. wattsi*, on the one hand, and *A. sabanus* on the other. It differs from the latter principally in having keeled, rather than smooth, ventrals; from *A. wattsi* (as can be seen from comparing species diagnoses) *acutus* is hardly distinguishable on squamation. This is in part due to the squamational diversity of the four races of *wattsi*, but in large measure reflects a real similarity; *A. wattsi* is probably the closest relative of *acutus*. The difficulty in diagnosing these forms also results from the fact that smaller scaled individuals of *acutus* have smaller scales all over; small ventrals are coupled with small head scales. The diagnosis must take this into account.

Anolis acutus is intermediate in size between *A. wattsi*, on the one hand, and the larger forms, like *bimaculatus* itself, on the other. It has not gone in for spectacular sexual dimorphism in scales and color (as has *sabanus*) or spectacular dimorphism in size (as has *bimaculatus*); it shows a balance of the two. Like its geographically distant neighbors, *marmoratus* and *oculatus* (also the sole anoline inhabitants of their ranges), *A. acutus* is ubiquitous and unspecialized in habitat.

All considered, it is tempting to speculate that all Lesser Antillean *bimaculatus* group anoles derived from Greater Antillean stock via an ancestor so close to the present form that, if I had a specimen before me, I would pronounce it *Anolis acutus*. That I have succumbed to this temptation will be evident from the general evolutionary discussion provided for the *bimaculatus* group below.

Anolis wattsi Boulenger

Anolis wattsi Boulenger (1894: 375)

Type. BMNH 1946.8.29.12–13 (*fide* Underwood, 1959: 217).

Type locality. "Antigua"; here restricted to the capital city of St. John's, Antigua, where this species is abundant and displays unequivocally the characteristics of the nominate subspecies.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals sharply keeled; interparietal separated from supraorbital semicircles by three or more scales, or, if by only two, then with less than 28 midventrals in the standard distance, or, if by only one, then with less than 23 midventrals in the standard distance.

Remarks. Anolis wattsi, as here understood, is an amalgamation of four, quite different, dichopatric forms. In two cases there is evidence of apparent character approach between two geographically approaching forms. Because ecological conditions in each case also become increasingly similar in concordance with geography, a case might be made for regarding the similarities of the anoles in the relevant areas as convergence in distinct species. Because several characters are involved in each case, and because some of these characters are not ostensible adaptations to ecological conditions, I regard the apparent character approach as evidence of evolutionary continuity, and therefore, as evidence of conspecificity.

In one case there is apparent divergence in a major diagnostic character concordant with geographical approach. If the two forms involved were absolutely distinct on the basis of any one of the several characters in which they differ, I would regard this character divergence as compelling evidence that full species level has been reached. In this case, however, though the differences separate more than 95 per cent of the specimens, absolute distinction has not been reached. On the basis of present information, therefore, I have little choice but to regard these forms as still conspecific.

There is definite evidence within one form of morphological divergence and distributional change since 1922. Clearly, the arrangement offered here of four subspecies is only temporary; speciation is here in a vividly dynamic state.

The deployment and major features of the four races are indicated in Figure 3. Details are presented under the relevant forms below; a discussion including the possible evolutionary history of the complex follows the subspecies accounts.

Anolis wattsi wattsi Boulenger

Anolis wattsi Boulenger (1894: 375)

Type. BMNH 1946.8.29.12–13 (*fide* Underwood, 1959: 217).

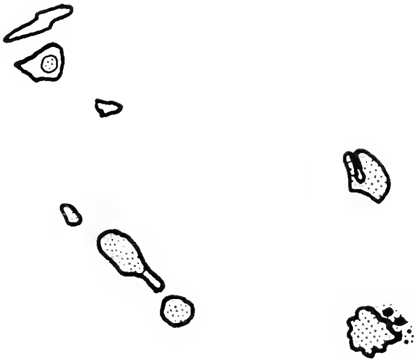
Type locality. St. John's, Antigua, by present restriction (see above).

Diagnosis. An *Anolis wattsi* combining the following characters: middorsals in the standard distance at midbody 13–19; male with orange-yellow throat fan; female with variable flank stripe always boldest posteriorly; suboculars usually blue.

Squamation. One hundred seventy-four specimens (98 males, 71 females, and 5 juveniles) are similar in squamation to other Lesser Antillean *bimaculatus* group

POGUS
(St. Martin; previously Anguilla)
Middorsals: 13-19.
Throat fan (♂): white.
Flank stripe (♀): absent.
Suboculars: variable.
Habitat: clumped in wet, shady pockets.

FORRESTI
(Barbuda)
Middorsals: 14-20.
Throat fan (♂): white.
Flank stripe (♀): bold anteriorly.
Suboculars: white to tan.
Habitat: well dispersed; all xeric.



SCHWARTZI
Middorsals:
19-24, St. Eust.
20-25, St. Kitts
21-26, Nevis
Throat fan (♂): yellow-orange.
Flank stripe (♀): bold posteriorly.
Suboculars: white to tan.
Habitat: clumped in wet, shady pockets in lowlands; infradispersed in highland forest.

WATTSI
(Antigua and cays)
Middorsals: 13-19.
Throat fan (♂): yellow-orange.
Flank stripe (♀): bold posteriorly.
Suboculars: blue.
Habitat: well dispersed; mesic and xeric.

Figure 3. The deployment and major features of the four subspecies of *Anolis wattsi*. See text.

anoles, except in the following features: the prenasal is posterodorsally elongate and frequently constitutes the entire dorsal border of the naris. The midventrals are sharply keeled and average smaller than the middorsals; from 16–26 (average 20) midventrals are contained in the standard distance at midbody. The middorsals are keeled or tectiform, and imbricate or subimbricate in males. From 13–19 (average 16) middorsals are contained in standard distance at midbody. The scales lateral to the middorsals show a graded but rapid decrease in size. There are 35–49 (average 42) dorsals in the standard distance six scale rows lateral to the dorsal midline. The subdigital dilations appear quite narrow in most specimens, and are sometimes not clearly of the raised type of Boulenger (1885) and Williams (1963). There are 17–22 (average 20) lamellae under the second and third phalanges of the fourth toe.

Coloration. In life, this is typically a bright and very pretty anole. Males have a basically brown dorsum, usually with a posterolateral green wash, and show faint, darker, transverse bands at least in their darker color phase; darkening seems to be associated with disturbance or capture throughout the range. The chin and snout are suffused with orange, as is the underside of the tail. Sometimes an orange suffusion extends over the posterior dorsum, tail, and hind limbs. The venter is pale to bright yellow, frequently with a green abdominal wash. The throat fan is rich orange-yellow with pale blue, blue-grey, or white scales; the fan scales turn grey in the disturbed phase. The subocular scales are typically bright sky blue; this blue usually extends brightly to the eyelids, and fades into the temporal area. A copper-tarnish green is frequently noticeable on the supraocular disk and sometimes includes the orbit generally.

Females are rich brown to dull grey-brown. There is a pale tan middorsal stripe bordered, and usually interrupted by, dark grey-brown, constituting a striped or ladder middorsal pattern. A pale flank stripe may be present from axilla to groin, but is boldest in the groin region, and usually set off from the ground color by dark grey-brown speckles that frequently coalesce into continuous streaks near the hind limb insertion. The venter varies from cream to yellow; the underside of the tail is yellow to orange. There is no green wash on the trunk. The orange of the chin and snout, and the copper-tarnish green of the orbit, may be reduced from the usual male condition to absence. The suboculars are normally blue, but this color is duller and less extensive than in males.

Although the degree and arrangement of chin spotting with black dots is variable in nominate *wattsi*, and not of diagnostic value, variation in this character is interesting. The mentals, anterior sublabials, and anterior gular scales are nearly white in ground color in preserved specimens (the yellow and oranges fade rapidly). Most Antiguan *wattsi* have small, subcircular, black dots fairly uniformly scattered over these scales. *Anolis wattsi* from the St. Kitts Bank is dingier and darker than the Antiguan form, and its chin spots reflect this difference: large and heavy. *Anolis wattsi forresti* from Barbuda is paler than any other subspecies; chin spots in this form are rather small and centrally located on the scales. Four females of nominate *wattsi* from interior SW Antigua (Body Ponds, MCZ 75697–700) have the large, heavy chin spotting typical of St. Kitts Bank individuals. One male from this same region (Boggy Peak, MCZ 55465) resembles *forresti* of Barbuda in having the spotting centrally located on the scales, and the scale margins relatively free of spots. In this specimen, however, the spots are very large and heavy—not like the fine speckles of *forresti.* The St. Kitts Bank and Barbuda extremes of chin spotting are shown in Figure 4.

Patterns of adult *Anolis wattsi wattsi* are shown on Plate 1.

Size and sexual dimorphism. Males of *A. w. wattsi* reach 58 mm snout-vent length (MCZ 75635, St. John's); females attain 46 mm snout-vent length (MCZ 64336, St. John's). Males as small as 39 mm (MCZ 75705, Johnson's Point) appear sexually mature; the presence of eggs in the oviducts demonstrates the sexual maturity of females as small as 36 mm (MCZ 68914, Gaylor's Estate).

Aside from the striking differences in coloration and pattern (see above), there is only average sexual dimorphism in size in *A. w. wattsi;* at maturity the sizes of the sexes overlap broadly. There is no significant dimorphism in head size. The standard distance is from 16–19 (average 18) per cent of the snout-vent length in both males and females. Williams (1962a) suggested that males have larger scales than females. Subjectively judged, this certainly seems to be true; I did not have enough equal-sized males and females to make a statistically significant objective assessment of this possibility. Since there is no average difference between the sexes in number of middorsal scales counted in the standard distance, I can only surmise that whatever actual differences in scale size exist are fully compensated for by the "crowding" (mentioned by Williams, 1962a), and consequent imbrication, of the middorsals in males.

Population structure and ecology. Barbour (1930b) regarded this form as rupicolous; this is an oversimplification. Although basically rupicolous, *A. w. wattsi* occurs on trees, bushes, and fence posts up to three feet above the ground. It shows a preference for shady stations, but occurs abundantly in very xerophytic regions, occasionally perching at open, sunny stations. Females and juveniles are more terrestrial and, therefore, more rupicolous than adult males; the latter characteristically perch twelve to twenty-four inches above ground level, but forage on the ground.

A. w. wattsi is less than infradispersed, but certainly not clumped; this corresponds to ecological conditions. In shady areas the species abounds; in xeric regions individuals usually are more scattered but find suitable stations wherever rocks or bushes provide even the slightest cover. Sugar cane fields, roads, and pastures provide at least some (though slight) barrier to complete infradispersion.

Retreat behavior in this form consists of ducking into holes and crevices in rocks or tree trunks, or frequently, running under detritus on the ground.

Distribution. Anolis wattsi wattsi is abundant all over Antigua in suitable habitats and occurs on every coastal cay that supports more than herb stage vegetation. This form also occurs in Castries, St. Lucia, where it apparently was recently introduced. MCZ 57221–2 and MCZ 58750 plus one untagged, collected by Proctor, bear only the datum "Castries." I, however, found this form only in the Botanical Garden (MCZ 71818–21), and never encountered it elsewhere. It may spread in St. Lucia, as neither of the other anoles occurring there seriously impinges on its basically rupicolous niche.

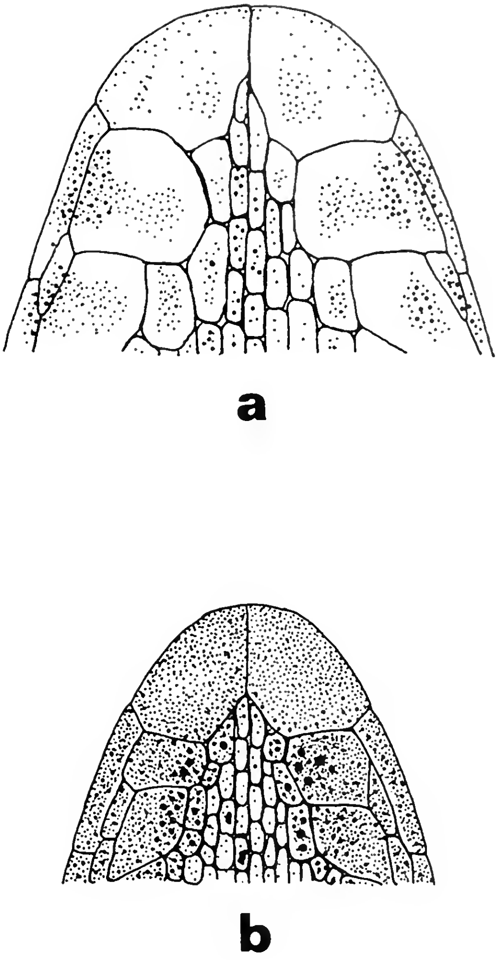


Figure 4. Extremes of pallor and dinginess in *Anolis wattsi* indicated by dark speckling on the mentals, anterior sublabials, and anterior gulars. (A) *A. w. forresti*, MCZ 75724. (B) *A. w. schwartzi*, JDL 209 (Type).

Relationships. Extreme northern Antigua (vicinity of Hodge's Bay), Long, Great

Bird, and Guana Islands (all off the northeast coast) are geographically, and ecologically, closer to the range of the Barbuda form, *A. w. forresti,* than any other parts of Antigua. Individual *wattsi* are sometimes paler in this area than elsewhere in their range. They lack the dinginess of the St. Kitts Bank *wattsi* representative, but, like that form and *forresti* from Barbuda, they may lack bright subocular blue. MCZ 75657, from Parham, and MCZ 75668 from Guana Island (both males from series of ten specimens), are examples. MCZ 75645–51, from Hodge's Bay, vary from the normal, bright condition of *A. w. wattsi* to notably paler, but all fit the diagnostic color characters of the subspecies. MCZ 75719, a male from Long Island (one of series of ten), has a throat fan of light, bright yellow. MCZ 75722, a female from the same Long Island series, has a flank stripe that is boldly accentuated throughout its length; MCZ 84987 and JDL 243, females from Great Bird Island, are similar. I regard these specimens, intermediate between nominate *wattsi* and *forresti* of Barbuda, as demonstrating the conspecificity of the two forms (see *Coloration*, under *A. w. forresti*).

Specimens of nominate *wattsi* from the mesic SW interior of Antigua may be very dark and dingy—thus resembling the *wattsi* representative of the St. Kitts Bank. MCZ 55465, from Boggy Peak, though lacking color notes from life, is clearly an example of this. MCZ 75691–700, from Body Ponds, were collected by me, and are all noted as being dingy in life. Of these, two females, MCZ 75698 and 75700, lack subocular blue, and could not be distinguished from St. Kitts Bank material on the basis of color. MCZ 75646, a male from Hodge's Bay, is an example with rather small scales; there are 19 middorsals contained in the standard distance at midbody. Five other specimens from scattered localities also are included in the range of scale size variation of specimens from St. Eustatius, the northernmost island of the St. Kitts Bank. Because overlap with St. Kitts Bank *wattsi* representatives occur in both coloration and squamation, albeit in a tiny number of specimens, I regard these forms as conspecific.

A. w. wattsi overlaps the scale size of the St. Martin (Anguilla Bank) representative of the species, but scarcely resembles it in other respects.

The only other previously named *wattsi* representative has been named twice and synonymized between the namings. It should be known as:

Anolis wattsi forresti Barbour

Anolis forresti Barbour (1923: 4)
Anolis wattsi, Underwood (1959: 217)
Anolis alter Williams (1962a: 463)

Type. MCZ 16170, W. R. Forrest coll., no date.

Type locality. "Barbuda"; here restricted to the major town, Codrington, Barbuda, where this form abounds, and displays unequivocally the characteristics of the taxon.

Diagnosis. An *Anolis wattsi* combining the following characters: middorsals in the standard distance 14–20; male with virtually white throat fan, and no dark, mossy, lateral body bars; females with variable flank stripe always boldest anteriorly; suboculars bluish white to pale tan.

Squamation. Eighty-two specimens (49 males, 31 females, and 2 juveniles) are similar in squamation to other Lesser Antillean *bimaculatus* group anoles, except in the following features: the prenasal is posterodorsally elongate: it always extends to the anterior level of the naris and frequently constitutes the entire dorsal border of the naris. The midventrals are sharply keeled and average smaller than the middorsals; from 17–23 (average 20) midventrals are contained in the standard distance at midbody. The middorsals are keeled or tectiform, and imbricate or subimbricate in males. From 14–20 (average 17) middorsals are contained in the standard distance at midbody. The scales lateral to the middorsals show a graded but rapid decrease in size. There are from 35–45 (average 39) dorsals in the standard distance six scale rows lateral to the dorsal midline. The subdigital dilations appear quite narrow in most specimens, and are sometimes not clearly of the raised type. There are 17–22 (average 20) lamellae under the second and third phalanges of the fourth toe. In squamation this form is essentially similar to the nominate race.

Coloration. In life, this is a rather colorless, drab, normally pale, grey-brown anole. There may be a faint posterior wash of green, giving some specimens an olive drab color. Males normally show little if any marking, except faint darker grey-brown transverse bands when disturbed; just the opposite occurs: specimens may be normally faintly banded, and become uniform and pale when disturbed. Some males have a general yellowish cast. The snouts of males are usually red-brown or copper tinted; the chin is cream to yellow. The bellies of males are dirty white to light, bright yellow. Usually the belly is brighter posteriorly: those with dirty white anterior venters normally have cream posterior venters; those with cream anteriorly may become light, bright yellow posteriorly. The underside of the tail is similarly cream to yellow. The throat fan is virtually white; there may be an all-over lemon yellow cast, or a faint posterior suffusion of the palest lime green. The scales of the throat fan are not colored differently from the adjacent skin. Color change is so slight that it does not affect the fan or fan scale color. The subocular scales are normally white; pale blue does occur rarely (e. g., MCZ 75743, Castle Rock) and in females and young males the suboculars are often very light tan. A tarnished copper green is frequently noticeable on the supraocular disk, and sometimes includes the orbit generally.

Females are light grey-brown. There is less ventral yellow, as a rule, than in males. The tarnished copper green of the orbital area may be quite absent. A pale tan to ash-grey middorsal stripe is bordered, but usually not interrupted, by darker brown or grey-brown. The flank stripe is well developed and frosty white on the shoulder; it fades out posteriorly, and is never set off by darker bordering pigmentation in the groin.

The pallor of *A. w. forresti* is indicated well by the chin spotting (see Fig. 4). The spots usually are small but, when large, are rather light and greyish. Spots invade the central portions of the mental halves and anterior sublabials from the sides of the head, but do not normally extend onto the anterior, posterior, or median margins of these scales, or onto the gular scales.

The patterns of adult *Anolis wattsi forresti* are shown on Plate 1.

Size and sexual dimorphism. Males of *A. w. forresti* reach 52 mm snout-vent length (MCZ 75726, Codrington); females attain 45 mm (MCZ 75730, Codrington). The smallest male that appears sexually mature is 38 mm (MCZ 75734, Codrington); the presence of eggs in the oviducts demonstrates the maturity of females as small as 38 mm (MCZ 68565, Derby Cave).

Aside from marked differences in pattern (see above) there is only average dimorphism in *A. w. forresti:* at maturity the sizes of the sexes overlap broadly. There is no significant difference in head size; the standard distance is from 17–19 (average 18) per cent of the snout-vent length in both males and females. As in *A. w. wattsi* (see above) whatever difference in scale size exists between males and females must be compensated for by scale crowding in males; the average number of middorsals counted in the standard distance is seventeen in both sexes.

Population structure and ecology. Like *A. w. wattsi*, the subspecies *forresti* is well dispersed throughout its range, though its preference for shade concentrates individuals somewhat. Shade, however, is available wherever there are bushes or rocks, so no real clumping into demes is discernible. Barbuda is, however, far more xeric than most of Antigua; the "wet pockets" that Williams (1962a, b) believed to exist in the sinkholes (called "caves" on Barbuda) are absent (see *Discussion*, below). Like *A. w. wattsi*, males of *A. w. forresti* usually perch no higher than about twenty-four inches and forage on the ground. Females and young are even more terrestrial and rupicolous. Stone walls are a highly favored habitat.

Retreat behavior is similar to that described for *A. w. wattsi*, above.

Distribution. This anole is found throughout Barbuda whenever suitable habitat occurs; it does not penetrate mangrove swamp (extensive in the north) more than a few yards beyond the point where the mangroves actually grow in water, but it does occur along the edges of the swamps.

Relationships. The presence of intermediates in color between nominate *wattsi* and *forresti* in extreme northern Antigua and on the islands off the northeast Antiguan coast is regarded as evidence of the conspecificity of the two forms. *A. w. forresti* resembles the *A. w. wattsi* representative on St. Martin in squamation and male throat fan color, but strong distinction in pattern characters argues against a common derivation of these forms (see *Discussion* following the subspecies accounts, below).

Though nominate *wattsi* and Barbudan *forresti* may be each other's closest relatives, the *wattsi* representative of the St. Kitts Bank is so similar to the nominate form that I did not distinguish them in the field. Dr. Albert Schwartz did, and repeatedly mentioned to me that he felt the St. Kitts Bank populations constituted a valid, different form. It was not until I examined squamation that I realized Schwartz was correct. This new form is therefore named:

Anolis wattsi schwartzi subsp. nov.

Type. MCZ 127088, J. D. Lazell, coll., 15 February 1966.

Type locality. Nevis Peak: South slope above Rawlings, 2500 ft., Nevis.

Diagnosis. An *Anolis wattsi* combining the following characters: middorsals in standard distance at midbody 19–26; male with orange-yellow throat fan; female with variable flank stripe always boldest posteriorly; suboculars usually white to tan.

Squamation. The following description is of the type (variation in 123 paratypes—77 males, 42 females, and 4 juveniles—is given in parentheses). The type is similar in squamation to other Lesser Antillean members of the *bimaculatus* group (as are the paratypes), except in the following features: prenasal posterodorsally elongate, forming the entire dorsal border of the naris (always extending at least to the anterior level of the naris; sometimes bordering dorsally on a nasal scale that includes the naris). The midventrals are sharply keeled and imbricate. There are 25 (19–28, average 23) midventrals in the standard distance at midbody. The middorsals are keeled (sometimes tectiform) and not imbricate (sometimes subimbricate). There are 22 (19–26, average 22) middorsals contained in the standard distance at midbody. The scales lateral to the middorsals show an abrupt decrease in size. There are 51 (44–60, average 52) dorsals contained in the standard distance six scale rows lateral to the dorsal midline. The subdigital dilations appear quite narrow (may be as dilated as in some other species, like *A. acutus* or *A. sabanus*), and are of the raised type (may not be clearly so). There are 22 (17–23, average 20) subdigital lamellae under the second and third phalanges of the fourth toe.

There is some geographic variation, indicating a north-south cline, in scale size best shown by the middorsals. Thirty-three specimens (13 males, 18 females, and 2 juveniles) from Nevis have 21–26 (average 24) middorsals in the standard distance at midbody, whereas 18 from St. Kitts (12 males, 5 females, and 1 juvenile) have

20–25 (average 23), and 63 from St. Eustatius (43 males, 19 females, and 1 juvenile) have 19–24 (average 22). The apparent collectors' bias for St. Eustatius (possibly because it is thought of as the "least known" of the three islands?) artificially compromises the difference between *schwartzi* and nominate *wattsi;* it is only in St. Eustatius individuals that overlapping middorsal counts have been found (see *Relationships,* below).

Coloration. In life, the type (an adult male) was dark, dingy grey-brown dorsally and could develop a faint olive tinge with vague transverse markings. The belly was dull, rather metallic looking, yellowish brown. There were orange suffusions on the snout, chin, and underside of the tail. The throat fan was deep orange with dull whitish scales that turned dark grey when the animal was handled. There was a hint of copper-tarnish green in the supraocular disk area, and the suboculars were off-white. The dark, heavy chin spotting is shown in Figure 4.

Preserved, the male paratypes are all very similar to the type. Color notes from life for those specimens collected by me indicate little more variation. All are dull and dingy, and most differ from nominate *wattsi* additionally in lacking subocular blue. Some blue was present in MCZ 75507 and 75509, males from a series of ten from Basseterre, St. Kitts, collected by me.

There is some variation in transverse banding. In about 20 per cent of males from St. Eustatius the anteriormost band, across the neck, is bolder than those on the back. This is also true of JDL 168, a male from Godwin's Gut, 2.5 miles northeast of Lambert's Estate Yard, 1000 feet, in northern St. Kitts. In most other specimens the nape band is no more (usually less) prominent than the back bands, and in some specimens no banding may appear at all. (See *Relationships,* below).

Females of *A. w. schwartzi* are very similar to females of nominate *wattsi.* They are duller and dingier than most Antiguan specimens, frequently lack orange tones, and have pale tan suboculars; but they have flank stripes best indicated in the groin region. They are dull grey-brown dorsally, and from dirty whitish to dingy golden ventrally. The pale tan or grey middorsal stripe is bordered, and frequently interrupted, by dark, slatey grey-brown. The patterns of the type and an adult female paratype are shown on Plate 1.

Size and sexual dimorphism. The type measures 43 mm, snout to vent, and is an adult male. The largest male (MCZ 75497, The Crater of The Quill, St. Eustatius) is 49 mm. The smallest male that appears sexually mature is 34 mm (JDL 212, from the type locality). The largest female examined is 43 mm (MCZ 75500, the Crater of the Quill); the smallest female with eggs in the oviducts is 37 mm (MCZ 75365, also from The Crater of the Quill). Although collectors' bias for St. Eustatius (especially the Crater of the Quill) probably artificially distorts appreciation of the real size range at maturity, it is clear that little sexual dimorphism in adult size is present in this form.

Sexual dimorphism in coloration and pattern in *A. w. schwartzi* is striking, and though the form is duller and dingier, it is basically similar to that in nominate *wattsi.*

In head size, material from Nevis and St. Kitts shows no significant dimorphism. In 13 males and 18 females from Nevis the standard distance is 16–20 (average 18) per cent of the snout-vent length. Variation is less (17–19 per cent) but the average for 12 males and 5 females from St. Kitts is exactly the same. On St. Eustatius, however, significant dimorphism is detectable. In 43 males the standard distance is 18–20 (average 19) per cent of the snout-vent length; in 19 females it is 17–18 (average 18) per cent. The significance of this geographic variation is discussed under *Relationships,* below.

There is not a significant average difference between the sexes in the number of middorsals, even in St. Eustatius specimens. I suppose that head size and scale size are correlated in such a way that larger headed individuals (males) also have larger scales, and that the difference is closely proportional.

Population structure and ecology. All three islands of the St. Kitts Bank have at least remnant rain forest at high elevations; on St. Kitts rain forest is extensive, while St. Eustatius is predominantly xeric. *A. w. schwartzi* occupies rain forest to the seemingly complete exclusion of the otherwise sympatric *Anolis bimaculatus bimaculatus*, and is infradispersed there. In the lowlands, *A. w. schwartzi* is definitely clumped in wet, shady pockets. Clearing for agriculture may have severely restricted suitable habitats, and better dispersion was probably the original condition. Human dwellings and buildings, however, do sometimes provide suitable habitat in the lowlands of the St. Kitts Bank islands, and *schwartzi* frequently is locally abundant around these, as well as in ravines and other naturally wet, shady areas. I was unable to locate any specimens of this form on the very arid, xeric Salt Pond Peninsula of St. Kitts, where no suitable habitat—either natural or artificial—seems to occur.

The rather different ecological relationships and manner of niche segregation observed between *Anolis bimaculatus* and *Anolis wattsi* on the St. Kitts and Antigua Banks, respectively, is discussed under *A. bimaculatus.* The altitudinal differences in population structure in *A. w. schwartzi* reflect the present geographic nature of niche segregation between this form and the largely sympatric *A. b. bimaculatus.* Ridiculous as it may seem, given the spectacular distinctions between these two species, I observed males actually contesting territories in the lowlands, and *A. w. schwartzi* is not always the loser.

Like *A. w. wattsi*, the present race is basically rupicolous, though it frequently perches on trees and shrubs up to three feet above the ground. Male perches are usually 18–24 inches above the ground, and foraging is done on the ground. Females and juveniles are more terrestrial than males. Retreat behavior is the same "into-or-under" type described for the nominate race.

An egg, presumably of this form (no other plausible reptile apparent), measures 10 by 5.7 mm, and was taken with JDL 184–6, south slope of South East Peak at head of West Farm Gut, 2000 feet, St. Kitts, on 12 February 1966.

Distribution. Throughout most of St. Kitts Bank, wherever suitable habitat occurs, up to about 3000-feet elevation; apparently absent from the entire Salt Pond Peninsula of St. Kitts.

Relationships. Anolis wattsi schwartzi is regarded as a subspecies because 10 per cent of the specimens from St. Eustatius agree with 3 per cent of those from Antigua in possessing 19 middorsals in the standard distance. Considering *schwartzi* as a whole, only 5 per cent agree with the 3 per cent of Antiguan specimens that have middorsal counts of 19; this is because specimens of *schwartzi* with such low counts (large scales) have not been found on St. Kitts or Nevis. I examined 124 specimens of *schwartzi* and 174 specimens of nominate *wattsi;* of these 298 specimens 12 had middorsal counts of 19, making a total overlap of 4 per cent. The other characters, like dinginess (as indicated by chin spotting) and subocular blue, in which these two forms differ markedly are not so readily quantified, but seem to show similar, very small percentages of overlap.

Antigua is not much further away from Nevis than is St. Eustatius (see Fig. 6), and Nevis *schwartzi* are more different from Antigua *wattsi* than are St. Eustatius *schwartzi.* Rather than interpreting this fact as character divergence between nominate *wattsi* and *schwartzi*, I suggest that it may indicate evolutionary continuity between *schwartzi* and the *wattsi* representative north of the St. Kitts Bank on St. Martin. This form's range is about as far away from St. Eustatius, geographically, as Nevis is, and as one proceeds towards it from Nevis to St. Eustatius, *A. w. schwartzi* approaches the new St. Martin form's characters not only in scale size, but in two other respects as well: (1) an increased tendency for the neck band to be well developed, and (2) the appearance of sexual dimorphism in head size. Character approach in these three respects, concordant to geographic approach, leads me to regard the St. Martin *wattsi*-like anole as a subspecies.

I collected fresh specimens—the first, apparently for four decades—in St. Martin in 1964. Noting their distinctive characters, I christened them with a brief, comparatively euphonious name that, according to the finest classical lexicons available to me, means nothing at all. Since that time, several other herpetologists have come to refer to this form by my "manuscript" name, and no reason exists to alter it. There follows an account of this, the last and northernmost, member of the *wattsi* complex.

Anolis wattsi pogus subsp. nov.

Type. MCZ 127052, J. D. Lazell, coll. 7 February 1966.

Type locality. Columbier Valley, French St. Martin.

Diagnosis. An *Anolis wattsi* combining the following characters: middorsals in the standard distance 13–19; male with virtually white throat fan and dark, mossy, vertical lateral bands; female with no flank stripe; suboculars sky blue, rust red, or virtually white.

Squamation. The following description is of the type (variation in 70 paratypes—42 males, 25 females, and 3 juveniles—is given in parentheses). The type is similar in squamation to other Lesser Antillean members of the *bimaculatus* group (as are the paratypes), except in the following features: prenasal posterodorsally elongate, extending beyond the anterior level of the naris, and forming the anterodorsal border of the naris (sometimes forming the entire dorsal border of the naris). The midventrals are sharply keeled and imbricate; there are 19 (14–20, average 18) midventrals contained in the standard distance at midbody. The middorsals are keeled (sometimes tectiform) and subimbricate (sometimes not imbricate). There are 15 (13–19, average 15) middorsals contained in the standard distance at midbody. The scales lateral to the middorsals show an abrupt (sometimes more gradual) decrease in size. There are 38 (35–45, average 38) dorsals contained in the standard distance at midbody six scale rows lateral to the dorsal midline. The subdigital dilations are fairly narrow (sometimes very narrow) and of the raised type (sometimes not clearly so). There are 20 (17–21, average 19) subdigital lamellae under the second and third phalanges of the fourth toe.

I have examined 68 specimens (40 males, 25 females, and 3 juveniles), all from St. Martin, collected by me in 1964 and 1966. In these the scales are larger than in three older specimens (all males) from the Anguilla Bank. In the fresh material there are 13–17 (average 15) middorsals in the standard distance at midbody; in the three older specimens (all males) there are 18, 18, and 19 middorsals in this distance. This difference is significant (p less than 0.05); its biological significance requires careful consideration.

The possibility that this difference results from preservational, or other, distortions in head-body proportions is strongly contradicted: in all three of these specimens the standard distance is 18 per cent of the snout-vent length, slightly less than the overall male average of 19 (see below).

One of the older specimens, MCZ 20986 (with a count of 18 middorsals), bears the data "St. Martin, Dutch West Indies. G. J. H. Molengraaff coll. 1883." The other two, MCZ 16597–7 (with middorsal counts of 19 and 18, respectively), bear the data "Anguilla Id., British West Indies, J. L. Peters coll. 1922." If one accepts these data as true, then Anguilla Bank *wattsi* seem clearly to have changed morphologically since 1922.

Coloration. Color change is far more pronounced and complex in this form than in other subspecies of *wattsi.* The type, an adult male, was grey-brown when first encountered, with clearly visible slatey transverse bands; the bands were narrow where they crossed the middorsum and widened and faded on the flanks; they were faintly bordered by coloration paler than that of the dorsal ground color. On the neck the anteriormost band was very bold, dark grey; it was well set-off by an ash-grey posterior border, and produced a distinctly collared appearance. The head was largely suffused with rust red. The belly appeared dirty white. The throat fan was virtually white, with the vaguest indication of a grey-green wash posteriorly.

When captured, the dorsal ground color paled to warm tan and a definite mustard yellow suffusion spread over the sides. The dark "collar" faded away almost entirely to grey smudges on the side of the neck. The remaining dorsal bands faded out almost to invisibility at the middorsum and along their more lateral, anterior edges; the remaining, posterior edges of each dorsal band darkened to a mossy, slatey greenish —giving the appearance of a pale animal with very dark lateral (not dorsal) bars. The dorsal surfaces of the head became spectacularly suffused with blue; this was a bright, sky blue over the entire orbital and subocular area, and faded anteriorly and posteriorly. The throat fan was wholly unaffected. The chin spots are fairly uniform, but rather light.

The colors of the 39 male paratypes that I collected were very variable. In some, dull greys and browns were the entire dorsal repertoire, and mustard yellow or greenish tints did not appear. In others, blue was well suffused on the head in what appeared to be otherwise the undisturbed color phase; in still others, various combinations of blue or blue-grey on the orbital region and rust or warm brown on the snout were encountered. Many were indistinguishable from the type in head coloration; others reversed the head color change correspondence to the dorsal pattern, but were equally bright in hues. The basic pattern and manner of pattern change, however, was similar in all specimens. The fan and fan scales are not differently colored, and not affected by color change. A tinge of tarnished copper green is usually visible on the supraocular disk.

Females are duller—usually altogether greys and browns dorsally. They pale, and a few show some mustard yellow lateral suffusion, when disturbed; most have either bluish or reddish suffusions on the head, or both. The suboculars are sometimes virtually white. There is no flank stripe at all. Females show a tiny, "pin stripe" middorsal line of dull tan or slightly metallic light brown. Female pattern is more somber, but similar to that of the male.

Ventral color, in both sexes, varies from dirty white or grey to a rather metallic light brown. Especially in females, there may be slatey speckles, smudges, or blotches on the venter. Chin spotting is extremely variable in both sexes, and not diagnostic.

The most boldly marked individuals collected were JDL 142, 146, and 150 (two males and a female from a series of ten), taken in the Grand Fond, Quartier d'Orlean, French St. Martin. Otherwise, there was no hint of divergence indicated in the four (three French and one Dutch) populations sampled.

The pattern, in both phases, of the type is shown on Plate 1, as is the pattern of an adult female paratype in the disturbed phase.

Size and sexual dimorphism. The type, an adult male, measures 44 mm, snout to vent. The largest male examined is 50 mm, (MCZ 20986, the previously noted Molengraaff specimen); the smallest male that appears mature is 39 mm (MCZ 75812, Colombier Valley). The largest female examined is 42 mm (MCZ 75818, Colombier Valley); the smallest female with eggs in the oviducts is 36 mm (MCZ 75825, Colombier Valley). The bias for collecting at Colombier Valley (36 of the 71 specimens) is my own, but it probably does not give a distorted view of size at maturity in this geographically very restricted form. As in other races of *Anolis wattsi*, sexual dimorphism in adult size is here rather weak.

Because females of *pogus* have such tiny middorsal stripes and wholly lack flank stripes, sexual dimorphism in coloration and pattern is here far less than in the other *wattsi* races.

In head size, however, sexual dimorphism is significant. In 43 males the standard distance is 17–20 (average 19) per cent of the snout-vent length; in 25 females it is 16–19 (average 18) per cent. Perhaps remarkably, the number of middorsals counted in the standard distance averages 15 in both sexes. (The three older specimens do not significantly alter this average, even though they have smaller scales.) This must mean either that larger headed males have less crowded scales, or that their scales are longer in close proportion to head size. Comparison of MCZ 75811, a 40-mm male with a middorsal count of 16 and a standard distance 19 per cent of its snout-vent length, and MCZ 75817, a female of the same size, with the same middorsal count, and a standard distance 17 per cent of the snout-vent length, indicates (albeit not wholly objectively) that the latter alternative is true: the male's middorsals are clearly larger, not at all less crowded. Perhaps the simplest (though certainly not the only) explanation of this fact is to postulate that head size and scale size are pleiotropic effects of the same genetic unit. Simple linkage of two different genetic units might produce more varied results than those observed, but is also possible.

Population structure and ecology. Diagnostic of Williams' (1962a) "*Anolis alter*" was occurrence in pocket populations in wet forest remnants. Ironically untrue of *A. w. forresti* (= *alter*), this is precisely the case in *A. w. pogus.* Locality designations like "Colombier Valley" and "Grand Fond" give an impression of large areas; actually, these places are small ravines: pockets of wet vegetation and shady stones quite comparable in total area to a football field. It is in these wet forest remnants that *A. w. pogus* abounds. These pockets, and *pogus*, occur today only on one Anguilla Bank island: St. Martin. No doubt, this form, or its immediately ancestral stock, occurred on Anguilla. There are specimens (MCZ 16596–7) to prove it, and such localities as Katouche Bay and Mango Garden were certainly once wet vegetation pockets. Charcoal burning or agriculture has totally devastated these areas, leaving eroded gullies and scraggly thornbush. I hoped that a few *pogus* might survive in cave entrances at Katouche Bay, or elsewhere along the northern coast of Anguilla, but despite an exhaustive search in February, 1966, I could find none. If *A. w. pogus* ever occurred on St. Barts, its demise there has been effectively the same, for no habitat comparable with that on St. Martin is present there today.

I sampled four pocket populations of this form in ravines selected for their comparatively large size and geographic coverage of the interior of St. Martin. There are perhaps a dozen other habitable pockets in the total subspecies range, which I estimate at a maximum of 22 square kilometers. On the ridges separating the ravines there is scrubby vegetation; I found no *pogus* on these ridges. Thus, this form is strikingly fragmented into demes and fulfills almost ideally the definition of "clumped" populations.

Once the proper, damp, shady, ravine habitats are entered, *A. w. pogus* is found in very large concentrations. I collected 26 specimens in an area of about 100 square meters at Colombier Valley, without making a discernible dent in the numbers around me. I took ten specimens from a 20 meter stretch of stone wall in the Grand

Fond, Quartier d'Orlean, and estimated I was collecting one out of every three seen. In the other localities—Loterie (French) and Cul-de-Sac (Dutch)—*pogus* was no less abundant. Although this form apparently has been severely curtailed in geographic range by human activities, it probably owes much of its present abundance in the areas where it survives directly to man: stone walls seem surely to be its ideal habitat.

In perch height, foraging habits, and retreat behavior, *A. w. pogus* is quite like other representatives of its species. The phrase "basically rupicolous" characterizes it well.

Distribution. So far as is known, presently confined to ravines in the interior uplands of St. Martin; previously, this form occurred on Anguilla and possibly (no evidence) on St. Barts.

Relationships. This is the most distinctive form of *Anolis wattsi*. It is regarded as a subspecies because *A. w. schwartzi*, of the St. Kitts Bank, shows character approach to it, concordant with geographical approach in three characters: increasing scale size, development of the neck band, and development of sexual dimorphism in head size (see *Relationships, A. w. schwartzi*, above). I regard its resemblance to *A. w. forresti*, principally in male throat fan color, as convergence accidentally resulting from two different sorts of selection pressures: character divergence from *Anolis gingivinus* in *pogus*, and open, arid ecology in *forresti* (see *Discussion*, below).

Assessment of the biological significance of the demonstrably larger scales of freshly collected *pogus* as compared to those of pre-1923 collected material would be simplified if I had more precise data on the older specimens (see *Squamation*, under this form, above). Three possibilities present themselves: (1) *A. w. pogus* were all smaller scaled forty years ago, and the whole subspecies has evolved towards larger scales; (2) the presently surviving populations had (as they now have) large scales forty years ago, and lowland populations, now extirpated, had smaller—or at least more variably sized—scales; (3) an average scale size difference existed between St. Martin and Anguilla populations, and that the older St. Martin example (MCZ 20986) is a chance sample from the overlap percentage of specimens. In any case, present *A. w. pogus* is different from its ancestors of only forty-five years back in two respects: it no longer occurs on Anguilla, and it has significantly larger scales.

I dismiss the possibility that the three older specimens bear faulty locality data because: (1) they were taken by two different collectors at two different localities; (2) evidence, in the form of tree stumps of large diameter, attests that *A. w. pogus* could have lived on Anguilla in the recent past; (3) what little pattern remains (mostly middorsally) indicates that in this respect these older specimens were *pogus*, and not one of the other forms; and, (4) they were all discovered in large series of *A. gingivinus*, the abundant species of the Anguilla Bank.

Discussion. Of all the races of *Anolis wattsi* described above, only *A. w. forresti* has been a center of nomenclatural confusion. Barbour (1923) described *forresti* on the basis of preserved specimens collected on Barbuda by W. R. Forrest. Barbour never saw living material, but the color characters he cites as distinguishing *forresti* are quite correct. Underwood (1959), unable to distinguish *forresti* and *wattsi* on the basis of preserved material, synonymized the former. Largely on the basis of the field notes taken by Auffenberg and King, Williams (1962a) described "*Anolis alter.*" I have been able to read these field notes in typescript form, revisit the collecting sites mentioned, and collect large series of fresh material from all over Barbuda. The Auffenberg-King field notes contain no actual misstatements of fact. However, four implications run through the relevant sections of these notes: (1) that the sinkholes, like Derby Cave, contain a distinctive plant association characterized by cabbage palm; (2) that the anoles in the sinkholes were observed to be distinct from those of the surrounding countryside; (3) that the anoles of the surrounding countryside were observed to be similar to *A. w. wattsi* from, for example, St. John's, Antigua; and, (4) that the anoles in the sinkholes were brightly colored ("red" and "green" are descriptive terms used frequently without modifying adjectives). Not one of these items is unequivocally stated, but all are implied; not one of these items is true. Occasional big trees and many dense clumps of cabbage palm (*Euterpe* sp.) are scattered all over the island of Barbuda. The same somber, pale, drab, little *Anolis wattsi* occurs all over Barbuda without a hint of geographic variation, and is not at all confined to palm clumps. All Barbuda *Anolis wattsi* are different from all Antiguan members of the species (though intermediates do occur in extreme northern Antigua and on the northeastern coastal cays). The specimen of "alter" collected by Auffenberg and King at Gaynor's Mill, in Antigua, has been darkened by strong formalin, but 17 better preserved specimens taken by three different collectors (nine collected by me) from this area are identical to typical specimens of nominate *wattsi*.

Auffenberg sent living specimens to Williams, and while he was somewhat disappointed by their lack of bright colors, Williams did not question the other implications in the story. The anoles from the sinkholes were clearly different from those in most of Antigua, and he named them anew.

Finally, Etheridge (1964) gave the range of *A. w. forresti* as Barbuda and Antigua (thus excluding nominate *wattsi* from its type locality). The simplicity of the real situation in no way merits the confusion that has accrued; I hope this confusion is herein laid to rest.

It is perhaps remarkable that a difference between *Anolis wattsi* on Antigua and Barbuda exists at all; the *Anolis bimaculatus* populations on these two islands (of the same bank) are not similarly differentiated. I can only suggest that Antigua and Barbuda are very different to a basically rupicolous anole; shade is permanently abundant on the former, more mesic, island, while shade on very xeric Barbuda is apt to be temporary, shifting, and very limited in extent. To the decidedly arboricolous *A. bimaculatus* representative, however, the two islands are similar. There are, of course, fewer trees on Barbuda (and fewer *bimaculatus* correspondingly), but the top of a Barbuda tree is in no way different from the top of an Antigua tree (from the lizard's viewpoint) once you have climbed up to it. In short, the conditions on the ground are generally different between the two islands, but the conditions in the trees are essentially the same; therefore, the anoles of the ground are different, while the anoles of the trees are the same. This explanation is, of course, pure speculation.

The differentiation of the other races of *A. wattsi* is less difficult to explain, perhaps, because one may appeal to geographic isolation. While Antigua and Barbuda were, presumably, part of a continuous land area during parts of the Pleistocene, the ranges of *A. w. schwartzi* (St. Kitts Bank) and *A. w. pogus* (Anguilla Bank) could never have been connected by land, either to each other or to the land areas of the Antigua Bank. Because Antiguan *wattsi* and St. Kitts Bank *schwartzi* are basically similar in coloration and pattern, their principal difference, scale size, might be entirely attributed to geographic isolation; there is certainly no evident selection pressure for, or adaptive value in, possessing smaller (or larger) scales, and no apparent linked or pleiotropic adaptive character.

A. w. pogus of St. Martin survives in habitats no more xeric than some in which *schwartzi* or nominate *wattsi* abound, and nowhere occurs in the very arid circumstances of *forresti.* Unless we postulate that *pogus* is directly derived from *forresti,* therefore, an ecological basis for the resemblance of these two forms is perhaps something of a puzzle. I suggested above that these resemblances (principally male throat fan color) are the result of convergence, and that other characters—such as scale size, neck banding, and sexual dimorphism in head size—indicate derivation of *pogus* from *schwartzi.* To reconcile the white throat fan of male *pogus,* and the lack of female flank stripe, with this view, I suggest character divergence between the sympatric species. The principal physical characteristic of male display in *A. b. bimaculatus* of the St. Kitts Bank is a huge nuchal crest; there is hardly any throat fan at all. Thus, perhaps, the large, bright throat fan of *schwartzi* has served as an excellent interspecies recognition character. In St. Martin, *A. gingivinus* has a small, but well-developed, prominently displayed, bright orange-yellow throat fan; *A. w. pogus* may have evolved a white throat fan as a response to selection pressure against interspecies confusion.

The same argument may be made for the presence or absence of the female flank stripe: *A. b. bimaculatus* has a rather vague anterior flank stripe; sympatric *A. w. schwartzi* has a distinct posterior flank stripe. *A. gingivinus* has a bold flank stripe from axilla to groin; sympatric *A. w. pogus* has no flank stripe at all. Similarly, character divergence reasoning may be applied to female middorsal pattern: vague in *bimaculatus,* bold in *gingivinus;* bold in *schwartzi,* very narrow and indistinct in *pogus.* In the field, *A. gingivinus* (with prominent flank and middorsal stripes) gives the impression of a longitudinally striped lizard; *A. w. pogus* possesses striking vertical bars.

Anolis wattsi, as a species, may have been derived directly from the very similar *Anolis acutus* of St. Croix. If this supposition is made, then either nominate *wattsi* of Antigua or *schwartzi* of the St. Kitts Bank seems closer to the ancestral stock than are *forresti* or *pogus.* Niche segregation seems far better developed between *Anolis bimaculatus leachi* of the Antigua Bank and the two *wattsi* forms there than it is between *A. b. bimaculatus* of the St. Kitts Bank and *A. w. schwartzi.* Further, Antigua Bank *wattsi* has abundantly occupied all of the available land areas on its bank, and has differentiated into two geographic races. *A. w. schwartzi* appears unable to inhabit much of the more xeric and open land area of the St. Kitts Bank, and shows only the slightest geographic variation through three islands. All this suggests *A. w. wattsi* as the oldest established and closest of the ancestral form.

Conversely, *A. w. schwartzi* is closest to *A. acutus* in squamation (the only one of the *wattsi* complex that impinges in ventral count), and geographically more proximate to *acutus* than is nominate *wattsi.* Too, though niche segregation is poorly developed in the lowlands of the St. Kitts Bank, all of these islands provide ecological zonation, and *schwartzi* and *bimaculatus* may well have originally evolved an ecological division of the available land areas on a geographic basis. *A. b. leachi* and *A. w. wattsi* lacked the possibility of such a solution to the sympatry problem, because their land areas lacked ecological zonation; vertical niche segregation throughout their ranges was an alternative. Character divergence (especially the male throat fan) is far more pronounced between *schwartzi* and nominate *bimaculatus* than between nominate *wattsi* and *leachi.* I personally find the arguments for *schwartzi* as the original *wattsi* stock (squamation, geographic proximity, and degree of character divergence) more convincing than those for nominate *wattsi.*

My proposed speculative evolutionary history of *Anolis wattsi* is, therefore, as follows: *A. acutus* stock arrived in the St. Kitts Bank from St. Croix, and there diverged into the form we know as *A. wattsi* today. Antigua was colonized from the St. Kitts Bank stock and diverged into *A. w. wattsi;* at this time *A. wattsi* of the St. Kitts Bank was developing into the present race *schwartzi.* Barbuda was colonized directly from Antigua, and ecological selection pressures (open, arid) differentiated *A. w. forresti.* The Anguilla Bank was directly colonized over water from the northern end of the St. Kitts Bank (St. Eustatius today) and *A. w. pogus* has developed in response to selection pressures for character divergence from *A. gingivinus.*

Of course, quite a different reasoning could be argued: *Anolis wattsi*, as we see it now, could be the result of waves of invasion from the west. *A. w. schwartzi* is the most similar to *A. acutus* in coloration and squamation combined, and thus the most recent arrival. This argument would imply, however, that *pogus* is the oldest (seemingly most different from *acutus*), and this might involve asserting that white throat fan, lack of flank stripe, and large scales are primitive. The first two might be rejected as character divergence, but the last is difficult to dismiss. All are contradicted as primitive by the evidence of bright (usually yellow) throat fans, flank stripes, and medium to small scales in *Anolis acutus* and the vast majority of other Lesser Antillean anoles of the *bimaculatus* group. Too, this implies independent acquisition, in each wave, of the *wattsi* karyotype (see *Relationships, Anolis acutus*).

All of this leads to the question of which came first, the *bimaculatus-gingivinus* stock, or the *wattsi* stock? Underwood (1959), not knowing of differentiation within *wattsi*, regarded it as the recent invader. The present arrangement of three forms (*bimaculatus, leachi,* and *gingivinus*) in two species (*bimaculatus* and *gingivinus*) on the one hand, and four forms (*wattsi, schwartzi, forresti,* and *pogus*) in one species on the other, destroys the clarity of Underwood's argument. However, the development of jaw sculpturing (see Etheridge, 1964), giant size, and the reduction of the throat fan in *A. b. bimaculatus* and *A. b. leachi* would seem to be more major divergences from the postulated ancestral condition than any changes visible in the *wattsi* representatives (scale size and color). Seemingly, *A. wattsi* must have colonized the Anguilla Bank after *A. gingivinus* was established there, for the burden of character divergence logically falls on the incoming—rather than the entrenched—form. If *gingivinus* resembles the ancestral condition (bright fan color, flank stripe, small scale size, and generalized, ubiquitous habits) and was widespread and abundant throughout the Anguilla Bank (as it certainly is today) then *A. wattsi* arriving as a waif propagule over water would have had to make radical shifts in characters to survive. The fact that Anguilla Bank *wattsi* has diverged from both its sympatric and its dichopatric relatives within the past four decades corroborates this view.

Etheridge (1964) has shown the existence of *wattsi* on Barbuda in the Pleistocene; *A. bimaculatus* was also present at that time on Barbuda, and had reached the level of differentiation it shows today in osteological characters at least. Assuming that evolutionary rates, at least in osteological features, are roughly comparable in Lesser Antillean *bimaculatus* group anoles (though there is no evidence that this is true), Etheridge's facts tend to support the view that *bimaculatus* was established (at least on Barbuda) before the *wattsi* stock arrived.

The relationships of *A. sabanus* are discussed under that form. It need only be said here that the similarities of *wattsi* and *sabanus* in size, habitat, behavior, and the manner in which sexual dimorphism is expressed do not permit as quick dismissal of close relationship as some of the obvious distinctions in squamation might suggest.

Anolis sabanus Garman

Anolis sabanus Garman (1887: 39)

Type. MCZ 6161, Lagois coll. The large male bearing the tag is here designated lectotype; five other untagged males are included in the present series.

Type locality. "Saba." As this species occurs nowhere but on this small island, and shows but minimal geographic variation, further restriction of the type locality seems unnecessary.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals smooth; width of ear opening, at middle of ear, contained in height of ear opening 2.3 or more times; no orange or red on orbital area; dark spots present.

Squamation. Eighty-three specimens (57 males and 26 females) are similar to other Lesser Antillean members of the *bimaculatus* group except in the following characters: the prenasal is posterodorsally elongate and frequently constitutes the entire dorsal border of the naris. The midventrals are quite smooth; there are 19–24 (average 22) in the standard distance at midbody. The middorsals average smaller than the ventrals in females (24–33, average 28, in the standard distance) but about the same size in males (19–25, average 22); the middorsals of males are frequently somewhat subimbricate, those of females are not. The scales lateral to the middorsals grade abruptly in males, and gradually in females, into smaller dorsal granules; in both sexes there are 30–40 (average 35) dorsals in the standard distance six scale rows lateral to the dorsal midline. The subdigital pads are well developed and clearly of the "raised" type of Boulenger (1885) and Williams (1963) in males, but reduced in females. Males have 24–28 (average 26), females but 21–25 (average 23) subdigital lamellae under the second and third phalanges of the fourth toe.

Coloration. This is the harlequin of Lesser Antillean anoles. Males vary from ash grey with a green cast to *café-au-lait* brown in ground color; large sooty black or slate blue spots crowd the dorsal surfaces. The orbital area is paler than the ground color, and is often blue-grey. A short vestige of a flank stripe is usually greyer or bluer than the ground color in the axilla, and frequently accentuated by coalescing spots above and below. Sometimes a number of large dorsal spots coalesce to form striking, broad stripes; MCZ 85573, from St. John's, is extreme in this respect. The ventral surfaces are light greenish yellow. The throat fan is light, bright greenish yellow shading toward orange-yellow at the anterior center. The fan scales do not contrast to their ground color, except in the most orange-yellow portion of the fan.

Females are generally paler than males, varying from grey or olive to light brown; their spots are reduced to mottlings and smudges, but still quite visible. A mottled, ladder, or sometimes striped middorsal pattern is indicated. The vague flank stripe is often better developed than in the male, and extends over the shoulder. The greenish yellow belly frequently has a metallic sheen.

Color change, to lighter or darker, is weakly developed in both sexes.

There is a definite cline in color from xeric coast (e. g., Flat Point) to the crater of The Mountain. At Flat Point (MCZ 75524–8) specimens show little yellow, tending toward grey or grey-green ventrally; above Little Rendezvous, at *ca.* 700 m (MCZ 75539–43), all specimens had a green cast, and one female (MCZ 75541) was described as olive all over with "rather bright green sides." Similarly, all three females from this elevation (MCZ 75541–3) had a coppery tinge to the head; this was occasional at The Windward Side and The Bottom, but was not found among three females taken at Flat Point (MCZ 75526–8).

Patterns of adult *A. sabanus* are shown on Plate 1.

Size and sexual dimorphism. Males of *Anolis sabanus* attain 69 mm snout-vent length (MCZ 6161, type); females reach 50 mm (MCZ 28521). The smallest males examined appeared sexually mature (MCZ 75540, from The Mountain above Little Rendezvous, and an untagged specimen with MCZ 28501, etc.) and are 44 mm snout-vent length. The smallest female examined (MCZ 75543, The Mountain above Little Rendezvous) is mature at 42 mm. Thus, adult sizes overlap considerably.

The considerable sexual dimorphism in color not withstanding, it is in squamation that *A. sabanus* is extreme. With respect to both middorsals and subdigital lamellae the sexes of this species are more different from each other in squamation than are several other pairs of forms (e. g., *bimaculatus* and *nubilus*) that I regard as full species. Males have strikingly larger middorsals and more lamellae than do females (see above).

The standard distance is 17–19 (average 18) per cent of the snout-vent length in both sexes; thus the middorsal scale size dimorphism is real, and not a result of proportional differences.

Population structure and ecology. Anolis sabanus is infradispersed and abundant all over Saba except in the driest areas. At Flat Point, for example, I found specimens decidedly clumped around the few bushes that provided shade. In behavior this species is far from ubiquitous; a peculiar fact, since it is the only *Anolis* on the island. *A. sabanus* stays close to the ground; males may perch as high as five feet, but females and young seldom go above three feet. Retreat behavior is usually either down or laterally into cavities and crevices. This species likes to remain pressed flat against a vertical substrate, and keeps the forelimbs more extended than is normal for other anoles. Males even display from this position: simply lifting the head at an angle before extending the very large throat fan. Barbour (1930a, 1935) was quite correct in asserting that *sabanus* is a basically rupicolous form; in fact, this species gives the most strongly geckolike impression of any in the Lesser Antilles.

Distribution. Anolis sabanus is confined to Saba, where it occurs from sea level to the top of The Mountain (870 m). The species does not occur on either the Diamond Rock or Green Island; the latter cay is thus the only bit of land I have encountered in the Antilles that has shrubs (two) but lacks *Anolis.*

Relationships. Barbour (1930a, 1935) argued cogently for a close relationship between *sabanus, wattsi,* and *acutus;* habitat and behavior amalgamate the first two, morphology bonds the second to the last. Then, Barbour (1937) turned around and confounded *acutus, wattsi,* and *forresti,* along with *Anolis gingivinus,* under the unrelated *A. krugi* of Puerto Rico. It is little wonder that Underwood (1959) believed none of Barbour's ramblings, and dumped this remarkable little species into his catch-all *Anolis bimaculatus.*

Anolis sabanus is probably the most immediately distinctive Lesser Antillean anole. Even pickled females show the dark spots that set them strikingly apart. The behavior of the species is bizarre. One cannot put characters like the manner in which sexual dimorphism is expressed into keys or diagnoses, but surely the dimorphic squamation of this species argues strongly for a long and independent evolution.

In the end, Barbour's initial view seems basically correct. *Anolis sabanus,* with its standard *wattsi*-type karyotype, is probably an immediate derivative of first *acutus*-type stock colonizing islands east of St. Croix; that stock has subsequently given rise to *wattsi* and the remainder of the *bimaculatus* group in the northern Lesser Antilles. The resemblances between *sabanus* and *wattsi* thus appear as holdovers from their common past; the differences between *sabanus* and its other relatives reflect its long isolation.

Anolis gingivinus Cope

Anolis gingivinus Cope (1864: 170)
Anolis virgatus Garman (1887: 41)

Type. BMNH 1946.8.29.18–20 (*fide* Underwood, 1959), W. J. Cooper coll.

Type locality. "Anguilla rock nr. Trinidad," here restricted to Sandy Ground, Anguilla.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior border of the naris; midventrals smooth; width of ear opening, at middle of ear, contained in height of ear opening less than 2.2 times; subdigital lamellae 17–24.

Squamation. One hundred seventy-five specimens (111 males, 61 females, and 3 juveniles) are similar to other Lesser Antillean *bimaculatus* group anoles except in the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris. The midventrals are smooth; there are 19–26 (average 22) in the standard distance at midbody. The middorsals average smaller than the midventrals; there are 20–29 (average 26) contained in the standard distance; the middorsals are subimbricate or inimbricate. The scales lateral to the middorsals grade rapidly into smaller dorsal granules; there are 39–50 (average 45) of these in the standard distance six scale rows lateral to the dorsal midline. The digital pads are broad and of the "raised" type. There are 17–24 (average 20) lamellae under the second and third phalanges of the fourth toe.

Coloration. In life, *Anolis gingivinus* varies from the usual olive drab to distinctly light greenish, or even rusty, in ground color. The venter varies from cream to bright yellow. The throat fan of males is well developed and yellow-orange in color, with white scales. Color change is merely to darker, enhancing the grey-brown pattern; greener individuals turn browner. The pattern consists basically of a very broad middorsal band, which may be lighter or darker than the ground color in the same individual at different times, and a bold, light flank stripe from shoulder to groin. In males, this pattern is often modified by the inclusion of spots or marbles of grey-brown. (Lazell, 1964c: 717.)

There is something of a geographic element in variation in this species, resulting, I believe, from the deme structure imposed by spreading its range over at least forty islands, cays, and rocks from Sombrero, throughout the Anguilla Bank, to the Ile Coco. Virtually every variant observed in *A. gingivinus* can, however, be found in a single population like that at Phillipsburg, St. Martin, or The Valley, Anguilla. Here are some of the extremes I noted elsewhere: palest and greyest, Scrub Island; brightest yellow bellies: Lower (= western) Prickly Pear Cay; brightest orange fans, Dog Island; palest yellow fans, Sombrero and Scrub Island; darkest and most uniform, Ile Coco; most regular oval spotting, Sombrero and Ile Tintamarre (= "Flat Island"); reddest, Guana Cay of Pelikan and Ile Coco.

Adults of both sexes are shown on Plate 1.

Size and sexual dimorphism. The largest male of *Anolis gingivinus* is 72 mm, snout to vent (MCZ 75603), and comes from Guana Cay of Pelikan; a female (MCZ 75605) from the same tiny islet holds the record for her sex: 53 mm. The distant Ile Coco supports a population that comes in a close second: a male 68 mm (MCZ 75630), and a female 51 mm (MCZ 75634). Elsewhere in its range, *A. gingivinus* rarely exceeds 65 mm and 48 mm, for males and females, respectively. The smallest apparently mature male is 42 mm (MCZ 75552, Sandy Ground, Anguilla),

PLATE 1

1. *Anolis acutus*: male, JDL 36; female, JDL 42; Christiansted, St. Croix.
2. *Anolis sabanus*: male, MCZ 75530; female, MCZ 75537; The Bottom, Saba.
3. *Anolis gingivinus*: male, MCZ 75544, Sandy Ground; female, MCZ 75555; The Valley, Anguilla.
4. *Anolis nubilus*: male, MCZ 82934; female, MCZ 82942; Redonda.
5. *Anolis wattsi wattsi*: male, MCZ 75635; female, MCZ 75641; St. John's, Antigua.
6. *Anolis wattsi forresti*: male, MCZ 75724; female, MCZ 75730; Codrington, Barbuda.
7. *Anolis wattsi schwartzi*: male, JDL 209 (Type); female, JDL 214; Nevis Peak.
8. *Anolis wattsi pogus*: male, JDL 100 (Type) shown in extreme color changes; female, JDL 107; Colombier Valley, St. Martin.

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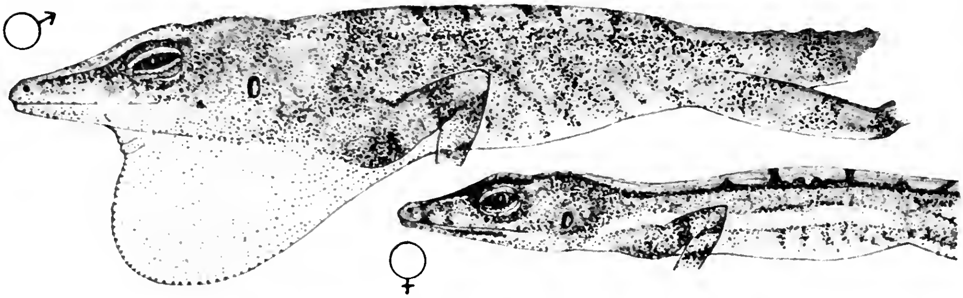

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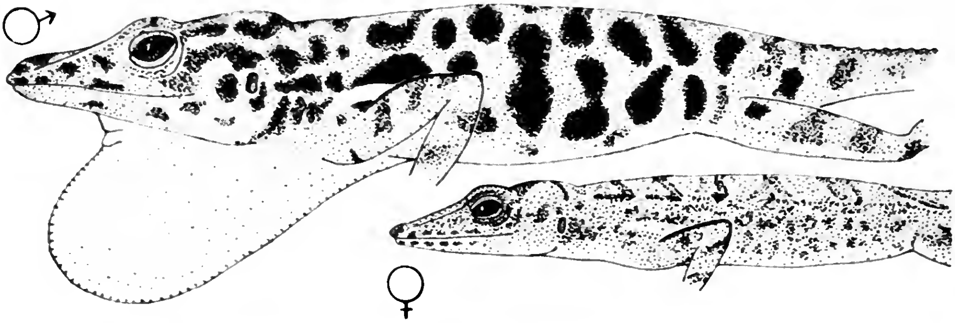

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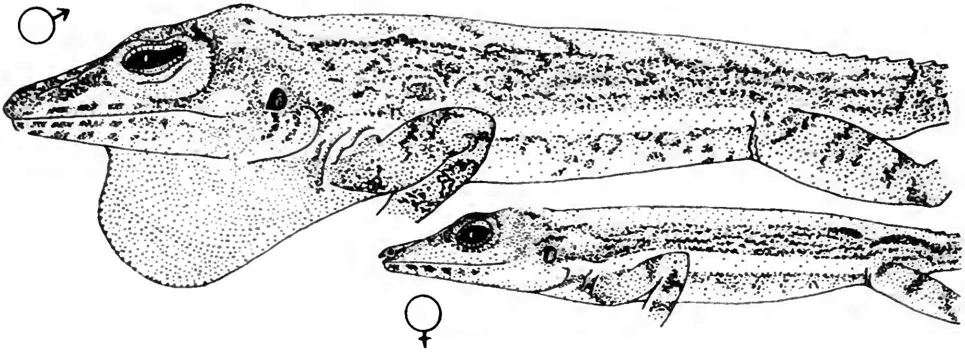

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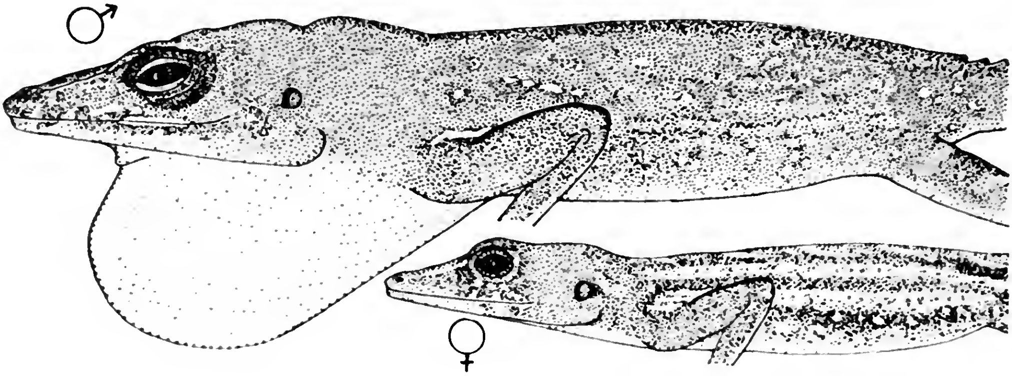

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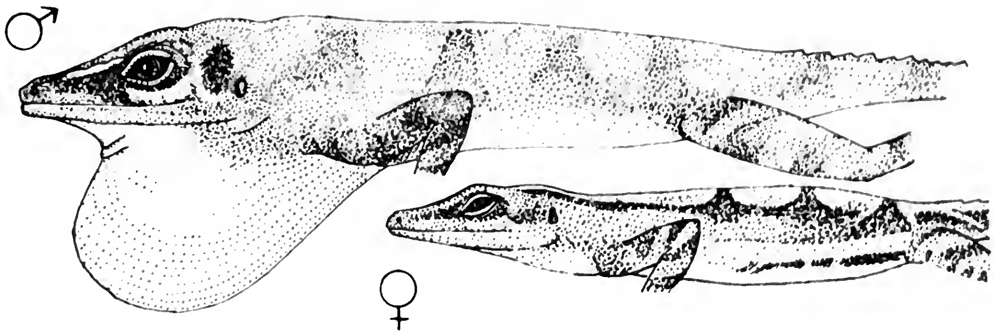

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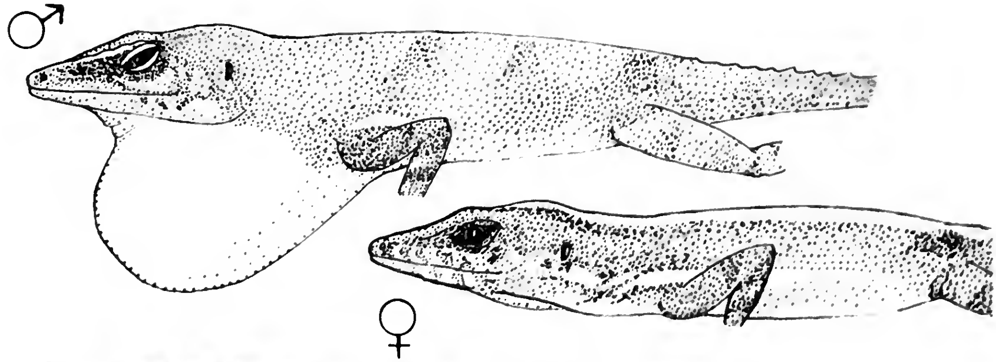

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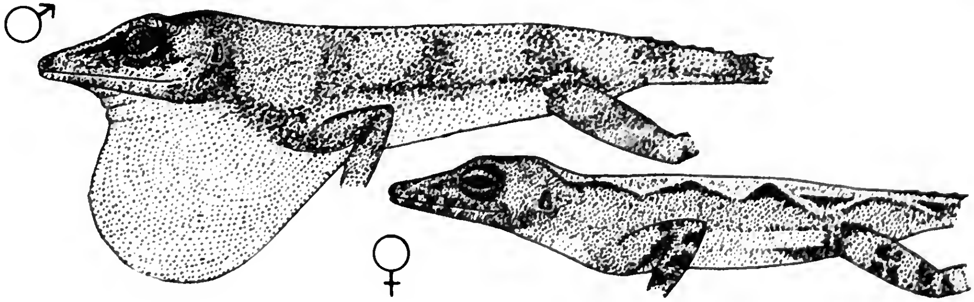

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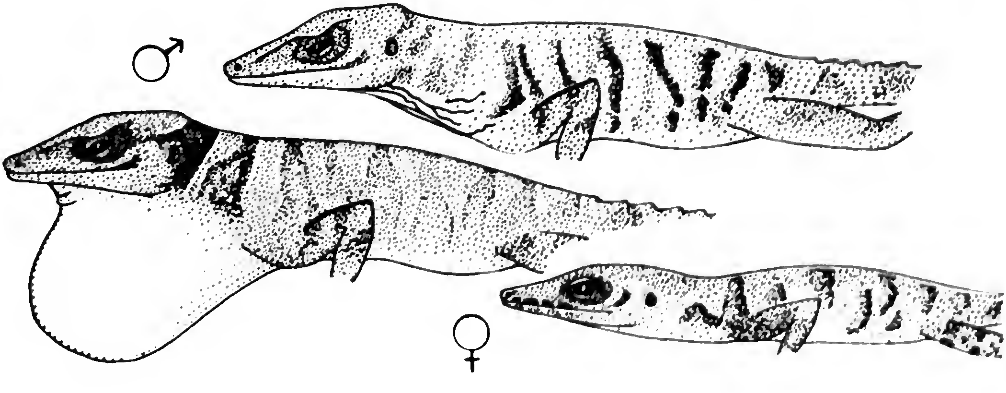

and the smallest mature female is 41 mm (MCZ 75555, The Valley, Anguilla). The fact that Guana Cay and Ile Coco have such large individuals and also agree in averaging more reddish than most other populations is interesting. The two islets are both small, but not otherwise especially similar: Guana Cay is high and steep, with but three or four small bushes; the Ile Coco is a low, flat, honeycombed limestone platform with patches of dense brush. Guana Cay is just south of St. Martin, and about twenty miles northwest of the Ile Coco; Guana Cay is about in the middle of Anguilla Bank, while the Ile Coco is its southern terrestrial terminus. I suggest that perhaps redness and large size are pleiotropic effects of the same gene, and that this gene has been independently acquired by founding populations, or coincidentally retained in stranded populations, on these two islets.

The sexes of *A. gingivinus* are remarkably similar; no sexual dimorphism is evident in squamation, and the standard distance is 17–21 (average 19) per cent of the snout-vent length in both sexes. In coloration and pattern the sexes are quite similar, except for the somewhat more complex markings and throat fan of the male. The tendency for females to have brighter yellow bellies than males is interesting; this feature may be a holdover from the presumably not distant *A. acutus* stock, which also possesses it. There is considerable overlap in adult sizes.

Population structure and ecology. As I have discussed this species elsewhere (Lazell, 1964c), it suffices here to say that *A. gingivinus* is ubiquitous in habits, quite like *A. acutus.* Even where it occurs with *A. w. pogus,* the species is abundant, and the two intermingle spacially and territorially at the rupicolous end of the *gingivinus* niche. *A. gingivinus* is infradispersed throughout the land areas it occupies, but, as I noted above, the fragmentation of its range into forty or more separate islands imposes a clumped deme structure upon it, from an evolutionary point of view.

Distribution. Anolis gingivinus occurs throughout the Anguilla Bank, on every rock and cay that supports more than herb-stage vegetation, and on Sombrero.

Relationships. In size, behavior, and the expression of sexual dimorphism, *Anolis gingivinus* is strikingly like *Anolis acutus.* The smooth ventrals, however, suggest *sabanus* or *bimaculatus.* The midventrals average larger than the middorsals; this is true of *sabanus,* if both sexes are amalgamated, but the opposite of the condition in either *acutus* or *bimaculatus.* A number of more subtle features, however, suggest proximity to *bimaculatus:* the stocky build; the prominent subotic bulge of adult males; the comparatively small throat fan; and, the presence of slight jaw sculpture in the largest males (e. g., MCZ 75603, discussed above). If I speculate that all of these features, as well as increased size and number of subdigital lamellae, are specializations of the *bimaculatus* stock over the original post-*acutus,* pre-*wattsi* stock that initially settled east of St. Croix, then *A. gingivinus* may be seen as an intermediate between these two stocks. That is, *gingivinus* may well be a product of the original post-*acutus* radiation that gave rise to pro-*wattsi* (on the St. Kitts Bank) and *sabanus* (on Saba); pro-*bimaculatus,* then, would be a derivative of *gingivinus,* originally on the Antigua Bank.

If the above speculative arrangement was correct, one might hope to find a population elsewhere that signalled the advance from *gingivinus* to pro-*bimaculatus,* but had avoided some of the extreme modifications of present-day *bimaculatus* that result from character divergence in sympatry with *Anolis wattsi.* Just such a form does, in fact, occur: *Anolis nubilus* of Redonda. *A. nubilus* is remarkably similar to *A. gingivinus,* and differs from it principally in ways (like number of subdigital lamellae) that indicate a shift toward *bimaculatus* (see *Relationships* under *A. nubilus*, below).

Anolis bimaculatus (Sparrmann)

Lacerta bimaculata Sparrmann (1784: 169)

Type. A specimen in the Museum de Geer Royal, Stockholm, *fide* Underwood (1959).

Type locality. St. Eustatius; no restriction seems necessary.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals smooth; width of ear opening, at middle of ear, contained in height of ear opening less than 2.2 times; subdigital lamellae 26–36; male with small throat fan entirely, or marbled with, yellow or orange; female without bold whitish spots or streak over hind limb insertion.

Remarks. Anolis bimaculatus is the giant of its group, with males of both subspecies frequently exceeding 110 mm, snout to vent. There is considerable geographic variation in apparent size and color within each of the subspecies, and the two seem to be diverging from each other in ways—like jaw sculpture, nuchal crest, and throat fan—that are of major evolutionary import. Nevertheless, I can find no character or combination of characters that will invariably separate the two forms, and thus retain them as conspecific. Geographically, these forms are simple: *A. b. bimaculatus* occurs on the islands of the St. Kitts Bank; *A. b. leachi* occurs on the islands of the Antigua Bank and has been introduced into Bermuda.

Anolis bimaculatus bimaculatus (Sparrmann)

Lacerta bimaculata Sparrmann (1784: 169)
Anolis edwardsi Merrem (1820: 45)
Anolis reticulatus Gray (1840: 114)
Anolis mayeri Fowler (1918: 8)

Type. A specimen in the Museum de Geer Royal, Stockholm, *fide* Underwood (1959).

Type locality. St. Eustatius.

Diagnosis. An *Anolis bimaculatus* with a green orbital region; spots, when present, frequently dominated by a large dark costal one on each side; male throat fan very small, extensible nuchal crest very large.

Squamation. One hundred ninety-seven specimens (113 males, 77 females, and 7 juveniles) are similar to other Lesser Antillean *Anolis* of the *bimaculatus* group except in the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris. The midventrals are smooth; there are 21–32 (average 26) contained in the standard distance at midbody. The middorsals average larger than the midventrals; there are 21–27 (average 23) in the standard distance; the middorsals are subimbricate or inimbricate. The scales lateral to the middorsals grade rapidly to smaller dorsal granules; there are 29–37 (average 33) in the standard distance six scales lateral to the dorsal midline. The digital pads are broad and raised; there are 26–35 (average 30) subdigital lamellae under the second and third phalanges of the fourth toe. I found no significant differences in squamation between the populations of this form on St. Eustatius (45 examined: 29 males, 15 females, 1 juvenile), St. Kitts (109 examined: 59 males, 46 females, 4 juveniles), and Nevis (43 examined: 25 males, 16 females, 2 juveniles).

Coloration. This is a basically green anole with green orbital skin; beyond those facts, it is an extremely variable species, and virtually the full range of variation may be seen in the St. Kitts population. Cochran (see Williams, 1962a: 457) describes a specimen near the gaudy extreme, but apparently lacking the ornate black and grey or brown trunk-spotting so frequent in this species. MCZ 75472, collected by me in Basseterre, showed the shades of pink, orange, yellow, green, and blue mentioned by Cochran, and had a large, sooty costal spot, and mottlings of grey-brown bordered black on the dorsal surfaces. MCZ 75464, collected by me at Willet's Estate, was virtually uniform green, shading to yellowish on the throat and white on the venter. There were no dark spots. MCZ 75469, collected by me at Basseterre (Fig. 22), is a near rival to this extreme. Most individuals of either sex, anywhere in the range of this subspecies, show at least the dark costal spot.

The notes quoted by Williams (1962a: 456–458) intimate the possibility of inter-island differences. Anxious to document such predictable (owing to isolation) differences, I paid very careful attention to colors and patterns in the field. The entire St. Eustatius population is much less variable than either of the larger island populations, and near the spotted and mottled extreme noted for MCZ 75472 above; all St. Eustatius specimens, however, are completely included within the range of Kittitian variation. The consensus, reported by Williams, that Nevis specimens are less spotted (or have the costal spot less distinct) is sharply contradicted by my specimens and observations: JDL 229, taken at Market Shop, is as spectacularly spotted as any animal of any species known to me; it has no more spots than, for example, MCZ 75472 from St. Kitts, and lacks the transverse mottling common to what I regard as the most patterned extreme; it has, however, very sharp definition of about 40 ink-black dots on each side of the head and body, about two dozen on the dorsal surfaces of the hind limbs, and even some on the forelimbs; the costal spot is one of the biggest and boldest: about half again the size of the ear. On the very next tree I collected JDL 230, a specimen with hardly any dorsal spotting at all, and quite without a costal spot; JDL 230 had as brilliant yellow a shoulder stripe, however, as I have seen (cf. King *in* Williams, 1962a: 457). In summation, then, *Anolis bimaculatus bimaculatus* is an exceedingly individually variable form, and no way of distinguishing specimens from the three islands on the basis of color can be found.

The ventral surfaces of this form vary from light green or yellow to white. The tiny throat fan of males is rarely used and highly variable: it may be all yellow or orange, or spotted or streaked with orange or yellow on a whitish ground; the scales may conform to the ground color, or be creamy to dull white. Females are so similar to males as to be quite inseparable on color characters when like-sized specimens are compared; they never attain the gaudy hues and bold markings that some old males achieve, however.

Color change from the normal green condition is to chocolate or blackish brown when upset. Color patterns of both sexes are shown on Plate 2.

Size and sexual dimorphism. The largest male examined is 114 mm, snout to vent (MCZ 75469), and comes from Basseterre, St. Kitts. The smallest apparently mature male is 62 mm (MCZ 75446), from Boven Bay, St. Eustatius. The largest female examined is 69 mm (MCZ 75473) from Basseterre; the smallest mature female is 52 mm (MCZ 75335) from Gilboa Hill, St. Eustatius. Because important inter-island size differences have been suggested to me by several people in conversation, and seem indicated by King's comments (*in* Williams, 1962a: 457), a closer scrutiny of the question is in order:

On St. Eustatius, 29 mature males range from 90 to 62 mm, snout to vent (MCZ 75325, Oranjestad, and MCZ 75446, Boven's Bay, respectively); 15 mature females range from 67 to 52 mm (MCZ 75319, Oranjestad, and MCZ 75335, Gilboa Hill, respectively).

On St. Kitts, 59 mature males range from 114 to 63 mm (MCZ 75469, Basseterre, and MCZ 65294, Golden Rock Airport, respectively); 46 mature females range from 69 to 54 mm (MCZ 75473, Basseterre, and JDL 167, 2.5 miles northeast of Lambert's Estate Yard, respectively).

On Nevis, 25 mature males range from 112 to 63 mm (JDL 230, Market Shop, and JDL 193, Charlestown, respectively); 16 mature females range from 66 to 53 mm (MCZ 28714, "Nevis," and MCZ 65290, Newcastle, respectively).

Therefore, no significant differences exist between the three island populations in minimum male size (62, 63, 63), maximum female size (67, 69, 66), or minimum female size (52, 54, 53). The only significant difference is in maximum male size between St. Eustatius (90) and St. Kitts-Nevis combined (114 and 112). On St. Eustatius a colubrid snake of the genus *Alsophis*, a presumed lizard eater, is prevalent; this snake does not occur on either St. Kitts or Nevis. Bearing in mind my remarks on "giant" (i..e., 100 mm plus) anoles made above (under "the genus *Anolis*"), it is possible to interpret the difference in maximum male sizes attained as a result of predation, and not as an indication of genetic differences between populations.

The sexes of *A. b. bimaculatus* overlap little in size at maturity, but are otherwise quite alike, barring the obvious distinction of the postanal plates in males.

The standard distance is 17–20 (average 18) per cent of the snout-vent length in both sexes.

Population structure and ecology. This species is abundant and infradispersed throughout the lowlands of all three islands; at high elevations it is absent, though I have taken a specimen at 1100 feet (JDL 167, forest edge, southeast rim of Godwin's Gut, 2.5 miles northeast Lambert's Estate Yard), and seen several others at the same locality. Clearing forest will presumably extend the range of this species altitudinally, if it is permitted to occur. *A. b. bimaculatus* is quite ubiquitous in habits, despite its large size and such seemingly arboreal adaptations as high lamellae counts. Males may perch as high as ten to fifteen feet above ground, but are usually at about three to six feet; they commonly forage with females and juveniles on the ground, and thus, frequently, with *Anolis wattsi schwartzi* (see "*Popultaion structure and ecology*" of that subspecies, and the general "*Discussion*" of *Anolis wattsi*). Whenever *A. w. schwartzi* occurs in the lowlands, the two species interact. Males frequently display at each other, and the very large fan of tiny *schwartzi* sometimes seems to deeply impress the virtually fanless, giant *bimaculatus*. I suspect that, originally, *A. b. bimaculatus* was far less abundant and widespread than it is today; an almost completely parapatric situation may have existed between the two species, with *bimaculatus* confined to open, arid areas and littoral, and *schwartzi* confined to shady woods. Clearing the forest for agriculture made possible a *bimaculatus* expansion into *schwartzi* territory; perhaps the two species, once largely geographically separated by ecological zonation on these high, first cycle islands, interact so vigorously today simply because they have not yet adapted to large-scale sympatry.

Distribution. Anolis bimaculatus bimaculatus occurs throughout St. Eustatius, St. Kitts, and Nevis, in open, sunny areas to at least 1100 feet elevation.

Relationships. This form differs significantly from *A. b. leachi* in the following respects: the nuchal crest is much more developed, and is extended to constitute the principal feature of male display; correspondingly, the throat fan is reduced to the minimum seen in any Lesser Antillean *Anolis*, and is considerably smaller (rather subjectively judged) than in *leachi;* jaw sculpture (noted by Etheridge, 1964) is much weaker in specimens of this form than in like-sized *leachi;* the costal spot is generally far more evident, and general vermiculation far less prevalent, in this form; the orbit is green rather than yellow. The last character is the best for separating all specimens, but the existence of *leachi* with decidedly yellow-green orbital skin (e.g., MCZ 75781, St. John's) leaves me no choice but to regard these two forms as still conspecific.

The relationships of the species are discussed under the following form.

Anolis bimaculatus leachi Duméril and Bibron

Anolis leachi Duméril and Bibron (1837: 153)
Anolis antiguae Barbour (1915: 74)
Anolis barbudensis Barbour (1923: 4)

Type. MNHN Ig. 34/1; T. Bell *leg.*, *fide* Underwood (1959).

Type locality. "Antilles," here restricted to St. John's, Antigua, capitol of the principal island on which the form occurs, and where it is abundant.

Diagnosis. An *Anolis bimaculatus* with predominantly yellow orbital skin; speckles or vermiculation on anterior trunk; usually not a large, dark costal spot on each side; male throat fan small, but well developed; extensible nuchal crest large, but not remarkably so.

Squamation. Ninety-five specimens (47 males, 41 females, and 7 juveniles) are similar to other Lesser Antillean *Anolis* of the *bimaculatus* group, except in the following features: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris. The midventrals are smooth (faint keeling may appear on some lateral ventrals; cf. Williams, 1962: 458); there are 20–30 (average 25) contained in the standard distance at midbody. The middorsals average slightly smaller than the midventrals: 21–32 (average 27) are contained in the standard distance; they are subimbricate or inimbricate. The scales lateral to the middorsals grade rapidly to smaller dorsal granules; 29–38 (average 34) granules are contained in the standard distance six scales lateral to the dorsal midline. The digital pad is the largest and most strikingly "raised" of *bimaculatus* group anoles; there are 28–36 (average 33) subdigital lamellae under the second and third phalanges of the fourth toe.

Coloration. The ground color of males varies from drab grey-green to brilliant yellow-green or blue-green; females from the drier parts of the range may be grey or grey-brown, without green. The orbital skin is basically yellow: sometimes quite bright, sometimes smudged with grey, and rarely light yellow-green. Grey to grey-brown vermiculation or small spots cover the anterior trunk and, usually, the head; females usually have a middorsal band relatively free of this dark marking. The ventral surfaces vary from light green or yellow to dull greyish white. The small throat fan of the male is yellow-orange to dull orange; the scales are usually paler than the skin, and frequently nearly white.

The full range of ground color variation may be seen at a number of localities: the north coast of Antigua (e. g., MCZ 57776–7, Hodge's Bay), or on Green Island, east of Antigua (MCZ 82108–9). The dullest individuals come from the most xeric regions: Barbuda (MCZ 75779–80, Codrington), Long Island, northeast of Antigua (MCZ 75783–4), and York Island, southeast of Antigua (MCZ 82110–5). Specimens from St. John's (e. g., MCZ 75781–2) may be as bright as any, or rather dull; I have a note dated 18.v.63 that all *A. b. leachi* seen at Body Ponds, northwest of Sweets Village, in the wettest part of interior Antigua, are very deep green with blue tones.

Several people (of admittedly ornithological leanings) have suggested that the name "*barbudensis*" Barbour (1923) is valid because less than 25 per cent of the Antiguan *leachi* population is as dull, or duller, in ground color as are all Barbudan specimens. That is to say, that if one were given a representative sample of *leachi* from all over its range, and picked the dullest individuals as "*barbudensis*," one would be right (i. e., they would be Barbuda specimens) 75 per cent, or more, of the time. If, however, one were given a series from, for example, Hodge's Bay, and one guessed the dullest specimens to be "*barbudensis*," one would be dead wrong

100 per cent of the time. The Barbuda type of *leachi* coloration is completely included within the Antiguan extremes of variation; Amadon (1949) and Mayr, Linsley, and Usinger (1953: 100) are perfectly clear on the point that this situation does not fit the 75 per cent rule for subspecies recognition. This situation in *A. b. leachi* may be instructively compared to the situation obtaining between *A. w. wattsi* (Antigua) and *A. w. forresti* (Barbuda): nominate *wattsi*, in the northern part of its range, sometimes approaches the diagnostic characteristics of Barbudan *A. w. forresti*: it never equals them.

Color change is from the normal green or grey to chocolate or blackish brown when upset. Color patterns of both sexes are shown on Plate 2.

Size and sexual dimorphism. The largest male *Anolis bimaculatus leachi* measured is 113 mm, snout to vent (MCZ 75779), from Codrington, Barbuda. That specimen was preserved 6.v.63, and the measurement was made 22.iii.65—after I had read Etheridge's (1964) account of the fossils from Barbuda; an 8 per cent shrinkage (see "Materials, Methods, Terms, and Concepts," above) would put this individual over 120 mm in life. Marks made in my field catalogue at snout tip and vent of the fresh dead animal are 123 mm apart; I regard this subspecies as the largest of all the *bimaculatus* group forms, and it certainly attains lengths today far in excess of that noted as maximal by Etheridge (1964). The following specimens may be noted for large size, as preserved: MCZ 16167, Barbuda ("*barbudensis*" type): 107 mm; MCZ 75783, Long Island northeast of Antigua: 109 mm; and, MCZ 75781, St. John's, Antigua: 111 mm. I can say with assurance that the two larger size classes of Barbudan fossils, which Etheridge regarded as representing two species, represent solely *Anolis bimaculatus leachi* (see remarks on "giant" anoles, under "The genus *Anolis*," above).

The smallest apparently mature males examined are both 68 mm, snout to vent (MCZ 65313–4), and are from Fort James, Antigua. The largest female examined is 70 mm (MCZ 66363), from Bermuda; a 69 mm specimen (MCZ 65306) is from St. John's Antigua. The smallest apparently mature female examined is 52 mm (MCZ 65311), from Fort James. Sexual dimorphism is not apparent in scales or proportions (standard distance 17–20, average 18, per cent of snout-vent length in both sexes), and very weakly indicated in color. With respect to size, however, dimorphism is quite sharp.

Population structure and ecology. This is an arboreal species: as close to a true crown dwelling form as occurs in the Lesser Antilles. Females and juveniles may rarely be encountered foraging on the ground, adult males virtually never. Perch heights for males vary from eight feet to as high as trees grow on the Antigua Bank; notes by T. Savage (with MCZ 65363–5) indicate that the introduced Bermuda population has retained its arboreal habits.

Though basically insectivorous, I recorded a specimen on Great Bird Island, northeast of Antigua (21.ii.66) eating prickly pear (*Opuntia*) fruit.

Because *A. b. leachi* is restricted to trees (or such substitutes as buildings), land clearing for agriculture has imposed a clumping effect on its otherwise infradispersed population structure.

Distribution. This form occurs throughout the Antigua Bank islands wherever there are trees; it has been introduced into Bermuda.

Relationships. The relationship of this form to *A. b. bimaculatus* is discussed under that form. It was suggested above that the species *bimaculatus* has been derived from an essentially *gingivinus* stock (see *Relationships*, *A. gingivinus*), and that the species originated on the Antigua Bank. *A. b. leachi* is essentially similar to *A. gingivinus*, except in the following particulars: it averages greener; it grows much larger; it is less notably striped; and (the chief distinction) it has more toe lamellae. All of these may be adaptations to a more arboreal way of life, and marked arboreality seems to be the way in which *leachi* has most effectively niche-segregated from *Anolis wattsi.* If a population of ancestral *Anolis bimaculatus* were isolated from *A. wattsi* sympatry after the initial adaptation away from the *gingivinus* stock had occurred, one might expect to see some, but not all, of these characters present in a species otherwise similar to *gingivinus.* I will argue below that *Anolis nubilus* is just that species.

Etheridge (1964) noted the remarkable jaw sculpturing of adult *A. b. leachi.* All specimens over 100 mm, snout to vent, could match the extreme of sculpture depicted by Etheridge, and one, MCZ 75783, from Long Island, northeast of Antigua, exceeds it. In this specimen, disjunct nodules and balls of bone are set in sockets in the markedly ornate dentary. The adaptive significance of jaw sculpture, or even its genetic basis, is open to speculation.

In summation, *Anolis bimaculatus* is the giant of the *bimaculatus* group (only one other form, a race of *A. marmoratus—ferreus* of Marie Galante—exceeds 100 mm). Gigantism seems possible where predation is light, or where the genetic potential to exceed *ca.* 100 mm is well developed and results in predator (kestrel and colubrid snake) immunity. The two races of this species are diverging in important respects (throat fan and nuchal crest size; color) that may result from niche-segregating adaptations to different races of *Anolis wattsi*

Anolis nubilus Garman

Anolis nubilus Garman (1887: 32)

Type. MCZ 6181, W. B. Richardson coll. I have tied the tag to the largest of the three specimens, labeled 6181, and regard it as the type; the other two specimens (fine examples of the species) will be regarded as untagged paratypes.

Type locality. Redonda.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals smooth; width of ear opening, at middle of ear, contained in height of ear opening 2.2 or less times; subdigital lamellae 26–33; male with large, virtually white throat fan; female with bold whitish spots or streak above hind limb insertion.

Squamation. Twenty-five specimens (19 males and 6 females) are similar to other Lesser Antillean *Anolis* of the *bimaculatus* group, except in the following features: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris. The midventrals are smooth; 20–28 (average 24) are contained in the standard distance at midbody. The middorsals average slightly smaller than the midventrals; 22–30 (average 26) are contained in the standard distance; they are subimbricate or inimbricate. The scales lateral to the middorsals grade rapidly to granules; 32–44 (average 38) are contained in the standard distance six scales lateral to the dorsal midline. The digital dilations are broad and "raised"; there are 26–33 (average 30) subdigital lamellae under the second and third phalanges of the fourth toe.

Coloration. Both sexes are a very dingy, dark grey-brown and can change to grey-green or grey-blue. The venter is dirty grey. The male throat fan is virtually white (very pale grey), usually with a very faint greenish or yellowish wash, and sometimes with faint blotches of these colors; the scales are white or pale grey. The orbital skin is sometimes slightly yellower than the rest of the head, but not distinctively colored. There are ashy or white flecks on the trunk and legs; these augment the vague longitudinal striping of the female, and are especially prominent over the hind limb insertion. The female has a flank stripe far better delimited than the male.

The color patterns of both sexes are shown on Plate 1.

Size and sexual dimorphism. The largest specimen ever collected, a male, is the type, MCZ 6181: 81 mm, snout to vent. Of the more recently collected material, the largest male is MCZ 82934, taken by me 2 August 1964: 72 mm; this is not as large as one of the paratypes, a 75 mm male. The smallest apparently mature male is 53 mm: MCZ 82940. The largest female is 52 mm: MCZ 82942. The smallest female with eggs is 50 mm: MCZ 82944. With only 25 specimens, only six of them females, I believe the available data on size is incomplete. Only two females are surely mature (those noted above); the species probably grows as large today as it ever did, though the effect of goats on the natural vegetation of Redonda may have so increased vulnerability to bird predation that large specimens are now very rare.

As in *Anolis bimaculatus*, sexual dimorphism is strong in size, weak in coloration, and nonexistent in squamation. In both sexes the standard distance is 17–20 (average 18) per cent of the snout-vent length.

Population structure and ecology. Anolis nubilus is not abundant, but occurs all over Redonda. Owing to the lack of trees, it seems to dwell mostly in the shade of large rocks close to ground. In the ruins of the old building and on the one tree (a *Casuarina*, apparently inedible even to goats), *A. nubilus* climb as high as they can get: about fifteen feet. This species must compete with the large, glossy black ground lizard, *Ameiva atrata*, for at least some of its food. Surely Redonda once supported more vegetation, and presumably *Anolis nubilus* then had an easier life. The feral goats should be extirpated on this remarkable island, whose only known nonflying vertebrates are species found nowhere else on earth. The sex ratio is apparently balanced despite the normal bias for male captures.

Distribution. Anolis nubilus occurs only on Redonda. This tiny islet is exceedingly steep-to, and rises nearly 1000 feet out of the sea. There is virtually no surrounding bank, and the full swell of the western North Atlantic pounds Redonda's cliffs. A tiny, nearly vertical gut on the leeward side provides the only access to the top of the islet up the cliffs; great blocks of basalt lie at the foot of this gut, and one's original entrance to Redonda is made by jumping onto these blocks as the boat goes past them. It is about like jumping from a moving elevator onto a card table, except that elevators give more notice of directional reversals. Getting on Redonda is easy compared to All-a-Wash or Kick-'em-Jenny (in the Grenadines), but getting on is just the beginning.

The islet is a great block of igneous extrusives: strata of basalt and the peculiarly conglomeratelike, porphyritic material so often the result of Antillean vulcanism. The top of Redonda is a rolling wold, and a favorite place of innumerable nesting sea birds; the gut provides a route for their guano to descend the cliffs, and it dries to a thick powder there. Because of its leeward location, a chimney effect is produced in the gut, and the guano dust, mixed with the volcanic sand weathered from the parent rock, tends to rise when disturbed. As one toils up the gut under the tropical sun, one is accompanied by a cloud of this dust, which soon mingles with one's own sweat to produce a wondrously aromatic and abrasive, though rather gluey, bath. At the top, jumbles of rocks and clumps of prickly pear rise gently to the old ruins, complete with a hedge of *Bougainvillea* and the single tree. This is the home of *Anolis nubilus.*

Relationships. Underwood (1959) provisionally synonymized this species with *Anolis lividus*, its closest neighbor to the south, on Montserrat. This has always seemed incomprehensible to me in view of the obvious distinctions between the forms: ear shape and coloration. It was quite surprising to me, therefore, when Dr. Albert

Schwartz (*in litt.*) reported that he, too, regarded *nubilus* and *lividus* as relatives (though not, I hasten to add, as synonyms). Assessments of relationship are always more subjective than we usually like to admit: I usually begin to associate a species when first encountered—whether consciously or subconsciously—with the other species it somehow looks like; this is long before any counts or measurements have been made, of course. To me, *Anolis nubilus* looked and acted like a near relative of *bimaculatus* or *gingivinus*, not like a near relative of *lividus* or its very close ally *marmoratus.* The male throat fan is large, as in the latter species; there is no indication of jaw sculpture, and the ear opening is far more oval than in *bimaculatus* itself (though that is true of *gingivinus* also). However, the manner of expression of sexual dimorphism (size more than color), the high lamellae counts, and the dull hues somewhat vindicate my original view; no more compelling lines of evidence are presently available.

I believe that *Anolis nubilus* was derived from the autochthonous Antigua Bank *bimaculatus* stock at a time not long after the *bimaculatus* stock had begun divergence from its *gingivinus* ancestor, and at about the same time as *bimaculatus* stock also colonized the St. Kitts Bank. Thus, *A. bimaculatus leachi* was evolving, as the original *bimaculatus*, away from *gingivinus* because of sympatry with *wattsi;* when it colonized the St. Kitts Bank, it remained in sympatry (or ecologically zoned parapatry) with an *Anolis wattsi*, and maintained enough of a parallel component in its evolution as a result to remain an *Anolis bimaculatus. Anolis nubilus*, the product of a contemporaneous colonization of Redonda, went out of *wattsi* sympatry, and retained both its basically *gingivinus*-like characters (full sized fan, oval ear, dull hues) and its pro-*bimaculatus* adaptations (high lamellae counts, large size); it has adaptively stagnated in these respects ever since. The faded fan and ashy markings of *Anolius nubilus* are certainly its own innovations.

Anolis lividus Garman

Anolis lividus Garman (1887: 32)

Type. MCZ 6167, S. Garman coll.

Type locality. Montserrat; here restricted to the principal town of Plymouth, where this species is abundant.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; midventrals smooth or weakly keeled; width of ear opening, at center of ear, contained in height of ear opening 2.3 or more times; eyelids yellow to red; no dark speckles or vermiculation on sides of neck.

Squamation. One hundred fourteen specimens (64 males, 44 females, and 6 juveniles) are similar to other Lesser Antillean *Anolis* of the *bimaculatus* group, except in the following features: prenasal posterodorsally elongate, extending to or beyond the level of the naris. The midventrals are usually weakly keeled, but sometimes smooth; there are 21–28 (average 25) in the standard distance at midbody. The middorsals are virtually the same size as the midventrals; there are 20–28 (average 24) in the standard distance; they are rather tubercular and sub- or inimbricate. The scales lateral to the middorsals grade rapidly to dorsal granules: 30–39 (average 35) in the standard distance six scales lateral to the dorsal midline. The digital dilations are quite ordinary, and of the "raised" type; there are 20–27 (average 23) subdigital lamellae under the second and third phalanges of the fourth toe.

I previously (Lazell, 1964a: 372) stated that the ventrals of *Anolis lividus* are always keeled, and that the direction of keeling is a diagnostic distinction from *Anolis marmoratus.* My own collections, made subsequently, provide a sufficient quantity of specimens to negate my previous view: the direction of keeling is more variable than I had supposed, and at least the midventrals may occasionally be smooth. (See *Relationships*, below, and *Anolis marmoratus*.)

Coloration. This is a basically green anole with yellow to red eyelids; the males are bright, and shade from brownish green on the head through plain or yellow-green on the trunk to blue-green on the tail. The females are olive-green or brown and have the dullest eyelid colors: yellow to orange; they have striped, ladder, or obsolete middorsal patterns. The ventral surfaces are cream, yellow, or light green.

The male throat fan varies from yellow to olive drab, and has white to green scales.

Both sexes turn darker and browner when upset.

All of the above variation can be seen in the Plymouth population. This species was seen and described alive by Underwood (1959: 199), and further described in detail by Auffenberg and King *in* Williams (1962: 456–460). Only the following points need to be added:

The light (whitish) spotting is an individual variation, not a result of color change; it is quite constant in those specimens that have it, and is enhanced by color change to the dark phase. Females may have light speckles as well as males, but these markings reach their extreme of boldness in the latter.

Specimens from the northwest part of the island average the yellowest: males are frequently bright yellow-green (e. g., MCZ 82032–7, Woodlands).

Specimens from the northeast part of the island average browner than most in Plymouth, and occasionally have dull orange or reddish brown blotches on the nape (e. g., MCZ 82035–7, Farm Estate).

Specimens from remnant rain forest on Mount Chance (e. g., MCZ 82042–3) are at the blue-green extreme of variation.

Adult color patterns are shown on Plate 2.

Size and sexual dimorphism. The largest specimen of this species I have seen is a male, 70 mm, snout to vent (MCZ 82044, Farm Estate); the smallest apparently mature male is 44 mm (MCZ 55701, Plymouth). The largest female examined was 52 mm (MCZ 82051, Farm Estate); the smallest mature female was 40 mm (MCZ 75394, Plymouth). Sexual dimorphism is far more striking in coloration than in size, and does not exist in squamation. The standard distance is 16–19 (average 18) per cent of the snout-vent length in both sexes.

Population structure and ecology. Anolis lividus is ubiquitous and infradispersed throughout Montserrat. Males usually perch from two to eight feet above the ground on a vertical substrate; females and juveniles may be anywhere, but tend to climb less high than males. Both sexes frequently forage on the ground. Generally, the species is extremely abundant, but individuals may be difficult to locate over about 2500 feet on the one high peak: Mount Chance. Field observations indicate a balanced sex ratio.

Distribution. This species is confined to Montserrat, and is found everywhere there.

Relationships. Underwood's (1959) association of this species with *A. nubilus* of Redonda does not fit with my views at all, as discussed under that form.

Anolis lividus and *Anolis marmoratus* are very closely allied. My collections have obliterated the one squamational distinction I thought valid (see *Squamation*, above). The extreme diversity of the twelve subspecies of *A. marmoratus* in morphological characters is a severe handicap in framing species level diagnosis. The eyelid color of *A. lividus* can be matched by the *marmoratus* races *desiradei* and occasionally *chrysops;* both of these forms have dark vermiculation, at least on the neck. *Anolis lividus* seems definitely to possess an evolutionary role uniquely its own, and no useful purpose would be served by allying it subspecifically with *marmoratus.*

Anolis marmoratus Duméril and Bibron

Anolis marmoratus Duméril and Bibron (1837, p. 139)

Type. MNHN Ig. 43. Plee coll.

Type locality. Capesterre, La Guadeloupe.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group combining the following characters: prenasal posterodorsally elongate, extending to or beyond the anterior level of the naris; ventrals smooth or weakly keeled; width of ear opening, at center of ear, contained in height of ear opening 2.3 or more times; eyelids either not yellow to red, or if so colored, then dark speckles or vermiculation present on the neck.

Remarks. This is the most complex rassenkreis in Lesser Antillean Iguanidae; twelve parapatric or dichopatric forms, distinct in coloration, and frequently in squamation, are found on the three banks of the Guadeloupéen archipelago. I previously (Lazell, 1964a) gave each of these forms detailed consideration and have provided an exhaustive general discourse on the species as a whole; this work should be consulted for information not given below. Presently, I shall repeat this information only through the diagnosis of each form; a comment, including information obtained since 1961 (when the collections for the 1964 report were made), is given for each subspecies; a general map of their ranges is provided (Fig. 5); finally, a discussion of the relationships of the species is given after the subspecies accounts. Here is a species upon which the physiographic and meteorologic peculiarities of the Lesser Antilles have combined to produce ecotypic races developed to a truly dramatic extent (see Introduction).

Population structure and ecology. All of the lowland races of *Anolis marmoratus* are, or were, evenly dispersed, rather than clumped, in population structure. Cultivation has cleared large areas, especially within the ranges of the races *marmoratus, setosus,* and *speciosus,* and this has limited the infradispersion of these forms somewhat. Except for *alliaceus,* which has a distinctive ecology (see below and Lazell, 1964a), all the remaining races occupy relatively dry country; they are abundant wherever bush or trees occur. Both sexes may forage on the ground; females and juveniles usually do. Males tend to perch on any vertical substrate, somewhat higher, on the average, than females: from three to ten feet.

Anolis marmoratus marmoratus Duméril and Bibron

Anolis marmoratus Duméril and Bibron (1837: 139)

Type. MNHP Ig. 43, no date, coll. Plee, *fide* Underwood (1959).

Type locality. Capesterre, La Guadeloupe.

Diagnosis. Dorsal scales in the standard distance 36 to 48 (average 42); 25 to 30 (average 28) subdigital lamellae; adult male green, changing to brown, snout suffused with orange; head, neck, and orbital area boldly marbled with bright orange; throat fan light orange-yellow scales. Adult female green, with an obsolete or dully striped middorsal pattern.

Comments. Fresh material from Bois Debut (JDL 282–291) provides a male larger than any other *Anolis marmoratus* ever recorded, except some *A. m. ferreus:* 82 mm, snout to vent (JDL 282). The smallest apparently mature male is 53 mm (MCZ 71219, Carangaise). Mature females range from 54 mm (MCZ 71222, Carangaise) to 48 mm (MCZ 71200, Bananier). There are 21–28 (average 25) middorsals in the standard distance. Adults are shown on Plate 2.

This form is confined to the plain of Capesterre: well-watered lowland to windward of the central, barrier range of La Guadeloupe.

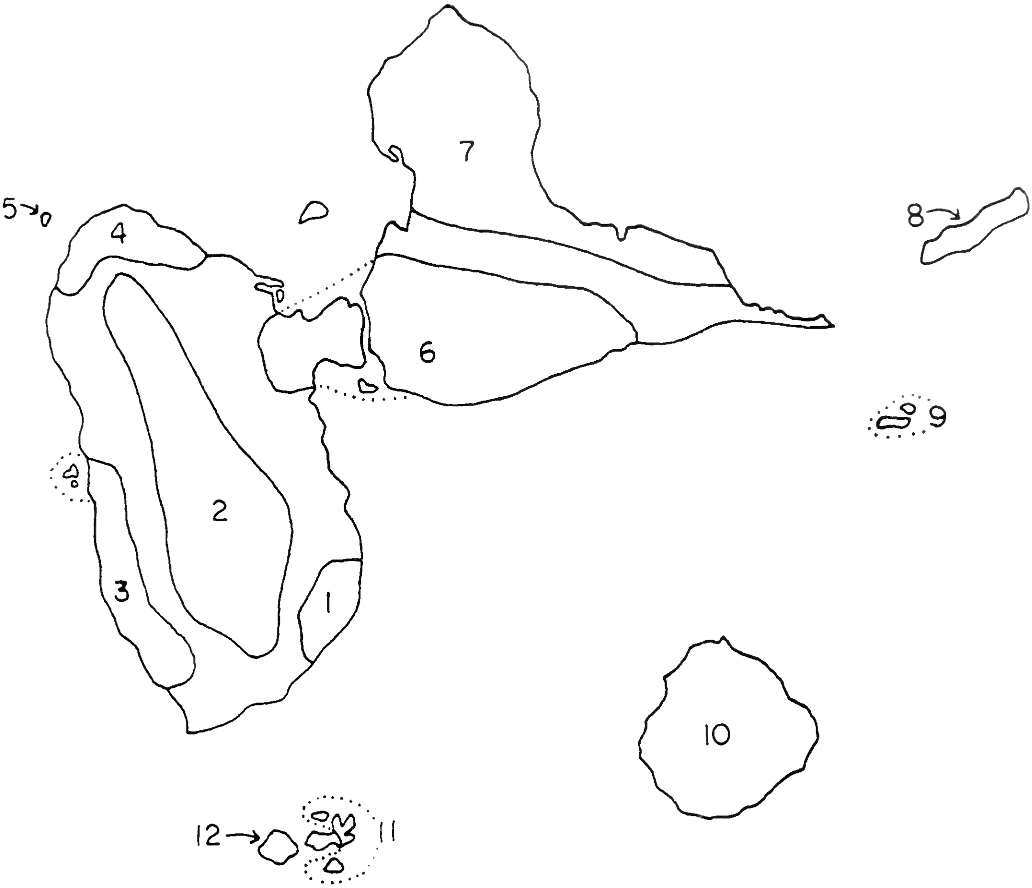

Figure 5. The Guadeloupéen archipelago, showing the ranges of the subspecies of *Anolis marmoratus:* 1. nominate *marmoratus;* 2. *alliaceus;* 3. *girafus;* 4. *setosus;* 5. *kahouannensis;* 6. *speciosus;* 7. *inornatus;* 8. *desiradei;* 9. *chrysops;* 10. *ferreus;* 11. *terraealtae;* 12. *caryae.*

Anolis marmoratus alliaceus Cope

Anolis alliaceus Cope (1864: 175)

Type. BMNH 946.8.28.96, *fide* Underwood (1959).

Type locality. Maison Forestier du Matouba, elevation 700 meters, La Guadeloupe.

Diagnosis. Dorsals in the standard distance 36 to 48 (average 42); 25 to 30 (average 28) subdigital lamellae; adult male green with no blue or bluish pigment in this ground color; palpebral area of orbit white in the light phase, changing to grey as the animal turns dark green; dark dots, tending to run together, scattered over the anterior and dorsal surfaces, and set off by pale cream to yellow borders; throat fan deep orange with green scales. Adult female green with mottled middorsal pattern and small light or dark dots anteriorly.

Comments. Fresh material includes a pair taken at Refuge Joseph Bourgeoise, south slope of Soufrière (JDL 292–3) and a magnificent male taken at Col des Mamelles (JDL 294). The largest male is 74 mm (MCZ 71338, Maison Forestier du Matouba); the smallest mature male is 48 mm (MCZ 71342, Maison Forestier du Matouba). The largest female is 57 mm

(MCZ 71344, Maison Forestier du Matouba); the smallest mature female is 43 mm (north ridge Morne Monstique *ca.* 650 m). There are 24–31 (average 28) middorsals in the standard distance. Adults are shown on Plate 2.

This is the form of the montane rain forest ecological zone.

Anolis marmoratus girafus Lazell

Anolis marmoratus girafus Lazell (1964a: 377)

Type. MCZ 71259, collected 14 August 1961 by J. D. Lazell.

Type locality. Vieux Habitants, La Guadeloupe.

Diagnosis. Dorsals in the standard distance 38 to 53 (average 47); 25 to 30 (average 28) subdigital lamellae; adult male blue-green to brown, always browner on the head and neck and always at least bluish on the posterior body and tail base; pale streaks and stipples, usually running together to form stripes that produce a reticulate pattern isolating dark spots, on the lateral trunk; throat fan pumpkin yellow with cream-colored to white scales. Adult female pale grey-brown with broken middorsal pattern.

Comments. Fresh material is from Les Ilets de Pigeon, off Malendure: MCZ 81863–7 (Nord), and 81868–72 (Sud). The largest male is the type: 75 mm; the smallest mature male is 56 mm (MCZ 71324, Boulliante), the largest female is 56 mm (MCZ 71286, Baillif); the smallest mature female is 42 mm (MCZ 71337, Malendure). There are 20–30 (average 25) middorsals in the standard distance. Adults are shown on Plate 2.

This is the form of the arid coast in the rain shadow of the central barrier range of La Guadeloupe.

Anolis marmoratus setosus Lazell

Anolis marmoratus setosus Lazell (1964a: 380)

Type. MCZ 70813, collected 11 August 1961 by J. D. Lazell, Jr.

Type locality. Pointe Allegre, La Guadeloupe.

Diagnosis. Dorsals in the standard distance 38 to 53 (average 47); 22 to 28 (average 25) subdigital lamellae; dorsal scales spinose, those of the nape region so much taller than broad that a distinctly furred effect is produced; adult male blue-green with sooty transverse markings and a dark stripe through eye indicated when changing to the dark phase; throat fan yellow with greenish scales; belly pale, but without yellow tint. Adult female without a middorsal pattern as such, but with a variegation of green, brown, slate, and white speckles and blotches on dorsum, and bold, dark streaks on the lateral venter.

Comments. Females may have striped, ladder, or obsolete middorsal patterns. The largest male is 69 mm (MCZ 70820, Deshaies), not the type as I previously stated (Lazell, 1964a: 381). The smallest mature male is 48 mm (MCZ 70816, Pointe Allegre). The largest female is 51 mm (MCZ 70829, Deshaies); the smallest mature females are both 44 mm (MCZ 10417 and 10425, Ste. Rose). There are 26–34 (average 30) middorsals in the standard distance. Adults are shown on Plate 2.

This is the form of the mesic coast at the north end of La Guadeloupe, where the barrier range is lowest.

Anolis marmoratus kahouannensis Lazell

Anolis marmoratus kahouannensis Lazell (1964a: 382)

Type. MCZ 70791, collected 28 August 1961 by J. D. Lazell, Jr.

Type locality. Ilet-à-Kahouanne, Guadeloupe Passage, northwest of La Guadeloupe.

Diagnosis. Dorsals in the standard distance 30 to 38 (average 33); 22 to 28 (average 25) subdigital lamellae; dorsal scales conical, producing a bulldog-collar-spike effect on the nape; adult male chartreuse (= bright yellow-green) with no markings except bluish washes on the head and chin;

belly bright yellow; throat fan bright yellow with yellow scales. Adult female chartreuse with a bright yellow belly and no markings except occasional traces of a ladder middorsal pattern.

Comments. Additional specimens are ASFS X6055–7 (two males and a female) collected by Richard Thomas on the Ilet-à-Kahouanne, 4 March 1963. The largest specimen is 73 mm: the type. The smallest mature male is 57 mm (MCZ 70795). The mature females are all either 47 mm (MCZ 70799) or 48 mm (the rest); a 43 mm female (ASFS X6057) does not contain eggs. There are 23–31 (average 27) middorsals in the standard distance. Adults are shown on Plate 2.

This form presumably owes its distinctiveness to isolation, rather than ecological zonation.

Anolis marmoratus speciosus Garman

Anolis speciosus Garman (1887: 45)

Type. MCZ 6172, collected by Richardson, March, 1886.

Type locality. Pointe-à-Pitre, Grande Terre.

Diagnosis. Dorsals in the standard distance 32 to 50 (average 40); 20 to 26 (average 23) subdigital lamellae; adult male green, without dorsal markings; venter brightly washed with yellow; orbital area sky blue; throat fan sulfur yellow with greenish scales. Adult female olive with ladder or striped middorsal pattern.

Comments. Additional specimens are MCZ 80533–4, "Guadeloupe," George Gorman coll., and MCZ 81883–91, Ste. Anne, Grande Terre, taken by me 13.viii.64. The largest specimen, a male, is 73 mm, snout to vent (MCZ 70978, Ilet-à-Cochons), not MCZ 70961, as previously stated (Lazell, 1964a: 385). The smallest apparently mature male is 48 mm (MCZ 70974, Abymes). The largest female is 52 mm (MCZ 70957, Baie Mahault); the smallest mature females are both 43 mm (MCZ 70945, Ste. Anne, and 70960, Baie Mahault). There are 26–35 (average 31) middorsals in the standard distance. Adults are shown on Plate 2.

This is the form of the main body of well-watered lowland to windward of the central barrier range of La Guadeloupe.

Anolis marmoratus inornatus Lazell

Anolis marmoratus inornatus Lazell (1954a: 386)

Type. MCZ 71036, collected 13 August 1961 by J. D. Lazell.

Type locality. Anse Bertrand, Grande Terre.

Diagnosis. Dorsals in the standard distance 38 to 53 (average 47); 20 to 26 (average 25) subdigital lamellae; adult male pale grey-green on trunk, rich brown on head; orbital area brown; belly pale lime-green; throat fan yellow with white to cream-colored scales; flank stripe indicated. Adult female pale grey-brown with striped middorsal pattern and flank stripe.

Comments. Females may have ladder middorsal patterns. Additional specimens are MCZ 81846–52, collected by me at Moule, Grande Terre, 9.viii.64. The largest specimen examined, a male, is 65 mm, snout to vent (MCZ 71049, town of Ste. Marguerite); my previous record of 75 mm, given for the type (Lazell, 1964a: 386) is in error, and resulted from a reversal of the digits in 57 mm, the correct measurement for the specimen. The smallest apparently mature male examined is 45 mm (MCZ 71025). The largest females are both 50 mm (MCZ 71018 and 81851, Moule); the smallest mature female is 40 mm (MCZ 71057, town of Ste. Marguerite). There are 26–36 (average 31) middorsals in the standard distance. Adults are shown on Plate 2.

The range of this form is dry; it is too far to windward of La Guadeloupe to be climatically affected.

Anolis marmoratus desiradei Lazell

Anolis marmoratus desiradei Lazell (1964a: 387)

Type. MCZ 71068, collected 14 September 1961 by J. D. Lazell, Jr.

Type locality. Grande Anse, La Désirade.

Diagnosis. Dorsals in the standard distance 32 to 50 (average 40); 22 to 28 (average 25) subdigital lamellae; adult male pale greenish with yellow wash on sides and yellow belly; dorsal surfaces extensively vermiculated with darker grey-brown; throat fan yellow with white to cream-colored scales; orbital area bright rust red; chin yellow with bold blue-grey streaking. Adult female grey-greenish with grey head and yellow belly; middorsal pattern obsolete or dully striped.

Comments. Previously (Lazell, 1964a: 388) I stated of females: "there is no indication of vermiculation." That is untrue, and results from failing to note the vermiculation of living females in my field notes, and then assuming that the preserved specimens (whose patterns I did not examine closely) were unmarked in life. Fresh material collected by me (MCZ 81872–82, Grande Anse) documents female vermiculation. The largest specimen measured, the type, was 80 mm, snout to vent, fresh dead. The smallest apparently mature male is 51 mm (MCZ 62211, Ravine La Rivière). The three largest females are 53 mm (MCZ 71107–8, and 71111, Pointe Double); the smallest mature female is 44 mm (MCZ 71098, Le Souffleur). There are 21–31 (average 26) middorsals in the standard distance. Adults are shown on Plate 2.

Anolis marmoratus chrysops Lazell

Anolis marmoratus chrysops Lazell (1964a: 389)

Type. MCZ 70649, collected 4 September 1961, by J. D. Lazell, Jr.

Type locality. Terre de Haut, Les Iles de la Petite Terre.

Diagnosis. Dorsals in the standard distance 30 to 42 (average 36); 22 to 28 (average 25) subdigital lamellae; adult male somber green-grey with bright yellow suffusion on the sides and bright yellow belly; vermiculations present on the anterior trunk and nape, at least, and dark dotting usually present on remaining dorsal surfaces; orbital area red-gold; chin entirely blue-grey; throat fan yellow with pale yellow scales. Adult female grey with yellow belly, an obscure striped middorsal pattern, and a brief flank stripe.

Comments. All three topotypic females (originally MCZ 70663–5) are missing in 1967; presumably they were traded or given away as a matter of curatorial routine, without consideration of the effect of this action on the type series. The largest male, the type, was 73 mm, snout to vent, fresh dead. The smallest apparently mature male is 62 mm (MCZ 70662, Terre de Haut). The largest females are both 48 mm (MCZ 70653 and 70655, Trou Canard, Terre de Bas); the only other remaining female is mature and measures 46 mm (MCZ 70654, also from Trou Canard, Terre de Bas). There are 23–30 (average 26) middorsals in the standard distance. Adults are shown on Plate 2.

Anolis marmoratus ferreus (Cope)

Xiphosurus ferreus Cope (1864: 168)
Anolis asper Garman (1887: 31)

Type. BMNH 1946.8.5.59, no collector, no date.

Type locality. Morne Constant, Marie Galante.

Diagnosis. Dorsals in the standard distance 22 to 33 (average 28); 25 to 30 (average 28) subdigital lamellae; adult male somber grey-brown becoming greener posteriorly; dorsum sprinkled with dark spots seldom coalescing to form short vermiculations; suffusions, often forming blotches, of yellow laterally; orbital area dull yellow; uniform blue-grey of chin often invading otherwise yellow throat fan with yellow scales. Adult female grey-brown to greenish with brief flank stripe, obsolete middorsal pattern, and a very pale yellowish belly.

Comments. The largest male examined was 119 mm, snout to vent, fresh dead (MCZ 70767, Vieux Fort); the smallest apparently mature male is 63 mm (MCZ

70769, Vieux Fort). The largest female is 65 mm (MCZ 70763, Grand Bourg); the smallest mature female is 50 mm (MCZ 70780, Courbaril). There are 19–26 (average 22) middorsals in the standard distance. Adults are shown on Plate 2.

Anolis marmoratus terraealtae Barbour

Anolis terraealtae Barbour (1915: 76)

Type. MCZ 10627, collected by Noble, no date.

Type locality. Pompière, Terre de Haut, Les Iles des Saintes.

Diagnosis. Dorsals in the standard distance 28 to 40 (average 33); 20 to 26 (average 25) subdigital lamellae; adult male grey-brown to green-brown, without dark speckles or vermiculations; large blotches of bright yellow laterally and on nape fading to suffusions on posterior body and belly; yellow of orbital area often confluent with yellow blotching of nape and trunk; throat fan yellow with yellow scales. Adult female grey-brown with a faint flank stripe briefly indicated and a striped or ladder middorsal pattern.

Comments. The largest specimen was 80 mm, snout to vent (MCZ 70687, Pointe Basse, Grande Ilet), fresh dead. The smallest apparently mature male is 54 mm (MCZ 70713, Pompière, Terre de Haut). The largest females are 54 mm (MCZ 70714–5, Pompière, and 70693–4, Pointe Basse, Grande Ilet); the two smallest mature females are 51 mm (MCZ 70695, Pointe Basse, Grande Ilet, and 70756, Ilet-a-Cabrit). There are 22–30 (average 26) middorsals in the standard distance. Adults are shown on Plate 2.

The range of this form is, like that of *desiradei, chrysops,* and *ferreus,* the arid lowland typical of those islands too low in elevation to stop significant rainfall. See the following form, however.

The type locality, on eastern Terre de Haut, is called "Pont Pierre" on some maps; this seems odd, as there is no bridge or likely place to put a bridge.

I could not find the type specimen, MCZ 10627, for my 1964 account, but expected it to turn up eventually as I examined the rest of the Lesser Antillean anoles; it has not. Underwood (1959) lists it as a specimen examined, but this means little, as he seems to have recorded specimens from bottle labels, and thus listed many specimens as "examined" that have not been in the collection for decades. Since the paratypes are present and serve to identify the form on scale characters, I see no present need to designate a neotype.

Anolis marmoratus caryae Lazell

Anolis marmoratus caryae Lazell (1964a: 394)

Type. MCZ 70666, collected 6 September 1961 by J. D. Lazell, Jr.

Type locality. The town of Terre de Bas, Terre de Bas, Les Iles des Saintes.

Diagnosis. Dorsals in the standard distance 38 to 53 (average 47); 20 to 26 (average 23) subdigital lamellae; adult male pale green, becoming bright green posteriorly; a faint wash of yellow on abdomen, rest of belly lime green; fine vermiculations coalesce on the back of the head and the nape to produce a grey appearance; posteriorly these fine vermiculations produce distinct pale grey transverse markings; a pale, whitish flank stripe accentuated in the costal region by a lack of vermiculation; throat fan bright yellow with yellow scales; orbital area cream-colored. Adult female pale grey-green with ladder middorsal pattern and striking flank stripe set off by dark speckles above and below.

Comments. Additional, fresh material was taken by me at the type locality (MCZ 81853–62) and on the northwest side of Pointe Sud (MCZ 81836–45) on 10–11.viii.64. One of the new males (MCZ 81854) measures 75 mm, snout to vent, after more than two years in preservative; this specimen was no doubt larger than the type (75 mm, fresh dead) when alive. The smallest apparently mature male is 56 mm (MCZ 81857, town of Terre de Bas). The largest female is 55 mm (MCZ 70682, town of Terre de Bas); the smallest mature female is 46 mm (MCZ 81845, northwest side, Pointe Sud). Females may have simply striped middorsal patterns. There are 27–34 (average 30) middorsals in the standard distance. Adults are shown on Plate 2.

The range of this form is a low snag island: Terre de Bas. It does impede sufficient cumulus to have a distinctly wetter climate than do the islands to the east of it.

Relationships. Although striking sexual dimorphism in color is apparent in nominate *marmoratus, alliaceus,* and *speciosus,* it is less notable in the other subspecies. Sexual dimorphism in size is better developed in this species, as a whole, than in *A. lividus,* less well developed than in *A. bimaculatus.* There is no significant dimorphism in squamation. Geological evidence, discussed under Evolution below, indicates that differentiation of some of the subspecies, like *kahouannensis, desiradei,* and *chrysops,* has probably been post-Wisconsin. Behavioral evidence with captives indicates that forms strongly distinct in coloration, like *marmoratus* and *speciosus,* would not interbreed directly; females of *marmoratus* that readily accept males of their subspecies in captivity do not respond to *speciosus* males. In the field there is a large zone of intergradation between these forms; they are presumably subspecies that have evolved as a single land area was colonized, not the result of separate colonizing populations that evolved independently until they covered enough geographic area to meet. The selection pressures for their distinctive color patterns must be strong, or the distinctions would never have arisen; in the zone of intergradation, selection pressures must cline with the characters: intermediate anoles do best in an intermediate habitat. Thus, it is not surprising that a zone of intergradation exists between two forms that, if abruptly transported into sympatry, may not interbreed.

If we suppose that the sum of genetic distinctions between *A. lividus* and *A. m. marmoratus* are no greater than between *A. m. marmoratus* and *A. m. speciosus* (an assumption surely faulty owing to the magnitude of the actual isolation of the two former), could we assume that *lividus* and *marmoratus* would introgress if transported into sympatry? Quite the contrary, the evidence is that these anoles are so color sensitive that they would not. The only *marmoratus* forms that have the eyelid color of *A. lividus, desiradei* and *chrysops,* are so different in general body coloration that a similar interpretation is in order.

Gorman and Atkins (1968b) found *A. m. marmoratus* and the very divergent subspecies *A. m. ferreus* to be karyotypically similar to each other, and to other Lesser Antillean members of the *bimaculatus* group, except *A. acutus* (see *Relationships* of that species) and *A. oculatus* of Dominica. It is not, therefore, possible to make much of a case for close relationship between the species *marmoratus* and *oculatus,* despite their geographic proximity.

Anolis oculatus (Cope)

Xiphosurus oculatus Cope (1879: 274)

Lectotype. USNM 10145, by present designation.

Type locality. Roseau, Dominica (see Lazell, 1962: 468).

Diagnosis. An *Anolis* of the Lesser Antillean section of the *bimaculatus* group (as here defined) in which the prenasal is subrectangular, and fails to extend posteriorly to the anterior level of the naris.

Remarks. Anolis oculatus is the most bizarre member of the *bimaculatus* group, and one of the most peculiar members of its huge and diverse genus. It is remarkable and distinct in ways that I could not have known about when I wrote the original report on the species (Lazell, 1962); also, it is remarkable and distinct in ways which I simply did not notice at the time of that report. My previous work on *A. oculatus,* while correct in major taxo-

PLATE 2

9. *Anolis bimaculatus bimaculatus*: male, MCZ 75469; female, MCZ 75473; Basseterre, St. Kitts.

10. *Anolis bimaculatus leachi*: male, MCZ 82108; female, MCZ 82109; Ten Pound Bay, Green Island, E of Antigua.

11. *Anolis lividus*: uniform male, MCZ 82044, Farm Estate; female, MCZ 82051, Farm Estate; spotted male, MCZ 82043; S summit, Mt. Chance, Montserrat.

12. *Anolis marmoratus marmoratus*: male, JDL 282; female, JDL 288; Bois Debut, La Guadeloupe.

13. *Anolis marmoratus alliaceus*: male, MCZ 71358; female, MCZ 71359; N ridge, Morne Moustique, ca. 650 m, La Guadeloupe.

14. *Anolis marmoratus kahouannensis*: male, MCZ 70791; female, MCZ 70796; Ilet-à-Kahouanne, NW of La Guadeloupe.

15. *Anolis marmoratus speciosus*: male, MCZ 70925; female, MCZ 70932; Gosier, Grande Terre.

16. *Anolis marmoratus girafus*: male, MCZ 71262; female, MCZ 71268; Vieux Habitants, La Guadeloupe.

17. *Anolis marmoratus setosus*: male, MCZ 70813; female, MCZ 70816; Pointe Allegre, La Guadeloupe.

18. *Anolis marmoratus inornatus*: male, MCZ 71036, Anse Bertrand; female, MCZ 71054; town of Ste. Marguerite, Grande Terre.

19. *Anolis marmoratus desiradei*: male, MCZ 71068; female, MCZ 71076; Grande Anse, La Desirade.

20. *Anolis marmoratus chrysops*: male, MCZ 70649, Terre de Haut; female, MCZ 70653; Trou Canard, Terre de Bas, Les Iles de la Petite Terre.

21. *Anolis marmoratus ferreus*: male, MCZ 70748; female, MCZ 70757; Morne Constant, Marie Galante.

22. *Anolis marmoratus terraealtae*: male, MCZ 70687; female, MCZ 70694; Pointe Basse, Grande Ilet, Les Iles des Saintes.

23. *Anolis marmoratus caryae*: male, MCZ 70666; female, 70672; Terre de Bas, Terre de Bas, Les Iles des Saintes.

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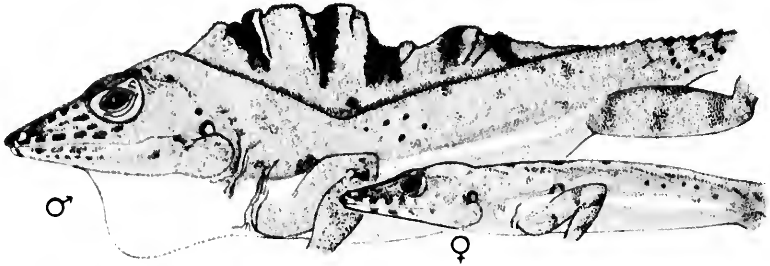

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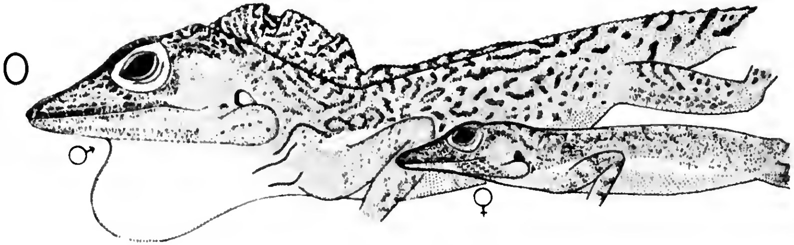

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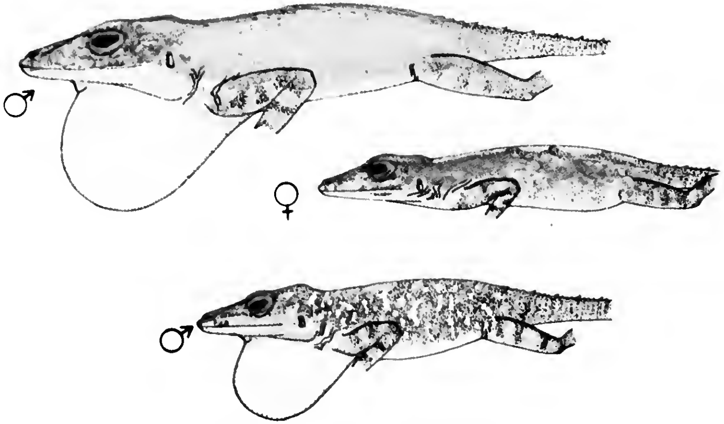

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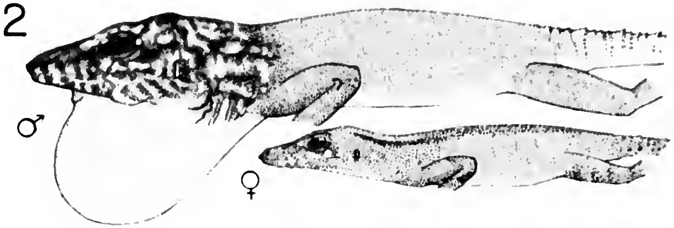

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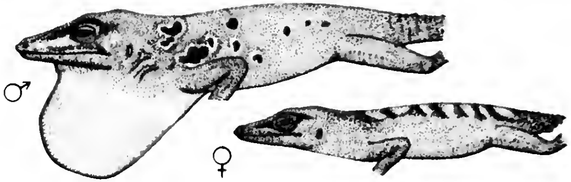

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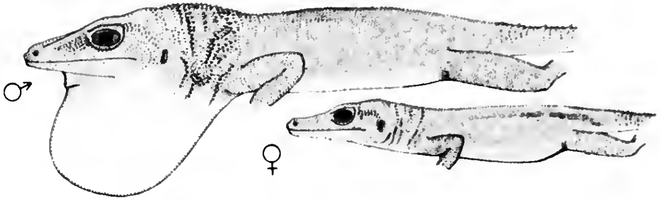

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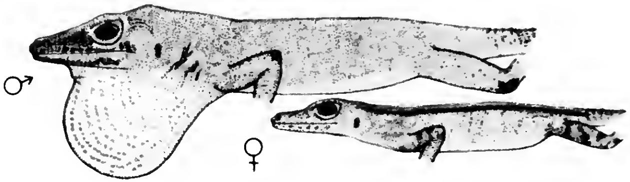

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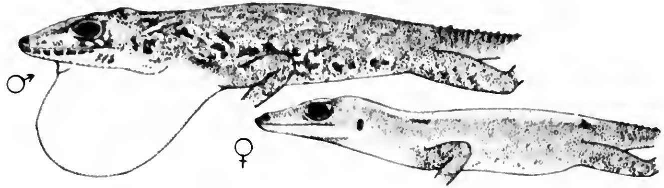

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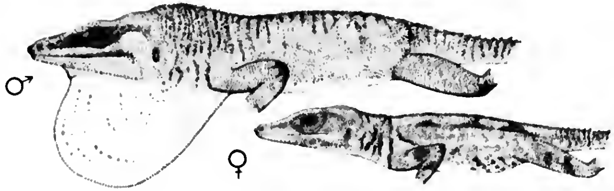

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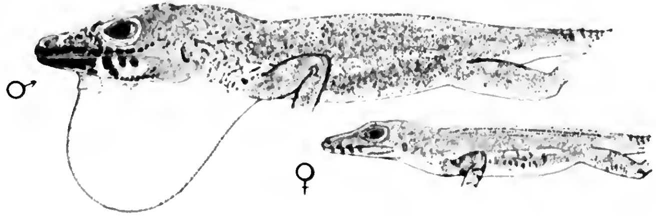

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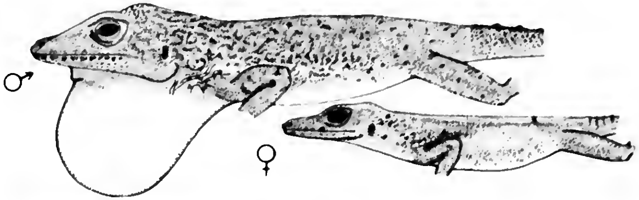

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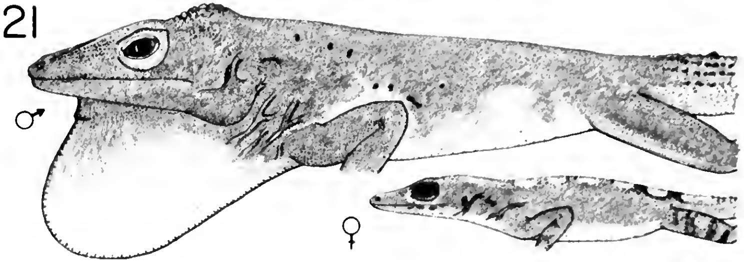

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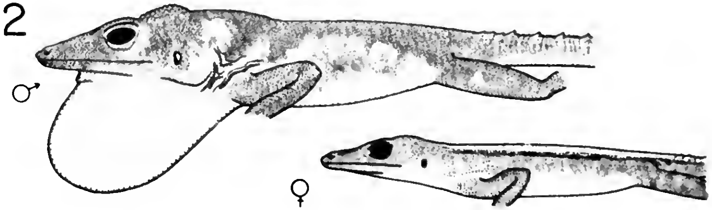

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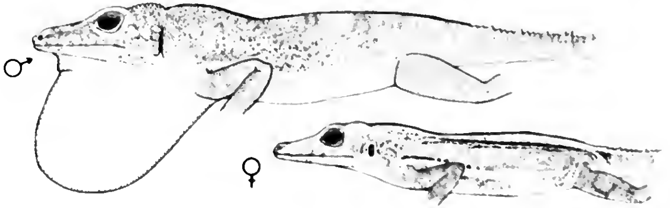

nomic features, was thoroughly unsophisticated. The paper was based largely on field observations, and I paid scant heed to the specimens once they were catalogued into the MCZ. Thus, I missed numerous specimens considerably in excess of what I stated to be the maximum sizes of three of the subspecies, and failed to note scale characters that not only separate *oculatus* from its relatives at the species level, but also aid in the recognition of the four subspecies.

Although I knew the adverse effect of formaldehyde on *Anolis*, I did not know of any "safe" alternative. My specimens were injected with strong formalin and unceremoniously dumped into a gallon jar of "cask rhum." This method of preservation certainly worked, but left a great deal to be desired in quality of material from the standpoint of color retention. After 24 hours in this witches' brew, the specimens were removed, wrapped in rhum-soaked newspaper, and packed in bisquit tins. I kept no field catalogs; the color notes and field data were written on bits of paper, in pencil, and packed with the specimens. The filled tins were shipped back by surface freight. Fortunately, I beat them to Cambridge, and was thus on hand to do the unpacking; otherwise much might have been lost.

In those days, the only air transport to Dominica was a single Grumman Goose that landed twice a week in the open roadstead at Roseau. The only real road on the island was the Trans-Insular, or Imperial, Road. It wound northeastward out of Roseau into the forest. It crossed the spine of volcanic peaks and descended to the windward coast. It wandered, a tiny ribbon of blacktop, through richly cultivated lands nearly to the northern end of Dominica, then turned west, crossed the low col between Morne Diablotin and Morne au Diable, called the Dos d'Ane, to Portsmouth. With good luck, one could make it from Roseau to Portsmouth in about six hours: an airline distance of about fifteen miles. With ill luck, one could not make it at all: far up in the mist of the cloud forest was an infamous slope called simply "The Slips." Many times I have been turned back there.

Another, much shorter, road went south out of Roseau along the leeward coast, then cut inland between Morne Anglais and Morne Plat Pays, descending to the little windward coast town of Grand Bay. As an alternative to the Imperial Road, for the short stretch between Canefield Estate and Pont Cassé, was the then brand new Layou Valley Road. Other than those roads, there were a few, disappointingly short, jeep tracks. In fact, most of my collecting sites were visited on foot or on horseback. It took me ten days on a horse to collect the windward coast of Dominica between Hatten Garden, where the Imperial Road descends, and Grand Bay. One can now drive to Castle Bruce, Rosalie, or even La Plaine —collecting sites along my route in 1959— in an hour or so from Roseau. A good road extends up the leeward cast now as far as Colihaut, and will shortly connect to Pointe Ronde and Portsmouth. It is said that "The Slips" no longer slip, but shortly it will no longer matter if they do.

I returned to Dominica in February 1966, to collect fresh alcoholics of the four subspecies. New roads have made important new collecting sites accessible for three of the forms, and new maps have made possible far more precise definition of their ranges. If Dominica and I have changed, at least *Anolis oculatus* remains the same. What is presented below both supplements and emends my original descriptions.

My previous account of this species (Lazell, 1962) provides considerable detail that will not be repeated here. The diagnoses given there, however, applied only to males, and were not as tight as they could be. I have recast them below, and a general map of the four subspecies is here provided: Figure 6.

I did not discuss squamation characters in 1962; these are noted below. A discus-

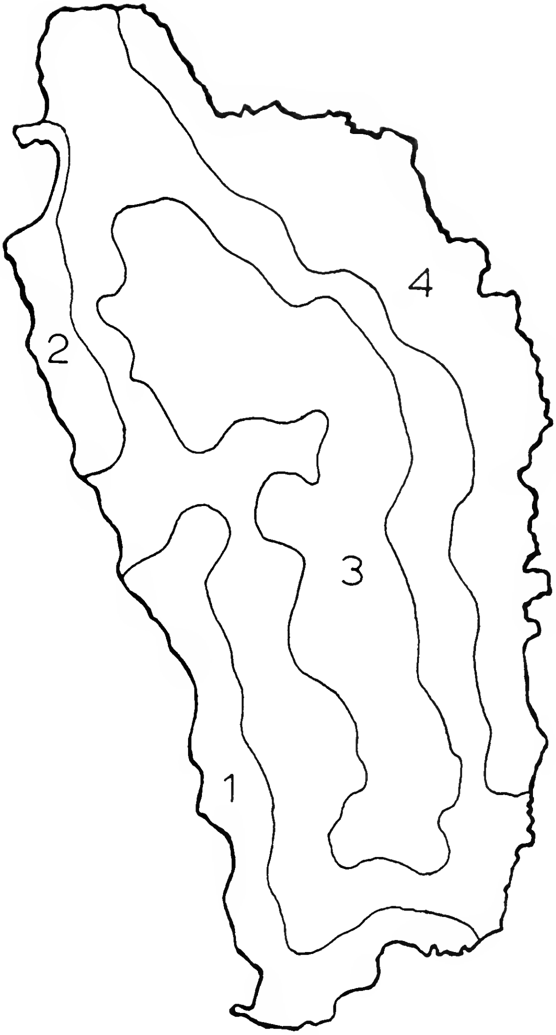

Figure 6. Dominica, showing the ranges of the subspecies of *Anolis oculatus*: 1. nominate *oculatus*; 2. *cabritensis*; 3. *montanus*; 4. *winstoni*.

sion of the relationships of the species is provided after the subspecies accounts. The races of *Anolis oculatus* conform to ecological zonation (see Introduction).

Anolis oculatus oculatus (Cope)

Xiphosurus oculatus Cope (1879: 274)

Type. USNM 10145 (see above).

Type locality. Roseau, Dominica.

Diagnosis. An *Anolis oculatus* with olive to grey-brown ground color; primary spots small, or vague, or absent; little if any black pigment surrounding primary spots of males; secondary spots vague or absent; venter pale yellow to white; male throat fan bright yellow with whitish scales; females with striped middorsal pattern.

Comments. Fresh material is from Goodwill, above Roseau (JDL 245–9) and Fond St. Jean, east of Grand Bay (JDL 273–7);

the latter a range extension. Mature males range from 79 mm, snout to vent (MCZ 60355, Hillsborough) to 44 mm (MCZ 60439, Second Layou River bridge, and JDL 273, Fond St. Jean). Adult females range from 58 mm (MCZ 60369, Roseau) to 42 mm (JDL 276, Fond St. Jean).

There are 20–27 (average 23) midventrals in the standard distance at midbody. There are 20–26 (average 23) middorsals in the standard distance in males, 21–31 (average 26) middorsals in the standard distance in females. There are 35–47 (average 41) dorsal granules in the standard distance six scales lateral to the dorsal midline. There are 18–24 (average 21) subdigital lamellae under the second and third phalanges of the fourth toe. The standard distance six scales lateral to the per cent of the snout-vent length in both sexes.

Adults are shown on Plate 3.

This is the form of the mesic southern end of Dominica, where the barrier range is at least at its lowest.

Anolis oculatus cabritensis Lazell

Anolis oculatus cabritensis Lazell (1962: 469)

Type. 60245, Lazell coll., 8.vi.59.

Type locality. The Cabrits (Prince Rupert Point), Dominica.

Diagnosis. An *Anolis oculatus* with grey or pale tan ground color, often overlaid with mustard yellow; primary spots large and bold, set off with ample black pigment in males; secondary spots run together to form irregular stripes or marbling; venter bright yellow to peach; male throat fan bright yellow with whitish scales; females similar but striped.

Comments. Fresh material fills in the range at Anse Gabriel, south of Colihaut (JDL 250–9). Adult males range from 81 mm, snout to vent (MCZ 60258, Pointe Ronde), to 55 mm (MCZ 60314, Picard). Adult females range from 59 mm (MCZ 60275, Pointe Ronde) to 48 mm (MCZ 60274, Pointe Ronde). There are 22–33 (average 28) midventrals in the standard distance at midbody. There are 22–30 (average 26) middorsals in standard distance in both sexes. There are 40–51 (average 45) dorsal granules in the standard distance six scales lateral to the dorsal midline. There are 18–24 (average 21) subdigital lamellae under the second and third phalanges of the fourth toe. The standard distance is 16–20 (average 18) per cent of the snout vent length in both sexes.

Adults are shown on Plate 3. This is the form of the arid coast to leeward of the great, central barrier range of Dominica.

Anolis oculatus montanus Lazell

Type. MCZ 60319, Lazell coll., 6.vii.59.

Type locality. Fresh Water Lake, Dominica.

Diagnosis. An *Anolis oculatus* with a green to nearly black ground color; both primary and secondary spots small and bright, black pigment surrounding several anterior spots in males; venter green, often metallic or coppery posteriorly; male throat fan very dark, dull ochre to orange with green or grey-green scales; females similar, usually striped.

Comments. Fresh material is from William Estate (Crete Palmiste), (JDL 206–6) and Brantridge (JDL 306), both in the middle of the range, and from Morne Anglais (JDL 316–323) at its southern terminus; I am once again indebted to Charles A. Winston, and his family, for this latter, excellent series, taken above his home at New Florida on the southwest slope of the mountain.

The largest male is 96 mm, snout to vent (MCZ 60344), from Fond Hunt; the smallest apparently mature male is 49 mm (JDL 321), from Morne Anglais. Mature females range from 64 mm (MCZ 60329, Fresh Water Lake) to 44 mm (MCZ 65930, Fresh Water Lake).

There are 21–27 (average 23), midventrals in the standard distance at midbody.

There are 18–24 (average 21) middorsals in the standard distance in both sexes. There are 32–40 (average 36) dorsal granules in the standard distance six scales lateral to the dorsal midline. There are 19–27 (average 22) subdigital lamellae in males, and 18–23 (average 20) in females, under the second and third phalanges of the fourth toe. The standard distance is 16–19 (average 18) per cent of the snout-vent length in both sexes.

Adults are shown on Plate 3. This is the form of the montane rain forest ecological zone.

Anolis oculatus winstoni Lazell

Anolis oculatus winstoni Lazell (1962: 472)

Type. MCZ 60467, Lazell coll., 29.vi.59.

Type locality. Woodford Hill, Dominica.

Diagnosis. An *Anolis oculatus* with a rich brown ground color; spots small, bright, little differentiated into primary and secondary rows, not surrounded by black pigment; venter peach to bright yellow; male throat fan deep pumpkin yellow with lighter yellow scales; females similar, but usually striped.

Comments. Fresh material is from the type locality, Woodford Hill (JDL 267–71). The largest male is 86 mm (MCZ 60525), from Castle Bruce; the smallest male is 56 mm (MCZ 60486, Woodford Hill). Mature females range from 64 mm (MCZ 80531), from Marigot, to 50 mm (MCZ 60624), from La Plaine.

There are 23–32 (average 28) midventrals in the standard distance at midbody. There are 22–30 (average 27) middorsals in the standard distance in both sexes. There are 37–48 (average 43) dorsal granules in the standard distance six scale rows lateral to the dorsal midline. There are 19–24 (average 22) subdigital lamellae in males, and 18–21 (average 20) in females, under the second and third phalanges of the fourth toe. The standard distance is 16–19 (average 18) per cent of the snout-vent length in both sexes.

Adults are shown on Plate 3. This is the form of the well-watered lowland to windward of the great, central, barrier range of Dominica.

Relationships. Gorman and Atkins (1968b) have shown *Anolis oculatus* to be karyotypically extreme among *bimaculatus* group anoles: it possesses two pairs of acrocentric macrochromosomes; no acrocentric autosomes are known in any other alpha *Anolis.* The prenasal scale is unique. Also, most males of this species show enlargement of the light scales in some of the spots, frequently to a remarkable (and pathological looking) extent; I have seen only a remote suggestion of this in some *Anolis marmoratus* (e. g., MCZ 81863, a male *A. m. girafus* from Ilet de Pigeon du Nord). *Anolis oculatus* is a rather large species with peculiarly low lamellae counts. Sexual dimorphism is variably expressed in size, color, and squamation, but is not striking in any of these respects.

It would seem that *Anolis oculatus* has long evolved in isolation, and lacks genuinely close relatives.

Anolis luciae Garman

Anolis luciae Garman (1887: 44)
Anolis trinitatis procuratoris Underwood (1959: 214)

Type. MCZ 6175 (not 6173, a series of 19 paratypes, as cited by Underwood, 1959: 213). S. Garman coll., 1887.

Type locality. St. Lucia; here restricted to the principal town and port, Castries.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined, in which the sublabials extend posteriorly as a series of scales notably larger than those surrounding them to or beyond the level of the posterior edge of the orbit.

Squamation. Two hundred fifty-three specimens of this species (175 males, 70 females, and 8 juveniles) have been examined. In addition to diagnostic characters, cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: There are 20–29 (average 25) midventrals in the standard distance at midbody; they are smooth, and the same size as the middorsals. There are 20–30 (average 25) middorsals in the standard distance. The dorsal granules decrease rather abruptly in size laterally; there are 33–42 (average 38) in the standard distance six scales lateral to the dorsal midline. The digital dilations are of undistinguished width and of the raised condition; there are 23–31 (average 27) subdigital lamellae under the second and third phalanges of the fourth toe.

Coloration. Anolis luciae is not a colorful species, though there is some geographic variation in hues. Males from Castries (MCZ 71685–9) are brown to olive with a tannish white belly and chin. The throat fan is very dingy: a greyish yellow or dull orange with white scales; it is frequently brighter posteriorly. The eyelids are pale greenish or tan to white. Color change is to pale apple green with blue tones laterally and on the extremities. The flank stripe is very vague and there is no dorsal pattern. Females (e. g., MCZ 71690) are similar, even duller and browner, show less color change, and have dark chevrons with whitish posterior borders to the tail base.

Specimens from Savanne Edmund (MCZ 71696–708), one of the type localities of "*procuratoris*" Underwood (1959), average darker; frequently the blue tones are extensive and deep, including a blue flank stripe and blue eyelids. Sometimes the bellies have a yellow wash. Throat fans vary from virtually plain grey with a faint greenish wash to brick red with green scales. Females frequently have a dark middorsal stripe in addition to the chevronate markings.

Specimens from the Barre de l'Isle (MCZ 71691–6), Marquis (MCZ 71769–75), between Londonderry and Gertrine (MCZ 71804–9: 13° 47′ N, 61° 00′ 30″ W, the other type locality of "*procuratoris*" Underwood), Dennery (MCZ 71810–7), Micoud (MCZ 71796–803), and Soufrière (MCZ 71786–95), span these extremes. Those from the Barre de l'Isle, Dennery, Micoud, Vieux Fort (MCZ 71737–43), and Moule-à-Chique Lighthouse (MCZ 71744–52) show better flank stripe definition and frequently the males show some dorsal chevronate pattern. Those from other parts of the range agree with Castries specimens. The overall pattern is thus of darker specimens in the interior highlands, paler specimens in coastal regions, and the most patterned specimens from the east and south. All of this variation is modal and clinal; no subspecies can be recognized.

I examined 54 specimens from the southernmost Maria Island (37 males, 10 females, and 7 juveniles), of which 10 (6 males and 4 females: MCZ 71776–85) were collected by me. Although many larger specimens in this population show a peculiar reticulate mottling of dark brown (this is vaguely visible, even in life, on these dark individuals), I cannot find characters that will separate it from the sum of the mainland variation.

The iris of most species of *Anolis* (all in the Lesser Antilles) varies from blackish brown to blue; the complete range, even to turquoise, may be seen in *A. luciae* from Castries, or anywhere else on St. Lucia.

Color patterns of adults are shown on Plate 3.

Size and sexual dimorphism. The largest specimen examined, an adult male, is 91 mm, snout to vent (MCZ 71697, Savanne Edmund); the smallest apparently mature male is 50 mm (MCZ 80450, Castries). The largest female is 63 mm (MCZ 71773, Marquis); the smallest mature female is 48 mm (MCZ 71817, Dennery).

The duller colors of females, and their patterning of chevrons, and frequently a middorsal stripe, are the principal sexual dimorphism; there is no indication of dimorphism in scales. The standard distance is 16 or 17 per cent of the snout-vent length in all specimens examined.

Population structure and ecology. Anolis luciae occupies most of its range alone; *A.*

extremus, from Barbados, and *A. wattsi*, from Antigua, have been introduced into Castries, and at least the former seems to be spreading. Nevertheless, *A. luciae* is not as abundant in most areas as might be expected of a species of ubiquitous habits without competition. Only on the southernmost Maria Island is this species really abundant, by ordinary Lesser Antillean standards. Males perch from three to twelve feet; females and juveniles tend to perch lower. Both sexes forage in bushes, trees, and on the ground; the species is thoroughly infradispersed throughout its range.

Field observations indicate a balanced sex ratio.

One might expect the small rupicolous *A. w. wattsi* to do well on St. Lucia in sympatry with *A. luciae;* it does not, however, seem to spread from the original collection site: the Botanical Garden in Castries. *Anolis extremus,* however, is abundant in Castries and its suburbs. I was convinced that it had spread from its 1962 range when I visited St. Lucia again in 1964. *A. luciae*, strangely, seems no less common within the *A. extremus* area, despite the apparent niche overlap.

Distribution. *Anolis luciae* occurs throughout St. Lucia and on its coastal cays that support more than herb-stage vegetation, like Pigeon (MCZ 71709–19) and the southernmost of the Maria Islands.

Relationships. Gorman and his colleagues have examined relationships of the *Anolis* of the *roquet* group in detail from the viewpoints of blood proteins (Gorman and Dessauer, 1965, 1966), karyotypes (Gorman and Atkins, 1967), and display behavior (Gorman, 1968). The summary work is Gorman and Atkins (1968b). My own morphological examinations confirm Gorman's views, and make possible definite assertions where he presented alternatives; I shall defer all but succinct remarks on the relationships of the species (see Evolution, below).

There is complete agreement: *Anolis luciae* is the closest living form to the ancestral stock of the entire group.

At some time prior to the acquisition of the enlarged sublabial scale row in *luciae*, there must have been two southward invasions of the primitive stock: the first gave rise to *A. griseus* and its derivative *richardi;* the second to *A. trinitatis* and its derivatives *aeneus*, *extremus*, and *roquet*. At least one extralimital colonization of the *luciae* stock, at a time subsequent to the initial development of the sublabials, gave rise to *A. bonairensis* far to the west. Thus, none of the other Lesser Antillean members of the group possess enlarged posterior sublabials, and *A. bonairensis* does only to an incomplete extent.

Anolis griseus Garman

Anolis griseus Garman (1887: 36)

Lectotype. MCZ 6164, S. Garman coll., 1887. I have tied tag 6164 to the finest adult male, a 117 mm specimen; the remaining five specimens should be recatalogued.

Type locality. St. Vincent; here restricted to the principal town and port, Kingstown (Garman's actual data read "Kingston"; a common error).

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined; sublabial scale row breaks up into undistinguished scales below eye; usually four or fewer scales of the supraorbital semicircles abut on top of head; if more, then interparietal separated from supraorbital semicircles; 11 or fewer (8–11) middorsals contained in ten per cent of the snout-vent length at midbody.

Squamation. Seventy specimens of this species (28 males and 42 females) have been examined. In addition to diagnostic characters, cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: There are 19–30 (average 25) midventrals in the standard distance at midbody; these are smooth, swollen, or tectiform, and much smaller than the middorsals. There are 15–18 (average 16) middorsals in the standard distance. The dorsals decrease abruptly in size laterally; there are 24–34 (average 29) dorsal granules in the standard distance six scale rows lateral to the dorsal midline. The digital dilations are broadly expanded. There are 28–31 (average 30) subdigital lamellae in males, 27–30 (average 28) in females under the second and third phalanges of the fourth toe.

Coloration. This is a mossy grey-brown anole with green or yellow-green tinges variably present dorsally, on face, limbs, and orbital area. The venter varies from pale greenish to yellowish grey. Some individuals (especially old males) have pink suffusions on the head. There are irregular dark spots and mottlings arranged in rough, forward-pointing V's across the dorsum; these are usually obscured middorsally by dark color in females. There is a vague, pale flank stripe indicated at least anteriorly; there is a bold, light bar or stripe across the forearm insertion. Chins vary from pale yellowish to grey and are usually mottled with darker grey. Both sexes have large throat fans: dull orange-yellow with virtually white to grey-green scales. Color change is merely to darker.

There is no apparent geographic variation in color, except that MCZ 82017, from the south rim of the old crater of Soufrière, at *ca.* 3000 feet was fairly dark.

Color patterns of both sexes are shown on Plate 3.

Size and sexual dimorphism. An adult male, MCZ 82926 (Kingstown), measured 136 mm fresh dead, and is 127 mm at present, snout to vent. Every male specimen examined, even including one 37 mm in the type series, has large, well-developed testes; I estimate that one like MCZ 82011 (Fancy), at 70 mm, is about as small as they actually breed. The largest female examined is 86 mm (MCZ 82015, Waterloo); the smallest with eggs is 57 mm (MCZ 82925, Colonarie River above South Rivers, *ca.* 1000 ft.). Females do not grow nearly so large as males, but are otherwise exceedingly similar in every respect of externals. Every specimen can be readily sexed by dissection.

The standard distance is 15–17 (average 16) per cent of the snout-vent length in both sexes.

Population structure and ecology. This is a "big tree lizard": it is big, it is decidedly arboreal, and, to cap the verbal ambiguity, it prefers big trees. Human depredations on big trees in the lowlands give a somewhat clumped appearance to its otherwise infradispersed population structure. Males tend to perch from six to twenty-five feet above the ground, females occasionally come lower. It is rare to see *Anolis griseus* on the ground; in Kingstown I have seen both sexes, however, come down on the ground to eat small red berries that looked like mulberries (and may have been). Large males are so arboreal, and live on such big trees, that collecting them can be very difficult; for this reason, my size record above may well be exceeded.

Field evidence indicates a balanced sex ratio.

Distribution. Anolis griseus is common throughout the mainland of St. Vincent, but I have not seen any on the coastal cays; perhaps they are too scrubby.

Relationships. This species seems to be a direct descendant of *Anolis luciae* and must be the direct ancestor of *Anolis richardi;* its relationship to the latter form will be given more detailed consideration under that species.

Anolis richardi Duméril and Bibron

Anolis richardii Duméril and Bibron (1837: 141)
Anolis occipitalis Gray (1840: 112)
Anolis stenodactylus Gray (1840: 114)
Anolis trossulus Garman (1887: 38)

Type. MNHN Ig. 53, Richard coll: *fide* Underwood (1959).

Type locality. "Tortola"; the species does not, and never did, occur on this small island in the British Virgins. I assume this to be a blunder, and suspect the real type locality was the somewhat similar sounding Tobago. I, therefore, revise the type locality to Crown Point, Tobago, where this species is abundant.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined; sublabial scale row breaks up into undistinguished scales below eye; usually four or fewer scales of the supraorbital semicircles abut on top of head; if more, then interparietal separated from supraorbital semicircles; twelve or more (12–15) middorsals contained in ten per cent of the snout-vent length at midbody.

Squamation. One hundred nineteen specimens (71 males, 38 females, and 10 juveniles) have been examined. In addition to diagnostic characters cited above, this species differs from other Lesser Antillean *Anolis* of the *roquet* group in the following features: There are 22–31 (average 27) midventrals in the standard distance; they are tectiform to sharply carinate, and smaller than the middorsals. There are 18–23 (average 21) middorsals in the standard distance. The dorsal granules decrease abruptly in size laterally; there are 29–41 (average 35) six scale rows lateral to the dorsal midline. The digital dilations are broadly expanded; there are 23–28 (average 26) subdigital lamellae in males, 22–26 (average 24) in females, beneath the second and third phalanges of the fourth toe.

Coloration. This species varies considerably in coloration geographically, and it is a temptation to describe at least one race; however, the sum of the variation is so gradually clinal that to do so would be misleading. Four series of specimens, collected by me, are missing from the material borrowed from the MCZ. They are from localities of crucial importance in assessing geographic variation in colors, and it is fortunate that I retained all the color notes and field sketches. These are MCZ Field Tags X-17824–7, Mabuya Cay off Carriacou, Grenadines; MCZ Field Tags X-17886–93, Point Saline, Grenada; MCZ 60773–7, 60780–6, one and one-half miles north of Point Saline, Grenada; and MCZ Field Tags X-18057–66, Crown Point, Tobago. All of these 34 specimens have been added to the sum of 119 specimens noted above in considering geographic variation in color and pattern, making 153 in all.

At Crown Point, Tobago, specimens vary from uniform dark green to greenish brown in ground color. Many, especially females, have dark speckles, sometimes arranged in oblique lines. There is frequently, but not always, a light area below the eye (suboculars and sometimes supralabials). Venters are pale grey-green, often with a yellowish wash; the chin may be similar, or washed with dull yellow. The throat fan, in both sexes, is dull orange with grey-green scales. Some specimens from Crown Point will match some specimens from any locality in the range of *Anolis richardi;* there are no populations composed of distinctive individuals. Color change is always merely to darker.

There are, however, some spectacular average differences. Individuals from Bequia, the extreme northern limit of the species range, and less than six miles from St. Vincent (but nearly 140 miles from Crown Point), may be rich forest green with deep blue suffusions on the head, especially pronounced under the eye. Their chins may be brilliant yellow with blue blotches, and set off from their throat fans by an area of blue-grey; the fans may be bright orange-yellow with white scales. On the other hand, Bequia specimens may have a few speckles, or remnant dorsal chevrons; their chins may be dull yellowish; blue tones may be absent, leaving merely a light subocular area; and their fans may be dull orange with grey-green scales.

At the opposite extreme of the Grenada Bank is Point Saline. Here, *Anolis richardi* may be a dusty grey-brown with extensive white piebalding on the head and anterior body; spotting is frequently heavy: sooty dots bordered by ash grey; the orbital area may be richly suffused with yellow. On the other hand, individuals may be olive, lack piebalding, have only a few spots and those not notably bordered, and lack orbital yellow.

Certainly, if Point Saline material were compared with Bequia material in the absence of specimens from the rest of the range, there would be no doubt about a racial difference at a 90–95 per cent level. However, the entire remainder of the species range, from southwestern Grenada through the Grenadines, is a gradual, continuous cline. The brilliant blue and yellow chin hues decrease in frequency at Mabuya Cay, and are rare in northern Grenada (e. g., 81992–5, Tufton Hall). White piebalding clines from an extreme at Point Saline (e. g., MCZ 81324) to occasional patches at St. George's (e. g., MCZ 81956 or 81958). Heavy spotting occurs as far north as Petite Etang, Grenada (MCZ 81985–91), a rain forest locality. As noted, the Tobago population looks as though it came right out of the middle of this cline, and is not extreme in any respect. In sum, I cannot justify subspecific recognition of even the Point Saline population.

Color patterns of adults are shown on Plate 3.

Size and sexual dimorphism. This is the largest Lesser Antillean anole. A male from Crown Point, Tobago, measured 140 mm, snout–vent, fresh dead (MCZ Field Tag X-18057); there are a number of preserved specimens over 125 mm (e. g., MCZ 83041–2, Store Bay, Tobago). Specimens from the Grenada Bank may not grow so large; a 115-mm male (MCZ 79064), from Bequia, Grenadines, is as large as any examined. Males as small as 70 mm (MCZ 81982, Corinth, Grenada) certainly appear mature, but so does MCZ 81983, from the same locality, and it is only 59 mm. The largest female examined is 77 mm (MCZ 83044, Store Bay, Tobago); the smallest mature female is 56 mm (MCZ 81980, Sugarloaf, or Levera Island).

As in *Anolis griseus,* this species shows little sexual dimorphism in color and squamation. The standard distance is 14–17 (average 15) per cent of the snout-vent length in both sexes.

Population structure and ecology. Like its very close relative, *A. griseus,* this is a "big tree lizard" throughout its Grenada Bank range. On Grenada proper, *A. richardi* is fairly infradispersed, except where human depredations have wiped out the big trees. In the Grenadines, a highly clumped structure is imposed by the fragmentation of the land areas, and the paucity of big trees. The ultimate extreme is a place like Mabuya Cay, off Carriacou: here, there is a single big tree on an otherwise scrubby little islet; about six *A. richardi* live on that tree, but the rest of the cay supports none. Obviously, this sort of thing is highly temporary from an evolutionary point of view: that tree has a limited existence, and may not be replaced; elsewhere, other suitable trees may be growing on islands not currently supporting the lizards. A state of constant change in the location of small demes must be the rule over most of the species range.

On Tobago, *A. richardi* occurs alone, and is ubiquitous. It is remarkable to see this giant species commonly perching low on fence posts or rocks; as one drives along the coast of Tobago, the huge old males, on virtually every coconut palm at about eye level, are a very prominent feature of the landscape.

Field evidence indicates a balanced sex ratio.

Distribution. Anolis richardi is abundant all over Tobago; I have not seen specimens from, or visited, Little Tobago, but certainly expect this species occurs there. On Grenada proper, this species occurs virtually everywhere, from arid coast to the top of Mt. St. Catherine (MCZ 81969). In the Grenadines, specimens have been examined from Sugarloaf (equals Levera Island, just northeast of Grenada), Carriacou, Mabuya Cay off Carriacou, and Bequia; except for the big islands (Carriacou and Bequia) the range of this species in the Grenadines must be in a constant state of flux, as discussed above.

Relationships. Anolis richardi and *A. griseus* are very closely related; in fact, when collecting in Tobago, and cognizant only of color characters, I concluded that the two forms were inseparable. That view was very hard to reconcile with the spectacular distinctions so evident between Bequia and St. Vincent specimens. Bequia is dry country, but *A. richardi* from other dry areas, like Point Saline, do not look much like them, and do look very much like *A. griseus.* The whole Grenada Bank shows a strong cline in characters: the closer *A. richardi* gets to *A. griseus*, the more distinct it is. This is classical Darwinian character divergence, except that nowhere do the two species occur in sympatry. Is dichopatric character divergence possible? It certainly is, provided individuals of one species are occasionally transported into the range of the other; they do not have to survive there, or establish a population: just get there, live a short time, and die.

Let us take a specific (imaginary) example: *A. griseus* (like *A. richardi*) likes big trees, such as coconut palm, and these are readily washed out to sea; the lizards climb, and seek shelter in the crowns, at times of crisis. A coconut palm, with a male *Anolis griseus* in its crown, washes off St. Vincent, and goes ashore on Bequia. The *griseus* is now in an area where all the available territories are held by *richardi;* even if he wins a perch site and successfully courts the *richardi* females, the two forms have evolved so long in isolation (before *richardi* reached the northern Grenadines, or before those islands were above water) that the result is gametic wastage. Certainly, any characters tending to exclude *A. griseus* individuals from breeding with *A. richardi* individuals will be selected for. Note also that all one needs to work this system is single individuals; it does not matter that they constitute a propagule: any individual *griseus* in *richardi* range contributes to the selection pressure for character divergence. Probably *griseus* are rarely rafted onto *richardi* islands south of Carriacou, but fairly frequently onto Bequia; probably *richardi* are quite frequently rafted onto St. Vincent. Character divergence is strong in colors, and Gorman (1968) has found a display behavior distinction; nevertheless, the two species are still far too similar to survive together. The facts cannot be reconciled with any explanation other than character divergence, so far as I know, and it is impossible, therefore, to regard forms that display character divergence as other than full species. The transferrin (Gorman and Atkins, 1968b) and squamation distinctions between the two forms add weight to this argument.

Anolis trinitatis Reinhardt and Lütken

Anolis trinitatis Reinhardt and Lütken (1863: 269)

Anolis vincenti Garman (1887: 46)

Type. A male measuring 70 mm, snout-vent length, in the "Universitetets Museum, Copenhagen," is said to be the type (Braestrup *in* Underwood, 1959). It should be given a catalogue entry of some sort, and have a tag identifying it affixed directly to it. Braestrup's translation of Reinhardt and Lütken's original color notes clearly identifies the species.

Type locality. Trinidad. Although this species does occur in Trinidad, that island is not within its natural range; it is an introduction. In addition, it is not very common there, and may be losing ground to the likewise introduced *Anolis aeneus.* To complicate matters, the two species hybridize. In the interests of taxonomic stability, I feel it is mandatory to revise the type locality to Kingstown, St. Vincent; this is the principal town and port within the natural range of this species, and it is abundant there.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined, in which the sublabials break up into undistinguished scales at the level of the orbit; five or more scales of the supraorbital semicircles abut, or, if fewer, then interparietal in contact with supraorbital semicircles; 37 or more dorsals in the standard distance six scale rows lateral to the dorsal midline.

Squamation. Two hundred forty-five specimens (168 males, 70 females, and 7 juveniles) have been examined. In addition to diagnostic characters cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: the ventrals are smooth; there are 22–33 (average 27) contained in the standard distance at midbody. The middorsals are about the same size as the ventrals; there are 25–34 (average 29) in the standard distance. The dorsals decrease abruptly in size laterally; there are 37–46 (average 42) dorsal granules in the standard distance six scale rows lateral to the dorsal midline. The digital dilations are quite ordinary; there are 23–29 (average 27) subdigital lamellae in males, 20–26 (average 24) in females, under the second and third phalanges of the fourth toe. The large number of specimens examined leaves me with the distinct impression that the number of lamellae, at least distally, increases with size or age; I have previously suggested this to be the case in other species of *Anolis* (Lazell, 1966), and the question is currently under investigation by the only sure method: raising living lizards.

An adult female *Anolis trinitatis*, MCZ 82061 (Kingstown), has the second through the eighth pairs of lamellae divided; this does not appear to result from injury, and is the only example of divided lamellae in *Anolis* known to me.

Coloration. At Kingstown, males are a bright green or blue-green shading to blue or blue-grey on the head, and to bright yellow on the mandibles and venter. The orbital area is blue to slatey blue-grey. The throat fan is butter yellow with pale bluish scales in most individuals. There is some striking variation: in some there are blue patches, and MCZ 82094 had a plain "white" (palest blue-grey) fan. Females are duller, show a vague flank stripe, and frequently have a mottled or herringbone middorsal pattern; the female throat fan is tiny and not distinctively colored.

Specimens from the extreme southeast (e. g., MCZ 82064–8, Brighton) average duller than in Kingstown.

Specimens from the extreme northwest (e. g., MCZ 82097–107, Chateaubelair Island) average yellower, and the orbital area is frequently distinguished from the ground color only by faint greyish mottling.

Specimens from the extreme northeast (e. g., MCZ Field Tags X-17692–701, Fancy; apparently missing from the MCZ collection at present, but well documented in my field catalogue) are the most striking: they show little blue, have a greenish wash on the male throat fan, and bright blue to sooty black orbits sharply set off from the ground color of the head.

Specimens from the mountainous interior (e. g., MCZ 82095–6, southeast rim old crater Soufrière, 3000 feet; or MCZ 82069–76, Colonarie River above South Rivers, 1000 feet) may lack yellow tones in the dorsal ground color, and be the darkest and bluest of all.

All of this variation is individual or the result of gradual clines; no subspecies can be recognized.

Adults are shown on Plate 3.

Size and sexual dimorphism. The largest male examined is 74 mm, snout to vent (one of MCZ 6178, Kingstown). The smallest apparently mature male is 46 mm (MCZ 81364, Rathomill). The largest female examined is 57 mm (one of MCZ 6178, Kingstown); the smallest mature female is 41 mm (MCZ 82063, Kingstown). Sexual dimorphism is striking in throat fan, strong in subdigital lamellae, and present in both size and color. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. Anolis trinitatis is ubiquitous and infradispersed everywhere within its natural range to at least 3000 feet elevation. Specimens rarely perch over ten feet above ground, but even adult males may perch on rocks or on the ground on the paramo-like heights of the Soufrière. Field observations indicate a balanced sex ratio.

Distribution. Anolis trinitatis occurs throughout St. Vincent, and on all its coastal cays, to at least 3000 feet.

This species occurs in a few areas of central, western Trinidad, where it was certainly introduced. The situation that obtains between *A. trinitatis* and its close relative *A. aeneus* has been the subject of copious publication, beginning with its original documentation by Kenny and Quesnel (1959) and continuing through the most recent of many papers by Gorman and his colleagues (see especially Gorman and Atkins, 1968a, 1968b, and works cited therein). I suggested to the other interested parties (Gorman, E. E. Williams, Underwood, Kenny, etc.) that the Trinidad situation was the result of direct introduction of *trinitatis* from southwestern St. Vincent and *aeneus* from southwestern Grenada (the Trinidad specimens are precisely like those from those areas today). At the time, my opinion was poorly regarded; it is a comfort to note that Gorman and Atkins (1968a) actually stress my precise point.

The anoles were introduced, and breadfruit saplings were surely their vehicle. Because of the drama surrounding H. M. S. *Bounty* in the years 1787–9, we tend to forget that Captain William Bligh was a man of enduring perserverance: he did go back to Tahiti, he did get more breadfruits, and he did bring them to the Royal Botanical Gardens at Kingstown, St. Vincent —just as he had been commissioned to do. And he didn't settle for that: by September, 1793, when Bligh returned to England, he had made two trips from Tahiti to St. Vincent, and delivered twice the requisite number of plants. The whole story is chronicled by Mackaness (1936).

The breadfruit plants were cultivated tenderly from cuttings to saplings before transport could be undertaken. However, by the early 1800's breadfruit had reached Grenada, and from there Trinidad and British Guiana. Today, it occurs throughout the Caribbean, even in non-British territories.

It is not remarkable that *A. trinitatis* did not become established elsewhere in the Antilles proper: at any port of entry it would meet well-adapted, exceedingly abundant, vigorous congeners. In Trinidad, however, the only native *Anolis* is the forest dwelling *A. chrysolepis planiceps* (name *fide* Vanzolini and Williams, 1970). The edificarian habitat was wide open. Each sapling was a perfect perch site for the Vincentian and Grenadian small anoles; each pot must have carried their eggs. It would seem that today *Anolis aeneus* has got the upper hand in the new territories, and *Anolis trinitatis* may ultimately survive only on the Vincentian soil from whence it came.

Relationships. This species and *A. aeneus* are very close. Hybridization certainly occurs in Trinidad, but the hybrids seem teratological (Gorman and Atkins, 1968a). *A. trinitatis* seems to be a direct derivative of the a pro-*luciae* stock, but *A. luciae* has diverged far away from it today. See Evolution, below.

Anolis aeneus Gray

Anolis aeneus Gray (1840: 114)
Anolis gentilis Garman (1887: 34)
Anolis roquet var. *cinereus* Garman (1887: 35)

Type. BMNH 1946.8.28.7. Presented by T. Bell.

Type locality. None given; here restricted to Point Saline, Grenada, where this species is abundant, and shows relatively constant characters at a populational level.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined, in which the sublabials break up into undistinguished scales below the orbit; five or more scales of the supraorbital semicircles abut, or, if less, then interparietal in contact with supraorbitals; 36 or less dorsals in the standard distance at midbody; axilla without dark, sooty pigment.

Squamation. Three hundred five specimens (198 males, 70 females, and 17 juveniles) have been examined. In addition to diagnostic characters, cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: the midventrals are smooth; there are 22–31 (average 27) contained in the standard distance at midbody. The middorsals are virtually the same size as the midventrals; there are 21–30 (average 26) in the standard distance. The dorsals decrease gradually in size laterally; there are 25–36 (average 31) in the standard distance six scales lateral to the dorsal midline. The digital dilations are quite ordinary; there are 21–28 (average 25) subdigital lamellae in males, 19–26 (average 23) in females, under the second and third phalanges of the fourth toe. As in *A. trinitatis,* I suspect a lamellae count increase concordant with age or size.

Coloration. This species is spectacularly variable in hues and patterns, and much of the variation is geographic. At Point Saline, Grenada, *Anolis aeneus* males are basically grey to grey-brown in ground color; many have a greenish wash. There is a dark grey peppering of spots, usually arranged in transverse bars; a distinctly metallic, bronzy sheen is prevalent within these markings. The venters are paler, dingy greyish. The throat fans vary from dull grey greenish, with similar scales, to lemon yellow with white scales. The orbital area may be bluish, but it is not in sharp contrast to the ground color. The females are grey-brown and may have a bold, dark, striped middorsal pattern, a single stripe, an obsolete pattern, or transverse bars; they lack a colorful throat fan. I have seen much Trinidad material alive, and find it indistinguishable from these; Underwood's (1959) description concurs; I have not seen Guyana (British Guiana) specimens alive, but MCZ 81283–92 (Georgetown) are precisely this anole.

Throughout the rest of the Grenada Bank, its natural home, *Anolis aeneus* varies from grey to brown to bright green, or blue and yellow; there may be spots of light, or dark, or transverse bands; throat fans may be bright or dull; the pineal may be surrounded by light, or dark, or shades between. There is so much variation that verbal description is wasteful; "typical" *Anolis aeneus* are shown on Plate 3; the geography of the variation in many features is shown in Figures 8–11. Names of the Grenada Bank Islands are given in Figure 7.

Though geographic variation here exceeds in apparent magnitude that seen in several species where good subspecies may be recognized, it is polytopic, discordant, and frequently gradually clinal. No subspecies can be usefully delimited.

Size and sexual dimorphism. The largest male examined from the Grenada Bank islands is 77 mm, snout to vent (MCZ 81805, Corinth, Grenada); I have seen larger specimens from Guyana, some in excess of 80 mm (e.g., MCZ 81283, 81285–6, Georgetown). The smallest apparently mature male is 45 mm (MCZ 81696, northernmost Tobago Cay, Grenadines). The largest female is 55 mm (MCZ 81817, Perserverance, Grenada); the smallest mature female is 39 mm (David Point, or Tonger Langue, Grenada). Sexual dimorphism, as in *Anolis trinitatis,* is striking in throat fan and notable in lamellae, coloration, and size. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. Anolis aeneus is abundant, infradispersed, and ubiquitous from the ground to ten or more feet above it. A strongly clumped structure, however, is imposed on the species as a whole by the fragmentation of its range into more than fifty islands and cays (see below). In the field, the sex ratio appears balanced.

At Point Saline, Grenada, I noted on 18 June 1964 several of this species devouring "mulberries" on the ground; others were seen doing the same around the Groome residence at Calliste, on Point Saline, on the same day. As when a rich horde of insects is uncovered, male territoriality seems forgotten, both sexes, and even a number of *Anolis richardi* joined in. The berries are small, dark red, tree-borne, and altogether like ordinary mulberries in appearance; I did not taste any, as I do not like mulberries.

Distribution. This species occurs throughout the islands of the Grenada Bank (Grenadines, Grenada, and cays) wherever more than herb-stage vegetation occurs. It has been introduced, from southwestern Grenada (the Botanical Garden is south of St. George's), into Trinidad and Guyana; on the former, at least, it is common and widespread in the central, western region of the island, and is reported from the inhabited (and bread-fruited) coastal cay of Gasparee. (See *Distribution, Anolis trinitatis,* above.)

Relationships and discussion. This species, I reason, must be a direct descendant of *Anolis trinitatis* (it retains the pale axilla), and the innovator of the $2n = 34$ karyotype (Gorman and Atkins, 1968b). Thus, it is also the direct antecedent of *A. extremus* and *A. roquet.* (See *Evolution,* below.)

The Grenada bank is a submarine platform low enough so that all of its nearly fifty islands may have been united as a single land mass during the last glacial height (0–40 fathoms). Throughout this bank, on every rock and cay that has so much as a single bush, from sea level to the highest volcanic peaks—nearly 3000 feet—swarms *Anolis aeneus.* This anole, like *A. gingivinus* previously described, is ubiquitous to the extent that one must regard each land area as the range of a single local population of interbreeding individuals; the species as a whole is fragmented only by water gaps. The largest, and second southernmost, island on this bank is Grenada. At its higher elevations Grenada extends well above cloud line and has extensive rain forests; its leeward coast is in an overspill area between the high peaks, and it, therefore, is quite wet also. The land areas of the remainder of the Grenada Bank are dry: southern Grenada; Glover Island, to the south of it; and the Grenadines, which stretch northward nearly to St. Vincent, almost 70 miles away. The northernmost of the Grenadines, Bequia and Mustique, as well as the small cays in their vicinity, get some rain as overspill from St. Vincent when the wind is from just east of north; this effect is small, however. Also, Carriacou, 1300 feet high, gets some rain owing to cloud line fluctuations, but once again very little. The remaining islands, scattered and in clusters, get no more rain than the open sea; rarely, and purely by chance. The islands vary from low, sandy cays covered with a nearly impenetrable tangle of manchineel and thornbush to tall basalt spires, like Kick-'em-Jenny, which is 700 feet high and looks like a church steeple but for a few clumps of bushes on the crags.

Anolis aeneus, occurring everywhere, may have reached the small islands by founding colonies, or may have been left on them as the water level rose. Certainly, founding goes on today, for even small sand bars, of a very temporary nature, have anoles as soon as they have bushes. Given the fortuitous circumstances of gene flow between populations of this species, and the diverse ecological conditions of the land areas, considerable geographic variation is to be expected. In fact, the variation in this species is so spectacular, and

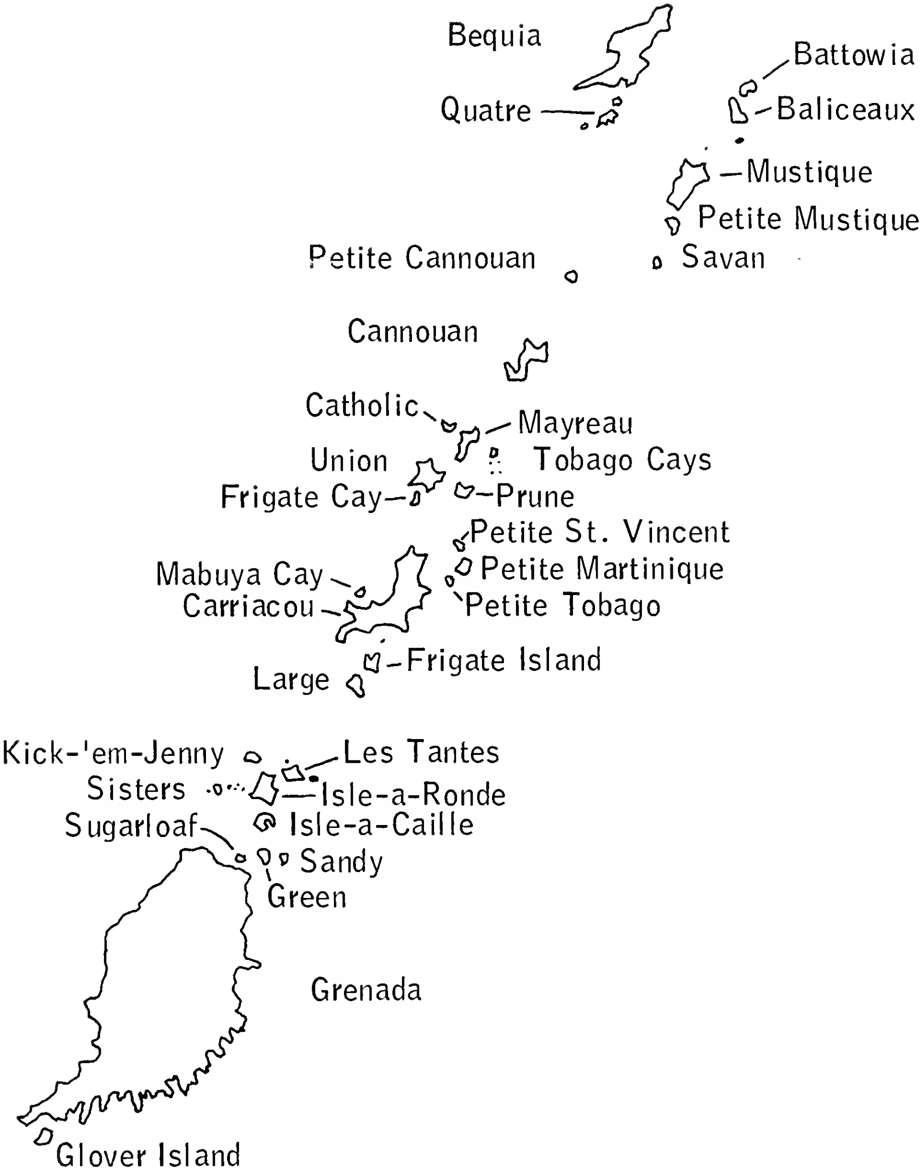

Figure 7. The Grenada Bank, giving names of islands mentioned in the text.

so discordant, that it is hard to visualize any pattern in it at all.

There is some correlation of variants and ecology: thus uniform green individuals occur only in wet forest areas (on mainland Grenada); banded individuals occur only in xeric places (southwest Grenada and some Grenadines). Beyond this, however, correlations fade. Some of the driest of the Grenadines, like Petite Tobago, have unbanded anoles; Bequia, a large, well-wooded, and fairly moist island, has anoles virtually identical to those of Kick-'em-Jenny—a dry basalt spire. The anoles of

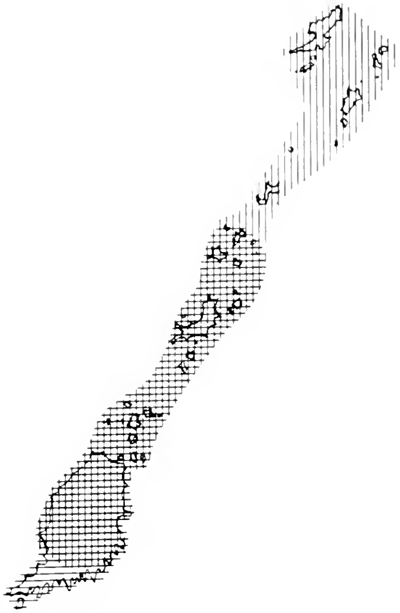

Figure 8. Variation in *Anolis aeneus*: pineal pigmentation: horizontal lines, white; vertical lines, black; intermediates may be black, white, grey, or pied.

Figure 9. Variation in *Anolis aeneus*: throat fan color: horizontal lines, yellow; vertical lines, grey; dots, individual variation including combinations of grey and yellow, and olive intermediates.

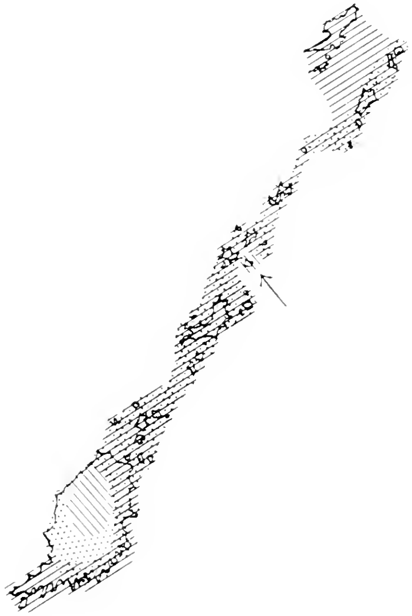

Figure 10. Variation in *Anolis aeneus*: markings on trunk: lines ascending left, uniform—no markings; dots, light speckles; lines ascending right, chevronate bands. Arrow indicates Prune Island.

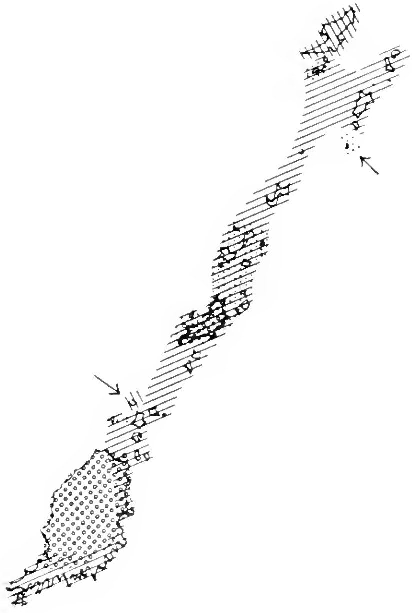

Figure 11. Variation in *Anolis aeneus*: ground color: lines ascending left, blue and yellow; dots, brown; lines ascending right, grey; open circles, green. Arrows indicate Savan and Kick-'em-Jenny.

Glover Island are somewhat different from those of adjacent Point Salines: darker, frequently greener, and often unbanded.

When water levels were lower, the present islands of the Grenada Bank may have been parts of a continuous land area occupied by *Anolis aeneus*. Geographic variation, I speculate, was neat, even if polytopic: bright colors (green, or blue and yellow) may have characterized wet country anoles, dull colors (grey or brown) dry country animals; similarly, banding may have been characteristic of xeric areas, uniform color or light speckles of rain forest. Rising water initially fragmented this species into local populations on islands of very diverse sizes, and thus of very diverse potentialities as sources of, and landing stages for, propagules. Subsequently, rafting from one island to another (and some far more than others) resulted in the chaotic scramble of phenotypes scattered about today. At least Kick-'em-Jenny may support this theory: it was probably a lone peak intermediate between a large lowland area (sea bottom today) and a high massif (Isle-a-Ronde, Isle-a-Caille, Les Tantes group); if the lowland was dry (grey or brown anoles, heavily banded) and the massif was wet (unicolored or speckled anoles of bright color), then Kick-'em-Jenny would be expected to have intermediates: perhaps banded anoles with bright colors.

Kick-'em-Jenny has no beaches and its sheer cliffs make a heavy, pounding surf of the swells coming across the shallow Grenada Bank towards it. Very few things have ever approached it on the water and lived to land there. If Kick-'em-Jenny had, when it became an island, banded, bright colored anoles, it should have them still, uncontaminated by new colonizers; it does.

Anolis extremus Garman

Anolis roquet var. *extremus* Garman (1887: 35)

Type. MCZ 6183, Garman coll. I have affixed the tag bearing this number to the largest male, and regard it as the type; the others in this series are regarded as paratypic.

Type locality. Bridgetown, Barbados.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined, in which the sublabials break up into undistinguished scales below the orbit; five or more scales of the supraorbital semicircles abut, or, if fewer, then interparietal in contact with supraorbitals; dorsals in standard distance 36 or less; axilla with dark, sooty pigment; head comparatively broad: width between orbits, across supraorbital semicircles at narrowest point, contained in standard distance less than four times.

Squamation. One hundred seventy-six (103 males, 39 females, and 34 juveniles) have been examined. In addition to diagnostic characters, cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: the midventrals are smooth; there are 20–29 (average 25) contained in the standard distance at midbody. The middorsals are about the same size as the ventrals: 20–28 (average 24) are contained in the standard distance. The dorsals decrease moderately in size laterally; 26–34 (average 30) are contained in the standard distance six scales lateral to the dorsal midline. The digital dilations are quite ordinary: there are 22–28 (average 26) lamellae under the second and third phalanges of the fourth toe; although the lowest counts come from females and juveniles, there is not a significant average difference between the sexes.

Coloration. This is a mossy looking green anole; there is usually blue-grey or lavender about the head, and lichenate black or dark brown markings on the anterior trunk; there may be small, light dots. The venter is yellow; the male throat fan is orange with yellow to greenish scales. Females are more olive green and generally duller than males; they lack a colorful throat fan, and may have striped or obsolete middorsal patterns.

There is some geographic variation: specimens from Ragged Point (MCZ 81904–8) are noted as being duller than most in Bridgetown, Speightstown, or Bathsheba, and tended more towards violet tones anteriorly. One from South Point (MCZ 81909) was virtually plain grey, with only a posterior wash of green; all (MCZ 81909–13) had bluish eyelids contrasted to darker orbits. Some of MCZ 81903–4, from North Point above Animal Flower Bay, were similar. Three series from as much of an "interior" as Barbados has (MCZ 81920–24, Castle Grant Hill, 1110 feet; MCZ 81925–29, Gun Hill; and MCZ 81940–44, Mount Hillaby, 1115 feet) average a shade greener, and sometimes have more light dots than most from elsewhere.

Specimens taken by me in Castries, St. Lucia (MCZ 71822–33) were identical to typical Bridgetown specimens in life. I have not seen living material from Bermuda, but there is not the remotest doubt about the identity of the preserved specimens examined.

Adults are shown on Plate 3.

Size and sexual dimorphism. The largest male examined is 83 mm, snout to vent (MCZ 80409, "Barbados"); the smallest apparently mature male is 46 mm (MCZ 75432, Ireland Island, Bermuda); the smallest Barbados male (MCZ 75285, St. Ann's Fort) and the smallest St. Lucian male (MCZ 56390, Castries) are both 53 mm. The largest female is 60 mm (MCZ 80414, "Barbados"); the smallest mature female is 42 mm (MCZ 75296, White Hall, Barbados). Sexual dimorphism is strong in throat fan, insignificant in lamellae, weak in size, but notable in color. The standard distance is 15–17 (average 16) per cent of the snout-vent length in both sexes.

I submit that MCZ 81903, taken by me at Bridgetown, 18 July 1964, holds the world's record as the smallest lizard ever taken with 6 pound test monofilament: 23 mm, less than .016 of an ounce.

Population structure and ecology. Anolis extremus is infradispersed, utterly ubiquitous, and exceedingly abundant all over Barbados. Thomas Barbour (1930b) notes of this species that it is "almost if not quite extinct on Barbados" (p. 112); that remark must certainly stand as one of the great verbal monuments of all time, but whether to a lizard's incredible fecundity, or a man's incredible myopia, I cannot be sure.

This species is abundant in Castries, St. Lucia; ubiquitous and infradispersed, it seems to be extending its range. I know nothing about its population structure on Bermuda, where *Anolis bimaculatus leachi* and *Anolis grahami grahami* also occur as introductions.

In the field, the sex ratio appears balanced.

Distribution. Anolis extremus is a native of Barbados, where it covers the island. It has been introduced in the recent past to Castries, St. Lucia, Bermuda, and the Centro Baleanico restaurant, Caracas, Venezuela (MCZ 110294–5).

Relationships. This species is very close to *Anolis aeneus*, on one hand, and *Anolis roquet*, on the other. It shares a transferrin with the former, a hemoglobin with the latter (Gorman and Dessauer, 1965, 1966); in display behavior it is unique (Gorman, 1968).

The axillary pigmentation makes a simple distinction between *extremus* and *aeneus*, especially when specimens (even preserved) are compared directly. Separation from *roquet* is more difficult; directly compared, *extremus* look notably broad headed; quantification is tricky, owing to the skull-covering soft tissues, the small size of the distances to be measured, and the location of the "center of the eye."

Anolis roquet (Lacépède)

Lacerta roquet Lacépède (1788)
Anolis martinicensis Suckow (1798)

Anolis cepedii Merrem (1820: 45)
Anolis goudotii Duméril and Bibron (1837: 108)
Anolis alligator Duméril and Bibron (1837: 134)

Type. None ever designated. This species is difficult to identify by conventional museum techniques, is remarkably variable, and has six subspecies that require description (below). It is imperative that a neotype be designated; that specimen is MCZ 81581, taken 29 July 1964 at Fort-de-France, Martinique (J. Lazell): an adult male 79 mm, snout-vent length.

Diagnosis. An *Anolis* of the Lesser Antillean section of the *roquet* group, as here defined, in which the sublabials break up into undistinguished scales below orbit; five or more scales of the supraorbital semicircles in contact, or, if fewer, then interparietal in contact with supraorbitals; 36 or fewer dorsals in the standard distance; axilla with dark, sooty pigment; head relatively narrow: width between orbits, across supraorbitals at narrowest point, contained in standard distance four or more times.

Remarks. Martinique and *Anolis roquet* require an introduction; Vandercook (1938) provides it:

> Martinique is steeply mountainous. Since its rainfall is nearly double that of the Leeward Islands, it is richly fertile. Fields that are level enough for the purpose are planted with bananas, coconuts, and cocoa, all of which add picturesqueness to the landscape. The many ravines and peaks that are too sheer for cultivation are covered with dense forest.

The ecological complexities of Martinique include all of the conditions I have described (see Introduction), from rain forest and rain shadow, through overspill and snags, to cays so low as to receive no more rainfall than the open sea.

Squamation. I have not found even significant average differences in squamation between the subspecies of *Anolis roquet.* I have examined 1,105 specimens (773 males, 251 females, and 81 juveniles). In addition to diagnostic characters, cited above, this species differs from other Lesser Antillean members of the *roquet* group in the following features: the ventrals are smooth; there are 19–27 (average 23) in the standard distance at midbody. The middorsals are virtually the same size as the ventrals: there are 19–27 (average 24) in the standard distance. The dorsals decrease gradually in size laterally; there are 25–35 (average 30) in the standard distance six scale rows lateral to the dorsal midline. The digital dilations are broad and raised; there are 23–30 (average 27) lamellae in males, 20–27 (average 24) lamellae in females, under the second and third phalanges of the fourth toe.

A discussion of the species and its relationships follows the subspecies accounts. A table of the characters of the subspecies is given in Table 2, and their ranges are shown in Figure 12.

Anolis roquet roquet (Lacépède)

Lacerta roquet Lacépède (1788)
Anolis martinicensis Suckow (1798)
Anolis cepedii Merrem (1820: 45)
Anolis goudottii Duméril and Bibron (1837: 108)
Anolis alligator Duméril and Bibron (1837: 134)

Type. MCZ 81581, by neotypic designation (above). J. D. Lazell coll., 29 July 1964.

Type locality. Fort-de-France, Martinique, by present restriction.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color dull, mossy green to brown, usually with blue, venter dirty whitish to yellow; slate grey irregular mottling on dorsum; light dots, when present, yellow to tan; throat fan yellow to light orange, sometimes white anteriorly, with white to cream scales, and often with dark, dingy streaks between scale rows; female mossy green to brown without a distinctive throat fan; bold striped middorsal pattern; when brown, stripes sooty black; venter dirty white to yellow.

Description of the neotype. This 79 mm adult male was rich, mossy green, shading laterally to blue. The dorsum was marked by dark grey-brown mottling; small yellow dots formed oblique rows, especially on the anterior trunk. The venter was yellow. The throat fan was yellow with cream scales and dingy streaks between the scale rows. This specimen and an adult female are shown on Plate 3.

Variation. I have examined 282 specimens of this form (187 males, 73 females, and 22 juveniles) of which 209 were collected by me. Variation is considerable, and has a geographic component. The Fort-de-France population is the standard: males are green with blue dorsally, and rarely lack oblique rows of yellow dots; their throat fans are yellow without white anteriorly. The females are green with bold dark dorsolateral stripes bordering a usually brown middorsum. The allocation of Lacépède's name is clear: no other subspecies has yellow spots. The names "*martinicensis*" Suckow and "*cepedii*" Merrem were proposed as direct replacements for *roquet;* not based on new material. The type of "*goudotii*" Duméril and Bibron (MNHN 791) is a young female typical of this subspecies. The four male syntypes of "*alligator*" Duméril and Bibron, MNHN 6791(3) and 784, are also typical of Fort-de-France material.

In the northeastern portion of the range (e. g., MCZ 82764–74 east end, Ilet Chancel), males average more heavily spotted than elsewhere, and the spots may be tan instead of yellow.

Specimens from southern coastal areas (e. g., MCZ 82239–50, Anse Gaffard; MCZ 82835–47, Rocher du Diamant; MCZ 82702–11, Ste. Luce) average browner than most, may have very bold dark markings, and may lack light spots.

Males from the Pilote valley (e. g., MCZ 82712–17, Rivière Pilote) are especially beautiful; in addition to rich green and blue, with bright yellow spots, their throat fans are usually bicolored: white anteriorly and bright, light orange with yellow scales posteriorly.

Size and sexual dimorphism. The largest specimen of *Anolis roquet roquet* examined is a male of this form, 86 mm, snout to vent (MCZ 82732, Abondance); the smallest apparently mature male is 49 mm (MCZ 66867, Anse Mitan). The largest female is 66 mm (MCZ 82132, Fort-de-France); the smallest mature female is 48 mm (MCZ 82701, Medecin). Sexual dimorphism is striking in throat fan and color, notable in lamellae and size. The standard distance is 15–17 (average 16) per cent of the snout-vent length in both sexes.

Population structure and ecology. This subspecies is ubiquitous and infradispersed throughout its range on the mainland of Martinique; island demes are on many coastal keys, the most isolated being Rocher du Diamant: an old basalt spire that is difficult to land on, owing to a lack of beach or strand. Males perch from rocks on the ground to about ten feet up; females are usually lower, but both sexes frequently forage on the ground.

This subspecies is not especially shy or wary.

The range of *A. r. roquet* is the broad, fertile, mesic region of Martinique, and the flanking range of hills that curve down the windward coast and then west to form the southwest peninsula. This region receives considerable rain as overspill from the high mountains to the north, and the snag effects of such small peaks as Vauclin, Gardier, and Bigot.

Distribution. This is the widest ranging subspecies, covering all of central and southern Martinique, except for the extreme southeast. From Fort-de-France, the range extrends east northeast to Morne Pavillon (MCZ 82632–41), then curves northeast to the coast at Habitation Mansard-Rancée (MCZ 82815–24), and north northeast to the Ilet Chancel (MCZ 82764–74). Along the windward coast, this subspecies occurs only as far south as Le François (MCZ 82592–601); then, through the south southwest curving spine of hills it ranges to the south coast (MCZ 82732–42, Abondance; ASFS X6395, 2 km northwest of Le Marin). To the west, its range is limited only by the available land areas of the Martinique Bank. (See map, Figure 12.) This is the mesic, overspill and snag portion of Martinique.

Anolis roquet summus subsp. nov.

Type. MCZ 81630; J. D. Lazell coll., 2 August 1964.

Type locality. Poste Forestiere, Tirage 38, Deux Choux, Martinique.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color bright yellow-green to plain green, without any blue; venter bright yellow-green to plain green; slate grey to sooty black irregular blotches or mottling on dorsum; light dots, when present, virtually white (very pale blue or green); throat fan deep orange with green scales; female similar or with a striped middorsal pattern boldest anteriorly; no distinctive throat fan.

Description of the type. This 70 mm adult male was brilliant green, above and below, in life. Sooty black mottling, running obliquely on the trunk, was prominent; several bright, very light blue dots were between the dark markings. The throat fan was very dark orange with bright green scales; there were vague dingy streaks between the scale rows. This specimen and an adult female are shown on Plate 3.

Variation. I examined 125 specimens of this form (74 males, 43 females, and 8 juveniles) of which 89 were collected by me. Male variation is confined to the extent of dark markings and the size and number of light spots. Dark markings may be heavy and bold, as in the type, or reduced; they are always present. Similarly, the light spots may be large and numerous, or absent: ASFS 18879 and 18881, from 3 km southeast of Le Morne Rouge, are extreme examples, respectively; the type is about average in this respect. Females are more variable. The standard female pattern is striped, with the stripes most prominent on the neck and anterior body, and sometimes absent posteriorly. Some females, like MCZ 82851 (Morne des Roseaux) or MCZ 82162 (Petite Savane, Montagne Pelée) are indistinguishable from males in dorsal pattern; all stages of intermediacy occur: this is not a polymorphism.

Size and sexual dimorphism. The largest male examined is 82 mm, snout to vent (MCZ 66845, Habitation Eden; the smallest apparently mature male is 49 mm (MCZ 82337, Vigie de la Calabasse, Montagne Pelée). The largest female examined is 62 mm (MCZ 82317, Habitation Eden); the smallest mature female is 48 mm (MCZ 82857, Morne des Roseaux). Sexual dimorphism is striking in throat fan, notable in lamellae, and weak in size and color. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. This subspecies is ubiquitous and infradispersed; from abundance at the lower elevations of its lofty range, it thins markedly past 2500 feet, and none have been collected over 3000 feet. Unlike both of the montane rain forest anoles (*A. oculatus montanus* and *A. marmoratus alliaceus*) of the *bimaculatus* group, this form is not a notable heliophile. The montane forms of the *bimaculatus* group are highly arboreal in the forest, staying close to the tree tops, and thus the sun; they are common near (or on) the ground only along watercourses, or at ponds, roads, and clearings. *A. roquet summus*, even in the deep gloom of the high forest at Morne des Roseaux, perch at about eye level, just as do their conspecifics in the rest of Martinique.

The range of *A. r. summus* is the highest mountain range in the Lesser Antilles; before agriculture cleared some areas, like the broad col between Montagne Pelée and the Morne Jacob massif, it must all have been rain forest.

This subspecies is not shy or wary, and is easily collected by noose.

Distribution. A. r. summus is found continuously through the mountains of northern Martinique from the great, smoking cone of Montagne Pelée to Absalon, above Fort-de-France. (See map, Fig. 12.) This is the montane rain forest ecological zone.

Anolis roquet majolgris subsp. nov.

Type. MCZ 81664; J. Lazell coll., 4 August 1964.

Type locality. Fond St. Jacques, north of Ste. Marie, Martinique.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color dark grey-green to mud brown; venter grey to dingy yellow; dull mottling on dorsum irregular and very little darker than the ground color; whitish blotches may be present on head or anterior trunk; throat fan dull grey anteriorly, often becoming yellow or blotched with yellow posteriorly; female mud brown above, dirty greyish below; no distinctive throat fan; pattern may be striped, obsolete, mottled, or absent, but it is always dull and very little darker than the ground color; no whitish patches, or light flank stripe on posterior body.

Description of the type. This 77-mm adult male was just plain brown above and grey below; the throat fan was plain, dull grey with grey scales; faint slatey mottling was discernible dorsally. This specimen and an adult female are shown on Plate 3.

Variation. I have examined 107 specimens of this form (76 males, 27 females, and 4 juveniles), of which 52 were collected by myself. When I remarked (under the genus *Anolis*, above) that some forms were "ideally camouflaged on a dung hill," this was the one foremost in my thoughts. Males may have oblique dark mottling better indicated than in the type (e. g., MCZ 81667, from the type locality), and such marking is common at the northern end of the range (see MCZ 82134–48, Le Lorrain). A vague, grey spot or two, lighter than the ground color, appears in some from the extreme southern end of the range (see MCZ 82530–39+3, Derrière Morne). White blotches on the head, throat, nape, or shoulder are an occasional feature throughout the range (e. g., MCZ 81665, from the type locality); yellow on the posterior throat fan is common throughout the range also. Females, when they show any pattern at all (e. g., MCZ 81671, from the type locality), are very dully marked.

The name *majolgris* is my own spelling for the Creole "grey throat fan."

Intergradation with *A. r. summus*, both between the range of that form and *majolgris*, and between *summus* and the sea along the north coast, has confused many observers. Green, in *A. r. summus*, results from yellow overlying bright blue. *A. r. majolgris* virtually lacks either color; deletion of the yellow overlay signals intergradation with a coastal race in *summus*. Thus *summus* × *majolgris* intergrades may completely lack yellow (and thus green) but still retain extensive blue. A bright blue anole, in this case, is quite intermediate between a solid green one and a plain brown one.

Size and sexual dimorphism. The largest male examined is 82 mm, snout to vent (MCZ 82520, Ste. Marie); the smallest apparently mature male is 51 mm (ASFS 18845, 4 km northwest of Ste. Marie). The largest female is 61 mm (MCZ 82537, Derrière Morne); the smallest mature female is 50 mm (82145, Le Lorrain). Sexual dimorphism is striking in throat fan, notable in lamellae, and weak in size and coloration. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. This subspecies is ubiquitous and infradispersed throughout its range. Individuals perch about eye level, on the average, with extremes from rocks on the ground to about ten feet. Both sexes commonly forage on the ground.

The range of this species is the well-watered lowland to windward of the great barrier range of northern Martinique; it is the wettest lowland on the island.

This subspecies is not shy or wary, and is easily collected by noose.

Distribution. *A. r. majolgris* occurs along the northern windward coast of Martinique from Derrière Morne to Le Lorrain. (See map, Fig. 12.) This is the form of the well-watered lowland to windward of Martinique's major mountain range.

Anolis roquet zebrilus subsp. nov.

Type. MCZ 81619; J. D. Lazell coll., 1 August 1964.

Type locality. Le Carbet, Martinique.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color pale grey-brown; venter dirty whitish to pale yellow; dark grey to sooty-black peppering on the dorsum, and often coalescing and combining with metallic bronze to form a chevronate pattern; whitish "frosting" on neck and anterior trunk; throat fan yellow to pale orange-yellow, usually white anteriorly, with white to cream scales, and, often, with grey streaks between the scale rows; female ashy grey-brown to olive peppered with slate grey to sooty black; no distinctive throat fan; pattern, when present, dully striped or mottled.

Description of the type. This 78-mm adult male was ashy grey in ground color; slatey peppering on the head coalesced into roughly longitudinal mottling on the nape, and sooty-black oblique streaking on the trunk. Rich bronze combined with the trunk streaking to produce four bold dorsal chevrons. The neck was frosted laterally with ashy white. The venter was pale yellow posteriorly, white anteriorly. The throat fan was light, bright yellow except for a white anterior quarter; the fan scales were virtually white. This specimen and an adult female are shown on Plate 3.

Variation. I examined 127 specimens of this form (89 males, 25 females, and 15 juveniles), of which I collected 66 myself. The general impression is of a black and white anole; there is no discernible geographic component in the variation, and all extremes may be seen at the type locality: males may completely lack the dark chevronate stripes (MCZ 81620), have dark mottling roughly longitudinally arranged on the dorsal trunk (MCZ 81622), or show pale, metallic bronze chevrons (MCZ 81621); some show great areas of white anteriorly (MCZ 81623). Females are frequently unmarked except for peppering or mottling, but may be striped (MCZ 81626), or may combine a striped middorsal pattern with the lateral components of the common male chevronate pattern.

Size and sexual dimorphism. The largest male examined is 82 mm, snout to vent (MCZ 82418, Morne-aux-Boefs); the smallest apparently mature male is 55 mm (ASFS 18552, 5 km northwest of Case Pilote). The largest female is 63 mm (MCZ 82423, Morne-aux-Boefs); the smallest mature female is 46 mm (ASFS 18561, 5 km northwest of Case Pilote). Both of the localities cited are about in the middle of the range. Sexual dimorphism is strong in throat fan, notable in lamellae and color, but rather weak in size. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. This subspecies is ubiquitous and infradispersed throughout its range. Individuals perch from ground level to about ten feet, averaging about eye level. Both sexes commonly forage on the ground.

The range of this subspecies is the exceedingly dry rain shadow of the great barrier range of Martinique: as arid and xeric as any area in the Lesser Antilles. This subspecies is very skittish and difficult to approach.

Distribution. *A. r. zebrilus* occurs along the northern leeward coast of Martinique from Case Pilote to Le Trou, south of St. Pierre. (See map, Fig. 12.) This is the arid coast to leeward of the island's principal mountain range.

Anolis roquet caracoli subsp. nov.

Type. MCZ 81601; J. D. Lazell coll., 31 July 1964.

Type locality. Pointe Caracoli, Presqu'île de la Caravelle, Martinique.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color smoky grey-brown to grey-green; venter grey to dull yellow; no dark peppering; slate grey, chocolate, or sooty black transverse dorsal chevrons; tiny whitish flecks may be present, and sometimes whitish patches on neck and anterior trunk; no light flank stripe on posterior body; throat fan yellow, usually white anteriorly, with whitish scales and dark, dingy streaks between the scale rows; females smoky grey-brown without dark peppering; no distinctive throat fan; striped dorsal pattern not in strong contrast to ground color; whitish patches frequent on neck and anterior trunk; no light flank stripe on posterior body.

Description of the type. This 73 mm adult male was smoky grey-brown in ground color and had five dark chocolate chevrons on the trunk, plus two more partial ones on the tail. The venter was grey anteriorly, and shaded to dull yellow on the abdomen. The throat fan was yellow except for a white anterior quarter; the fan scales were cream; prominent, dark, dingy streaks were between the fan scale rows. This specimen and an adult female are shown on Plate 3.

Variation. I examined 44 specimens of this form (30 males, 12 females, and 2 juveniles), of which I collected 20 myself. There is very little variation. The greenest specimen was a rather pretty lichen green: MCZ 81603, from the type locality. Some show vague mottling in the ground color (e. g., MCZ 81602, from the type locality), but this is a far cry from the peppering of *A. r. zebrilus*. Females are all smoky, and have an obscure striped middorsal pattern.

Size and sexual dimorphism. The largest male examined is 79 mm, snout to vent (ASFS X443, 3 km northeast of Tartane); the smallest apparently mature male is 54 mm (MCZ 82286, the Lighthouse). The largest female is 58 mm (MCZ 81610, Anciens Cachot, Baie du Tresor); the smallest mature female is 51 mm (MCZ 66926, Chateau Duduc). Sexual dimorphism is striking in throat fan and color, notable in lamellae, but weak in size. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. *A. r. caracoli* is ubiquitous and infradispersed; there are presumably demes on the tiny Ilet Lapin and Ilet Tresor, a few yards off the steep cliffs of the Presqu'île. Individuals perch from the ground to about ten feet, just as in the other subspecies. The range of this form is arid and xeric: it is so far east of the mass of Martinique as not to receive more rainfall than the open ocean.

This subspecies is wild, shy, and difficult to noose.

Distribution. *A. r. caracoli* occurs on the eastern end of the Presqu'île de la Caravelle. (See map, Fig. 12.) This bit of land is too far windward of Martinique's mountains to be climatically affected.

Anolis roquet salinei subsp. nov.

Type. MCZ 81675; J. D. Lazell coll., 5 August 1964.

Type locality. Pointe des Salines, Martinique.

Diagnosis. An *Anolis roquet* combining the following color characters: male ground color light, bright green to ash grey-brown; venter cream to yellow; slate grey to sooty black dorsal chevrons; no dark peppering; tiny whitish flecks present, but no large whitish patches; throat fan yellow, becoming white anteriorly, with cream to white scales; no dark dingy grey streaks between fan scale rows; females ash grey-brown above, grey to yellowish below; no distinctive throat fan, striped or mottled dorsal pattern not in strong con-

TABLE 2. TABLE OF THE PRINCIPAL IDENTIFYING CHARACTERISTICS OF THE SUBSPECIES OF *ANOLIS ROQUET*. SEE TEXT.

	Ground Color	Venter	Dark Markings	Light Markings	Throat Fan Skin	Throat Fan Streaks	Throat Fan Scales	Females
ROQUET	green to brown with blue	whitish to yellow	slate mottlings	yellow to tan dots	yellow to light orange	±	white to cream	bold stripped pattern
SUMMUS	green	green	sooty mottlings	bright whitish dots	dark orange	±	green	green belly
MAJOLGRIS	dull grey green to brown	grey to dingy yellow	vague mottlings	none (faint spots)	dull grey ±yellow	±	dull grey ±yellow	brown, vague pattern
ZEBRILUS	grey-brown	whitish to yellow	blackish peppering (sooty chevrons)	whitish "frosting"	yellow ±white	±	white to cream	peppered
CARACOLI	grey-brown to grey-green	grey to dull yellow	sooty chevrons	whitish "frosting"	yellow ±white	+	whitish	no posterior streak
SALINEI	light green to grey-brown	cream to yellow	sooty chevrons	light flank stripe	yellow ±white	–	white to cream	posterior streak

trast to ground color; no whitish patches; flank stripe indicated on posterior trunk.

Description of the type. This 72-mm adult male was pale green without blue tones dorsally, and dull yellow below. Sooty black coalesced to form four narrow chevrons across the trunk. Tiny, virtually white flecks were scattered on the dorsal trunk. The throat fan was bright yellow shading to white on the anterior quarter; the scales were cream to white in correspondence. A pale flank stripe was present on the posterior trunk. This specimen and an adult female are shown on Plate 3.

Variation. I examined 87 specimens of this subspecies (50 males, 32 females, and 5 juveniles), of which I collected 52 myself. Variation is principally in male ground color. All males taken by me at Ste. Anne (MCZ 82177–82) were very light, bright green. At all other stations individuals ranged from this hue to ash-grey. Many males lack all indication of a flank stripe. Females are all ashy, have a dorsal pattern, and a vague, light flank stripe on the posterior body.

Size and sexual dimorphism. The largest male examined was 78 mm, snout to vent (MCZ 82177, Ste. Anne); the smallest apparently mature males is 54 mm (MCZ 82192, Pointe des Salines). The largest female is 62 mm (MCZ 82183, Ste. Anne); the smallest mature female is 47 mm (MCZ

Figure 12. Martinique, showing the ranges of the six subspecies of *Anolis roquet*: 1. *A. r. roquet*. 2. *A. r. summus*. 3. *A. r. majolgris*. 4. *A. r. zebrilus*. 5. *A. r. caracoli*. 6. *A. r. salinei*.

82147, Pointe des Salines). Sexual dimorphism is striking in throat fan and color, notable in lamellae, and weak in size. The standard distance is 16–18 (average 17) per cent of the snout-vent length in both sexes.

Population structure and ecology. This subspecies is ubiquitous and infradispersed; demes occur on the Ilet Cabrits (MCZ 81653–7), and the windward coast cays adjacent to the mainland range (e. g., 81658–63, Ilet Chevalier). As with the other forms of this species, individuals perch from the ground to about ten feet, and both sexes frequently forage on the ground.

The range of this species is so far southeast of the mass of Martinique that it receives little more rainfall than the open ocean. It is as arid and xeric as any area in the Lesser Antilles.

This subspecies is skittish, wary, and often hard to collect.

Distribution. A. r. salinei occurs in extreme southeastern Martinique from the Ilet Cabrits and 3 km southeast of Le Marin (ASFS 18678–9) northward along the windward coast to Pacquemar (MCZ

82722–31). (See map, Fig. 12.) This peninsula is southeast of the main body of Martinique. It is very low in elevation, and consequently very arid and xeric.

Discussion. As is evident from the preceding descriptions, identification of *Anolis roquet* to subspecies is very difficult except in life. The subspecies *caracoli* and *salinei* are the most difficult; I cannot distinguish between their intergrades with *roquet*, and do not really know what to call insular intergradient populations such as MCZ 82754–63, from Loup Garou.

Because of wind direction and the lay of the land, coastal cays tend to have anoles like those on the mainland southwest of them, rather than immediately adjacent. This is apparent on the Ilet St. Aubin, adjacent to the range of *majolgris:* MCZ 81611–18 combine characters of *roquet*, *majolgris*, and *caracoli*, as do those from the town of Trinité (MCZ 82540–51). This holds true all the way south to the cays off Le François, which harbor anoles combining features of *roquet* and *salinei* (e. g., MCZ 82775–84, Ilet Oscar), rather than being ordinary *roquet*, like those of the adjacent mainland (e. g., MCZ 82592–601, Le François).

It is evident from the map that a large portion of Martinique is zones of intergradation. The huge, roughly triangular area from the range of *A. r. summus* southeast to the range of *A. r. roquet* is notable: in its western, highland stretches influence from *A. r. majolgris* combines with the other two races to produce a homogeneous and rather distinctive beast (see especially MCZ 82612–21, La Duchene). I would name this as a seventh subspecies if it had any characteristics of its own; to name a three way intergrade, however recognizable and widespread, seems to me to be an inexcusable obfuscation of the real biological situation.

It has taken me six years, complete with over four months of collecting on Martinique, to finally decide to name subspecies. That naming provides the simplest and best method of describing and discussing the spectacular geographic variation in *Anolis roquet* can be challenged. Certainly, the lack of squamation differences, compounded by close convergence in the three chevronate forms (*zebrilus*, *caracoli*, and *salinei*), makes the case for parapatric subspecies far weaker than it is in either *Anolis marmoratus* or *Anolis oculatus*.

Relationships. Anolis roquet is the culminating species of its group. It shares the diploid chromosome count of 34 with both *A. aeneus* and *A. extremus* (Gorman and Atkins, 1967). It is distinct from the former in both hemoglobin and transferrin (Gorman and Dessauer, 1965, 1966) and in axillary pigmentation. It shares hemoglobin and axillary pigment with the latter. It is distinct from all in display behavior (Gorman, 1968). Further discussion is provided under Evolution, below.

EVOLUTION

> I am trying to pursue a science that is beginning to have a good many practioners but that has no name: the science of four-dimensional biology or of time and life.
>
> —G. G. Simpson (1953)

"Evolution" is a compound of many phenomena; without a fossil record of considerable depth, historical evolution—phylogeny—becomes foggy, speculative, and requires great imagination to reconstruct convincingly (even if perhaps incorrectly). Nevertheless, the garland of islands that makes up the Lesser Antilles provides a stage of incomparable quality for all of evolution's acts. *Anolis* have been players of extraordinary action: here we have at least a little of everything in the repertoire. But the curtain has been up a long time: if we believe Schuchert (1935), for about thirty million years. It is possibly fortunate, from the point of view of man's space and time, that we have missed so much: there is so much now to be seen.

Extinction. Since the passing of the Dodo, the strange, isolated animals of oceanic islands have been noted for their

PLATE 3

24. *Anolis oculatus oculatus*: male, JDL 245; female, JDL 249; Goodwill, above Roseau, Dominica.
25. *Anolis oculatus cabritensis*: male, JDL 250; female, JDL 256; Anse Gabriel, S of Colihaut, Dominica.
26. *Anolis oculatus montanus*: male, JDL 260; female, JDL 265; William Estate, Crete Palmiste, Dominica.
27. *Anolis oculatus winstoni*: male, JDL 267; female, JDL 270; Woodford Hill, Dominica.
28. *Anolis luciae*: male, MCZ 71865; female, MCZ 71690; Castries, Saint Lucia.
29. *Anolis extremus*: male, MCZ 81892; female, MCZ 81898; Bridgetown, Barbados.
30. *Anolis trinitatis*: male, MCZ 82054; female, MCZ 82062; Kingstown, Saint Vincent.
31. *Anolis aeneus*: male, MCZ 81733; barred female, MCZ 81736; striped female, MCZ 81734; all from Large Island, Grenadines.
32. *Anolis griseus*: male, MCZ 82927; female, MCZ 82932; Kingstown, Saint Vincent.
33. *Anolis richardi*: male, MCZ 81954; female, MCZ 81958; St. Georges, Grenada.
34. *Anolis roquet roquet*: male (the neotype), MCZ 81581; female, MCZ 81588; Fort-de-France, Martinique.
35. *Anolis roquet summus*: male (Type), MCZ 81630; female, MCZ 81639; Poste Forestiere, Tirage 38, Deux Choux, Martinique.
36. *Anolis roquet majolgris*: male (Type), MCZ 81664; female, MCZ 81672; Fond St. Jacques, Martinique.
37. *Anolis roquet zebrilus*: male (Type), MCZ 81619; female, MCZ 81626; Le Carbet, Martinique.
38. *Anolis roquet caracoli*: male (Type), MCZ 81601; female, MCZ 81648; Pointe Caracoli, Martinique.
39. *Anolis roquet salinei*: male (Type), MCZ 81675; female, MCZ 81648; Pointe des Salines, Martinique.

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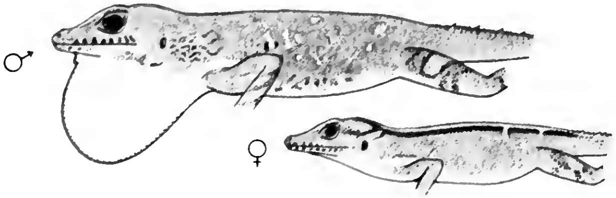

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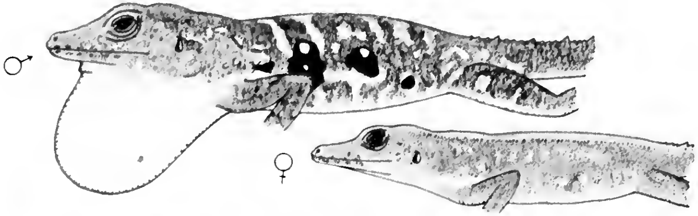

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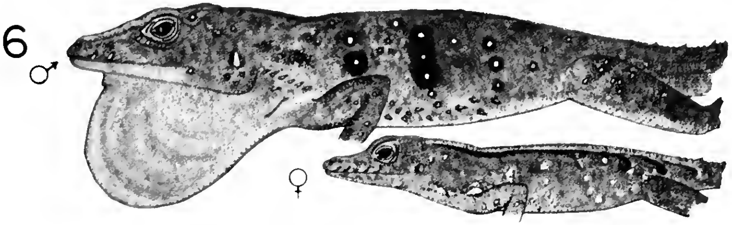

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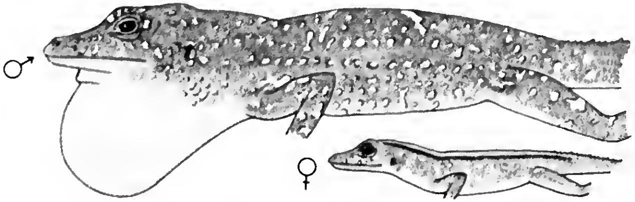

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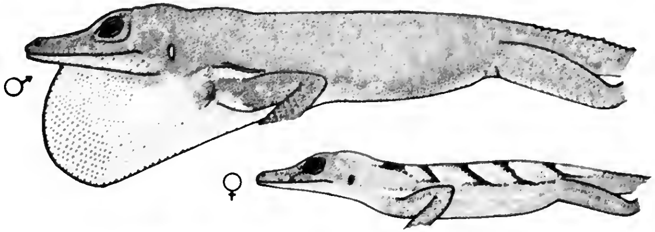

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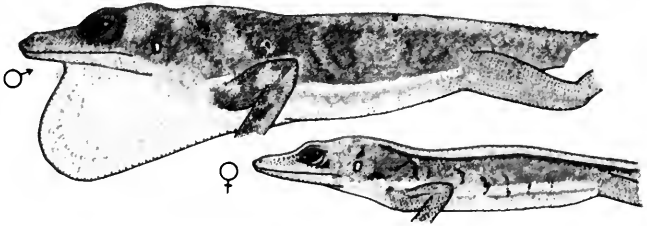

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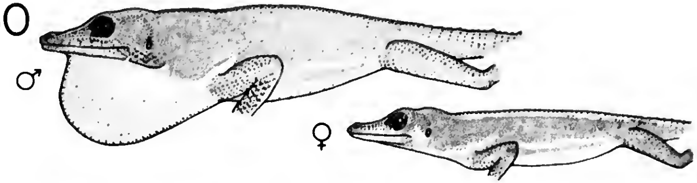

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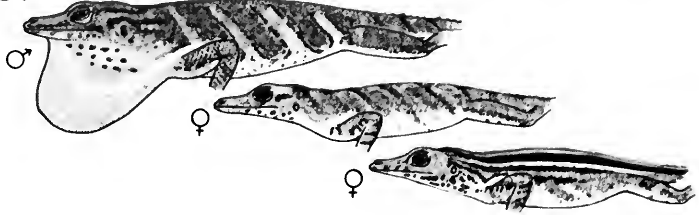

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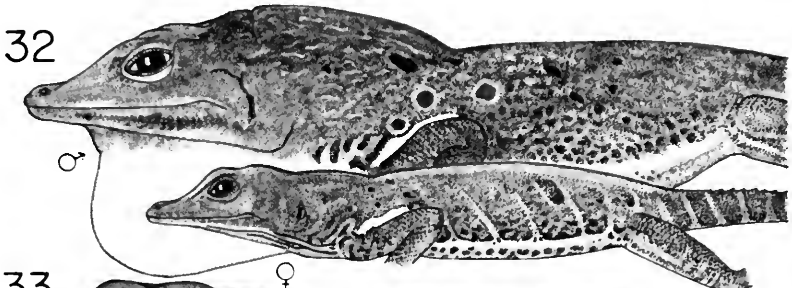

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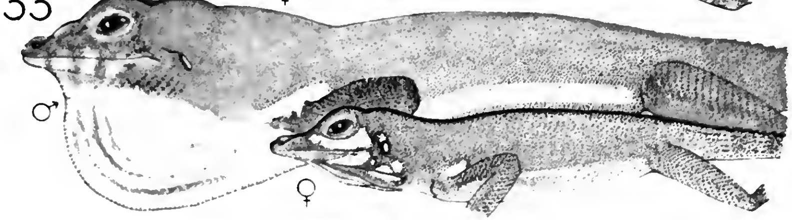

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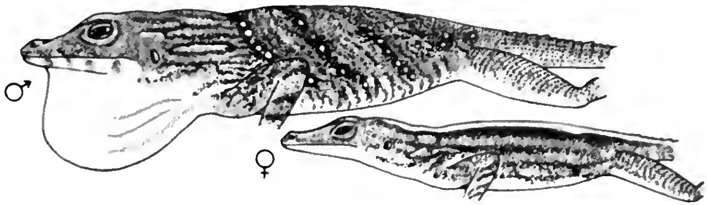

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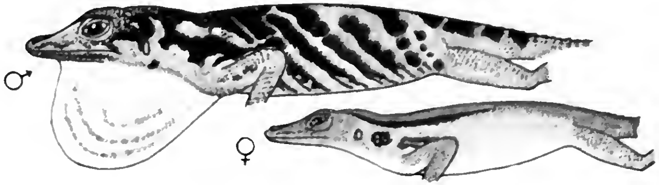

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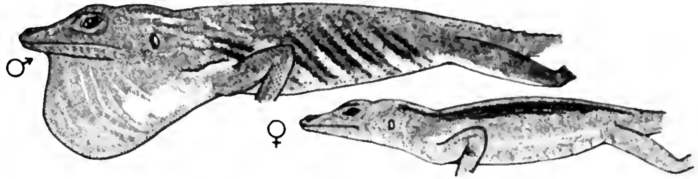

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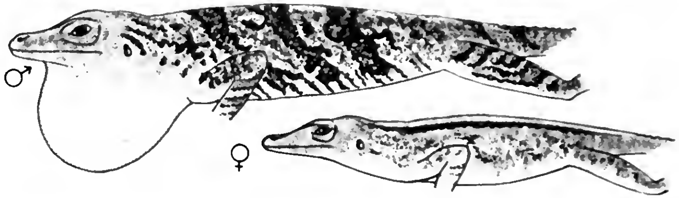

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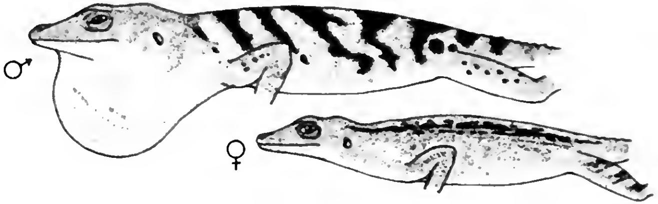

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ability to become quickly extinct. It is encouraging to look at the Lesser Antillean anoles in this respect, for present evidence indicates that this is one of the major evolutionary phenomena that they have indulged in the least.

One population of a form still living seems to have been extirpated: *Anolis wattsi pogus* occurred on Anguilla as recently as 1922.

What has been the causal agent of this extirpation? Of one thing we can be sure: it has not been the infamous mongoose. Mongooses have been introduced into St. Croix, St. Martin, St. Kitts, Nevis, Antigua, La Guadeloupe and Grande Terre, Marie Galante, Martinique, St. Lucia, St. Vincent, Grenada, and Barbados. That leaves out quite a few islands, including Anguilla, from which *A. w. pogus* has vanished. Thomas Barbour (1930a, b) was the principal proponent of the theory that mongooses have wiped out lizards; aside from his classical remark on the extinction of *Anolis extremus* (1930b: 112), he also claims that both *A. griseus* and *A. trinitatis* (= *vincenti*) are "rare" and "a prey to the mongoose." Of St. Vincent he says simply, "most of the species of this Island are extinct"; with the dubious exception of one snake (two others well represented), I do not know of any species that are missing from the original Vincentian roll call. I do not wish to be misunderstood, there is no more devout deprecator of the mongoose than I: *Herpestes* is a nasty, smelly, disease-carrying, and thoroughly wretched beast; its contribution to the great faunal losses of the Antilles cannot be denied (see e. g., Lazell, 1967b). The mongoose, however, has not been significant with respect to *Anolis.*

Man, if his populations are not stabilized, will push other populations to their demise; however, it seems doubtful that even man can exterminate any form of Lesser Antillean anole before major starvation die-off decimates his own species. The Lesser Antilles are islands of little land, and man has not been kind to what there is; already the majority of the islands are thoroughly parasitic, depending utterly on the infusion of money directly from mother governments to maintain their human numbers. Such an artificial situation cannot long prevail; some day, not too distant, there will be many fewer people living in the Lesser Antilles than there are today. Considering man's established predilections, however, things will no doubt get worse before they get better.

Phylogeny. Taxonomy and evolutionary biology are frequently stated to be more art than science by critics seeking to bring these areas of interest into disrepute. As a taxonomist and evolutionary biologist, I delight in this criticism, and here embrace its basic thesis. What has preceded has been largely a recitation of empirically determined, objective facts; there have been a few speculations and hypotheses, but these have largely been expressed with the trepidation of a scientist teetering at the very brink of his factual margin. There is no relevant or important fossil record of Lesser Antillean iguanid lizards, and probably never will be. To reconstruct the evolution of the groups on an objective foundation is impossible. I shall reconstruct it, then, on a subjective basis. The result cannot be shown to be either right or wrong; one need not believe it or disbelieve it; there is no need to like it or dislike it; there is no necessity to even look at it. In what follows, I shall make abstract representations of real objects and arrange them in patterns that appeal to me. The couching of phrases in speculative terms now ends, but I practice no deception. Even as a mobile constructed out of odd bits of hospital apparatus is not medicine, so this is not science. In all respects, it is the purest of art.

In constructing the phylogenies, I shall make the assumption that each major character has originated only once. For a karyotype, for example, this seems quite likely to be true of probabilistic necessity;

for a character like the loss of ventral keeling, it is far less sure. Keeled and smooth ventrals must each have evolved many times in the history of the genus *Anolis*; my assumption of once only within the two species groups with which I deal could certainly be challenged.

The *Anolis* of the *bimaculatus* group are fascinating. In Figure 13 I present my view of their phylogeny. At stage 1, *acutus* stock, already established on St. Croix, and previously derived from the Greater Antilles, colonized the St. Kitts Bank; the 2n = 29 (male) and 2n = 30 (female) karyotype, with nine metacentric macrochromosomes, originated. There was no change in the condition of the ventrals (heavily keeled), and only minor shifts in trivial characters like scale size. The new karyotype was the single alteration.

At stage 2, this "pro-*wattsi*" stock colonized the little island of Saba; ventral keeling began to weaken: I postulate no other change at this stage; the karyotype remains as developed at stage 1.

At stage 3, massive emigration and colonization took place. Bypassing the already full islands of the St. Kitts Bank, and missing tiny Redonda, propagules still retaining some ventral keeling landed in Montserrat, Guadeloupe, and Dominica. The peculiar 2n = 31 (male), 2n = 32 (female) karyotype of *oculatus* arose subsequently on the latter island. Also at this stage, a northward invasion put anoles on the Anguilla Bank that had or developed smooth ventrals, as did *sabanus*, who stayed at home. The incipient southern species of *marmoratus* and *lividus* thus retained some ventral keeling and had unmodified ear shapes; their alterations in the process of speciation have been in trivial features like scale size, body size, and (principally) in coloration. The Saba stay-at-home, incipient *Anolis sabanus*, still resembled its stage 2 progenitor (and living *Anolis wattsi*) strikingly in size, habitat, and behavior. Its alterations were in sexual dimorphism, coloration, and, as noted, loss of ventral keeling. Incipient *gingivinus* stock was probably quite similar, exhibiting only changes from *sabanus* stock in body size, coloration, sexual dimorphism, and (very slightly) ear shape. This last feature is the beginning of a new trend.

At stage 4, *wattsi* stock invaded the Antigua Bank from the St. Kitts Bank, and Anguilla Bank "pro-*bimaculatus*" stock arrived as well: the first case of sympatry existed. With sympatry came strong selection pressures for obvious changes: body size, coloration, and ear shape diverged in the *bimaculatus* line, *sensu stricto*, and the *wattsi* stock. Also at this time, *marmoratus* stock invaded the Marie Galante Bank; changes here are trivial ones of size, scale size, and color: the form resulting is still regarded as conspecific with *marmoratus*.

The final stage 5 returned a lineage to the St. Kitts Bank as *bimaculatus* proper, and colonization of Redonda by this same stock occurred. St. Kitts Bank *wattsi* invaded the Anguilla Bank to establish sympatry with *gingivinus*. The tiny Sombrero Bank acquired *gingivinus*, and Les Iles des Saintes were colonized by *marmoratus*. If one uses degree of subsequent differentiation as a guide, that order is reversed, and Sombrero has been the last colonized; in fact, *gingivinus* may have arrived on Sombrero by human transport. None of the changes occurring at this stage involve more than body size (average), scale size, or color. Thus, *Anolis nubilus* resembles its *bimaculatus* ancestor in such basic features as ear shape, but is innovative especially in color. The other populations, similarly, are races distinguished by color or scale size (or both) or, like Sombrero *gingivinus*, not distinguished at all.

The *Anolis* of the *roquet* group are simpler (Fig. 14). The group originated as an autochthon on St. Lucia, and had undistinguished sublabial scales. At stage 1, St. Vincent was colonized, and the *griseus* stock developed some ventral keeling.

At stage 2 the primitive St. Lucian stock

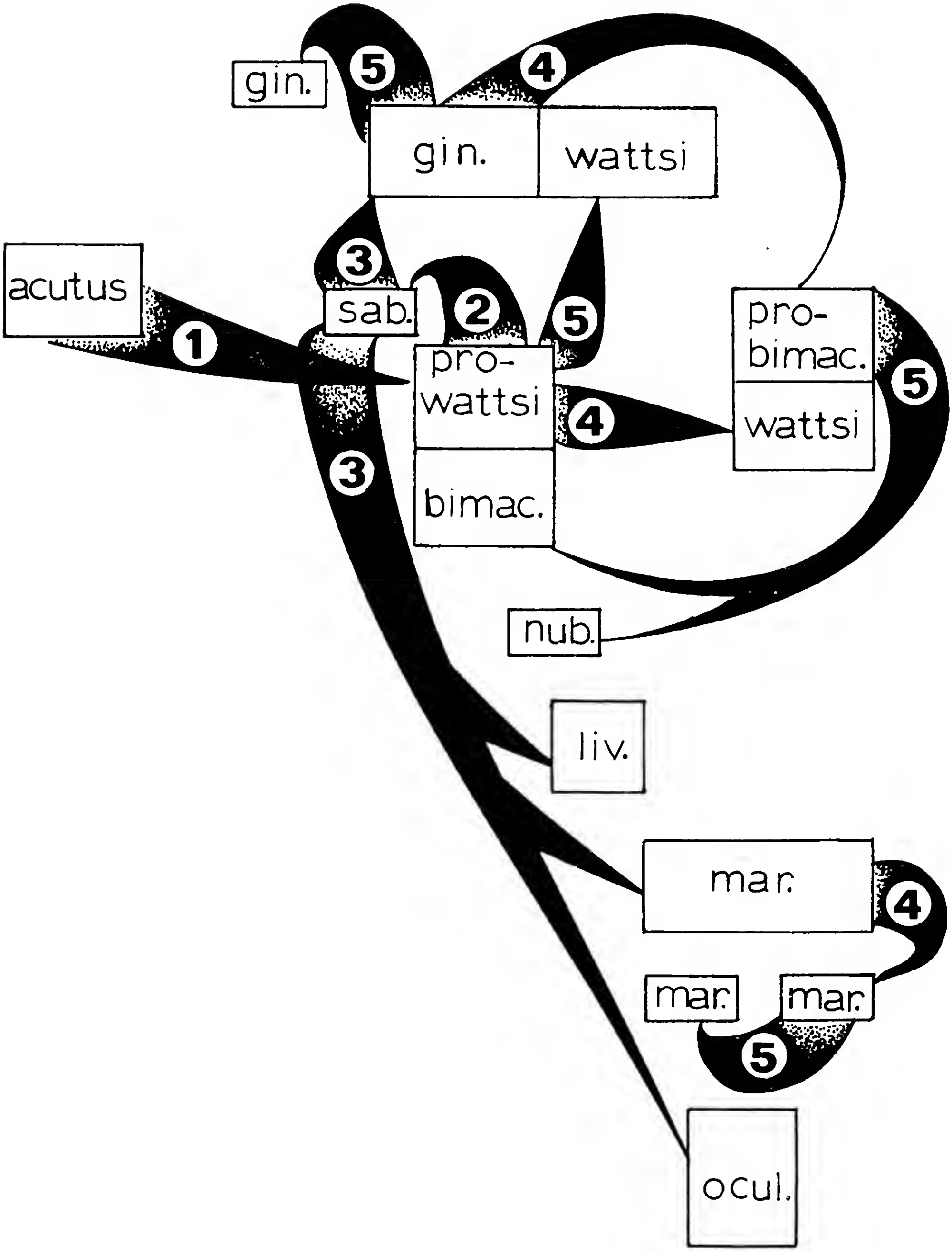

Figure 13. A hypothetical, diagrammatic scheme of the evolution and zoogeography of the species of Lesser Antillean *Anolis* of the *bimaculatus* group. Boxes represent banks; divisions within boxes represent species, not islands. Numbers indicate chronology of invasions: 1, the earliest; 5, the latest over-water colonizations; post-Colombian introductions (*A. b. leachi* to Bermuda; *A. w. wattsi* to St. Lucia) are not indicated. The same number indicates only approximate contemporaneousness: a more refined breakdown is possible. See text.

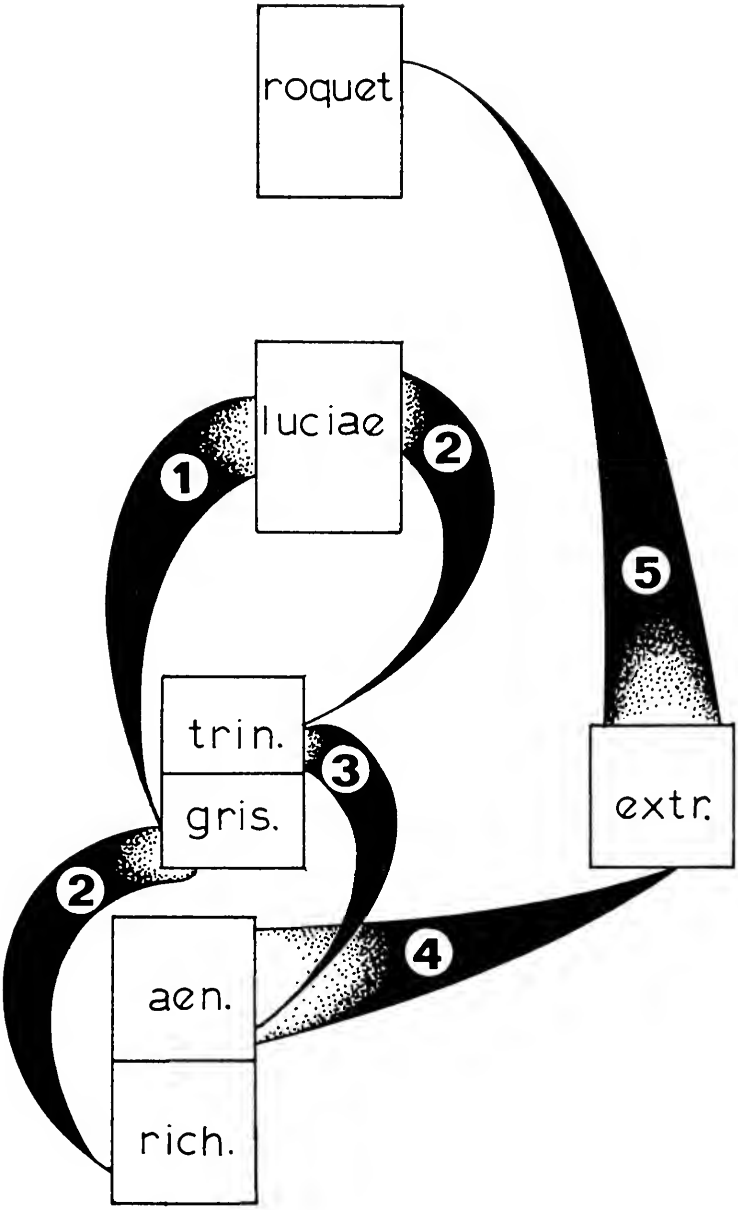

Figure 14. A hypothetical, diagrammatic scheme of the evolution of the Lesser Antillean *Anolis* of the *roquet* group; the general plan is as in Fig. 13. Extralimital colonizations (*A. luciae* stock to Bonaire and Blanquilla; *A. richardi* to Tobago) have been omitted. Post-Colombian introductions (*A. trinitatis* to Trinidad; *A. aeneus* to Trinidad and Guyana; *A. extremus* to St. Lucia) are not indicated. See text.

reinvaded St. Vincent, to give rise to *trinitatis*, a species retaining smooth ventrals. Also at this stage, *griseus* stock colonized the Grenada Bank, giving rise to *richardi*, a species continuing the trend towards ventral keeling.

Stage 3 saw a second invasion of the Grenada Bank: this time by *trinitatis* that subsequently developed the *aeneus* karyotype of $2n = 34$. The axilla remained unpigmented.

At stage 4 *aeneus* stock reached Barbados, and the resultant *extremus* developed the dark axilla. Probably at this stage, also, the *luciae* stock, with its peculiarly enlarged sublabials well in process of development, invaded far westward of the ancestral homeland: to Bonaire and Blanquilla (not shown in Fig. 14).

At stage 5 the culminating invasion of Martinique from Barbados was made, and *Anolis roquet* was born. At this or a later date (but almost certainly not by human agency), *richardi* stock reached Tobago (not shown in Fig. 14).

Except for the characters mentioned at each stage above, none of the modifications in *roquet* group evolution has involved characters other than body and scale size, and (principally) coloration. The striking distinctions between, for example, *Anolis richardi*—a giant with a short head, long legs, keeled ventrals, and little sexual dimorphism—and *Anolis aeneus*—a small form of unmodified proportions, with smooth ventrals and strong sexual dimorphism in color and throat-fan size—are attributed by me wholly to character divergence in sympatry on the Grenada Bank.

Evolutionary rates. Evolution may proceed with remarkable rapidity in populations of small size that are well isolated. Although simple, idealistic formulas for generalized biological phenomena are a commonplace today, no one seems yet to have presented such a formula for evolutionary and invasion rates. A classic example of such a simple, idealistic formula is the Hardy-Weinberg equilibrium. This is not a mathematical description of any real phenomenon, but rather an idealized formulation for a generality that never, in fact, does occur in nature: no two alleles are ever selectively neutral or equal, for example. What the formula provides is a readily calculable standard to which real gene frequencies and real frequency changes may be compared. Certainly, this is a most useful formula.

The specific question arises: What minimum number of generations is required for an allele to sweep a population, whose size is stabilized by extrinsic limiting factors (e.g., land area, food supply, etc.), given that its possessors have maximum competitive success (i.e., the rate of sweep is maximal)? I am deeply indebted to Miss P. Beth O'Sullivan, formerly a student of mine in biology, for pointing out the formula that provides the answer.

If $N =$ the number of individuals in a stable population, $X =$ the number of offspring produced per individual, and $G =$ the minimum number of generations required for an allele (appearing initially in one individual) to sweep the population, then: $X^G = N$.

Or, solving for G: $$G = \frac{\log N}{\log X}$$

G may also be taken as the minimum number of generations required for an invader to establish a stable population beginning with a propagule of one (i.e., a fertilized female). In our equation, X would optimally be the maximum number of offspring per individual produced in a lifetime; using the average number of offspring produced in a lifetime tends to increase G, but is more realistic. Thus, G is either the maximum evolutionary rate or the maximum rate of territorial conquest. It is, of course, meaningful to round G up to the nearest whole number.

While there is very little empirical data on values for G, even in artificially selected populations, neither N nor X is especially difficult to determine within pragmatic limits in many natural populations. Therefore, the formula has immediate practical application as a means of accounting for both proposed rates and observed phenomena that might otherwise be difficult to explain.

For example, the population of *Anolis*

gingivinus on Sombrero might be expected to speciate at a visibly rapid rate. In fact, in applying the formula, if there are 100 *Anolis* on the island (a generous estimate), and six offspring are produced per individual in a reproductive lifetime (a low estimate), then the entire population could achieve distinction from its parental stock in only three generations. A generation (or reproductive lifetime) for these *Anolis* is probably about three years; thus, the entire population could be altered in less than a decade.

Considered from this point of view, it is perhaps not so remarkable that the tiny Ilet-à-Kahouanne, in the Guadeloupéen archipelago, has a distinct, endemic form of *Anolis,* despite its proximity and apparent ecological similarity to the mainland, and despite the fact that it has presumably been a separate island less than 10,000 years. There are surely less than 1,000 *Anolis* on this cay, and they presumably reproduce at close to the typical *Anolis* rate. Very rapid evolution is well within reason under these circumstances.

Several people have objected to this formula without, apparently, understanding it. For example, critics are proud to point out that, on the average, only one-half of an individual's offspring, in diploid organisms, will inherit the allele in question. Precisely, but that is *on the average.* The formula describes the maximal situation. It is no less likely that an anole may be the parent of six offspring, all of whom inherit the allele in question, than that a human parent may have six children, all of the same sex. As anyone living in an urban area can attest, this phenomenon occurs with dreary regularity. In any case, one may correct for this average by merely dividing X by two before proceeding.

Another, more amusing criticism is that the formula is invalid because a single allele does not make a species level difference, or even a subspecies. This criticism apparently reflects the belief that genes move through populations by some sort of osmosis, rather than by whole organisms replacing other whole organisms. The maximum speed at which one allele can sweep a population, by individuals—of course—replacing other individuals, is identical to the maximum speed an entire new karyotype and genome can sweep the population. Obviously, since the formula is the same for maximum invasion rate, it applies to whole organisms, whether they be different in one allele or a million.

It bears repeating that this formula, like the Hardy-Weinberg equilibrium, does not describe any real evolutionary event in nature. It is an ideal standard—a limit—which actually evolving populations may approach. Its value, like the value of the Hardy-Weinberg equilibrium, is that real occurrences may be compared to it, once the factual data from nature have been ascertained.

Dichopatric character divergence. When I returned from field collecting in the southern Lesser Antilles in 1964, I attempted to convince E. E. Williams, E. O. Wilson, George Gorman, and other interested persons of the reality of character divergence between presently wholly dichopatric species: *Anolis richardi* and *A. griseus.* The geographic variation in the former, as described above, cannot be explained in terms of ecology and appears to be exactly what one would expect of classical character divergence. It came as something of a surprise to me to find this phenomenon elucidated in detail by Williams (1969), especially as I had not had success in convincing anyone of the reality of the phenomenon previously. Williams, however, attributes the size difference between *Anolis marmoratus ferreus* and its neighbors to dichopatric character divergence (called by Williams, modification by "failed invasions" or "nudge effect"). This size difference, far more trivial* now that it was known to be when Williams wrote,

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* See the new size records for the other subspecies, especially nominate *marmoratus.*

is closely comparable to the size difference between St. Kitts and St. Eustatius *Anolis b. bimaculatus,* for example, and those populations are not even racially distinct. Because *Anolis* all start life small, size is a highly dubious character to employ taxonomically in this group. Its genetic basis is unknown, and it would not serve to identify any but that small percentage of the largest individuals. I have discussed gigantism in Lesser Antillean anoles under "Systematics," above, in some detail.

That *Anolis richardi,* has, though still dichopatric, diverged in characters away from *Anolis griseus,* presumably by means of selection against gametic wastage resulting from failed invasions, seems unassailable on present evidence. I am gratified that my theory has found acceptance even before its best example was described in print.

In conclusion, the taxonomy presented here is for the moment, not for all time. In ten years time *Anolis griseus* may have succeeded in invading islands of the Grenada Bank held weakly, nor not at all, by *Anolis richardi.* At present, the two species are so ecologically similar that, while invasion appears to be frequent, establishment of populations is not yet feasible. On Trinidad, two ecologically similar, previously dichopatric, forms now compete with each other (and, possibly, rare, fertile hybrids between them) for a large and desirable realm; it is too soon to tell which genotype will succeed. On St. Lucia, *Anolis extremus* is expanding despite its closely similar, if primitive, relative *Anolis luciae;* the distantly related (ecologically and morphologically) *Anolis wattsi wattsi* seems barely able to maintain a toe-hold in this land to which it was introduced by man. In the Guadeloupéen archipelago, totally occupied by *Anolis marmoratus,* races as bizarrely distinct as nominate *marmoratus* and *setosus* seem forever doomed to conspecificity by the topography of their island, while dichopatric forms as insipidly similar as *chrysops, ferreus,* and *terraealtae* proceed to speciate with respect to such a seemingly adaptively irrelevant character as the size of their scales.

Anolis wattsi pogus has transformed in forty years, before our very eyes.

The processes that make species are complex and, in the Lesser Antilles, dramatically dynamic; so are the processes that make the Lesser Antilles. These islands and their *Anolis* will repay future study, I have no doubt.

ACKNOWLEDGMENTS

My original entrance into the West Indies in general (1957) and the Lesser Antilles in particular (1958) was sponsored by the late Margaret M. Cary, naturalist and entomologist, of Philadelphia. My continuing work there was supported through sale of specimens to the Philadelphia Zoological Garden in 1958 and 1959; for this I am especially indebted to Dr. Roger Conant. From 1959 through 1963 field work was sustained through purchase of specimens by the Museum of Comparative Zoology, Harvard University; for this I am especially indebted to Dr. Ernest E. Williams. In 1964 and 1965 my work was sponsored by grants from the Evolutionary Biology Committee of Harvard University. My final field work was sponsored in part by the New York Zoological Society; for this I am especially indebted to Dr. H. G. Dowling. Part of that last expedition, and all work done since completion of field work, has been strictly out-of-pocket.

Similarly, Dr. H. G. Dowling, Adjunct Professor, University of Rhode Island, has incurred considerable personal and financial loss, especially in the efforts of borrowing and transporting huge quantities of museum specimens; for this I am genuinely grateful. Dr. Dowling, and Dr. V. H. Hutchison, University of Rhode Island, have read and criticized the manuscript in its entirety. Dr. Albert Schwartz, of Miami, has loaned extensive material from his pri-

vate collections and given invaluable advice. Mr. John Alexander assisted me in the field.

Lastly, and most deeply, I owe my thanks to the people of the Lesser Antilles, who fed me, sheltered me, humored me, saved my life a dozen times, and—most of all—inspired me. It is no small trial to live with a lizard hunter, and I have never been an easy man.

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APPENDIX: PARATYPES OF NEW FORMS

Anolis wattsi schwartzi

NEVIS: MCZ 16213–5; Charlestown: JDL* 187–92; 6 mi. E of Charlestown: MCZ 38375–6; Newcastle: JDL 198, MCZ 64339–44; Golden Rock Estate: ASFS 19563, ASFS 19542–5; White Bay: ASFS 19583–4; Nevis Peak: JDL 210–18. ST. KITTS: MCZ 28696–9; Basseterre: MCZ 75504–13; Godwin's Gut, 2.5 mi. NE Lambert's Estate Yard: JDL 168; S slope Southeast Peak, at head of West Farm Gut, 2000′: JDL 184–6; 1.2 mi. SW Lodge: ASFS 19523–5. ST. EUSTATIUS: MCZ 54708 (+ 1 untagged), MCZ 12334–6, MCZ 16538–43 (+ 1 untagged); Oranjestad: MCZ 75474–83, ASFS 19624–8; 1 mi. NE Oranjestad: ASFS X4659–61; The Quill, upper slopes at crater: ASFS 19597–615; Inside the Crater of the Quill: MCZ 75352–71, MCZ 75494–503; Behind the Mountain: MCZ 75489–93; Boven Bay: MCZ 75484–8.

Anolis wattsi pogus

ST. MARTIN: MCZ 20986; Colombier: MCZ 75798–825, JDL 101–09; Loterie: JDL 115–24; Cul-de-Sac (Dutch portion): JDL 127–36; Grand Fond, Quartier d' Orlean: JDL 152–6. ANGUILLA: MCZ 16596–7.

Anolis roquet summus

MARTINIQUE: Poste Forestiere, Tirage No. 38, Deux Choux, MCZ 81631–42; Deux Choux: MCZ 82486–92, MCZ 82858–61; Habitation Eden: MCZ 66845–7, MCZ 82311–20; Morne des Roseaux: MCZ 82848–57; Vigie de la Calabasse: MCZ 82321–37; Absalon: MCZ 82394–403; Propête: MCZ 82478–85; Montagne Pelée: MCZ 82158–66; SE slope Montagne Pelée, 2700 ft.: ASFS 18787; 5 km N Le Morne Rouge: ASFS 18577; 3 km N Le Morne Rouge: ASFS 18581; 3 km SE Le Morne Rouge: ASFS X466–9; 7 km SE Fond St. Denis: ASFS 18540; 3 km SE Le Morne Rouge: ASFS 18878–98; 4 km S Colson: ASFS 18875–7; 1 km S Colson: ASFS 18878; 4 km SW Ajoupa-Bouillon: ASFS X6621, ASFS 18728.

Anolis roquet majolgris

MARTINIQUE: Fond St. Jacques: MCZ

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* All JDL specimens are now in the MCZ.

81665–74; Derrière Morne: MCZ 82530–9 (+ 3 untagged); Le Lorrain: MCZ 82134–48; 1 km E Le Lorrain: ASFS 18827–30; 3 km SE Le Lorrain: ASFS X6483–92; Ste. Marie: MCZ 82518–29; 4 km N Ste. Marie: ASFS X425–8; 2 km SE Ste. Marie: ASFS X6454–7; 4 km NW Ste. Marie: ASFS 18831; Marigot: MCZ 82505–17.

Anolis roquet zebrilus

MARTINIQUE: Le Carbet: MCZ 81620–29, MCZ 82167–76; Case-Pilote: MCZ 82404–15; 1 km NW Case-Pilote: ASFS 18504–15; 5 km NW Case-Pilote: ASFS X454–61, ASFS 18541–64; Fond Capot: MCZ 66848–55, MCZ 82382–93; Le Trou: MCZ 82427–36; Morne-aux-Boeufs: MCZ 82417–26; 3 km SW Morne Vert: ASFS 18669–71; 2 km S St. Pierre: ASFS 18662–4.

Anolis roquet caracoli

MARTINIQUE: Pointe Caracoli: MCZ 81602–7; Anciens Cachots, Baie du Tresor: MCZ 81608–10; Lighthouse, Presqu'île de la Caravelle: MCZ 82280–9; Chateau Dubuc: MCZ 66924–6; 3 km NE Tartane: ASFS 18767–81, ASFS 1816–7, ASFS X443–7.

Anolis roquet salinei

MARTINIQUE: Pointe des Salines: MCZ 81643–52, MCZ 82187–96; Grande Anse des Salines: ASFS X6396–7; Ste. Anne: MCZ 82177–86; 1/2 km SE Ste. Anne: ASFS 18675–6, ASFS 18680–7; 1 km NE Ste. Anne: ASFS 18688–702; 1/2 km N Ste. Anne: ASFS X448–53; 3 km SE Le Marin: ASFS 18678–9; Pacquemar: MCZ 82722–31. ILET CHEVALIER: MCZ 81658–63. ILET CABRITS: 81653–7.

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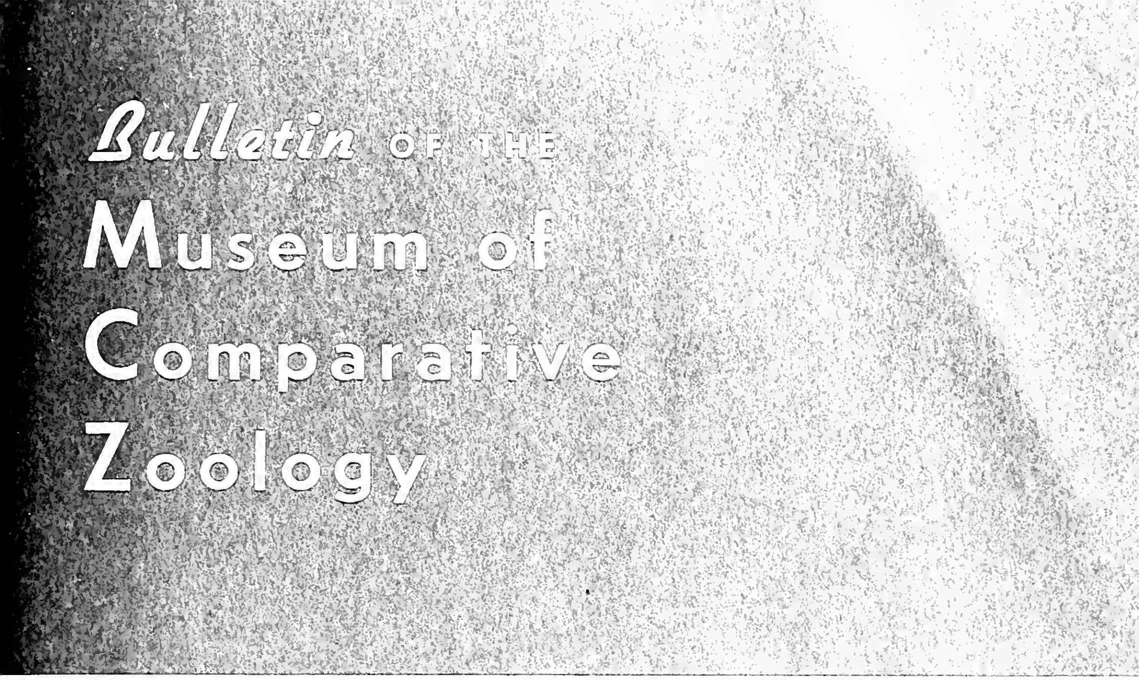
Addendum to

THE ANOLES (SAURIA, IGUANIDAE) OF THE LESSER ANTILLES

JAMES D. LAZELL, JR.

Bulletin of the Museum of Comparative Zoology
Volume 143, Number 1, 15 February 1972
Page 104, Column 2, Line 36

Fieldwork for the paper was partly supported by NSF grant No. G 19727 to R. C. Rollins. Publication was supported by NSF grant B 019801X to Ernest E. Williams.



Bulletin OF THE
Museum of
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Ecology of Fishes in the Amazon and Congo Basins

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PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN 1863–
BREVIORA 1952–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
OCCASIONAL PAPERS ON MOLLUSKS, 1945–

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ECOLOGY OF FISHES IN THE AMAZON AND CONGO BASINS

TYSON R. ROBERTS

Abstract. Some relationships between the great diversity of fishes and physical and biological aspects of the environment in the Amazon and Congo basins are discussed. Aspects of physical environment considered are rainfall regimes; stabilizing influence of forests; seasonal fluctuations in water level; white water, clear water, and black water; relative accessibility of Amazon and Congo basins to marine fishes; tidal conditions in the lower Amazon; shoreline and islands; river anastomoses and connections with adjacent basins; stream captures; unique or peculiar biotypes; causes of massive mortality of fishes. The main adaptive significance of parental care in Amazon and Congo fishes is evidently related to reproduction in deoxygenated waters. The following topics are considered under biological interactions: fishes with brilliant coloration or conspicuous markings; association of similarly colored species of fishes in mixed schools; fishes of minute size; responses to predation; and partitioning of food resources. About one third of the paper is devoted to discussion of trophic adaptations and feeding habits. The topics considered are predatory fishes; scale-eating characoids; fin-eating characoids; feeding habits of "parasitic" trichomycterid catfishes; parallelism in feeding habits of "weakly electrogenic" fishes in the Amazon and Congo basins; plankton-feeding fishes; deposit feeders; and feeding habits of characins and other fishes in Amazonian rainforest streams.

INTRODUCTION

An overwhelming proportion of the species of fishes in continental fresh waters are primary freshwater forms. This means that they are unable to live in salt water, and have had a long history separate from that of marine fishes. The great majority of these freshwater fishes are members of a single group, the Ostariophysi. In contrast to tropical marine shore fishes, which have had only one principal center of radiation—the Indo-Pacific—ostariophysans in Africa, South America, and Eurasia have radiated largely in isolation from one another. Asia and Africa, of course, share many ostariophysan elements. There is some indication that the South American and older African ostariophysan elements had a common origin. The formation of the Amazon basin provided the opportunity for a remarkable radiation of Ostariophysi. The Amazon and Congo basins have more kinds of fishes than any other river basins in the world, and both exhibit a high degree of endemism.

One of the principal reasons tropical fish faunas are richer than temperate ones is that they have not been as adversely affected by glaciation. Pleistocene glaciation probably caused extinction or withdrawal of marine shore fishes in the higher latitudes, especially in the North Atlantic (Briggs, 1970). It is unlikely that fishes live more than a few miles inward under the ice caps. Freshwater fishes in most of North America and northern Eurasia were wiped out by Pleistocene glaciation. Western Europe now has a depauperate fish fauna of only about 60 species, all or almost all derived from stocks that populated the area in postglacial times.

It may be well to express here my suspicion that the richness of the Congo and Amazon fish faunas is not necessarily ancient. Fishes have undergone considerable diversification, with great increase in the number of species, in lakes less than five million years old. I do not believe that lakes represent the only ecological situation in which explosive adaptive radiations of fishes have occurred. It is conceivable that the present Amazonian fish fauna, with its large number of species, is the product of only a few million years of evolution from an original stock of two or three hundred founder species. Some of the founders, of course, would represent groups of considerable antiquity.

Draining two and a quarter million square miles, the Amazon basin is the largest river basin in the world. Its mouth discharges an average of three to four million cubic feet of water per second. The Congo, discharging 1.4×10^6 cubic feet per second from slightly over one and a half million square miles, is the second largest. The vast area of these basins, with abundant water and varied habitats, undoubtedly contributes to the large number of fish species in them. Habitats such as streams with high gradients or streams draining dry ground (igarapés de terra firma) are sometimes separated by hundreds of miles. Meandering creates a regular succession of habitats in the main courses of the big rivers. The high percentage of the basins at base level, along with the relatively stable existence of so much aquatic habitat, favors the existence of very large numbers of individuals, which in turn is conducive to the existence of large numbers of species (Preston, 1962).

As of 1967 (the last year for which the Zoological Record has been issued) approximately 1300 species of fishes had been recorded from the Amazon and 560 from the Congo (including the Lualaba River but not lakes Bangweolu and Moeru). The Mississippi basin, in comparison, with an area (1,244,000 square miles) almost as large as that of the Congo basin, has only 250 species. It is unlikely that many species remain unrecorded in the relatively well-studied Mississippi, but the numbers known from the Amazon and Congo will undoubtedly increase considerably as systematic studies continue.

The limnology, seasonal changes and some biological aspects of the rivers, lagos, flooded forest (igapó) and streams (igarapés) that constitute the main habitats of Amazon fishes are described by Sioli (1964, 1967) and Fittkau (1964, 1967). The ecology of fish habitats in the cuvette centrale of the Congo basin, similar in many respects to that in the Amazon, is described by Gosse (1963) and Matthes (1964). McConnell (1964) described the ecological groupings of fishes and effects of the seasonal cycle on the fishes in the Rupununi savanna of British Guiana. Many of her remarks are applicable to the Amazon basin, especially to the savanna parts of it. Most, if not all, of the species in the Rupununi are present in the Amazon. McConnell (1969) reviewed some factors contributing to speciation in tropical freshwater fishes, and many of her remarks apply indirectly or directly to fishes in the Amazon and Congo basins. Knöppel (1970) reported in detail on the stomach contents of a large number of fish species from small rain forest streams near Manaus. Myers (1947, 1949a) gave a general account of Amazonian fishes and their ecology.

The main part of this paper is divided into two sections. The first section deals with the interactions of fishes and physical aspects of environment in the Amazon and Congo basins, the second section with biological interactions among fishes in the Amazon and Congo basins. The rest of this introduction provides a brief sketch of the main groups of ostariophysans and other fishes under consideration. Readers familiar with these groups may turn directly to the main part of the paper if they wish. In drafts of this paper I tended to include extraneous notes about species occurrence, etc., which might distract readers interested mainly in the discussion of ecology and adaptations. These notes, indicated by arabic numerals in the text, are given at the end of the paper. They are of concern primarily to systematists and zoogeographers.

Ostariophysi—the Predominant Fishes in Both Basins

In the Amazon 43 percent of the fishes are characoids, 39 percent siluroids, and 3 percent gymnotoids. In the Congo 15 percent are characoids, 23 percent siluroids, and 16 percent cyprinoids. All of these fishes belong to the order Ostariophysi, which thus comprises 85 percent of the Amazon's and 54 percent of the Congo's fish fauna. Ostariophysi differ from all other fishes in the manner in which some of the neural arches and ribs of the first four vertebrae are modified into an apparatus, the Weberian apparatus, which conducts vibrations from the swim bladder to the inner ear. There is no precise understanding of how the Weberian apparatus affects sound (and pressure?) perception, nor is much known about the effects of sound on the behavior of ostariophysans in nature. It is generally agreed, however, that they are "acoustic specialists," and that their worldwide predominance in fresh waters is somehow linked with the Weberian apparatus. Experimental work with various ostariophysans indicates that their auditory sensitivity and range is greater than in many other fishes. Of considerable interest is whether they have directional hearing, i. e., can localize the source of a sound by means of their auditory apparatus. Most fishes apparently have nondirectional hearing, but directional hearing evidently occurs in several groups (see Moulton and Dixon, 1967: 195). The only freshwater fishes thought to have directional hearing are Ostariophysi and perhaps mormyroids. Kleerekoper and Chagnon (1954) and Delco (1960) reported directional hearing in three species of North American minnows. Whatever the nature of its role in perception, it seems highly likely the Weberian apparatus has increased the opportunities for interactions between fish species.

Characoids. Characoids or characins are mostly laterally-compressed, open-water fishes, active in the daytime, many of them silvery or iridescent. They usually have jaw teeth, often of a highly complex nature (Roberts, 1967), and invariably lack barbels. With few exceptions, they are not known to produce biologically significant sounds (almost all fishes produce noises incidental to feeding and locomotion). Of the large groups of fishes inhabiting the earth's fresh waters, characoids (as a group) exhibit the least tolerance for salt or brackish water. They occur only in Africa and Central and South America. Their presence in Central America undoubtedly is the result of recent invasion, and it is unreasonable to believe that they could have reached Africa and South America by way of Europe and North America without leaving the least trace of their passage (Myers, 1966). The only fossils identified with certainty as characins are African, or South or Central American (Weitzman, 1960). In the light of evidence for Continental Drift and for characoid antiquity (Greenwood et al., 1966; Roberts, 1969) it is reasonable to think that characins were present in South America before it separated fully from Africa.

Gymnotoids. Gymnotoids, the so-called electric eels, all have specialized electrogenic and electrosensory organs. The quality of the electric discharges is characteristic of each species. The gymnotoid that has received the most scientific attention, the famous electric eel (*Electrophorus electricus* Linnaeus) studied by Alexander von Humboldt, Faraday, and others, has a very powerful discharge. The discharges of other gymnotoids are too weak for us to sense without the help of instruments and have only recently come to our attention. We are just beginning to appreciate the roles played by gymnotoid electric organs in object location and in intra- and interspecific behavior. Many of the species have specialized trophic structures, and at least some are highly active at night, hiding or even burying in sand during the day. Their mode of swimming is peculiar (Lissmann, 1958; Greenwood et al., 1966: 383–384). The geographical restriction of gymnotoids to part of South and Central America indicates that the group had a later origin. Their greatest diversity (18 genera and 35 species) is in the Amazon basin. They are almost as well represented as this in the Guianas and the Orinoco basin. Outside these areas their diversity declines markedly. A few species, belonging to wide-ranging genera, occur north as far as southern Central America (a single species reaching Guatemala) and south to the Plata basin. They are almost absent west of the Andes (a single wide-ranging species reaching coastal Ecuador), and are absent in the numerous Atlantic coast drainages between the mouths of the Rio São Francisco and the Rio Paraíba. Gymnotoids were derived from characoids.

Siluroids. Siluroids or catfishes typically are denser-than-water, bottom-dwelling fishes with flattened bellies and nocturnal habits. The dentition usually consists of numerous simple conical elements in bands of varying thickness. The barbels, usually two or three pairs, sometimes (as in Bagridae) four pairs, are almost invariably present (one exception in South America, none in Africa) and serve as tactile and gustatory organs. In the African Mochokidae (represented by 37 species in the Congo) the barbels are highly branched. In contrast to characins, catfishes are noisy. They produce sound from various anatomical structures; the most familiar catfish sounds are due to stridulation between pectoral spine and girdle. Of the 31 families of catfishes recognized by Greenwood et al. (1966), eight occur in Africa (three of them endemic) and 14 in South and Central America (all but Ariidae endemic). Catfishes are more widely distributed geographically than any other ostariophysans, and their inter- and intrafamilial relationships are not well understood. Two of the living families (Ariidae and Plotosidae) are predominantly marine. Representatives of a South American endemic family, the Aspredinidae, occur along the Guiana coast (Myers, 1960a). Several people are working on the morphology and classification of catfishes on a worldwide basis, and much new information relevant to their zoogeographic history will be available soon. The startling diversity of endemic catfishes in South America and the presence in southern South America of the only two species in the family Diplomystidae, the most primitive of living catfishes, indicate that catfishes, like characoids, were in South America long ago, certainly in the Mesozoic.

Cyprinoids. Minnows, the only group of cyprinoids in the Congo basin, more or less resemble characins except they have protrusible jaws and frequently one or two pairs of small barbels, while jaw teeth and adipose fin invariably are absent (most characins and catfishes have a rayless adipose fin behind the dorsal fin). The lower pharyngeal teeth, however, are highly modified and despite their lack of jaw teeth minnows exhibit considerable diversification in feeding structures, as shown by Matthes (1963) for African forms. The cyprinoids are perhaps more diverse in North America and certainly much more diverse in Asia than they are in Africa. It is generally thought that they originated in Asia. However this may be, the number of minnow species in Africa is very high, especially in Ethiopia, Southern Africa, and in the rockier headwaters of many of the bigger tropical rivers, including the Congo.

Non-ostariophysan Primary and Secondary Freshwater Fishes

South America is not rich in the number of major groups of freshwater fishes it harbors. The only primary freshwater fishes in South America other than Ostariophysi are a genus of Lepidosirenidae, two genera of Osteoglossidae, and two genera of Nandidae. The secondary freshwater fishes (*sensu* Myers, 1949b) consist of Cichlidae, Cyprinodontidae, Poeciliidae, Galaxiidae, and Percichthyidae. All of these families of primary and secondary fishes excepting Galaxiidae and Percichthyidae are present in the Amazon basin, and all of them excepting Poeciliidae and Percichthyidae also occur in Africa.

The primary and secondary freshwater fish fauna of Africa is much more complex. It can be broken down into three main categories: 1) groups shared with South America—ostariophysans excluding Cyprinidae, Lepidosirenidae, Osteoglossidae, Nandidae, Cichlidae, Cyprinodontidae, and Galaxiidae; 2) groups shared with Asia, and which probably originated in Asia—perhaps complicated by the fact that they may have been centered in India when India was closer to Africa than to Asia—Notopteridae, Cyprinidae, Mastacembelidae, Anabantidae, and Ophiocephalidae or Channidae; and 3) an unparalleled assemblage of archaic primary freshwater forms known only from Africa—Polypteridae, Denticipitidae, Pantodontidae, Phractolaemidae, Kneriidae, Mormyridae, and Gymnarchidae. Practically all of the families reach their greatest diversity in Africa in the Congo basin, excepting Nandidae, Denticipitidae, and Gymnarchidae, which are unknown from there. The weakly electrogenic mormyroid fishes parallel gymnotoids in many ways (see pp. 140–141).

INTERRELATIONS BETWEEN FISHES AND THE PHYSICAL ENVIRONMENT IN THE CONGO AND AMAZON BASINS

Since the Amazon and Congo basins straddle the equator, they have two rainfall regimes. Most of the Amazon basin lies south of the equator, and in this portion the rainy season is generally from December through April or May. During the rest of the year the rain decreases somewhat. In virtually the entire Rio Branco basin, the Rio Negro basin north of Uaupés, and most of Colombian Amazon, on the other hand, the rainy season is generally from March to November or December, or from May through August, and the dry season (at least in the savanna area of the Rio Branco) is somewhat more pronounced. In the Congo basin the great Ubanghi River from north of the equator and the smaller but numerous southern tributaries are in high water at opposite times of the year; thus the maximum and minimum average rates of flow of 75,000 and 50,000 cubic meters per second at Kinshasa are close. The water level in the Amazon River is mainly determined by contributions from southern tributaries and run-off from melting snow in the Andes. Snow melts during much of the year, and rainy seasons are prolonged (it may rain a lot during the so-called dry season). The bulk of these contributions comes at somewhat different times of the year. The relative difference between maximum and minimum water levels in the lower courses of the Amazon and Congo rivers, although considerable, is less than in any other river in the world. The absence of a period of severe desiccation has no doubt enhanced the evolution of rich faunal diversity.

Forests and relative environmental stability. Today forests cover a large part of the Congo and Amazon basins but this has not always been so. During much of the Recent and Pleistocene periods the forests retreated and advanced in response to cyclical climatic changes. Their present range lies somewhere between the greatest and least extents of the past. In the Amazon basin much of Brazil's Roraima Territory is "campo" or savanna. Great tongues of campo extend between the southern tributaries of the Middle and Lower Amazon. Montane forests and gallery forests along the great tributaries and the main Congo and Amazon rivers were the portions of forest that would have suffered least from long dry periods. Certainly some montane forests persisted, and perhaps the main gallery forests never disappeared. The forests undoubtedly mitigated the adverse effects of dry periods on the fish fauna. On a shorter time scale, they contribute greatly to over-all wetness and temperature stability in the basins. Forest soils and swamps retain a vast quantity of water, which is relinquished throughout the year. Transpiration keeps the air laden with moisture and lengthens the rainy season.

Seasonal fluctuations in water level. Seasonal fluctuations in water level have profound effects on feeding, reproduction and dispersal of fishes (Matthes, 1964; McConnell, 1964). During high water more food is available, and many fishes move into the flooded lands to feed and to reproduce. Growth is rapid and fishes are widely dispersed. As the waters go down, food becomes scarcer for most fishes except predators. Losses to predation are greatest during low water, when fishes are least dispersed. The effects, however, are not nearly so great as in savanna rivers such as the Zambesi, in which the flow during the marked dry season is a small fraction of that during flood time, and massive fish mortalities are an annual event except in unusually wet years. The seasonal fluctuations mean that certain habitats exist only part of the time, and this must play a very important role in fish distribution. It should also be noted that these cyclic changes are more predictable than some other kinds of variability (especially in the temperate zones), and allow adaptive responses to evolve, thus increasing the effective environmental heterogeneity—and increasing rather than decreasing the species diversity.

The forest streams may be flooded in the wet season or go down so much in the dry season that the fishes must either leave or accommodate to great changes. Such constantly changing conditions alter drastically the local faunal composition. During any intensive collecting in the Amazon or Congo, a good proportion of species obtained in a given locale are likely to be either recently arrived or in the process of moving away from habitats that became unfavorable. Thus a rotenone collection in an igarapé may yield 70 or 80 species, but only a third or less will be represented by fair numbers of specimens. Even when such a collection comprises one or two thousand specimens from a stretch of igarapé one mile long, it frequently happens that a dozen or more species are represented by a single specimen. The indications are that most of these came from populations established elsewhere, that their presence is largely due to chance, and that they will soon disappear unless additional individuals enter the igarapé. However, the species composition of adjacent igarapés that superficially look alike may differ markedly. Occasionally an igarapé has numbers of a species that is absent or represented by a single specimen in collections from other igarapés nearby. Investigation of the physical and biotic components might provide an explanation in some instances, but I suspect that, in addition to subtle differences in environment, chance plays a major role. The fact that many species are represented by widely separated populations over the entire basins probably contributes to evolution and maintenance of species diversity. Certainly it is difficult to conceive of the rapid extinction resulting from biotic factors of species dispersed in so broad a manner. Furthermore, the pattern suggests a favorable model for allopatric speciation.

Physical and biological nature of white water, clear water, and black water rivers. The big rivers of the Amazon basin are of three main types: white water, clear water, and black water. These types are not absolute. Some rivers are intermediate between white and clear, others between clear and black; some rivers may be clear water in the dry season and white water in the rainy season. However, the main Amazon river (known as the Solimões above Manaus) is white water year round, and its largest tributary, the Rio Negro, is black water year round. White water (its color actually tan or café-au-lait) is due to suspended earth; the white water rivers arise in the Andes and are constantly eroding the alluvium from their steep banks. Proceeding up the Solimões from Manaus one is impressed by evidence of landslides (terras caídas) from the steeper banks, some of which must release tens of thousands of tons of earth into the river. The resulting white waters are relatively rich in salts compared with other Amazonian waters (Gibbs, 1970). Because of the silt, they are opaque, and light does not penetrate more than two or three feet, usually much less. Thus they do not support photosynthesizing plant life. The *p*H of the white waters ranges from 6.2 to 7.2 (in part from Sioli, 1967: 31–34).

Seen from a distance or from the air, the black water rivers appear quite black. In a glass the water is the color of weak tea and is quite clear. The black water rivers of Amazonas apparently originate in lowland areas with bleached, sandy podsol soils (Klinge, 1967). These soils, and perhaps decaying organic matter in the flooded forests, provide humic coloring substances which give the water its characteristic tint. Light is effectively cut off about three to six feet below the surface. The mineral content is precipitation dominated (Gibbs, 1970) and so low that the water may be considered "distilled water slightly polluted with organic compounds." Virtually no primary productivity occurs in black water rivers. Furthermore, the black waters are highly acid, with *p*H ranging from 3.8 to 4.9 (Sioli, 1967: 34).

The characteristics of the basins and the water chemistry play profound roles in determining the distribution and abundance of animals in the Amazon basin. In the evenings an incredible variety of moths and dipterous insects, including numerous species of mosquitoes, are commonly attracted to boats plying a white water river. In the daytime one is liable to be bitten by hordes of Simuliidae. On the other hand, during 25 days and nights spent on the Rio Negro (above Manaus) at widely different times of the year, I failed to encounter a single biting insect (to my immense relief!) and noted that even moths were relatively scarce. It may be that the extremely acid conditions of the black waters in the Rio Negro are lethal for most aquatic insects. Perhaps largely because of the absence of insects, terrestrial animals such as frogs and lizards (relatively abundant along the Solimões) were seldom encountered in my ramblings along the shore. Fish populations are probably lower here than elsewhere, although there is no data to support this. In the black water and white water rivers most of the food available for fishes must come from terrestrial sources (Marlier, 1967) or floating vegetation. There is probably very little food for nonpredaceous fishes in the main Rio Negro, which presumably find most of their food in habitats peripheral to the main stream, especially during periods of high water. In the white water rivers earth slides probably bring considerable amounts of plants and lower animal life that serve as food directly into the main channels, and production along the main watercourse by floating vegetation probably is also greater. Men who have learned to fish in the Rio Negro are sometimes conceded to be the best fishermen in Amazonas. Some black water rivers are known as "rios de fome" because there is little food to support the population. Extremely little human habitation is found along the main Rio Negro between Manaus and the mouth of the Rio Branco. The only towns are small and usually located near the mouths of clear or white water affluents. Along the Solimões River habitations occur every quarter- or half-mile over long stretches. The "moradores" usually have flower and vegetable gardens and small feijão plantations. The Solimões has large towns and cities, but these are usually some distance up black water rivers or just downstream from a large black water outlet, which provides a degree of protection from insects.

The clear water rivers are more diverse in origin and possess a broader range of *p*H values—from 4.5 to 7.8—than black and white water rivers, indicating that they are chemically (and biologically) a heterogeneous assemblage. The only character they share is the relative lack of organic coloring materials and suspended matter (Sioli, 1967: 33–34).

In the Congo basin the rivers can be similarly classified according to their waters. The southern tributaries are mostly black water, and during part of the year the main Congo River is a deep-tinted brown, approaching black water. The Ubanghi River is white, however, when it passes its flood waters to the Congo River. At this time contributions from the southern black water tributaries are at their lowest. The Ubanghi is the only true white water tributary in the Congo basin; the rest are either black water or clear water. The main Congo River never becomes sufficiently laden with silt to be considered a white water river. In the Congo River, as in the Amazon, food chains must originate largely on the land. The relatively recent introduction and widespread establishment of *Eichhornia* in the Congo basin must have greatly increased the relative contribution of floating plants to food available in the main river courses. There are many varieties of floating plants in the Amazon basin, including *Eichhornia*, but these are little in evidence along the main river channels. Along much of the Congo River *Eichhornia* is extremely abundant. Its roots offer haven and presumably food to many small species of fishes and to the young of many larger species of catfishes, characins, and mormyroids in Stanley Pool (personal observation).

Relative accessibility of Amazon and Congo basins to marine fishes. Most of the African continent is relatively high above sea level, and marine fishes ascending rivers usually do not get very far inland (Marlier, 1967). Most fishes in the cuvette centrale of the Congo are primary freshwater fishes (*sensu* Myers, 1949b). Two families, Cyprinodontidae and Cichlidae, are secondary freshwater fishes that have undergone extensive radiations in fresh water. The remaining secondary freshwater fishes in the cuvette centrale belong to four families—Clupeidae, Eleotridae, Centropomidae, and Tetraodontidae—which are better represented in salt water than in fresh water. The particular groups involved, however, entered the fresh waters of Africa a very long time ago, and must have invaded the Congo basin via other river systems instead of directly from the sea. The clupeids are members of the Pellonulinae, also present in fresh water in tropical Asia.[1] All but two or three of the eleven or twelve species of Pellonulinae in the Congo basin appear to be endemic. The Eleotridae are represented by a single small species, *Kribia nana*. This species, or one closely related to it, is found in many rivers in West Africa. The genus is known only from fresh water. The Centropomidae are represented by *Lates niloticus*, present in most of the bigger rivers of tropical Africa. Finally, the Tetraodontidae (with two species of *Tetraodon* in African rivers outside the Congo basin) are represented in the Congo by four species, three of them endemic. Not a single sporadic marine invader has been reliably recorded from the Congo River above the lower rapids.[2]

In contrast to the Congo, the Amazon basin is relatively open to invaders from the sea. Fourteen families of fishes that are predominantly marine have species widely distributed in the Amazon basin. The elasmobranch families Carcharhinidae and Pristidae, each with a single species in the Amazon, are probably sporadic invaders.[3] Clupeidae (herrings) are represented by five species, at least two endemic; Engraulidae (anchovies) by a dozen species, about half endemic; Belonidae (needlefishes) by three species, two endemic; Hemiramphidae (half-beaks) by a single species, *Hyporamphus brederi* (Fernandez-Yepez) (Collette, personal communication); Mugilidae (mullets) by a single species of *Mugil;* Synbranchidae by *Synbranchus marmoratus* (widespread in streams and swamps throughout most of tropical Central and South America); Sciaenidae (croakers or drums) by about ten species, several endemic; Eleotridae by two tiny species of the genus *Microphilypnus* Myers (1927), both endemic; Achiridae (flatfishes) by about nine species, most endemic; Tetraodontidae (puffers) by a single species, *Colomesus psittacus;* and, Batrachoididae (toad-fishes) by an endemic species, *Thalassophryne amazonica* (Collette, 1966a). Thus slightly more than 50 species of fishes belonging to predominantly marine families are widespread in the Amazon basin. About half of them are endemic species. In most instances the ancestral populations probably invaded the Amazon basin directly from the sea. In addition to these 50, many more marine species have been recorded from the lowermost Amazon, especially from Pará. As noted by Marlier (1967) the great extension of brackish waters in the mouth of the Amazon and along the coast has undoubtedly facilitated invasion of the Amazon basin by marine forms. In like manner such conditions must have favored the marine invasion by catfishes of the subfamily Aspredininae, which belong to a family (Aspredinidae) otherwise found only in fresh water. The three genera and four species of Aspredininae are restricted to the lowland, muddy coast of Guiana and Amazonia, occurring in the sea, in brackish waters, and in the estuaries and tidal portions of rivers, including the Amazon delta (Myers, 1960a).

Tidal conditions in the lower Amazon and effect on fish life. Many marine and estuarine fishes ascend the lower courses of tropical rivers with the rising tide. Fishes apt to do this in the lower Amazon delta area include species of Centropomidae, Mugilidae, Belonidae, Sciaenidae, Pomadasyidae, Lutjanidae, Ariidae, Atherinidae, Carangidae, Clupeidae, Engraulidae, and Dasyatidae. Tidal bores (pororóca) occur in much of the delta area (Branner, 1884), and the highest tides are said to exert their influence as far upriver as Santarem. The periodic rise in water level (occurring with great rapidity and force in certain areas) inundates vast areas, submerging terrestrial plants and insects upon which fishes then feed. This regular addition of terrestrial food plus the higher titre of nutrients resulting from mixing with sea water, probably make the mouth and delta the most productive area in the Amazon basin. The variation in the seasonal availability of food is probably least marked here. Schwassmann (1967: 214) reported that schools of *Anableps* near Pará moved close to shore with every rising tide and thought this was correlated with increased feeding on shore insects floated off by the rising water.

Shoreline and islands. The importance of shoreline and islands in the ecology of fishes in the Middle Congo River is stressed by Gosse (1963: 124–138). The islands so characteristic of the Middle Congo River vastly augment the amount of shoreline. It is interesting to note the important role in the development of these islands played by a succession of plant types, from the aquatic grasses such as *Echinochloa* and *Vossia* (les prairies flottantes) which stabilize shifting sand banks to the mature forest on the oldest islands which are not inundated by normal floods. The amount of food available from terrestrial sources, of course, is proportional to the amount of shoreline. In addition, stabler bottom, resulting from slower currents along shore, and clearer water permit greater development of planktonic and benthic plants and animals. Higher plants fringing the shores provide shelter from currents and predators as well as food for the adults and young of many species. Calm and deep places downstream from sand banks and islands and backwaters in which mud and organic detritus accumulate provide particularly suitable habitats for bottom-feeding fishes such as *Labeo, Citharinus,* and *Tilapia.* During the period of high water many of the islands are partially flooded, thus adding to the inundated areas accessible to fishes for feeding and reproduction. In a given section of the Middle Congo River fish productivity probably bears a strong relationship to the number and size of the islands present in it.

The contributions of islands and shoreline outlined above for the Middle Congo also apply to the Amazon. In the evening many small fish (especially characins) move close to the shoreline in order to feed and larger fish including predators and catfishes probably come inshore from deeper waters. In the daytime Curimatidae and Hemiodontidae are to be found feeding over sandy bottom near shore. Beginning about 40 miles above its confluence with the Solimões and continuing some 350 miles upstream, the Rio Negro exhibits a multitude of islands that no other river in the world can rival. For this entire distance there are very few stretches without islands, and such stretches are never more than five miles long. Often there are two or three big islands abreast of each other, and a straight line across the Rio Negro where it attains its greatest widths (15–18 miles) may intersect a dozen islands. High shoreline coefficient, however, cannot make up for the unproductivity of the waters of the Rio Negro, the shores of which must be among the least productive in Amazonas.

River anastomoses and stream captures. "River anastomoses" or interconnections occur in the interior of the Congo basin as well as in the Amazon. Thus the Congo River above Coquilhatville has a series of connections (Chenal de Bosesela, Chenal de Nyoi, etc.) with the Giri River (a large tributary of the Ubanghi), and some of these have connections between themselves. What is probably the greatest complex of river anastomoses in the world occurs between the Solimões and the Rio Japurá in the vicinity of Fonte Boa (Furo Boia, Furo Auati-Paraná), portions of which were explored by the EPA expedition in 1968 (see Acknowledgements). The Auati-Paraná, a navigable furo connecting the Japurá and Solimões and having numerous connections with smaller tributaries, is 125 miles long. Such anastomoses perhaps play a role similar to that of islands in making the flooded forest more accessible to fishes. They must also facilitate dispersal of fishes. It seems likely (although the maps I have do not show any) that connections between the Rio Negro and Solimões exist some 500 miles above their confluence. Such features frequently do not show up on maps, largely because they occur in relatively uninhabited and economically unimportant areas. Even with aerial surveys the smaller connections must be difficult to trace with certainty, and since in any case they would not be navigable, there has been little reason to map them. And of course maps cannot take into account all the minor changes in stream courses and the extent of flooding, which varies so much from year to year. During exceptionally wet years the interconnections available for fish dispersal must be greatly augmented. Since interconnections such as the Auati-Paraná have little or no sources of their own, the direction of flow in them presumably depends on the water level in the rivers they connect. Thus if the Solimões is higher than the Japurá, the Auati-Paraná must flow towards the Japurá, and vice versa; if the water level is similar in both rivers, it has little or no current. If the level of both rivers should drop below that of the Auati-Paraná, it might be drained until only disconnected pools are left.

The Amazon basin has important connections with other basins. The largest of these, the Canal de Casiquiare, links the Rio Negro and Rio Orinoco in Venezuela's Amazonas Province. In Colombia the Amazon basin reputedly is linked to the Magdalena by the Japurá, to the Guaviare (which flows into the Orinoco) by the Uaupés, and to the Inírida (also flowing into the Orinoco) by the Guaniá (an affluent of the Rio Negro). The Mapuera links the Rio Trombetas and Essequibo. In Mato Grosso the Amazon basin supposedly is linked to the Paraguai by the Tapajós and the Guaporé. The Tocantins is linked to the São Francisco. The Casiquiare is a good-sized waterway throughout the year. Some of the other connections probably are broken during particularly dry years. Haseman (1912) was unable to find any connections between the Amazon basin and the Rio Paraguai. It seems likely, however, that within the recent past most of these connections permitted faunal exchanges. The Casiquiare undoubtedly has provided an easy route for exchange of fishes between the Orinoco and Amazon; many species have been recorded from it.[4]

The Orinoco basin and Guiana undoubtedly have been areas of diversification of the fish species independent of the Amazon (as evidenced by large numbers of endemic gymnotoids and doradid catfishes in the Orinoco and such peculiar forms as *Lithoxus* in the Guianas). Exchange between these basins and the Amazon basin has undoubtedly enriched the fish faunas of all three. Despite existing Amazonian connections, however, the fish faunas of the São Francisco and Magdalena retain marked peculiarities (a surprisingly large number of endemic genera of pimelodontids and species of characins in the São Francisco; an extensive radiation of *Astyanax*-like forms in the Magdalena).

There also are some connections between the Congo basin and river systems adjacent to it. Poll (1957) indicated "occasional hydrographic confluences between the Ogowé and Congo" (without stating where they are) as an explanation for the presence in the Ogowé of a number of fish elements characteristic of the Congo. Connections have been reported with the Nile in the region of Garamba; with the Chad basin by affluents of the Ubanghi, Gribingui and Ouham; and with the Zambesi by affluents of the Lualaba (Bell-Cross, 1965). As Gosse (1963: 152) noted, some of these hydrographic connections occur in swampy areas, thus facilitating exchange of certain fishes only.

The Congo and Amazon basins evidently have been growing by stream capture at the expense of adjacent basins. A very important capture was that of the Lualaba, which probably connected earlier with the Upper Nile. The capture apparently occurred at a place named "les portes de l'Enfer" (Poll, 1957: 60). Map study indicates that southern tributaries of the Congo River captured numerous headwaters of westward flowing rivers in Angola. There is a theory that the Tocantins was a separate basin before it was captured by the Amazon. To my knowledge there are no reports of important Amazon or Congo tributaries being captured by adjacent basins. If this is true, it represents a mechanism by which the Amazon and Congo could have gained species from adjacent basins with little or no release of species into them.

Special biotopes. The Congo and Amazon basins provide instances of endemic fishes that are restricted to the special biotopes in which they evidently originated. Several peculiar genera and species (most of them catfishes and cichlids) known only from the lower rapids of the Congo (Poll, 1959, 1966; Roberts, 1968) are almost certainly endemic there and unlikely to be found away from the rapids biotope. Two lakes in the central bowl of the Congo appear to have endemic fishes: lac Tumba has an apparently endemic genus of Characidae (*Clupeopetersius*), an endemic species of catfish (*Eutropius tumbanus*), and an endemic subspecies of cichlid (*Tylochromis lateralis microdon*), and lac Fwa has two endemic genera of Cichlidae (*Cyclopharynx* and *Neopharynx*) and an endemic species of the cichlid genus *Haplochromis* (*H. rheophilus*) (Poll, 1957: 60). The peculiar characoid *Paraphago*, known only from lac Leopold II at Kutu, is probably a relict, rather than an endemic form and may yet be found elsewhere.[5]

As noted by Marlier (1967), all of the present Amazonian lakes are shallow, very young, and markedly dependent on the water level in the rivers with which they are linked; the fishes in them move in and out from the rivers. Although geologically old lakes are absent in the Congo and Amazon basins, the temporary shallow lakes have undoubtedly been a hydrographic feature for a fairly long time. It may be well to consider the possibility that many fishes of the Congo and Amazon are essentially lacustrine forms that must frequently resort to the rivers to find suitable habitats. (This is not to deny the existence of many strictly riverine forms that seldom, if ever, enter lakes, such as cynodontids, various catfishes and gymnotoids, etc.) There is evidence that during wetter times in the Pleistocene much of the interiors of the Amazon basin (Marlier, 1967) and of the Congo basin were covered by a large lake or a series of lakes. One would expect that such conditions had important consequences for the evolution of fishes.

The Amazon does not have any rapids of magnitude comparable to those in the Congo. Nevertheless, four strange genera of trichomycterid catfishes are known only from the São Gabriel rapids on the Rio Negro (Myers, 1944). It seems likely that exploration of other rapids such as those of the Araguaia will divulge peculiar endemic forms. Amazonian headwaters in the Andes provide a great amount of high-gradient stream habitats. The principal fishes found in the highlands streams are astroblepids, loricariids (especially *Ancistrus* and related forms), various trichomycterids and small pimelodontids, and various Tetragonopterinae of small to moderate size. The paucity of this fauna and other evidence suggests it is relatively recent (personal communication from G. R. Smith). The only highly distinctive group that appears to have originated in the Andes is the Astroblepidae. In this family a single genus has speciated extensively. The Himalayas, on the other hand, are the center of distribution for a rich assemblage of highly modified hill stream and mountain torrent fishes (predominantly cyprinoids and siluroids). It is unclear why the Andes have such a relatively poor fish fauna.

Although there are no important mountain ranges in the Congo basin, it is highly probable that several of the species of *Barbus* described by Poll (1967a) from the elevated headwaters of tributary streams in Angola are localized endemics. In most of the big river systems of Africa the greatest representation of endemic *Barbus* species is to be found in rocky headwaters in relative isolation from the richer lowlands fauna.

Extreme physical environmental factors and their effects on fish life. McConnell (1969) hypothesized that biotic pressures are of far greater importance than climatic or physical factors in the evolution of tropical freshwater fishes. There are, however, major physical environmental factors which have met with highly varied evolutionary responses. Concerning highly acid waters (black waters with a *p*H figure sometimes much lower than 5 are a major environmental feature of the Amazon and Congo basins), we have virtually no precise evidence of how the fishes have responded. The blood of most temperate-water fishes is unable to exchange O_2 and CO_2 at *p*H's as low as those in which many tropical freshwater fishes live. Some Amazonian fishes apparently occur only in white or clear waters, perhaps because they are unable to adapt physiologically to the acid conditions encountered in black waters. Certainly many Amazonian fishes are characteristic of black waters, and some of them seem able to reproduce only in water so acid that it would kill many kinds of fishes.

Attention should be called to the "friagens" or cold spells, which cause fish mortalities in the Brazilian territory of Acre and in other parts of Upper Amazonas. Bates (1892: 289) observed mortality of fry of different species of characins at Tefé that he ascribed to a very sudden and quite considerable drop in temperature caused by southerly winds. (Reference cited by J. G. Myers, 1935: 20). According to Geisler (1969), fish mortalities accompanying a friagem may be due not to a drop in temperature, but to the uprising of water with little or no oxygen.

The nonbiotic factors that have had the most obvious, or at least best understood, effects on the evolution of tropical freshwater fishes are deoxygenation and drought. A variety of physiological, morphological, and behavioral adaptations of South American and African freshwater fishes permit them to survive such conditions. Many of these adaptations are well known (see Carter and Beadle, 1931; McConnell, 1964: 132–134) but some probably remain undiscovered. Lewis (1970) documented the morphological and behavioral adaptations that permit cyprinodontids in habitats otherwise totally deficient in O_2 to utilize the O_2-charged water of the first few millimeters immediately below the surface.

Several circumstances lead to waters deficient in O_2 in the Amazon and Congo basins. Black waters, with relatively low *p*H and reducing properties, are particularly subject to deoxygenation. Stagnation occurs in receding flood waters when masses of newly drowned vegetation rot; in lagos that become overgrown with floating vegetation; in the lower courses of some tributaries (such as the Purus and Tapajós) when they are dammed at the confluence by rising water in the main river; and in pools (including those in rapids) during low water. In exceptionally dry years when many igarapés and lagos dry up completely and even big rivers may be reduced to a series of largely disconnected pools, the stagnation must be incredible. At such times massive mortality of fishes is apt to occur. Gadow (1909: 447) reported a prolonged drought on the island of Marajó, in the mouth of the Amazon, that caused swamps and lakes to dry up to the extent that the alligators in them migrated towards the rivers, and many thousands died in the attempt. Spruce (1908, vol. 1: 118) reported that the waters of the Tapajós are sometimes dammed by the Amazon and are rendered stagnant for several weeks, during which time the water is considered very unwholesome. (References cited by J. G. Myers, 1935: 19.) In the Amazon and Orinoco basin stagnation of the waters seems to be associated with some kind of non-specific epizootic which kills fishes and other vertebrates (J. G. Myers, 1935).

In 1839 a drought occurred in the Rio Negro which brought on forest fires, and immense quantities of fishes killed by the heat and drought lay on the sandbanks (Schomburgk, 1931: 181–182). In 1926 during an exceptionally severe dry season in the Rio Negro-Rio Branco area a great fire blazed for over a month destroying vegetation along the lower Rio Negro, and it is said that fishes succumbed (Carvalho, 1952). Fire probably has had little long-term effect on the rain forest.

The occurrence of fires in the rain forest is an example of "less predictable" variability, and the fishes probably show little adaptation to them. In savanna regions, however, where fires are more regularly occurring, fishes may have evolved adaptations to them. The burrowing or estivating habits of lepidosirenids, *Synbranchus*, and other forms may well enhance the probability of their survival in regions frequently subjected to fires.

The role of fire in the ecology of South America undoubtedly has increased since the arrival of man (see Sternberg, 1969:

418–422), and it may be that fires of such magnitude as those of 1839 and 1926 would not have occurred along the Rio Negro unless set by man. In the Rio Uraricoeira area near the Ilha Maracá, I accompanied a fazendeiro who was setting the grasslands of his fazenda ablaze toward the end of the dry season (in April 1969) in order that the tough grass on which his cattle could not feed would be replaced by tender green shoots when the rain came.

Beebe (1945) reported an astonishing variety of fishes from a small "all but dried up mud-hole" in northeastern Venezuela. Some 34 species, comprising six catfishes (a trichomycterid, three callichthyids and two loricariids), fifteen characins, a gymnotid (*Hypopomus*), four cyprinodontoids, six cichlids, *Polycentrus schomburgkii*, and *Synbranchus marmoratus*, were taken from malodorous mud and decayed vegetation covered by damp slime (but no free water) in what was left of a drying pool that had been "almost unswimmable" slime for weeks. He estimated that in another week or ten days without water all would have perished. Of the 15 characins, two are air-breathers. *Copeina* and some of the others perhaps utilize oxygenated water immediately below the surface in a manner similar to that of cyprinodonts. *Copeina* is characteristic of swampy places and stagnant backwaters. But it is difficult to imagine how *Astyanax, Creagrutus, Moenkhausia, Paragoniates, Pristella* and *Serrasalmus* could have survived in such a habitat for as long as they did. Most of the species found in this Venezuelan mud-hole occur in the Amazon basin.

Significance of parental care in Amazon and Congo fishes. McConnell (1969) stated that many tropical freshwater fishes have some form of parental care and implied that biotic factors such as predator pressure are of far greater importance than climatic factors in the evolution of such behavior. This seems to apply to cichlid fishes in lakes Victoria, Tanganyika and Nyasa but not to the riverine fishes of tropical Africa and South America. Whereas an overwhelming proportion of the rich endemic cichlid fauna of these three lakes practice oral brooding, such behavior is far less common in riverine Cichlidae in Africa, and in South America, where it has been reported only in some species of *Geophagus.* The explanation for this remarkable behavioral dichotomy probably lies in relatively simple considerations. In the still, clear littoral waters of the lakes the eggs and young are less readily dispersed and far more susceptible to visually oriented predators. Under riverine conditions the eggs are likely to be separated from the parents by current; moreover, in the black waters and white waters of many tropical rivers, the eggs and young would be extremely difficult to detect visually by predators, and perhaps even more important, by the parents themselves.

In tropical riverine fishes of Africa, South America, and Asia, parental care occurs mainly in fishes in which adults spend at least part of the time in swamps or other oxygen-deficient habitats; many are capable of air-breathing. These fishes, if they reproduce in such habitats, are usually obliged to care for the young. In African and South American lungfishes a nest is constructed that is subsequently guarded and aerated by the male. Notopteridae, osteoglossoids, and Pantodontidae are air-breathers and guard the young. *Gymnarchus,* which is probably capable of air-breathing, makes a floating nest of plants in dense swamps; it is the only mormyroid known to guard the young. Young *Gymnarchus* have external gills with numerous fine filaments and a highly vascularized, enlarged yolk sac, both structures playing an important role in gas exchanges. No other mormyroids have such structures. Parental care might be expected of *Polypterus;* none has been recorded. In Asia the largest group of freshwater fishes with parental care is the air-breathing anabantoids. These fishes typically build a floating froth nest of air bubbles in which the eggs are deposited. The bubbles may provide a supply of oxygen. Usually one or both parents stay near the nest to protect and maintain it. Froth nests have been attributed to the African characoid *Hepsetus* (which is not known to be an air-breather, but may leave its young in habitats likely to be oxygen-deficient). Nesting habits are also ascribed to characoids of the family Erythrinidae. Erythrinids tend to enter swampy regions, and *Hoplerythrinus* is evidently capable of air-breathing. *Callichthys* and *Hoplosternum*, South American air-breathing catfishes, construct froth nests, whereas the related *Corydoras*, which probably are not air-breathers, generally scatter their eggs amidst plants. In most characoids, although courtship and selection of spawning site may be highly complex, parental behavior probably ends once the eggs are deposited. There are no records of parental care in gymnotoids, excepting the unconfirmed report (Du Bois-Reymond, 1882) that *Electrophorus* (the electric eel) practices oral brooding. In *Electrophorus* a highly convoluted oral epithelium facilitates air-breathing (Carter, 1935). (There is also reason to think that *Gymnotus*, which is related to *Electrophorus*, takes the young into its mouth.) It would appear that the great majority of fishes in the Amazon and Congo have no parental care. As pointed out by McConnell (1969: 63–64) many Amazonian fishes engage in upstream spawning migrations (piracema), producing extremely large numbers of eggs per female, all or most of these eggs being laid at one time at the start of, or early in, the rainy season. In all such fishes parental care is very probably nonexistent. None of the fishes with modifications for breathing air participate in piracema.

A remarkable exception to the general rule that non-air-breathing characoids lack parental care is provided by *Copella*, the spawning and parental care of which have been the subject of several reports by aquarists (for detailed extracts from the literature and additional references see Breder and Rosen, 1966: 163–165). The main events seem clear enough. The eggs are actually deposited out of the water. A pair about to spawn station themselves at the surface beneath an overhanging object (presumably the underside of a leaf in nature) that is about three or four inches above the water. With bodies close together, the pair leap and momentarily adhere to the object. After repeated trials, the actual spawning begins. Half a dozen to a dozen eggs are deposited with each leap, until sixty or more eggs are left lying close together (but not on top of one another) in a clump of spawn resembling that of a snail. Afterwards the male returns every twenty to thirty minutes and splashes the eggs with water by making vigorous fin and body movements. Between splashings the male is stationed at a spot some distance from the eggs. The eggs hatch in two or three days, and the fry drop into the water and spend the next few days near the surface (summarized from Stoye, 1935). This fish occurs throughout much of the Amazon in backwaters and swampy places where deoxygenation is likely. This fact, as well as its small size, habit of frequently resting at the surface, and somewhat cyprinodontlike appearance suggest that it can utilize the oxygen-rich layer of water at the air-water interface. The aquarists' accounts of its spawning, parental care, and behavior of its fry are suggestive of adaptations to permit reproduction by fishes in habitats almost totally deprived of oxygen.[6]

BIOLOGICAL INTERACTIONS OF FISHES IN THE AMAZON AND CONGO

Apart from predator-prey and host-parasite relationships, with one exception there are no recorded instances of biological interactions between Amazon or Congo fishes and animals of other classes. The exception is commensalism of chironomid larvae attached to Loricariidae and Astroblepidae in the Amazon recorded by Freihofer and Neil (1967). Insects aside, invertebrates apparently are of minor consequence in the Amazon and Congo river systems. Almost all of the marine groups with which tropical reef fishes display so many complex symbiotic and commensal relationships are absent, and nothing has taken their place. The relatively scarce molluscs and crustaceans exhibit little diversity compared to those of tropical reefs. Excepting parasites, then, almost the only animals with which the fishes can interact are other fishes.[7]

Conspicuously marked Congo and Amazon fishes. Africa and South America are famous for brightly colored and strikingly patterned fishes, most of which regularly find their way into the aquarium fish trade. Such fishes are not evenly distributed among the river systems of the two continents. In general, more brightly colored fishes occur in forest rivers than in savanna rivers; and more in black water or clear water rivers than in white water rivers. The highest proportion of brightly colored fishes occurs in the river systems and in the fish groups with the highest numbers of species. The great majority of brightly colored fishes in the aquarium trade of Africa come from the Congo. The most brightly colored of all freshwater fishes are some of the small Amazonian Characidae. The trend toward more distinctively marked representatives in the Congo and Amazon basins affects almost all groups of fishes in Africa and South America. To cite just two examples from Africa: the catfish genus *Synodontis* is represented by 15 species in the Volta basin and 37 species in the Congo. None of the Volta species can match the bright colors or contrasting patterns of the Congo species *S. angelicus*, *S. ornatus*, *S. ornatipinnis*, *S. flavotaeniatus*, *S. decorus*, *S. nummifer*, and *S. notatus*. Again, the Volta has three species of the characoid genus *Distichodus*, all with indistinct vertical bars and drab colors, while the Congo has eleven species of *Distichodus*, all but two of them distinctively or even strikingly marked. Equally good examples could be drawn from the Characidae, the cyprinid genera *Labeo* and *Barbus*, and the anabantoid genus *Ctenopoma*. The major exceptions to the trend in Africa are the uniformly drab or cryptically colored mormyrids, in which nonvisual sensory structures are highly specialized and the eyes are reduced. In South America the gymnotoids constitute a similar exception. These bright colors and striking markings are evidently meant to advertize the presence of their possessor. The bright colors, unlike those of many gaudy tropical birds and insects, are not confined to mature males, but generally appear at an early age in all individuals. If the fishes were distasteful, venomous, or harmful in some way, we could make an hypothesis that their coloration warns away predators. At least for the majority of characoids, however (which provide most of the best examples of brilliantly colored fishes both in the Amazon and in the Congo), there is no indication whatever that they are inedible or dangerous in any way to predators. It would seem, although there are no data available to support this, that the brightly colored characins are just as subject to predation as drably colored ones, if not even more. In this respect the colors advertizing their presence are probably a disadvantage. Many of the small, brightly colored Amazonian characins form schools. This is true of the most brilliant characins of all, the neon tetras and cardinal tetras. Most of these brightly colored characins live in black water or clear water igarapés, a habitat that can be highly temporary (see p. 122). Thus populations frequently are split up or dispersed, and species recognition and schooling habits are probably important means of reconstituting populations.

Association of species of Amazonian characoids in mixed schools. Myers (1960b), Géry (1960), and McConnell (1969) recounted examples of generically distinct but similar appearing South American characoids that form mixed schools of two or more species. Myers (*ibid.*, p. 207) reported that the small characoids *Creagrudite maxillaris* and *Creagrutus phasma*, which look very similar, were collected together (it is unknown whether they were schooling together). He suggested that they appear to form an instance of Batesian mimicry, with *Creagrudite* the model and *Creagrutus* the mimic. Re-examination of fishes identified as *Creagrudite* from the same area (upper Orinoco-upper Rio Negro) revealed among them another species of *Creagrutus*, which appears to be *C. melanzonus* (Myers and Roberts, 1967). All three species have a blackish crescentic humeral blotch and are closely similar in appearance. Géry (1960) suggested that similar cheirodontines and tetragonopterines that school together both benefit from the association, and thus the mimicry is Müllerian. Géry (*ibid.*, p. 37) labelled the schools "protective associations" but did not identify the nature of the protection the association supposedly provides. As noted by McConnell (*ibid.*, p. 130) the facts are not available to show what advantages the fishes gain from such mimicry. Perhaps it permits small numbers of isolated individuals of two (or more) species to form a nucleus for aggregation with increased chances that breeding populations eventually will be reconstituted. Moynihan (1968) discussed several instances of mimicry that seem to facilitate flocking in neotropical mountain birds.

Amazon and Congo fishes of minute size. Consideration of the fishes in the Amazon and Congo that have minute body size as adults indicates that this is primarily a response to biotic pressures. In the Amazon, where biological interactions among fishes perhaps are greater than anywhere else in the world, we find more minute freshwater fishes than anywhere else, including: the smallest oviparous and the smallest viviparous cyprinodonts in the world (*Fluviphylax pygmaeus* and *Poecilia minor*); one of the smallest needlefishes (*Belonion apodion* Collette, 1966b); two tiny species of Eleotridae (*Microphilypnus* Myers, 1927); and minute catfishes in several subfamilies of Trichomycteridae, a number of them smaller than any other catfishes. Excepting the needlefish, which is very slender, every one of these is less than an inch long when fully adult. All excepting the catfishes are secondary freshwater fishes and belong to groups whose presence in the Amazon can be thought of as "marginal." Large poeciliids are absent in the Amazon except for three good-sized species of *Poecilia* that have penetrated no further inland than Pará. *Poecilia minor* itself seems confined to the Lower Amazon. It is known from only two collections (separated by more than 100 years) within 100 miles or so upstream from Obidos. *Poecilia scalpridens*, the only other poeciliid in the interior of the Amazon, and not much larger than *P. minor*, is known from a few localities in the Middle and Lower Amazon. *Fluviphylax* is a phyletically isolated form widespread in the Amazon basin. Its relationships evidently lie either with Procatopodinae, a subfamily otherwise restricted to Africa, or with Fundulinae (found mainly in North and Central America) rather than with Rivulinae (the only other subfamily of Cyprinodontidae in the Amazon basin) (Roberts, 1970a). Large gobioids occur in fresh water in many places throughout the tropics where primary freshwater fishes are poorly represented. Although a number of large gobiids and eleotrids have been recorded from the mouth of the Amazon, the two minute species of *Microphilypnus* are the only gobioids known from its interior. A third species of *Microphilypnus*, perhaps the smallest one, occurs in the Orinoco basin (Myers, 1927). The Congo eleotrid, *Kribia nana*, while considerably larger than *Microphilypnus*, is nevertheless a very small fish. It is the only gobioid in the interior of the Congo. Until recently the cyprinodont *Aplocheilichthys myersi* was the smallest fish known from the Congo basin. We may note that at least some of these little fishes (*Fluviphylax*, *Poecilia minor*, and *Kribia*) apparently reproduce all year round; probably they all do. Their size may permit them to utilize food resources unexploited by adults of other fishes. And it may place them below the size threshold for attack by most predaceous fishes.

The best African example of a fish group with an essentially marginal distribution, except for unusually small species in the midst of the richest lowland faunas, is provided by the Kneriidae. The species of *Kneria* and *Parakneria*, some of which are 80–150 millimeters long, are now known from high gradient streams around virtually the entire periphery of the Congo basin (Poll, 1966; 1969, map on p. 360) but have yet to be found in the cuvette centrale or in the main rapids of the Congo River, where one might expect ecological conditions would be suitable for them. The kneriid *Grasseichthys gabonensis* Géry (1964), only 18–20 millimeters in standard length and very slender, was discovered in 1964 by Géry in forest streams in Gabon and by myself in forest streams in the western part of the cuvette centrale. This is now the smallest known species of fish in the Congo basin.[8]

Adaptive responses to predation. McConnell (1969) noted the high number of predatory fishes in the Amazon (which she felt was relatively higher than in African fresh waters) and suggested that this permitted more prey species to co-exist. (The converse may also be true.) Of adaptations displayed by Amazon and Congo fishes that lessen the toll of predation for their possessors, reference should be made to the alarm substance and fright reaction in Ostariophysi, Kneriidae, and Phractolaemidae (Pfeiffer, 1963, 1967); the ability of gymnotoids to withstand mutilation (Ellis, 1913); the cryptic body form and coloration of such fishes as *Farlowella;* the heavy (and frequently spiny) body armor of many catfishes (especially in the families Doradidae and Loricariidae); and the protective dorsal and pectoral fin spines of most catfishes. In some catfishes these spines are very sharp and venomous, as in the Amazonian caratai, *Centromochlus heckelii,* and other auchenipterids. In other catfishes the spines are stout and can be locked in erect position. *Centrochir crocodili* (Humboldt) of the Rio Magdalena is called "mata-caiman" after the wounds it inflicts on crocodiles attempting to swallow it (Eigenmann, 1922: 47). It is said in Ghana that crocodiles sometimes are killed trying to swallow *Auchenoglanis occidentalis.* Many catfishes in the Amazon and Congo basins are equally equipped with pectoral and dorsal spines, and once they grow to a certain size they presumably are seldom preyed upon by predators that swallow their prey whole. The spines do not protect them from piranhas, which bite out chunks rather than swallow their prey whole, or from attack by various kinds of candirú (see pp. 136–138). On the other hand, the electric eel of the Amazon (*Electrophorus electricus*) and the electric catfishes of Africa (*Malapterurus*) may be entirely exempt from predation. *Malapterurus* only an inch or so long are capable of producing a jolting shock (personal observation).

Partitioning of food resources, and trophic adaptations. Another obvious aspect of biological interaction or accommodation in Congo and Amazon fishes is the partitioning of food resources. Food-place, food-time, and food-type partitioning are probably equally important. The basic dichotomy of ostariophysans into nocturnal and diurnal groups (siluroids and gymnotoids vs. characoids and cyprinoids) is mentioned in the introduction. The habitat preferences of many of the fishes in the Amazon and Congo are in many instances closely linked with feeding habits. Many of the fishes have highly modified trophic structures, some of which are quite peculiar. Interestingly enough, for some of the most peculiar types of feeding we have examples of convergence between fishes of the Amazon and Congo basins. It has been said that riverine fishes of tropical Africa and South America exhibit less trophic specialization than cichlids in lakes Victoria, Tanganyika, and Nyasa and that this is due largely to relative year-round availability of food in the lakes in contrast to marked seasonal abundance and dearth of food in the rivers. The observation and the reasoning, it seems to me, while they may be relevant in savanna rivers having extreme seasonal vicissitudes, do not apply to the Congo and Amazon rivers. In any event, it should be remembered that fishes are capable of fasting for considerable periods, provided they get an adequate share of the resources available during times of abundance. A more important reason for the relative paucity of fishes with highly specialized trophic structures in savanna rivers is probably faunal impoverishment resulting from drought. The diversity of feeding habits of fishes in the Amazon and Congo is perhaps as great as one could expect given the nature of the food available. Were it not for partitioning of food resources and concomitant evolution of specialized feeding behavior, the astounding number of fishes present in the Congo and Amazon probably would be unable to coexist. Partitioning of food resources apparently has proceeded to the point where utilization and cycling of energy and materials are very efficient. The upper limits of partitioning presumably are determined by complicated factors such as the variety of foods and their relative availability in space and time; and the capacity of fishes to exist (e. g., by fasting or facultative feeding) when such resources are unavailable, and to reproduce when they become available. Food resources cannot be partioned indefinitely, because a point would be reached where individual parcels of energy and materials are too small to support populations big enough to have sufficient probability of survival, even in habitats where catastrophic (i.e., nonbiological) causes of extinction tend to be minimal.

The main categories of food in the big tropical rivers are relatively few, namely, 1) other fishes; 2) insects, both aquatic and terrestrial, and aquatic insect larvae; 3) higher plants, including fruits and leaves fallen into the water and roots growing out into the river from the banks, as well as some aquatic plants; and 4) mud or earth, including interstitial organisms, dead organic matter, and possibly bacteria. Each of these categories seems to be highly partitioned among the fishes and to have evoked various kinds of trophic, behavioral, and morphological adaptation. It should be noted that some lake cichlids that are highly specialized for feeding on plankton and molluscs would find little or none of their predilected food in rivers of the Amazon or Congo basins.

Predatory fishes. It would appear that nowhere else on earth have fishes evolved as many manners of preying on other fishes as in the Amazon. Excluding fin-eaters and scale-eaters, in the Amazon over 40 species of characoids alone are primarily or exclusively piscivorous. The more voracious species of *Serrasalmus* (known as piranha chata in Brazil) bite out chunks from larger fishes. Géry (1963: 615–616) noted that for each species of *Serrasalmus* in the voracious subgenera *Pygocentrus* and *Taddyella* there is a geographically corresponding species in the less specialized subgenus *Serrasalmus*. He hypothesized a parallel evolution of sympatric species in which the less aggressive *Serrasalmus* (known in Brazil as pirambebas) benefited from association with *Pygocentrus* and *Taddyella*.

Several of the most archaic fishes of the Amazon and Congo basins are rapacious predators. Some species of *Polypterus* (e. g., *P. senegalus*) are insectivorous, but the two largest species—*P. endlicheri* and *P. congicus*—are piscivorous. The African osteoglossoid *Heterotis* is a filter-feeder, but the Amazonian *Osteoglossum* is piscivorous (feeding mainly on characins), as is *Arapaima gigas* (the largest osteoglossoid), which sometimes feeds on *Osteoglossum*. The African *Hepsetus*, which appears to be the most primitive characoid (Roberts, 1969), is a voracious piscivore, as are a number of phyletically isolated (and perhaps primitive) South American characoids.[9] This should not come as much of a surprise, for a remarkable number of survivors of archiac fish groups throughout the world—viz., lampreys, sharks, chimaeras, gar-fishes, bowfin, tarpon, and pikes—are extremely effective piscivores. Far from inhabiting situations geographically or ecologically isolated and open to relatively few organisms (as do survivors of some archaic invertebrate groups), these modern predaceous representatives of archaic fish groups are frequently dominant forms in shallow seas and especially in lowland rivers (e. g., the Congo) where the fish fauna is exceptionally rich.

Scale-eating and fin-eating characoids. South America has several scale-eating characoids (Roberts, 1970b). Four genera and about ten species are present in the Amazon (scale-eating has yet to be verified for all of them). Eating scales appears to be of major importance in the mode of living of these fishes. Several of the species have been observed actually feeding on scales from other fishes, and scales generally predominate in their stomach contents. Their teeth are obviously specialized for removing scales. They generally attack fishes larger than themselves, which presumably usually escape without being killed. Although the Congo is rich in characoids, no scale-eaters have been reported there. The only other freshwater scale-eating fishes are cichlids from lakes Nyasa, Tanganyika, and Victoria.

The Congo, on the other hand, has a remarkable group of fin-eating characoids, all in the family Ichthyboridae (Matthes, 1961). Most but not all members of this family will probably be implicated as fin-eaters. The small *Microstomatichthyoborus katangae* feeds on aquatic insect larvae. *Gavialocharax* (from Cameroun), with its wonderfully elongated jaws, probably is a fin-eater, as are the species of *Belonophago* (from the Congo). As with scale-eaters, they attack fishes much larger than themselves. The fin-eater diet, rich in bone minerals, probably was prerequisite for the development of the exceedingly hard, platelike dermal armor (derived from scales) present in *Belonophago* and *Phago*. Daget (1967) reported that *Ichthyborus besse besse* in the Chad basin is a fin-eater, while *Ichthyborus besse congolensis* in the Lualaba seems to have readopted secondarily the diet of a micropredator. Daget (*ibid.*, p. 142) suggested that the difference in feeding habits between the two subspecies might be explained thus: in Katanga the "ecological niche" of fin-eaters is occupied by *Phago* and *Eugnathichthys*, while *Ichthyborus*, probably less well adapted to fin-eating, has its diet restricted to small fishes and invertebrates; in the Chad basin, on the other hand, *Ichthyborus* has no competitors (no other ichthyborids occur there) and occupies only the "ecological niche" of fin-eaters. In the Amazon the only known fin-eaters are in the genus *Serrasalmus* (e. g., *S. elongatus*), and they tend to utilize other foods to a considerable degree.

Feeding habits of the Amazonian catfishes known as candirú. Candirú is an Amerindian name for certain catfishes which attack other fishes and, occasionally, man. (For a delightful account of candirú attacks on man, see Gudger, 1930.) Very little is recorded concerning their feeding habits. About 30 species have been described from the Amazon basin, representing two unrelated families of catfishes, Cetopsidae and Trichomycteridae. The trichomycterid candirús belong to four subfamilies, Pareiodontinae, Stegophilinae, Vandelliinae, and Tridentinae. During fieldwork with EPA in October and November 1968 many candirú species were collected, some of them in considerable numbers, and observations were made on their feeding behavior. Most were collected with a fine-meshed wire basket (open at one end) baited with fresh fish heads, or with a fine-meshed dipnet and a fresh fish head suspended in the water on a string. Large catfish heads worked best.

Cetopsis coecutiens (Lichtenstein) gets at least a foot long and two inches in diameter, and is the largest candirú in Amazonas. On several occasions I saw this species taken in open water in midday, on hooks baited with pieces of fresh fish. Its back is deep sky-blue, its belly milk white. It was never taken at night or by means of my fish heads. *Hemicetopsis candiru* (Spix) reaches about eight inches in length and its whole body has a pinkish or reddish hue, especially in somewhat smaller specimens. The largest specimens tend to have a more greyish cast. It is apparently active only after dark. At first none of this species were collected. Then one evening, finding myself without fresh material for bait, I tried some old fish heads from previous fishing that had been tied to the boat, and got a fair number of *Hemicetopsis candiru* and virtually no other species. (Earlier it had been noted that, in general, fish heads were most efficacious as candirú bait while very fresh.) Later on, fishing was carried out with fresh and rotten fish heads simultaneously, with the finding that *Hemicetopsis* came only to rotten baits. In this it differs from all other candirú. *Pareiodon microps* Kner reaches about eight inches long and its body is uniformly grey. It was more commonly captured than any other candirú with fish heads used as bait. On several occasions 50 to 100 were captured in a baited wire basket within an hour or two and on one occasion about 300 were caught in less than an hour. They came mainly in the first hour or two after nightfall and seemed to prefer fresh baits. *Hemicetopsis candiru* and *Pareiodon microps* feed by biting out circular chunks. If they are unsuccessful in removing a bite, they leave a nearly perfect circular scar. *Pareiodon* or *Hemicetopsis* eight inches long leave a scar about a half inch in diameter. Stomachs of these fishes frequently contain a half dozen or more round chunks of flesh or viscera. There is no evidence that either *Pareiodon* or *Hemicetopsis* enter the gill chambers or suck the blood or body fluids of other fishes.

The majority of candirú belong to trichomycterid subfamilies, Stegophilinae, Tridentinae, and Vandelliinae. These range in size from less than an inch long and extremely slender to perhaps six inches long. In Stegophilinae and Tridentinae, which are closely related, the mouth is wide, and teeth in both jaws are very numerous and arranged in several rows. In Vandelliinae the mouth is relatively narrow and the teeth are few and in only one or two rows in both jaws. According to Eigenmann (1918), Reinhardt in 1858 was the first to record that a species of candirú (*Stegophilus insidiosus* Reinhardt, from the Rio das Velhas, Rio São Francisco basin) enters the gill chambers of other fishes. Eigenmann (1918) recorded similar behavior for a species of Vandelliinae (*Branchioica bertonii* from the Rio Paraná). During the EPA fieldwork a number of Vandelliinae and Stegophilinae were obtained directly from the gill chambers of fishes caught on hook and line, usually large catfishes, and their stomachs were frequently gorged with blood. Stegophilinae and Vandelliinae were readily caught by using fresh fish head baits. *Pseudostegophilus nemurus* (Günther) were observed on only one occasion, at midday, when our boatmen were unusually successful in catching dourada and filhote (catfishes of the genus *Brachyplatystoma*) by hook and line. One specimen dropped out of the gill chamber of a dourada after it was landed and was positively identified. The *Pseudostegophilus* appeared in numbers and were darting about near the surface, even jumping clear of the water in evident excitation. Other than on this occasion, dusk and the first hour or so after nightfall appeared to be the time of greatest activity for Vandelliinae and Stegophilinae. *Pseudostegophilus*, with its handsome golden-hued body and dark cross bars, is the most colorful candirú, which further suggests that it is more diurnal than other species.

Kelley and Atz (1964) published a photograph of *Vandellia* attacking goldfish in an aquarium and reported that after gorging on blood the *Vandellia* settled to the bottom of the aquarium. Vandelliinae, except for their eyes and viscera, are generally transparent in life. *Plectrochilus* has a longitudinal black mark on the caudal peduncle and fin. Vandelliinae are slender fishes but are capable of considerable abdominal expansion to receive blood. There is no evidence that either Vandelliinae or Stegophilinae spend protracted periods in the gill chambers of another fish; perhaps members of both subfamilies gorge themselves fairly soon after entering and then swim out. Haseman (1911: 315) stated that *Vandellia* and other trichomycterids lie buried in sand bars. When disturbed the *Vandellia* "rise like a flash and bury themselves again in an instant, leaving a small round hole where they re-entered." He reported collecting four hundred *Stegophilus* buried in the sand in an igarapé near Santarém; however, his remark that these were "minute and could be seen by the millions in this locality, where the water was too shallow to permit the presence of large fishes of any kind" indicates they may have been Tridentinae instead of *Stegophilus*. McConnell (1964: 116) reported *Trichomycterus* (*Pygidium*), minute trichomycterids (Tridentinae ?), and *Hemicetopsis* amidst a large variety of other fishes (mostly catfishes) hiding in crevices and hollows in logs in a creek of the Rupununi River in British Guiana.

On one occasion I watched a fisherman return from spearing a pirarucú (*Arapaima gigas*, the largest scaled fish in Amazonas). In the bottom of his canoe were several specimens of a very dark stegophiline (identified in the field as *Ochmacanthus reinhardti*). The fisherman indicated that many such candirú had been clinging to the pirarucú as he hauled it into the canoe. Upon examining the gill chamber of the pirarucú, I could not detect any indication of damage to the tough gill filaments and strongly doubt that the *Ochmacanthus* obtained any blood from the gill filaments or elsewhere. Perhaps they were feeding on mucus, which is abundant on pirarucú. *Ochmacanthus* observed on sandy bottoms in relatively clear water were always light colored. I suspect they can change color to match the substrate, whether it be light sandy bottom or the dark body of a pirarucú.

Mr. Jonathan Baskin, who is studying the family Trichomycteridae, called to my attention the scale-eating habit of the stegophiline *Apomatoceros alleni* Eigenmann. The mouth of this species is capable of being everted to form a discoid sucker about twice as wide as the head, and is provided with numerous bands of teeth. The evidence of scale-eating is provided by examination of an alizarin preparation and radiographs of two specimens (105 and 111 mm, catalogued as no. 109804 in the fish collection of the Academy of Natural Sciences of Philadelphia), the alimentary canals of which are partially filled with scales about 3 millimeters long.

The food habits of the Tridentinae are unknown. All are small (usually an inch or less in length). We collected several species of this subfamily by using rotenone in shallow, forested backwaters wth deeply tinted, clear water at localities along the Rio Solimões between the Rio Purus and Rio Içá, but no observations were made on their behavior.

Amazonian fishes with trophic structures for straining minute organisms from midwater. Production of phytoplankton is practically lacking in most Amazonian waters and zooplankton is often absent. In black waters and white waters this is probably due mainly to the low penetration of light. The big black water rivers with wide mouth-bays have very little primary production of phytoplankton, partly because the water is highly acid and extremely poor in inorganic ions and nutrients. An insignificant amount of phytoplankton, mainly of desmids, and more surprisingly, a certain amount of zooplankton may be present. The principal biotopes in which phytoplankton develops are the mouth-bays of clear water affluents, such as the Tapajós and the Xingú, and the shore lagoons or lagos of white water rivers. In some places veritable plankton blooms occur. The shore lagoons are often favored fishing grounds. Fishes are scarce in the mouth-bays, however, and the main consumption of the phytoplankton produced in them may happen in the white water rivers into which they flow (Sioli, 1968).

A number of Amazonian fishes have trophic structures that could permit them to utilize plankton. Böhlke (1953) described a minute (25–30 mm) herringlike characid from the upper Rio Negro, *Thrissobrycon pectinifer,* with "otter-board" maxillaries in a nearly toothless mouth and about 25 long gill rakers on the lower limb of the first gill arch. Böhlke inferred that it is an open-water, schooling planktophage. Amazonian clupeids and engraulids tend to be predators, but *Cetengraulis jurnensis* Boulenger, with about 40 long, finely denticulate gill rakers on the lower limb of the first gill arch, is probably planktophagous. The Amazonian fishes with the most highly modified apparatus for straining minute organisms from the water are the catfishes of the genus *Hypophthalmus* and the characin *Anodus elongatus* and one or two of its close relatives. In these presumably planktophagous catfishes and characins the mouth is toothless and the gill slits are extremely long. The gill membranes are free from the isthmus. The gill openings and gill arches extend anteroventrally almost to the symphysis of the lower jaw, so that virtually the entire floor of the oropharyngeal cavity is lined with gill rakers. The gill rakers on all of the gill arches are elongate and exceedingly numerous. There are no less than three very distinct species of *Hypophthalmus* in the Amazon. At least one of them gets to be two feet long. In Brazil they are called mapará. The ventrally directed eyes and laterally compressed body with its complicated system of criss-crossing lateral line canals make the genus readily recognizable. The trophic structures are highly distinctive. The opening of the mouth is large and its roof is smooth. Most of the gill rakers are borne on the elongate lower limbs of the gill arches. A 300-millimeter specimen of *H. edentatus* has about 240 gill rakers are borne on the elongate lower of the gill rakers tapers off at either end of the gill arch, but most of them are extremely long, about 15–17 millimeters. Rakers on succeeding arches are almost as numerous as those on preceding arches, and only slightly shorter. The first two arches bear rakers on the leading edge only; the full length of the trailing edge of these arches supports a strong membranous flap the height of which is about one-half of the length of the gill rakers. The third and fourth arches bear rakers on both leading and trailing edges, and no flap. The fifth arch bears rakers on its leading (free) edge. The mouth, branchial arches, and gill covers can be held in such a position that all water leaving the gills must first pass through a fine sieve formed by the rakers (observed by manipulation of preserved specimens). The tips of the gill rakers of the trailing and leading edges of the third, fourth, and fifth gill arches meet to form a ΛΛΛΛΛ-shaped sieving mechanism. For this to be completely effective all the water must exit through the third and fourth gill slits. The membranous flaps on the trailing edges of the first and second gill arches presumably prevent water from exiting through the first and second gill slits. *Hypophthalmus* form large schools and undergo extensive migrations. They are one of the most important food fishes in the lower Tocantins and are among the fifteen or so commonest species in the fish market at Manaus.

The highly streamlined *Anodus elongatus* appears to have an even more perfect straining mechanism than *Hypophthalmus*. Both leading and trailing edges of its first four gill arches bear rakers, and the fifth arch bears rakers on its leading (free) edge. The upper limbs of the arches are about two-thirds as long as the lower limbs and bear correspondingly fewer rakers. The number of rakers is only slightly reduced on successive arches. The first arch of a 200-millimeter specimen bears 80 + 110 rakers, most of which are 10 or 11 millimeters long. The dorsal edge of each raker bears two rows of about 100 or more tiny denticles approximately 0.2–0.3 millimeters long and 0.1 millimeter apart. The denticles of adjacent rakers mesh to form an exceedingly fine sieve. The stomach is thin walled and the intestine relatively straight. In the specimens examined by me, collected by the Thayer Expedition, the stomachs are empty. A related form, *Eigenmannina melanopogon*, from the upper Amazon has exceedingly numerous gill rakers, and is also presumably planktophagous.[10]

In the Congo basin none of the catfishes or larger characins are planktophagous. The small characin *Clupeopetersius schoutedeni* Pellegrin in Lake Tumba is a pelagic planktophage (Matthes, 1964: 43, figs. b and d, pl. 1), as are some endemic Congo species of Pellonulinae.

Parallelism in the feeding habits of mormyroids and gymnotoids. The nature of the electric faculties and their biological significance in gymnotoid and mormyroid fishes is now under intensive investigation; evidently a great deal remains to be discovered and understood (the best general review is still Lissmann, 1958). This independent evolution of weakly electrogenic freshwater fishes in Africa and South America is a particularly striking example of parallelism because of its novelty and the pervasiveness of its effects. Some 18 genera and 35 species of gymnotoids have been recorded from the Amazon basin. Undescribed Amazonian species are present in most important museum collections and the group is in great need of systematic revision. Ten genera and 93 species of mormyroids have been recorded from the Congo basin. It is believed that all mormyroids and gymnotoids possess both electrogenic and electrosensory faculties, and this has been verified for at least one species in almost every one of the genera. In both groups it is apparent that virtually all aspects of the morphology and behavior have become specialized and integrated with the electric faculties. Certain aspects remain uninvestigated. For instance, it is known that electrosignalling functions in territorial and aggressive behavior in gymnotoids and mormyroids, but its (presumably important) role in sexual behavior has not been described in either group.

The parallels in habitat selection, mode of locomotion, and feeding habits between gymnotoids and mormyroids are intimately bound up with their electric faculties, although this has not been fully appreciated and much remains to be learned concerning it. It is my belief that elucidation of the interrelations between electric behavior and feeding habits in mormyroids and gymnotoids will contribute materially to understanding the evolutionary history and perhaps the very origin of both groups. The strongest evidence that electric behavior has profoundly affected feeding habits in mormyroids and gymnotoids lies in the repeated development in both groups of highly peculiar and remarkably similar trophic structures, e. g., diverse types of elongated tubular mouths with weak jaws and feeble dentition. These structures evidently permit efficient exploitation of a rich bottom fauna of small worms and wormlike insect larvae (e. g., enchytraeids and chironomid larvae) which other fishes can use only marginally or not at all. (For food habits of gymnotoids, see Ellis, 1913. Little comprehensive information is available on mormyroid food habits. For food habits of Congo mormyroids, see Matthes, 1964. Observations of mine and a few published accounts confirm that some mormyroid species feed heavily on chironomid larvae.) It seems likely that several factors enter into this relationship between electric faculties and feeding habits. The nocturnal behavior of some gymnotoids and mormyroids may mean that they are feeding actively when such wormlike prey is most susceptible to predation. But this in itself seems insufficient to account for the successful exploitation evidenced. Two further possibilities merit consideration. The first is that mormyroids and gymnotoids are able to locate such minute prey electrosensorily. I think this highly likely. The second is that the weak electric emanations of gymnotoids and mormyroids affect these prey in a manner that makes them more susceptible to predation. Either of these last two possibilities (or both acting together) would, in my opinion, go a long way towards explaining the evolution of almost all of the more peculiar trophic modifications exhibited by mormyroids and gymnotoids. I would go even further, and suggest that the interrelation between electrical faculties and feeding played a decisive role in the initial divergence of the gymnotoids and mormyroids from nonelectrically specialized ancestors.

Bottom feeding fishes with generalized trophic structures. Roughly a third of Amazonian and Congo fishes are bottom feeders. Mormyroids and gymnotoids, and Chilodontidae and Hemiodontidae among the characoids, are highly selective in removing food items from substrate. Most bottom feeders, however, including members of the large South American characoid family Curimatidae, cyprinids of the genus *Labeo,* and many catfishes, ingest considerable amounts of substrate with their food. No serious efforts have been made to determine what part of the ingested material these fishes digest. Obviously this will be difficult to work out. The food may be in virtually unrecognizable condition before ingestion, and is liable to be taken in with all sorts of nonnutritional material. Nevertheless, partitioning of food resources probably occurs in these bottom feeders. At first glance, the manner of ingesting quantities of bottom material might seem to preclude fine selection of food resources, but I expect this contention would disappear if we had more information about habitat selection and substrate preference of the bottom feeders.

One of the main reasons African characoids are less diverse than those in South America appears to be that in Africa other fish groups pre-empted certain major food resources. Mormyroids and cyprinoids, to cite what appear to be the two most important examples, appear to have largely or entirely taken over bottom feeding niches that might otherwise have been available to characoids. None of the African characoids, with the possible exception of *Citharinus*, have bottom feeding habits comparable to the Prochilodontidae and toothless Curimatidae of South America. In the Congo the cyprinoid genus *Labeo,* which parallels the family Prochilodontidae in certain respects, is represented by at least 22 species, most of them endemic. Much of the present diversity of African and South American characoids is probably due to relatively late radiations, and in Africa these radiations occurred in competition for food resources with a greater number of other fish groups.

Trophic specialization evidently played a major role in the adaptive radiation of characoids. The variety of characoid teeth, from simple conical elements to highly unusual forms of multicuspid teeth, is unparalleled by any other living group of vertebrates except mammals. The peculiar modes of tooth formation and tooth replacement characteristic of characoids apparently arose early in their history and provided the main morphological variations that led to the evolution of diverse feeding habits. These have been described and discussed elsewhere (Roberts, 1967).

Feeding habits of fishes in small Amazonian rain-forest streams. The stomach contents of 49 fish species from three rain-forest streams near Manaus were reported on by Knöppel (1970). His main conclusions (pp. 343–346) were:

1. Terrestrial insects (especially ants), aquatic insect larvae (especially Ephemeroptera and Trichoptera), and vegetable remains are major items in the stomach contents.
2. Most species exhibit considerable variability in the items ingested, and stomach contents of various families are relatively uniform.
3. Stomach contents of the same species collected at different times of the year (May, July, and November) are generally similar.
4. The fishes find their food in the whole living space, even those species that appear to be adapted to certain zones in the stream.
5. Distinct specialists in food ingestion are not present in the forest streams studied.
6. Neither the structure of the snout and denture, nor the morphological structure of the alimentary canal, nor even the intestinal ratio can be used as indices to the feeding habits.

The last three conclusions are too sweeping even as broad generalizations, and are not entirely in accord with statements in the main body of Knöppel's paper. Thus *Helogenes* and *Pyrrhulina* "picked up food nearly exclusively at the surface . . . yet most fishes find their food at the bottom" (*ibid.*, p. 341). The stomach contents of *Hoplias, Bryconops, Poecilobrycon, Iguanodectes, Pyrrhulina, Steatogenys, Eigenmannia, Curimatus, Chilodus, Cichla,* and many other forms reported on by Knöppel are precisely what one would expect from the morphology of their trophic structures. The numerous, sharp conical teeth of *Hoplias* are clearly those of a piscivore, and Knöppel found that adult *Hoplias* ingested only fishes (*ibid.*, p. 272). The fan-shaped teeth of *Poecilobrycon* and *Iguanodectes*, with numerous small cusps, are adapted to feeding on filamentous algae, and Knöppel found that considerable amounts of filamentous algae were ingested by *Iguanodectes* and *Poecilobrycon*. Dentition of similar appearance occurs in many small characids, and it is predictable that filamentous algae is an important food item for at least some of them. Concerning intestinal ratios, adult Curimatidae have extremely convoluted intestines, and this corresponds with their habit of ingesting large amounts of fine detritus, only a small (?) portion of which is nutritional. In six specimens of *Curimatus spilurus*? from 26.0 to 42.3 millimeters in standard length Knöppel found "sand (40%) and detritus (54%) in all stomachs"; in one stomach there was plant matter (*ibid.*, p. 276). While juvenile *C. spilurus* have "only a few concentric coils on the stomach sac" (*ibid.*, p. 335), I find that a 100-millimeter specimen has 21 concentric intestinal coils, some partly folded over on themselves, the entire mass filled with mud and occupying a space considerably greater than the space occupied by the stomach. The intestines are also extremely convoluted in *Curimatus latior*. Knöppel found that the stomach of a 151-millimeter specimen of this species contained "gray-black, very fine sand, and some larger grains" (*ibid.*, p. 276). One can also learn to recognize the morphology of trophic structures indicative of a mixed diet. Characid omnivores, for example, usually have moderate numbers of tri- to quinqui-cuspid teeth.[11]

The generalization about the relative lack of narrow trophic specialists in such small Amazonian streams is partly valid. Most of the highly specialized predatory characoids, such as piranhas and scale-eaters, are entirely absent. The commonest piscivore is probably *Hoplias,* which swallows its prey whole. Many nonpredaceous characoids with highly specialized trophic structures do not occur in small streams. Hemiodontidae, Prochilodontidae, and most genera of Anostomidae are absent. On the other hand, few fishes are more "distinct specialists in food ingestion" than the leaf fish *Monocirrhus polyacanthus,* one of the species studied by Knöppel, which feeds exclusively on small live fish (see Liem, 1970). Rhamphichthyid gymnotoids also have specialized means of ingesting their small prey.

ACKNOWLEDGMENTS

Thanks to Dr. P. E. Vanzolini, Director of the Museu de Zoologia of the University of São Paulo, I was able to participate in fieldwork of the Expedição Permanente da Amazônia on the Rio Solimões from September 20 to November 5, 1968. This provided an opportunity to see fishes in a great variety of habitats. EPA is a continuing joint effort of the Museu de Zoologia, Instituto Nacional de Pesquisas da Amazônia, and Museu Goeldi. It is financed by the Fundação de Amparo à Pesquisa of the state of São Paulo. The rich collection of fishes being assembled is kept at the Museu de Zoologia, under the curatorship of Sr. Heraldo A. Britski, to provide the basis for a systematic revision of the Amazon fish fauna.

I wish to thank M. Pierre Brichard for helping me to get acquainted with the fishes of Stanley Pool, and Sr. Willy Schwarz for providing me with an opportunity to visit the lower Rio Negro and Rio Jauaperi. Many colleagues have shared with me information about fishes from the Amazon and Congo. In this respect I must particularly thank Prof. George S. Myers. Very helpful comments on drafts of this paper were provided by Dr. Gerald R. Smith, Dr. Robert R. Miller, and Prof. Myers.

NOTES

1. Poll (1964) described *Congothrissa* from the cuvette centrale and designated for it a new family, Congothrissidae. Its relationships are discussed by Poll et al., (1965) and Thys van den Audenaerde (1969). It probably should be referred to the Pellonulinae.

2. The record of *Arius africanus* Günther from Stanleyville (Nichols and Griscom, 1917: 716) is probably a mistake. The specimen upon which it is based should be in the American Museum of Natural History. A recent search for it there was unsuccessful and it is presumed lost.

3. Specimens of sharks and sawfishes from the Amazon River have yet to be examined by persons competent to identify them. The Amazonian shark presumably is *Carcharhinus leucas,* the same species that occurs in Lake Nicaragua. A shark that probably was this species was photographed at Iquitos (Myers, 1952). Both *Pristis pectinatus* and *P. perrotteti* might be expected, at least in the lower Amazon. The Museum of Comparative Zoology possesses a watercolor by J. Burkhardt of a specimen of *Pristis perrotteti* taken by the Thayer Expedition at Pará on August 14, 1865, with the pencilled comments "Je possède un morceau du bec de ce poisson de Monte Alegre" and "M. le Col. Michille m'a dit qu'on en avait pris de'le Rio Madeira, au-dessus de Borba."

4. *Gnathodolus bidens* Myers (1927), a remarkable anostomid, is known only from the type specimens collected at the Orinoco-Casiquiare bifurcation.

5. Poll (1959: 160–161) considered the possibility of endemic fish species in Stanley Pool and concluded that there probably are none. Of 13 species he listed that were known only from Stanley Pool, five were subsequently recorded from Yangambi (Poll and Gosse, 1963).

6. The fish aquarists have observed depositing its eggs out of water is definitely not *Copeina arnoldi* Regan, but is probably either *Copella nattereri* Steindachner or *Copella compta* Myers (personal communication from G. S. Myers). Neal Foster has called my attention to the account of "*Copeina arnoldi*" spawning on a leaf above the water in their aquarium by Nieuwenhuizen (1964: 156–159), which is illustrated by excellent photographs. The fish in the photographs are *Copella.*

7. Most of the main rivers and streams in the Amazonian lowland are relatively poor in numbers of kinds and of individuals of molluscs and crustaceans. This is also true of the Congo. The paucity of these two groups is particularly striking when compared to their richness and abundance in lowland streams of portions of Southeast Asia. Aquatic leeches also seem to be more abundant in Southeast Asia. Perhaps molluscs, crustaceans, and leeches would be less abundant in Southeast

Asia if the dominant ostariophysans there were characoids instead of cyprinoids. G. R. Smith informs me that shrimp are fairly abundant in some Amazonian headwaters. This may be related to the relative paucity of their fish fauna. Many molluscs and crustaceans presumably would find black water habitats acidic and too poor in calcium and white water habitats too silty.

8. *Grasseichthys* is not the only minute kneriid in Africa. *Cromeria nilotica*, which attains a maximum standard length of about 28 millimeters, occurs in the main courses of the White Nile, Upper Niger, Mayo-Kebbi, and Volta rivers. It evidently spends much of its time buried in the sand. Because of its larval appearance, it was suggested at one time that *Cromeria* might be the young of an undescribed species, but no other kneriids have ever been reported from any of the basins in which it lives.

9. The characoid *Agoniates* is remarkable in feeding on other fishes when it is very small. On October 15, 1968, five specimens about 1–1½ inches long were caught in the Rio Solimões above Florianopolis. The stomach of each one was bulging with two or three cichlid young 5–8 mm long. Young *Agoniates* have rapacious dentition similar to that of adults. At this size most predaceous characoids (e. g., *Hydrocynus*) are probably insectivorous. *Agoniates* grows to about 150 mm.

10. *Anodus* and *Eigenmannina*, constituting the subfamily Anodontinae, are placed in the family Curinatidae by Eigenmann and Eigenmann (1889), Regan (1911), and Greenwood et al., (1966). This relationship, if true, is of considerable interest because in other Curimatidae gill rakers are absent or greatly reduced. All or almost all of the species are deposit feeders with highly convoluted intestines. Observations of mine indicate that *Anodus* is closely related to *Hemiodus*. The relationships of the families Hemiodontidae, Curimatidae, and Prochilodontidae to each other and to other characoid families are worth study.

11. Most of the small- to medium-sized Amazonian Tetragonopterinae (roughly 140 species) probably feed on whatever comes in their way (McConnell, 1969), benefiting greatly from insects falling into the water or emerging from aquatic larvae. The medium- to small-sized African characids allied to *Alestes* (about 40 species in the Congo) probably have similar feeding habits. In a remarkable instance of parallelism, the complex dentition of many small species of South American Tetragonopterinae (comprising a high proportion of species in the five largest genera of Characidae) is practically identical to that in small species of African Alestiinae. In these small characids of both continents, there are typically two rows of teeth in the upper jaw and two rows in the lower jaw; in the upper jaw the outer row consists of four to six relatively small and widely spaced tricuspid teeth, the inner row of eight to 16 multicuspid teeth; in the lower jaw the outer row consists of eight to 16 multicuspid teeth, the inner row of two relatively small conical teeth near the symphysis of the jaws. Occlusion apparently occurs only between the inner row of teeth in the upper jaw and the outer row in the lower jaw. Usually the number of cusps in these teeth is from three to five, but there are forms with as many as 20 cusps on each tooth. Some of the South American forms have conical teeth on the maxillary but these are usually small and apparently with little or no functional significance; the African forms invariably lack maxillary teeth. Poll (1967b) figured the dentition in most of the Congo species. In very general terms, the species with few cusps probably tend towards insectivory; those with intermediate numbers of cusps to mixed insectivory-herbivory; and those with the most cusps to herbivory.

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Bulletin of the
Museum of
Comparative
Zoology

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CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 143, NUMBER 3
27 JUNE 1972

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN 1863–
BREVIORA 1952–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
OCCASIONAL PAPERS ON MOLLUSKS, 1945–

Other Publications.

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FOSSIL SUIDAE FROM KANAPOI AND LOTHAGAM, NORTHWESTERN KENYA

H. B. S. COOKE[1] AND R. F. EWER[2]

CONTENTS

Abstract. During 1965–1968, expeditions from the Museum of Comparative Zoology, Harvard University, discovered and worked three deposits of fossiliferous sediments in the area southwest and west of Lake Rudolf, northwestern Kenya. One of these, Ekora, furnished relatively little material, but good assemblages came from Kanapoi and Lothagam. Fossil Suidae are fairly abundant and the material includes a number of excellent skulls and mandibles. Most of the suid specimens are assigned to the genus *Nyanzachoerus*, first recorded by L. S. B. Leakey in 1958 from Kanam, Kavirondo Gulf, Kenya. The most abundant Kanapoi suid is here named *Nyanzachoerus pattersoni*, differing from the type species *N. kanamensis* mainly in having stouter cheek teeth and a shorter diastema. A second Kanapoi species has much enlarged low-crowned third molars, with folded enamel, and it is named *N. plicatus*. The third new species, *N. tulotos*, is not present at Kanapoi but is distributed throughout the thick Lothagam-1 sequence. Its third molars are smaller than in the other species but the third and fourth premolars are larger; enlarged third and fourth premolars are one of the significant features of *Nyanzachoerus*. The upper canines have closed or nearly closed roots; the lower canines tend to be U-shaped towards the base. The skulls resemble *Hylochoerus* in general size and morphology but the braincase is more elevated. There is strong sexual dimorphism and the zygomatic arches are expanded, developing hollow bony protuberances or bosses in the male. A few fragments, which may be *N. pattersoni*, occur in Lothagam–1 and *N. plicatus* occurs in

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Lothagam–3. Only *N.* cf. *plicatus* occurs at Ekora, which is stratigraphically younger than Kanapoi. At Kanapoi there are scraps of a very large *Notochoerus*, possibly close to *N. capensis* Broom, and a smaller form resembling the Kaiso species *N. euilus* Hopwood; the latter also occurs in Lothagam–3 and is known to occur in the lower Omo beds (Shungura Formation). Both *N. pattersoni* and *N. plicatus* occur in the Mursi Formation ("Yellow Sands") in the Omo area, dated at 4.05 million years. The Lothagam beds are cut by a basalt dated at 3.71 million years, thus providing a minimum age for the entire sequence. The Ekora Beds are estimated to be a little younger than the Mursi Formation, which must be closely equivalent to the Kanapoi beds and Lothagam–3. The base of the Lothagam sequence is probably close to 5.5 million years. Correlations with other formations are suggested.

INTRODUCTION

Since the publication of Leakey's survey of the East African fossil Suidae (1958), a substantial amount of new material has been recovered from various deposits in this region, in many cases including more complete specimens that make it possible to modify or extend earlier work. In particular, a recently discovered deposit at Kanapoi, southwest of Lake Rudolf in northwestern Kenya, has yielded suid material that probably constitutes the finest collection yet found at any single fossil locality in Africa. There are a number of well-preserved skulls, some of them almost complete, and good lower dentitions also. Another new locality at Lothagam Hill, 40 miles north of Kanapoi, has furnished a single complete skull, a number of mandibles, and other remains. It would appear from a close study of the collections that most of the material from these two deposits must be assigned to the genus *Nyanzachoerus*, of which there are two very different new species at Kanapoi and a third new one at Lothagam. The specimens extend greatly our knowledge of this extinct genus. Other genera and species of Suidae are represented both at Kanapoi and at Lothagam, but the material is scanty and incomplete so that specific diagnosis is difficult. Although this account deals with all the suid remains from these sites, it is concerned mainly with *Nyanzachoerus*.

The Kanapoi locality (Fig. 1) was discovered in 1965 by an expedition from the Museum of Comparative Zoology, Harvard University, which had been working for several years in the Miocene beds of Turkana, northwestern Kenya. A short general account of the local geology and preliminary list of the fauna was published by the leader of the expedition, Professor Bryan Patterson (1966), and the age of the deposit was tentatively assessed as early Pleistocene (Villafranchian). The base of the sediments is not exposed, but the sequence consists of more than 200 feet of material ranging from clays to conglomerates. A lower division of clays, silts and some sandstones can be recognised, and appears to be essentially lacustrine in origin; nearly all the suid material came from these deposits. The upper division consists mainly of coarser clastic debris mixed with layers of finer sediments and it is probably fluviatile in origin. Capping the sediments is a basaltic lava, with reversed magnetic polarity. Samples from one spot have provided potassium-argon ages of 2.5 ± 0.2, 2.9 ± 0.3, and 2.71 ± 0.26 million years (Patterson, Behrensmeyer and Sill, 1970). The fossil material includes the distal end of a hominid humerus (Patterson and Howells, 1967), which is possibly *Australopithecus* (but not *Paranthropus*). As will be discussed later, the faunal evidence suggests an age for the sediments considerably greater than that given by the Kanapoi basalt, although there is no field evidence for any erosion interval below the lava, nor was evidence seen to suggest that it is intrusive. (See footnote on page 226.)

The Kanapoi sediments and the overlying basalt were traced northeastwards for about 15 miles to Ekora (Fig. 1). At this locality only the uppermost Kanapoi beds are exposed but the basalt is overlain by a group of silty to gritty sediments, the top of the sequence being concealed. Some

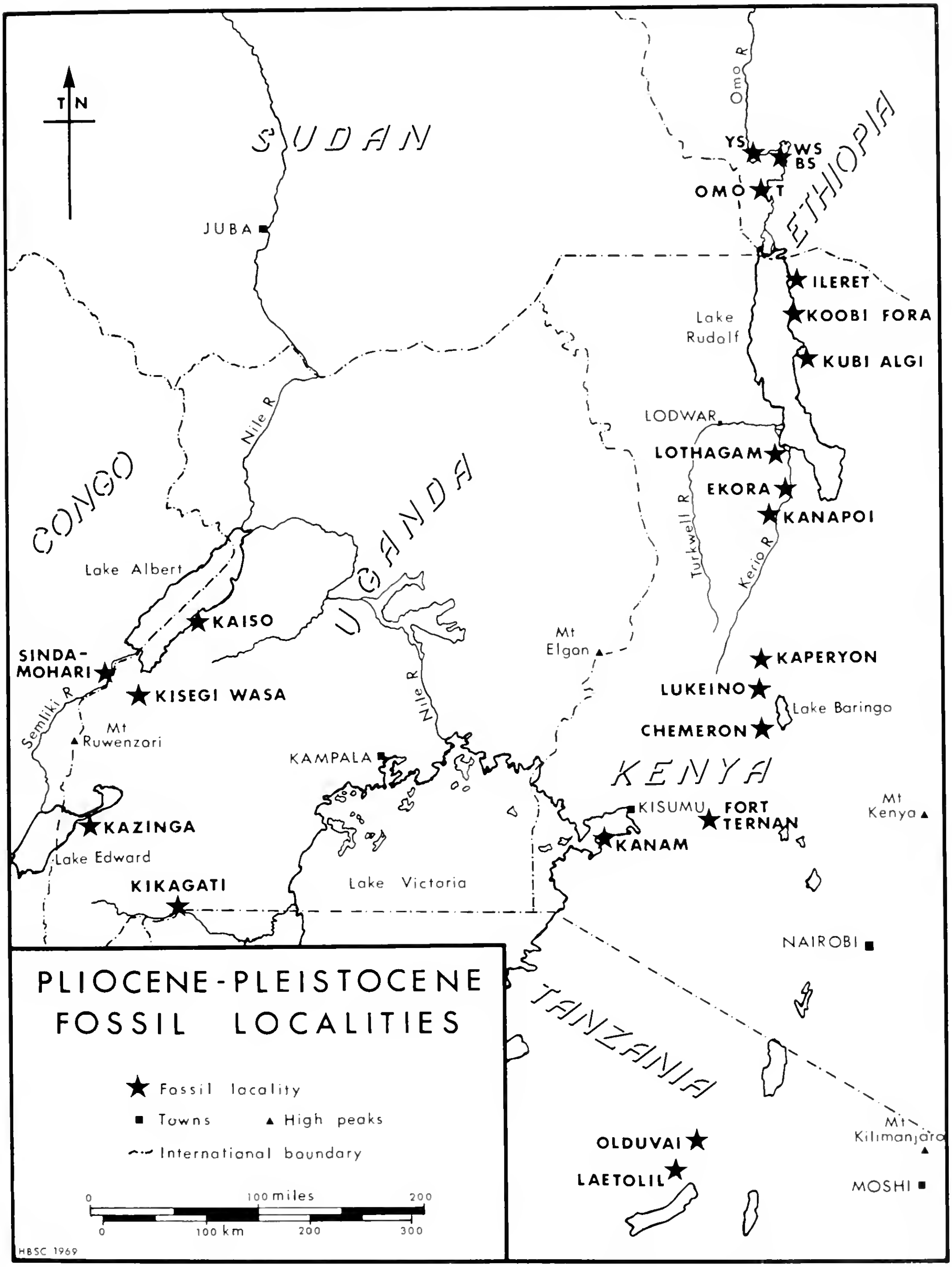

Figure 1. Map of part of East Africa to show the principal Pliocene-Pleistocene fossil localities. In the Omo area, north of Lake Rudolf, the abbreviations used are as follows: T—type area (Shungura Formation); WS—"White Sands" and BS—"Brown Sands" (Usno Formation); YS—"Yellow Sands" (Mursi Formation).

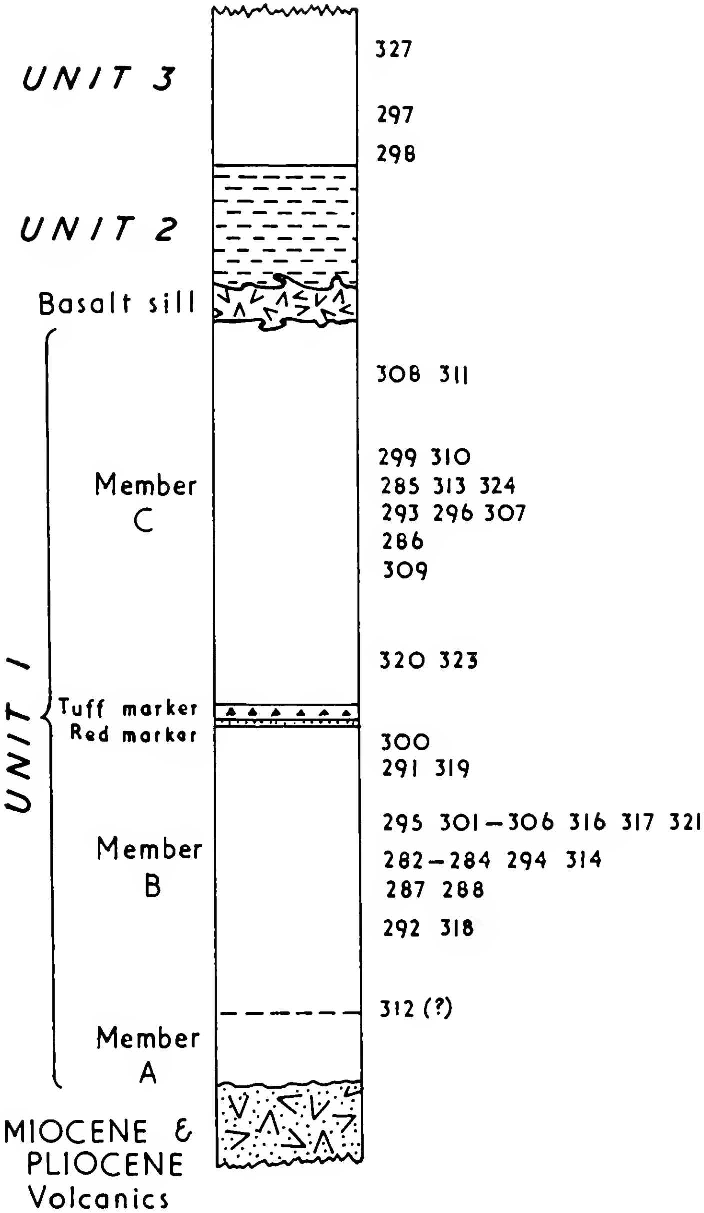

Figure 2. Composite columnar section of the Lothagam sequence, 2000 feet thick, showing the horizons from which the suid specimens were recovered. (*Stratigraphy after Miss A. K. Behrensmeyer.*)

excellent proboscidean remains were recovered from these Ekora beds, but only a few fragmentary suid specimens were found.

In 1967, the expedition continued its work in northwestern Kenya at another new locality at Lothagam Hill, some 40 miles north of Kanapoi on the west side of Lake Rudolf, not far from the deltas of the Kerio and Turkwell rivers (Fig. 1). The

TABLE 1. STRATIGRAPHIC DISTRIBUTION OF SUIDAE FROM LOTHAGAM, KANAPOI, AND EKORA

	LOTHAGAM				
	Unit 1 Memb. B	Unit 1 Memb. C	Unit 3	KANAPOI	EKORA
Nyanzachoerus pattersoni	cf.	cf.		x	
Nyanzachoerus plicatus		x	x	x	cf.
Nyanzachoerus tulotos	x	x			
Nyanzachoerus spp.	x	x		x	
Notochoerus cf. *capensis*				x	
Notochoerus cf. *euilus*			x	x	
Suidae indet.	x			x	

fossil material comes from several horizons within a thick sedimentary sequence that rests unconformably on Miocene/Pliocene lavas and associated boulder conglomerate. Hominid material was found but is undescribed (Patterson, personal communication). The area was mapped in 1967 by Dr. W. D. Sill and again, in more detail, in 1968 by Miss A. K. Behrensmeyer, who recognised three sedimentary units (Patterson et al., 1970). The lowest (Unit 1) is 800 to 1500 feet thick and consists of coarse conglomerate near the base (Member A), followed by irregular alternations of fine conglomerates, thinly bedded sandstones, silts, and occasional shales or tuffaceous shales. Near the middle of this sequence there is a conspicuous red silty band overlain by about 30 feet of tuff, which forms a useful "marker" horizon between the upper two members of the unit (see Fig. 2). The best suid material comes from Member B; the lower horizons of Member C furnished very little suid material, but these fossils were again moderately plentiful higher up. The beds of Unit 1 appear to represent fairly continuous and rapid deposition on an aggradational plain, probably a delta. Unit 2 comprises some 250 feet of lacustrine clays and silts, almost devoid of fossils; a fairly substantial time must have been involved in the deposition of this unit. Unit 3 comprises more than 300 feet of medium to coarse-grained clastic sediments, probably of fluviatile origin; the top of the sequence is concealed. Only a few fossils have come from these upper beds. The contact between the fluviodeltaic deposits of Unit 1 and the lacustrine beds of Unit 2 is obscured by an intrusive basaltic sill, about 80 feet thick, so that their exact mutual relationship is uncertain. A potassium-argon age of 3.71 ± 0.23 million years has been obtained for this basalt, thus providing an upper limit for the age of the whole of the Lothagam succession (Patterson et al., 1970). Figure 2 gives a diagrammatic columnar section for the sequence and shows the horizons from which the principal fossil suid specimens were derived.

Table 1 lists the suids identified from Kanapoi, Lothagam, and Ekora. The whole assemblage suggests that the Kanapoi beds could not be older than the top of Unit 1 at Lothagam, but might be as young as the fluvial deposits of Unit 3. The Ekora beds are younger than the Kanapoi beds, but there is no reason to believe that a long gap intervenes. Even if the base of the Pleistocene extends back as far as 3.0 million years, the Ekora beds are probably Upper Pliocene. The Kanapoi beds must also be Upper Pliocene and Unit 1 at Lothagam Middle Pliocene.

THE GENUS *NYANZACHOERUS*

The type species of the genus, *Nyanzachoerus kanamensis*, was established by Leakey in 1958 and was based on three specimens from Kanam West, Kenya. The holotype is a left mandibular ramus having the canine and cheek teeth, but lacking incisors (British Museum Natural History [BMNH] no. M 15882). The first paratype is a fragment of a right mandibular ramus with RM_2 and RM_3 (Kenya National Museum, Nairobi [KNM]). The second paratype was an upper right third molar (BMNH M 16383) found 15 years later at the same site as the holotype and believed by Leakey possibly to belong to the same individual. However, the upper molar is well abraded, whereas the holotype M_3 is very little worn, so that this possibility can be excluded. Furthermore, the upper molar is rather short in relation to the lower third molars (42.5 mm as against 50.5 mm) and there is a good possibility that this tooth belongs to another species; it is, in fact, very close to the new Lothagam species, *N. tulotos,* in which the upper molars average 40.8 mm in length and the lowers 41.7 mm. Accordingly, the second paratype must be treated with caution and is here regarded as representing an undetermined suid, probably not *N. kanamensis.*

The genus was originally diagnosed by Leakey (1958) as follows:

> "A genus of Suidae with enlarged 3rd and 4th lower premolars resembling those of *Tetraconodon* Falc., but more laterally compressed. Upper and lower molars closer to those of *Sus* than of *Potamochoerus.* Lower canines of verrucose type."

The specific diagnosis for *N. kanamensis* was as follows:

> "A species of *Nyanzachoerus* of medium size and with the length of the dental series P_3 to M_3 greater than 150 mm. 2nd premolar much reduced, compared with the very large P_3 and P_4. The index $P_{3-4} \times 100/M_{1-3}$ above the range of *Sus* and *Potamochoerus.*"

The enlargement of the third and fourth premolars, which may be regarded as the essential basis for the establishment of the genus, is apparent in all the new material, both in the lower and in the upper dentitions. The second premolars are not correspondingly enlarged but retain about the size relationship to the molar teeth that is normal in *Sus* or *Potamochoerus;* they *appear* reduced because of the contrast in size to the adjoining third premolar. The enlargement of the premolars is not, in fact, very like that found in *Tetraconodon* (or in *Conohyus*), and there is no indication of any connection with the Indian forms. The degree of enlargement and the relative proportions of the teeth vary with the different species now recognized. A revised diagnosis for the genus and for the type species may now be given.

Class *MAMMALIA* Linnaeus 1758
Order **Artiodactyla** Owen 1848
Infraorder **Suina** Gray 1868
Family SUIDAE Gray 1821
Genus *Nyanzachoerus* Leakey 1958

Revised diagnosis. A genus of Suidae with cheek teeth similar to *Potamochoerus* in basic structure but tending to be more hypsodont and with main cusps of molars more distinctly columnar; third and fourth premolars relatively enlarged and more hypsodont than in *Potamochoerus.* Lower fourth premolar with three roots. Incisors similar to those of *Potamochoerus.* Upper canines oval to flattened oval in cross section, bearing little or no enamel, and with closed or nearly closed roots. Lower canines U-shaped or heart-shaped in cross section near the base, becoming more verrucose or triangular towards the tip; thin, weakly grooved enamel on two lateral faces; roots partially closed or open. Strong sexual dimorphism exhibited in size of canines and massiveness of skull; hollow bony protuberances or bosses on zygomatic arches present in male, weak or absent in female. Corpus of mandible heavy and contrasting markedly with unusually thin bone forming the angle.

Type species: *Nyanzachoerus kanamensis* Leakey 1958.

Nyanzachoerus kanamensis Leakey

Nyanzachoerus kanamensis Leakey, 1958: 4, pl. 1.

Revised diagnosis. A species of *Nyanzachoerus* somewhat larger than the extant *Hylochoerus.* Lower third molar with three pairs of lateral pillars and small to moderate posterior pillar on the talonid; length about two and one-fourth times breadth. Molars brachyodont, less columnar in structure, and relatively narrower than in *N. pattersoni.* Premolar series (P_2–P_4) about 60 per cent of the length of the molar series; P_3 more than half the length of M_3 and narrow, with length/breadth ratio about 1.9; P_4 shorter and wider than P_3, with length/breadth ratio about 1.3. Diastema from canine to P_2 substantially longer than length of premolar series P_2–P_4. P_1 apparently absent. Upper dentition not certainly known.

Holotype. BMNH M 15882: left mandibular ramus with canine and cheek teeth, but lacking incisors.

Paratype. KNM-KW: fragment of right mandibular ramus with RM_2 and RM_3.

Locality. Kanam West, Kavirondo Gulf, Kenya.

Horizon. Probably Plio-Pleistocene or Upper Pliocene.

Remarks. There is a considerable resemblance between the lower dentitions of *N. kanamensis* and the new Kanapoi species *N. pattersoni.* In the latter, however, P_3 is shorter and wider, having a length/breadth index of about 1.3 (instead of 1.9), and P_4 is slightly longer, but stouter, than the corresponding tooth in *N. kanamensis.* M_1 and M_2 have about the same width in the two species, but these two molars are longer in *N. kanamensis* than in *N. pattersoni.* In keeping with the relatively narrower and more elongate cheek teeth in *N. kanamensis,* the mandible is also more elongate and the diastema between P_2 and the back of the alveolus of the lower canine is much longer than in *N. pattersoni* (67.5 mm compared with 48–50 mm).

TWO NEW *NYANZACHOERUS* SPECIES FROM KANAPOI

Nyanzachoerus pattersoni sp. nov.*

Text-figures 3–6; Plates 1–9

Diagnosis. A species of *Nyanzachoerus* somewhat larger than the extant *Hylochoerus.* First premolars vestigial or absent. P^4 considerably narrower than M^3. Upper third molar with two pairs of lateral pillars and talon, length about 1.6 times breadth; brachyodont, maximum height of unworn third molar approximately 70 per cent maximum breadth. Lower third molar with three pairs of lateral pillars and stout posterior pillar, length about twice breadth. P_3 and P_4 robust, with length/breadth ratios of about 1.3 and 1.1 respectively. P_4 about two-fifths as long as M_3. Diastema from lower canine to P_2 substantially shorter than length of the premolar series P_2–P_4. Upper and lower premolar series (P2–P4) 60–70 per cent of the length of the molar series. In the male, maxillary flanges present round the bases of the canines but not particularly strongly developed; opposite the flanges there are slight thickenings at the level of the nasopremaxillary suture. Zygomatic protuberances extremely large in the male; towards the back they are deep dorsoventrally, appearing pear-shaped when viewed from the side, with lower margin not horizontal but curving downwards to approximately the level of the palatal plane. Female without maxillary flanges and with reduced zygomatic protuberances.

Holotype. KNM–KP 239: almost complete skull and associated mandible of adult female, together with the atlas and a damaged thoracic vertebra.

Paratype. KNM–KP 264: damaged skull and associated incomplete mandible of old male.

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* *N. pattersoni* has been referred to in several preliminary faunal lists as *Nyanzachoerus* species "A."

Locality. Kanapoi, northwestern Kenya.

Horizon. Kanapoi sediments; probably Upper Pliocene.

REFERRED SPECIMENS

Cranial (in approximate order of dental age). KNM–KP 222: fragment of right maxilla with Rdm^4 and part of RM^1. KP 244: almost complete skull of immature (subadult) individual with M^3 in alveolus; back of occiput missing. KP227: part of skull of immature (subadult) individual with M^3 in alveolus; cranium and snout missing. KP223: incomplete skull of young adult; occiput and snout missing. KP201: part of right maxilla of young adult with cheek teeth preserved. KP231: incomplete snout and partial palate of old female, lacking teeth except part of RM^3 and base of left canine.

Mandibular (in approximate order of dental age). KNM–KP 221: parts of left and right mandibular rami with milk teeth and RM$_1$. KP 266: part of left mandibular ramus with canine, milk teeth, RM$_1$ and RM$_2$. KP 213: part of left mandibular ramus of subadult with LP$_3$–M$_2$ and LM$_3$ partly erupted. KP 255: part of left mandibular ramus of young adult with LP$_4$–M$_2$. KP 256: part of right mandibular ramus of young adult with RP$_4$–M$_3$. KP 263: part of left and right mandibular rami of adult with LP$_3$–M$_3$ and roots of RP$_2$–M$_3$. KP 240: parts of left and right mandibular rami of adult with LM$_2$–M$_3$, RM$_3$ and roots of anterior cheek teeth. KP 258: part of left mandibular ramus of adult with LM$_3$ and roots of LP$_4$–M$_2$; fragment of right mandibular ramus without teeth. KP 219: damaged mandible of old individual; incisors and canines broken or missing. KP 259: part of left mandibular ramus of an old individual with LM$_2$ reduced to dentine and LM$_3$ almost patternless.

Cheek teeth. A number of isolated and fragmentary teeth are referred to this species; of these measurements only on the following are included in the tables: KNM–KP 205 (RM$_1$ and LM^2); KP 220 (RM$_2$); KP 228 (RM$_1$); KP 260 (RM$_2$).

Postcranial. KNM–KP 215: left tibia, some bones of the left pes and right manus, associated with tooth fragments and a right lower canine. KP 243: right tibia and right third metatarsal.

DESCRIPTION

The Holotype Skull and Mandible

The holotype skull (KNM–KP 239) is unusually well preserved, the only major damage being the loss of the nasals and the roof of the skull. The occipital crests are missing and the left zygomatic arch is incomplete. The tip of the premaxilla on the left side is lost, but two of the three incisors are present on the right side, as well as the socket for the third incisor. Both canines are preserved and the cheek teeth on both sides are intact (Pl. 1). Associated with the skull, and fitting to it, is a well-preserved mandible, with a few of the cheek teeth intact and others damaged (Pls. 2, 5).

The skull is about the same size as that of *Hylochoerus* and closely resembles the latter in general architecture. The zygoma, however, is more inflated, like that of *Phacochoerus* and the snout is rather more like that of *Sus* or *Potamochoerus.* The vertex length is estimated to have been approximately 480 mm and the zygomatic breadth was about 270 mm compared with 430 and 250 mm respectively in *Hylochoerus.* The vertical height of the crest of the occiput above the palatal plane was approximately 15–20 mm more than in the forest hog, but this is about in proportion to the rest of the skull. The muzzle is rather narrower, the width across the maxillae between the front edges of the infraorbital foramina being only about 50 mm compared with 70 mm in *Hylochoerus.* In the forest hog this foramen lies directly above the boundary between M^1 and M^2; in the fossil it is directly above the back half of P^3. As in *Phacochoerus,* the back-

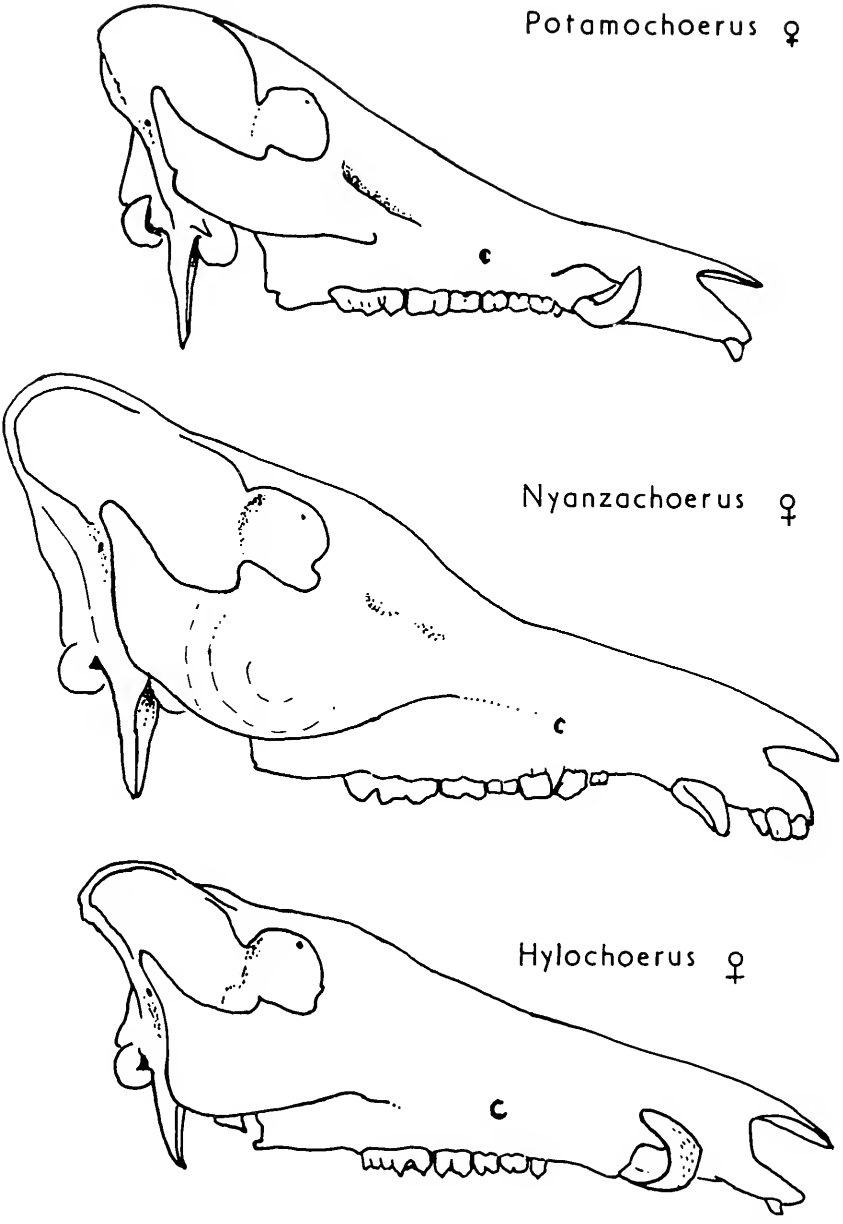

Figure 3. Reconstruction of the skull of the holotype (female) of *Nyanzachoerus pattersoni* (centre) compared with *Potamochoerus* (above) and *Hylochoerus* (below). The specimens are aligned on the front of the orbit and have the occlusal plane horizontal. × ¼.

ward flare of the maxillary portion of the zygomatic arch commences a good deal further forward than in *Hylochoerus*. The difference in contour will be seen in the comparative drawings in Figure 3. The effect is to make the braincase appear relatively longer and the snout shorter than in *Hylochoerus*. The "droop" of the snout below the plane of the cheek teeth is slightly exaggerated by fracturing, but was rather more pronounced than in *Hylochoerus* and less extreme than in *Phacochoerus.*

The back of the occiput, as far as it is preserved, is like that of *Potamochoerus* or *Phacochoerus* and there is no sign of the median vertical ridge that occurs in the forest hog. Although the occipital crests are lost and the upper part of the skull is damaged, it is clear that the crests were not quite as wide as in *Hylochoerus.* It is also clear that the contour of the frontoparietal region was flat or slightly depressed although not to the extent seen in *Hylochoerus* (described by Ewer [1958] as having "a highly characteristic collapsed appearance, like a badly baked cake"). The top of the braincase is higher and the slope of the frontoparietal region is a little steeper in the fossil than in the forest hog. The occipital condyles and glenoid cavity are relatively higher above the occlusal plane, although this is not nearly as exaggerated as in *Phacochoerus.* The glenoid itself is moderately wide from front to back, as in *Hylochoerus*, and is quite unlike the narrow transversely elongated bar found in *Phacochoerus.*

In correlation with the more elevated glenoid, the zygomatic portion of the squamosal slopes up more steeply from the jugal than in *Hylochoerus;* the external ear openings are considerably higher and the ascending ramus of the lower jaw must also have been higher in the fossil.

In *Hylochoerus*, both the jugal and the squamosal underlying the zygomatic wart are thickened to form a protuberance that breaks the smooth contour of the zygoma. As already noted, this thickening is exaggerated in the fossil, forming a distinct and rather knoblike dilation. Despite the fact that the inner surface of the zygoma is slightly hollowed out beneath it, the bone in the centre of the protuberance reaches a thickness of 32 mm; the jugal is also vertically much deeper than in *Hylochoerus*, the lower border of the expanded portion drooping considerably. Behind the rounded posterior margin of the 'knob,' however, the posterior part of the zygoma is extremely slender, as in *Potamochoerus.* As will be seen in the account of the paratype (Pls. 2 and 3), this zygomatic knob is excessively exaggerated in what is believed to be the male of the same species, the holotype being regarded as a female.

From the palatal aspect, the general resemblances to *Hylochoerus* are again apparent, in part because of the similar basic outline of the zygomatic arches. There are, however, a number of differences. The greater vertical distance between the palatal plane and the glenoids and occipital condyles has already been mentioned. The paramastoid processes would therefore be expected to be longer than in *Hylochoerus;* although the tips have been broken off, the robust basal portions suggest that this was indeed the case. The auditory bullae are slender and subtriangular in cross section and are much less inflated than those of *Hylochoerus.* The posterior ends of the palatines are damaged, but the parts that remain do not suggest any major difference from *Hylochoerus.* The palatine notch, however, is much narrower; in fact no wider than in *Potamochoerus.*

The general shape of the palate in the holotype is somewhat intermediate between that of *Hylochoerus* and *Potamochoerus*, largely because the fossil lacks the expanded bony buttresses that contain the roots of the canine teeth in the forest hog. However, the shape of the anterior part of the palate and premaxilla is like that of *Hylochoerus* in being expanded between the canines and in tapering both behind and in front of them, rather than being parallel-sided as in *Potamochoerus.* (In the larger male, as will be seen later, the palate is much more hylochoerine.)

The upper dentition is virtually complete. In life all three incisors were present, although the third incisor is missing from the holotype and is represented only by the root cavity, filled with matrix. The first and second incisors are both large teeth, almost equal in size; the alveolus of I^3 shows that this tooth also was large. The I^1 is well worn, but the shape of the dentine area suggests that its morphology was much the same as that of the less worn I^2. The latter tooth shows a structure comprising a broad anterior cone and a narrower posterior cone; on the posterointernal flank of the hinder cone are two small tubercles or conelets. In front of the foremost of these conelets, and thus lying on the lingual surface of the crown between the main cones, is a small fovea enclosed by a thin lingual ridge, almost like a weak cingulum. Comparison with the living African forms is not meaningful as the incisors in all three forms are specialized in one way or another; other comparisons are difficult to make as these teeth are seldom found in fossils. The structure of the incisors is very similar to that shown in the second premolar.

The upper canines are small, being comparable in size, position, and angle of emergence, with the corresponding teeth in *Potamochoerus.* As in the latter, there is an anterior wear facet that is practically at right angles to the axis of the skull. The bases of the canines were surrounded by thin extensions of the maxillary bone, but there is no indication of the vertical "wings" exhibited by *Potamochoerus.* Morphologically the canine is unlike that of *Potamochoerus, Sus,* or *Hylochoerus.* In cross section it is oval, slightly pointed anteriorly and flattened posteriorly, as well as slightly flattened dorsally and ventrally (see Fig. 5). This is similar to the shape found in the tips of very young canines of *Phacochoerus.* There is a thin coating of enamel, apparently confined to the tips of the teeth, and this is smooth except for weak longitudinal ridges or striations. The small size of the tusks, despite the fact that they belong to an adult animal, suggests that the canines have closed roots, or roots that are nearly closed. There is a strong morphological resemblance to the canines of "*Promesochoerus mukiri*" and "*Ectopotamochoerus dubius*" (Leakey, 1965), although there is no other close resemblance to those species.

There is a short diastema between the back of the canines and the front of the small second premolar. In the centre of this gap, on the left side, there is what might possibly be the mark of a root for a very small P^1, but it is not at all certain that this tooth was ever present; there is no corresponding mark on the other side. Relative to the molars, the third and fourth premolars are extremely large, as compared with those of *Sus* or *Potamochoerus.* The first molar is worn down to dentine, with only traces of enamel. The second molar is well worn, and the third molar is in moderate wear with the hindmost large cusp of the talon in early wear. The dentition thus represents a young adult, presumed to be female. The details of the cheek teeth will be included in the systematic account of the dentition.

The mandible, which fits the skull, lacks the left mandibular ramus behind the third molar and also the upper part of the ascending ramus on the right side. In size and general morphology, it is very similar to the jaw of *Hylochoerus,* being fairly thick in the corpus to a point anterior to the level of the back of the symphysis. However, the canines are relatively smaller than in *Hylochoerus* and, consequently, the symphysial region is not so broad and flat and is therefore somewhat like *Potamochoerus* in this respect. The arch of the incisors is intermediate between the condition in the two living forms.

All six incisors are present, and they correspond in size relationships and general morphology to those of *Potamochoerus.* As in the bushpig, there is a ridge along the posterior (upper) face of the enamel in each incisor, although in the fossil the ridge is more marked than in the bushpig, so that this aspect of the tooth is broadly triangular in section. The demarcation between the base of the enamel and the roots is more clearly marked than in *Potamochoerus.* The tips of the four central incisors are worn in a straight line at the front of the jaw, but the tips of the third incisors extend only to a position about half way along the body of the second incisor, as in *Potamochoerus,* and their tips are only slightly worn.

The lower canines are of the verrucose type and resemble those of *Hylochoerus* in being slightly convex on both lingual and buccal faces, lacking any indication of the broad concavity or groove typically present on the buccal face in *Potamochoerus.* The tooth is more compressed laterally than in *Potamochoerus* or *Hylochoerus* and the lingual face is only slightly longer than the buccal one. There is no enamel on the posterior face, even beyond the area of abrasion. The enamel is fairly thin and has the same texture as in *Potamochoerus.* The wear facet on the tip of the posterior face, matching that of the upper canines, is vertically oriented and at right angles to the long axis of the skull. It is virtually indistinguishable from the lower canine of "*Ectopotamochoerus dubius*" Leakey (1965).

Of the cheek teeth, the right third premolar, both second premolars and both third molars are preserved intact; the left third and fourth premolars are damaged posteriorly, and the left second molar is slightly damaged, but the remaining teeth are broken away. Details of the teeth are included in the systematic account of the dentition, given below. As the first molars are missing and the P_4 is damaged, the descriptions of these teeth are, of necessity, based on referred specimens.

The Atlas of the Holotype

Associated with the holotype skull were three vertebrae, a well-preserved atlas that fits the skull, a mid-thoracic vertebra, and an incomplete centrum. The thoracic vertebra is incomplete and in poor condition but corresponds reasonably closely with the seventh vertebra in *Hylochoerus,* both in size and general morphology.

Figure 4. Diagrammatic sagittal section of the roof of the neural canal in the atlas vertebrae of A, *Phacochoerus* and B, *Nyanzachaerus pattersoni.* The thick line shows the area of attachment of the rectus capitis dorsalis muscle. The arrow indicates the direction of the neural canal.

The atlas is very similar in size to that of *Hylochoerus* but is a little more massive in construction. The wings do not have the unusual, almost rectangular outline characteristic of *Phacochoerus* but are more rounded, as in *Potamochoerus* and *Hylochoerus,* the resemblance being closer to the latter. The fossil atlas is relatively deeper dorsoventrally than in any of the extant species, but this is due more to thickening of the bone and larger dorsal and ventral tuberosities than to enlargement of the neural canal or difference in shape of the articular facets. In none of the extant species is the ventral tubercle very large, whereas in the fossil there is a conspicuous downward conical bulge behind the rim of the anterior articular cavity, which tapers off towards the middle of the centrum. In the three extant species the atlas bears a roughened central area in the anterior region of the neural arch. This represents a somewhat tendinous attachment of the deepest fibres of the rectus capitis dorsalis muscle. In the warthog this roughened area is oriented almost at right angles to the line of the neural canal and to the plane of the wings of the atlas. The roof of the neural canal is therefore deeper at its anterior than at its posterior margin (Fig. 4a). In *Hylochoerus* there is considerable individual variation, but the roughened surface always slopes obliquely backwards so that it forms a more acute angle with the neural canal and the plane of the atlantal wings; its posterior margin forms a raised hump on the neural arch. The difference is presumably related to the carriage of the head, which is much more vertical in *Phacochoerus* than in *Hylochoerus*. In the fossil the condition is much as in *Hylochoerus*, with the facet sloping backwards so that its posterior margin lies midway between the anterior and posterior margins of the neural arch (Fig. 4b). Presumably this reflects the more or less normal carriage of the head in *Nyanzachoerus*.

The Paratype Skull and Mandible

The skull of the paratype (KNM–KP 264) is badly damaged at the back so that the entire basicranial region is lost. The frontal and orbital margins are damaged and the whole of the left zygomatic arch is missing. The right zygoma is fairly complete except in the temporal region. There is also an isolated fragment comprising a large part of the back of the parietal and occiput, with portions of the adjoining temporal areas. Unfortunately, it is incomplete and no direct contact with the skull remains. In the illustrations (Pls. 2 and 3) it has been placed in its approximate position. Also isolated is a fragment of the temporal around the external auditory meatus; it displays a long vertical process above the ear opening, even more developed than in *Hylochoerus*. The cheek teeth are partly preserved on both sides but are in very advanced wear and the anterior teeth are almost featureless; the premolars are broken off at the roots on the right side.

The skull is substantially longer than that of the holotype, with an estimated vertex length about 10 cm greater. The entire nasomaxillary region is very much wider than in the holotype and extremely like that of *Hylochoerus* in outline, but more massive. The basically *Hylochoerus*-like morphology is obscured by the fact that the jugal region is expanded into an enormous boss or protuberance so that the bizygomatic breadth is in the vicinity of 480 mm, i. e., 80 per cent of the vertex length, as compared with about 55 per cent in the holotype and in *Hylochoerus*. The animal's appearance in life must have been extraordinary. At first it was considered that this represented a species different from the holotype, but there are so many similarities in general morphology and in the dental characters that this consideration is most improbable. Accordingly, the specimen is now regarded as a large old male of the same species, and it is inferred that there was very strong sexual dimorphism. This point will be discussed in more detail later. Comparative measurements (including estimated measurements) on the two specimens are given in Table 2.

Although the supraorbital foramina lay in the missing portion of the braincase, the two grooves leading to them are present and these are flanked on the outer side by strong ridging as in *Hylochoerus*. However, in the forest hog the region between the grooves is raised and forms a rounded hump, which continues down the nasals; in the fossil, this area is flattened, as is also the nasal region generally. The flat nasal area meets the maxillae on either side at a fairly abrupt edge, like that in *Potamochoerus* (and in the holotype) so that the snout does not have the rounded contour seen in *Hylochoerus*. The bony flanges surrounding the upper tusks are very similar to those of *Hylochoerus*, as is also the shape of the premaxillary region. The zygomatic arch begins to flare out immediately behind the infraorbital foramen and the contours of the maxilla-lacrimal and maxilla-jugal regions correspond exactly to those in the holotype. As in the holotype, the anterior margin of the jugal protuberance slopes outwards and backwards to reach its maximal lateral extension at approximately the level of the orbit; from this point it turns in abruptly, so that the posterior margin is virtually at right angles to the skull and the protuberance does not extend back beyond the orbit. The ventral surface of the jugal is turned outwards, somewhat in the manner found in *Phaco-*

TABLE 2. MEASUREMENTS OF SKULLS OF *NYANZACHOERUS PATTERSONI* COMPARED WITH *HYLOCHOERUS MEINERTZHAGENI* AND *POTAMOCHOERUS PORCUS**

	Holotype KP 239 ♀	Paratype KP 264 ♂	Referred KP 231 ♀	*Hylochoerus* MA 1 H 1† ♂	*Potamochoerus* MA 1 Po 6† ♂
Vertex length	480 e	580 e		428	357
Basilar length	425	500 e		375	307
Bizygomatic breadth	c270	c480		246	171
Greatest breadth across nasals	53	71		56.5	60
Breadth of muzzle between infraorbital foramina	48	66	49	71	27
Parietal constriction		76		96	25.5
Palatal length	301	352		283	234
Palatine notch width	28.5	28.0	28	40.5	17.0
Breadth of palate					
— between $M^3 - M^3$	33	40	35	46	23.5
— between $P^2 - P^2$	52.5	73	59	59	38.5
Premaxilla breadth over $I^3 - I^3$	69	95		51.5	40.5
Diastema $I^3 - P^2$	72	101		119.5**	81.5
Diastema $C - P^2$	39.5	c35	c40	35.0	31.5
Length premolar series	51.9	68.0	c61.5	24.5	35.0***
Length molar series	95.2	99.1	c99.5	77.0	70.0
Length $P^2 - M^3$	147.0	161.6	c161.0	101.5	105.0***

* In this and all the subsequent tables, measurements are given in millimetres. The abbreviations "c" (for circa) is employed before a figure to indicate an approximate measurement; the abbreviation "e" is used after a figure to denote an estimated figure. A + sign following a figure indicates that the figure given is accurate but the original dimension was greater. "d" indicates tooth worn to dentine only.

** I^1 — P^2 *** omitting P^1

† Specimens in the osteology collection of the Kenya National Museum, selected as the best match for the relevant fossil material from the viewpoint of sex and dental age.

choerus, but its lower surface is damaged and details cannot be seen.

In the palate, in the region between the cheek teeth, there is very little difference from that of the holotype, and the palatine notch is of comparable size. However, anteriorly the palate widens to accommodate the enlarged canines and the premaxillae taper much more than in the holotype. Only the sockets of the six incisor teeth remain, and these are a little larger than in the holotype skull. The left canine is broken off in the plane of the palate but its outline is easily seen. The shape is oval with the ventral surface slightly flattened and the dorsal surface flattened and slightly grooved (Fig. 5). The elongation is anteroposterior as in the holotype skull. The long axis is thus oriented in the opposite direction to that in a *Hylochoerus* tusk and closely resembles the condition found in *Phacochoerus*, though not nearly as exaggerated. As far as can be determined, this portion of the canine at least is devoid of enamel. There is at the centre only a very small pulp cavity or root canal, and it is inferred that the roots are closed or nearly closed. Relative to the size of the skull, the canines are very modest in size and probably did not protrude more than 8–10 cm from the bony bosses. They emerged almost parallel to the palatal plane.

The cheek teeth are in a very advanced state of wear, all but the third molar being virtually patternless. The second premolar is a little larger than in the holotype. It is possible that P^1 was present on the left side in the middle of the diastema, as there is a scar in this position, but there is no similar indication on the right side. On the left side the crowns of the premolars are missing and only the roots remain. The third molars are in advanced wear. They are of approximately the same size as those of the holotype and have exactly the same cusp pattern, the only obvious difference being that the enamel is thicker.

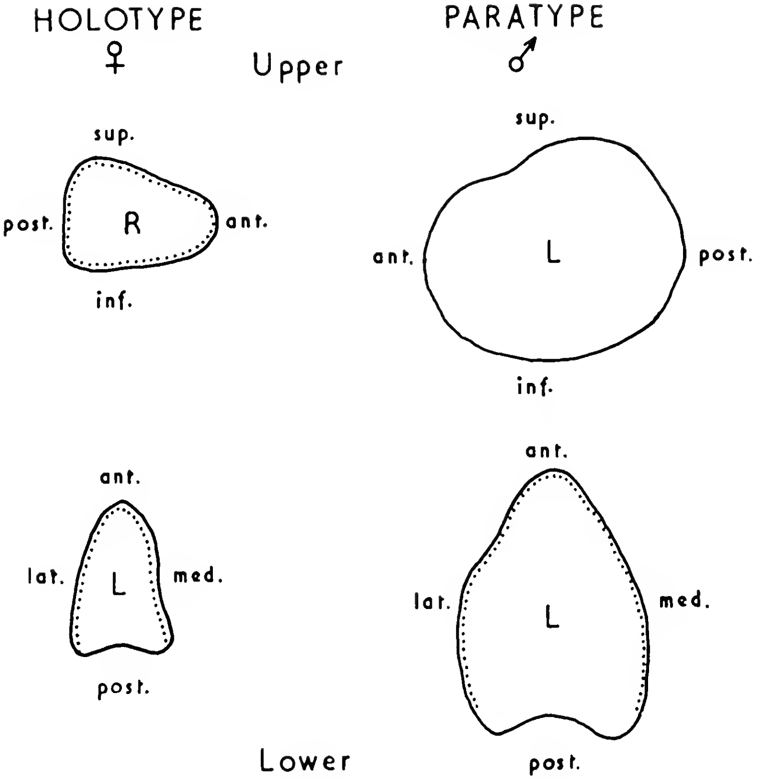

Figure 5. Sections through upper and lower canines of *Nyanzachoerus pattersoni*, near the border of the alveolus. The dotted line indicates the zone covered with enamel. Abbreviations: R—right; L—left; sup.—superior; inf.—inferior; ant.—anterior; post.—posterior; lat.—lateral; med.—median. All nat. size.

The isolated back portion of the cranium differs both from *Potamochoerus* and from *Hylochoerus*. The braincase between the temporal lines is flattened or smoothly concave, having neither the collapsed appearance of *Hylochoerus* nor the convexity of *Potamochoerus;* it is, indeed, a little like this region in *Phacochoerus*, suggesting that the orbits were slightly elevated, though not nearly as much as in the warthog. The skull clearly extended much further behind the orbits than it does in *Phacochoerus*. The back of the occiput is the same size as that of a large *Hylochoerus,* which means that, relative to the length of the skull, the occiput is somewhat narrower. The vertical median ridge, so conspicuous in *Hylochoerus,* is absent.

Associated directly with the skull, and undoubtedly belonging to the same individual, are the left and right mandibular rami. Both are broken off behind the third molars and through the canine alveoli; no part of the symphysis is preserved. The corpus is almost twice as thick as the mandible of the holotype and it is also considerably deeper. Of the cheek teeth, only the third molars remain intact, the anterior teeth being represented in the jaw only by roots; however, incomplete, well-worn second molars of both sides were found with this material and most probably belong to the same mandible. There are also three fragments of canines that do not quite join the pair in the jaw itself. The left canine is partly preserved within the jaw and it has a cross section of the verrucose type. The long axis is anteroposterior and the mesial (topographically dorsal) and lateral faces are almost equal in length. These faces are gently convex but are weakly grooved near the front so that there is a very slight anterior "keel." The posterior face has a broad groove, so that the cross section is almost heart-shaped (Fig. 5). The lateral faces are covered with thin enamel, which is very weakly striated; the posterior face has no enamel and the root, although open, is free of enamel.

Snout and Palate of Old Female

This partial skull (KP 231) was assembled from numerous fragments and represents the incomplete snout and palate of an old female. A fragment of third molar shows that the teeth were in an advanced stage of wear. The nasal area is broken at about the supraorbital foramina and the palate at the back of the palatine notch; the palate lacks the premaxillae and the front of the nasals. Unfortunately not possessing any actual contact, is an isolated fragment showing the back of the right orbit, the postorbital process and the parietal crest. This region is missing from the holotype but the fragment, which comes from a small-tusked and therefore presumably female skull, is virtually identical with the corresponding portion of the (assumed male) paratype. It is therefore of interest, as it lends further support to the identification of the holotype and paratype as the two sexes of a single species.

The right canine is missing but the left canine is broken off at about the margin of the alveolus. It is almost equidimensional, measuring 28.5 mm anteroposteriorly and 27.5 mm vertically. The upper surface is slightly flattened as also is the lingual surface. The pulp cavity, as in the paratype tusk, is extremely small, measuring only 10.5 × 6.7 mm on the broken surface. The bosses surrounding the canines are much less developed than in the old male skull but are decidedly larger than in the holotype. The breadth across the canines at their point of emergence from the alveolus is estimated to be about 125 or 130 mm as compared with 97 mm in the holotype and about 180–190 mm in the paratype.

The width across the muzzle at the infraorbital foramina is almost identical with that of the holotype (see Table 2), and the commencement of the outward flare of the zygomatic arch is also very similar to that of the holotype. In the holotype the nasal area is severely damaged by weathering and the form of the nasals cannot be determined. In this specimen, however, it can be seen that the nasals are flat but turn down rather sharply on either side to contact the premaxillae and maxillae below the level of the top of the snout. In transverse section, the shape of the snout would thus be a trapezoid with rounded corners. In this it differs from *Hylochoerus,* where the nasals turn down less sharply and form a continuous curve with the premaxillae and maxillae, so that the transverse section has the form of a simple arch, slightly flattened above.

Young Adult Skull

This specimen (KP 223) lacks the greater part of the braincase and occiput and also the palate and snout in front of the second premolars. The zygomatic arches are lost and the whole skull is crushed sideways and distorted. The third molars on both sides are preserved in an early stage of wear. In all the morphological features that can be studied, there is close agreement with those of the holotype. The frontoparietal area, which is badly damaged in the holotype, is partly preserved in this specimen, and the width across the parietals at the supraorbital processes is estimated to be 130–135 mm; the corresponding measurement for the holotype on a reconstruction is 130–140 mm. The parietal area is slightly concave between the supraorbital processes and the orbits are thus raised slightly above the mid-line of the frontoparietal area. This is very similar to the corresponding area in *Hylochoerus* but in the fossil the back part of the parietal rises instead of collapsing.

The Immature (Subadult) Skull

A well-preserved skull (KP 244) represents a subadult individual in which the second molars are in wear but the third molars are still unerupted. The fourth premolar is erupted to the level of the grinding surface and shows traces of wear, but the third premolars are incompletely erupted. There is no sign of a P^1. The right canine is broken off but the left is complete. It is newly erupted and the tip is bluntly rounded, without a wear facet. Even at this early stage, the tusk has a greater diameter than that of the holotype female, and there are already small bony bosses around the roots of the canines. There is a good possibility that this is the skull of a young male.

The rest of the skull agrees extremely well with the features shown in the holotype. The zygomatic arches are, unfortunately, missing on both sides. The roof of the skull is less damaged than in the other two specimens. The frontoparietal region is broad and flat. The area in front of the orbits continues the upward sloping plane of the snout but the area behind them is more nearly horizontally oriented. The contour of the skull therefore shows a slight angulation at the level of the orbits and does not run in an almost straight line from snout to occiput, as it does in *Potamochoerus*. The parietal constriction is much wider than in *Potamochoerus* of corresponding age, and the temporal line behind the orbits overhangs the braincase slightly. The upper margins of the orbits are broken, but they must have been level with the frontal surface or even have been very slightly elevated. The auditory bullae are somewhat peculiar, being slender, almost triangular in cross section and very pointed. The specimen is illustrated in Plate 10.

The lacrimal suture can be clearly seen, and the body of the lacrimal bone has the almost square shape found in *Potamochoerus* of similar age. The upper edge is prolonged into a fine tongue of bone running forward between the maxilla and the frontal, terminating just posterior to the nasal suture, very much as happens in *Phacochoerus*. The suture between the jugal and the maxilla slopes forwards and downwards from the anterior margin of the lacrimal as in *Phacochoerus*, whereas in both *Hylochoerus* and *Potamochoerus* the suture runs directly down in line with the front of the lacrimal. Thus, although the body of the lacrimal is short and *Potamochoerus*-like, the conformation of the sutures at the anterior end of the bone is phacochoeroid. This, presumably, is related to the inflation of the zygoma to form the large protuberance that has been described in the holo- and paratypes. Unfortunately the zygoma is not preserved and the juvenile condition of the zygomatic knob is therefore not shown. The anterior part of the jugal, forming the front of the arch is, however, preserved with little or no distortion on the right side of the skull. Both the jugal and the part of the maxilla anterior to it show the characteristic outward flare, and it is apparent that a zygomatic knob of some sort must have been present. We made a reconstruction of the zygoma on the assumption that the knob must end at the level of the back of the orbit, and refraining from making the knob itself any larger than is necessary in order to preserve a reasonably smooth contour on the outer surface. When this had been done, it was found that the knob, as restored, resembled very closely that of the holotype adult female. This is satisfactory, since it is to be expected that in a character showing strong sexual dimorphism an adult female should resemble a juvenile male. The restoration therefore lends support to the original opinion that the paratype and holotype represents the two sexes of a single species.

Mandible of an Old Individual

Specimen KP 219 is an almost complete mandible, presumed to belong to a male individual because of the relatively large sockets for the canines. The roots of four incisors are in position at the front of the symphysis, but the lateral area is broken away as far as the back of the canine sockets; the exact shape of the front of the mandible cannot be determined. The symphysis is long, being about the same length as the cheek teeth series. The lower border of the symphysis is in line with the middle of the fourth premolar. The symphysis is thus longer than in the holotype. The corpus of the mandible is very thick, although less massive than in the paratype (Pl. 4). The ascending ramus is broken off on the left side, and on the right the coronoid process and most of the condyles are missing; the angle, however, is preserved. In contrast to the heavy mandibular rami, the bone forming the angle is surprisingly thin. The lower border, although ridged internally—presumably in relation to the insertion of the internal pterygoid muscle—is not thickened along the outer margin. In this it resembles the mandible of *Potamochoerus* and differs from those of *Hylochoerus* and *Phacochoerus*.

All the cheek teeth are present. They are heavily worn but the characteristic enlargement of the premolars and typical pattern on the M_3 are clearly shown (Pl. 8). From the size and shape of the canine sockets, it is inferred that the canine was like that of the paratype, but a little smaller.

The Upper Dentition

The upper dentition is complete only in the holotype skull (KP 239). The cheek teeth are also intact in a fragment of skull that consists of the right maxilla from P^2 to M^3, together with the area above them up to the nasal suture line and the front of the jugal (KP 201). The cheek tooth series is also complete, but in very poor condition, on the right side of the palate of the paratype (KP 264). Partial series are present in two subadult skulls (KP 244, 227) and in the crushed skull of a young adult (KP 225). The overall measurements for the palate and dentition in the holotype and paratype have been given in Table 2. The range of variation in size, and average values for the upper cheek teeth are given in Table 3.

The cheek teeth are very similar to those of *Potamochoerus* in general structure but are slightly more hypsodont, and in the molars the main cusps are more distinctly columnar. The third and fourth premolars are decidedly more hypsodont in the fossil, as well as being relatively very much enlarged. In a subadult *Potamochoerus*, the height of P^4 is 91 per cent of the maximum breadth, compared with 114 per cent in the fossil; for M^2, the corresponding figures are 73 per cent in *Potamochoerus* and 87 per cent in the fossil. The third molar is slightly longer in proportion to its breadth than in the bushpig, but the lateral columns in the fossil are less massive, more conical, and better separated so that the crown does not have as compact an appearance. The talon is wider in the fossil. The enamel is actually only very slightly thicker than in *Potamochoerus* so that in proportion to the size of the crown it is relatively thinner, and the dentine areas in the enamel islands are therefore more conspicuous. Length/breadth ratios for a typical *Potamochoerus* are included in Table 3.

In the tooth measurements given in the tables that follow, "length" is the greatest length, measured on premolars across the cingulum just above the roots, on first and second molars on the occlusal surface, and on third molars from the front cingulum to the back of the talon; "breadth" is in

TABLE 3. AVERAGE DIMENSIONS OF UPPER CHEEK TEETH OF *NYANZACHOERUS PATTERSONI*

		Range	*N* *	*S.D.**	Mean	Typical *Potamochoerus*
P^2	length (L)	11.2 – 13.2	5	0.711	12.1	18.0
	breadth (B)	6.7 – 8.9	5	0.806	7.4	6.5
	L/B	1.48– 1.8			1.64	1.54
P^3	length	20.2 – 26.8	6	2.013	23.7	13.2
	breadth	18.5 – 20.8	6	1.126	19.8	10.5
	L/B	1.19– 1.30			1.22	1.26
P^4	length	18.0 – 20.3	7	0.950	19.1	13.0
	breadth	21.0 – 24.2	6	1.187	22.4	13.5
	L/B	0.80– 0.89			0.86	0.97
M^1	length	18.5 – 23.0	7	1.629	21.2	17.0
	breadth	17.3 – 20.1	5	0.958	18.8	16.5
	L/B	1.05– 1.19			1.13	1.03
M^2	length	26.3 – 32.0	9	2.006	28.7	22.0
	breadth	23.8 – 28.4	8	1.421	24.9	21.0
	L/B	1.12– 1.29			1.22	1.05
M^3	length	48.5 – 51.6	7	1.192	49.8	29.5
	breadth	28.8 – 32.4	6	1.231	31.2	20.5
	L/B	1.51– 1.73			1.60	1.44
$P^2 - P^4$		49.5 – 68.0	7	7.876	55.6	36.2
$M^1 - M^3$		96.0 –102.0	6	2.987	98.1	68.5
$P^2 - M^3$		146.1 –162.0	5	6.904	153.7	104.7
$\frac{P^2 - P^4}{M^1 - M^3}$		0.49– 0.71	5		0.60	0.53

* *N* denotes the number of specimens in each sample; *S.D.* is the standard deviation.

all cases measured at the base of the enamel at the widest part of the tooth (usually the anterior pair of columns in the molars); "height" is maximum height of enamel, measured on the buccal side in upper teeth and on the lingual side in lower teeth. In canines measurements are made at the alveolar margin (except where otherwise stated); the least diameter is found first and the maximum is measured at right angles to it (in lower teeth these are, respectively, the posterior face and the anteroposterior dimension). In incisors, "length" is transverse, parallel to the edge of the premaxillae, and "breadth" is anteroposterior; "height" is height of enamel above roots on the anterior face along the axis of elongation of the tooth.

Upper Incisors

The upper incisors are preserved only in the holotype specimen and have been described fully in the account of that specimen. The dimensions are given in Table 4.

Upper Canines

The upper canines are intact only in the holotype and the subadult skull, but in

TABLE 4. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER INCISORS

Specimen No. (KP)	Tooth	Transverse (length)	Antero-posterior (breadth)	Height
239	RI^1	19.5	11.5	11.0+
	RI^2	21.2	8.5	9.0+
	RI^3 alveolus	(14.0)	(9.5)	–

TABLE 5. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER CANINES

Specimen No. (KP)	Position	Maximum	Minimum	Length
239	left	22 m	16 m	37+b
	right	20 m	17 m	39+b
264	left	34 a	25	–

a – within alveolus
m – at margin of alveolus
b – from margin of boss

TABLE 6. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER P^2

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
244		Very slight	12.0	6.7	6.0
239	left	Slight	11.2	7.0	6.2
	right	Slight	11.6	6.8	6.5
201		Moderate	12.6	7.4	(6+)
264		Moderate	13.2	8.9	8.0
Mean			12.1	7.4	
Standard Deviation (S.D.)			0.711	0.806	

the paratype the cross section of the root can be seen. Its flattened oval shape is unlike that seen in any living form. The canines of the female have enamel only at the tips and resemble those from Olduvai Bed I which have closed or nearly closed roots; there can be no doubt that the same is true for the tusks of the holotype. The cross section of the broken canine in the paratype shows a great thickness of dentine, absence of enamel, and a very small pulp cavity. Measurements are given in Table 5.

Upper Premolars

P^2 of both sides is preserved in the holotype, the right P^2 in the paratype and in the broken maxilla (KP 201), and the left P^2 in the subadult skull. Measurements are given in Table 6. This tooth is small and oval or subtriangular in outline, with a stout cusp anteriorly and behind it a cusp of almost equal height on a broad and pustulate cingulum. A cingular ridge extends along the lingual side and partly encloses a long and narrow fovea.

P^3 is a robust tooth of subtriangular shape, broadest at the back. There is a very strong main cone that is divided near the top into two cusps (paracone and metacone). From the anterior crest, a steep shallow ridge runs to the anterointernal border, where there is a small cingulum and weak cingular cusp. A corresponding ridge runs diagonally backwards to the posteroexternal corner and meets a high, slender cingulum cusp. The main cone forms the full width of the crown anteriorly but at the posterointernal corner there is a well-developed cusp extending about half the height of the main cone. The essential structure is rather like that of *Potamochoerus*, but the main cone is much stouter and the major axis runs more diagonally across the crown. Measurements are given in Table 7.

TABLE 7. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER P^3

Specimen No. (KP)		Stage of Wear	Length	Breadth	Height
227		Almost unworn	(26.8e)	20.5	(c22)
244		Almost unworn	20.2	(21.4e)	26.6
239	left	Moderate	22.7	18.6	18.2+
„	right	Moderate	23.5	18.5	18.5+
201		Heavy	23.8	19.2	13.5+
264		Extremely heavy	24.9	20.8	5.0+
Mean			23.7	19.8	
S.D.			2.013	1.126	

TABLE 8. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER P^4

Specimen No. (KP)		Stage of Wear	Length	Breadth	Height
244		Almost unworn	20.1	23.5	27.0
227		Very slight	20.3	24.2	21.5
223		Slight	19.4	21.8	17.9+
239	left	Moderate	18.2	21.1	15.0+
"	right	Moderate	18.0	21.0	13.5+
201		Heavy	18.0	22.5	11.5+
264		Extremely heavy	19.8	(c23)	5.0+
Mean			19.1	22.4	
S.D.			0.950	1.187	

P^4 is essentially like that of *Potamochoerus* but enlarged and relatively much higher crowned. There is a strong double outer cone (paracone and metacone) the crests of which are much less separated than in *Potamochoerus.* On the lingual side lies another cone (protocone) which, although smaller than the main buccal cones, rises to the same height. Spurs from the two buccal crests project towards the lingual cusp, leaving a central fovea or narrow longitudinal cleft. Anterior and posterior cingula rise to two-thirds the height of the main cusps and fuse with the flanks of the lingual cone but do not "wrap around" it as they do in *Potamochoerus.* With moderate wear, as in the holotype, a large single island develops from the paracone and metacone, and on the lingual side there is a smaller enamel island developed from the protocone. The pustules or conelets on the cingulum seem to be composed only of enamel, and wear does not result in exposure of any dentine. Although essentially like the corresponding tooth of *Potamochoerus* in structure, there is also a slight resemblance to the upper fourth premolars in the Indian forms *Conohyus* and *Sivachoerus*—but in these genera P^4 has an inner cingulum not present in either *Potamochoerus* or *Nyanzachoerus.* In *Potamochoerus* P^4 is narrower than M^1 and no more than two thirds as broad as M^2; in *Nyanzachoerus* P^4 is broader than M^1 and about 90 per cent as broad as M^2. Dimensions for P^4 are given in Table 8.

The Upper Molars

As has been stated above, in general structure the molars are very like those of *Potamochoerus* except for the slightly

TABLE 9. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER M^1

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
227		Moderate	22.5	–	7.0+
244	left	Moderate	23.0	19.2	9.5+
"	right		22.8	20.1	10.5+
239	left	Heavy	19.3	18.3	0.5+
"	right		18.5	17.3	1.0+
201		Heavy	20.8	19.3	3.5+
264		Heavy	21.2	–	–
Mean			21.2	18.8	
S.D.			1.629	0.958	

Table 10. *Nyanzachoerus pattersoni* dimensions of upper M^2

Specimen No. (KP)	Stage of wear	Length	Breadth	Height
205	Unerupted	29.6	23.7	22.0
227	Slight	31.8	28.4	20.7
244 left	Early	31.7	24.6	19 +
〃 right		32.0	24.8	19 +
239 left	Moderate	29.8	25.5	8 +
〃 right		27.5	24.1	10 +
201	Moderate	30.7	23.8	12.5+
264 left	Extremely heavy	26.3	(24e)	5 +
〃 right		26.3	(24e)	5 +
Mean		29.7	24.9	
S.D.		2.006	1.421	

greater hypsodonty and the more decided separation of the main paired pillars (Pls. 5, 7). Because of its early eruption, M^1 quickly becomes a featureless tract of dentine, but fairly early wear stages are shown in the subadult skull (KP 244) and in a fragmentary immature skull (KP 227). It has the usual "five-spot" arrangement with an anterior and a posterior pair of columns and a median column between them. Small accessory cusps lie between the main columns on the lingual side. The front and back have well-developed cingula, the anterior one running almost the width of the tooth. The second upper molar is simply an enlarged version of the first molar. With advancing wear both these teeth tend to become broader and, as the cingula are worn, also shorter. The breadth across the anterior pair of pillars is only a trifle less than that across the posterior pair.

The third molar is a subtriangular tooth, distorted so that the buccal length is greater than the lingual. There is an anterior cingulum like that in the first and second molars together with an enlarged talon. A median column separates the first and second pair of pillars and another lies between the second pair and the talon. The columns of the talon tend to form a continuation of the "2 + 1" cusp pattern on the crown of the tooth, with a pair of lateral pillars (of which the lingual is the larger) followed by a posterior one. There is, however, some variation in the degree of de-

Table 11. *Nyanzachoerus pattersoni* dimensions of upper M^3

Specimen No. (KP)	Stage of wear	Length	Breadth		Height	
			Anterior	Talon	Anterior	Maximum
223 left	Early	51.4	30.7	21.4	18+	19.5
〃 right		49.0	(30e)	21.0	17+	(20+)
239 left	Moderate	48.7	32.2	18.7	18.5+	20+
〃 right		48.5	31.4	18.6	17+	18+
201	Moderate	50.0	28.8	19.8	19+	21
264 left	Very advanced	51.6	31.8	20.0	10+	16+
〃 right		49.1	32.4	21.0	11+	19+
Mean		49.8	31.2	20.1		
S.D.		1.192	1.231			

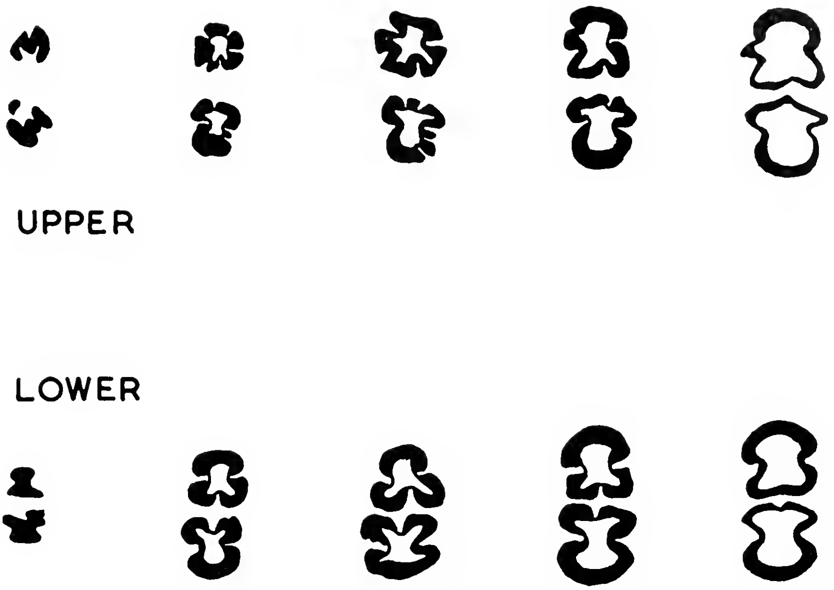

Figure 6. Generalized reconstruction of a pair of lateral columns in upper and lower molars of *Nyanzachoerus pattersoni* to show changes in the form of the enamel islands with increasing wear. The lingual side is at the top of the drawing. Approximately nat. size.

velopment of these talon cusps; the buccal and posterior pillars may be so small that the larger lingual pillar becomes effectively a posterior pillar.

The pattern of the enamel islands in the molar teeth with advancing wear is similar to that found in *Potamochoerus*, but the dentine areas are relatively larger and so the pattern is more obvious. The columns are not simple cones that wear to expose a circular core of dentine but are vertically grooved so that the enamel is infolded. The buccal columns are essentially bilobed, the buccal segment being transversely elongated, while the inner segment is axially longer and initially trilobate. The lingual columns are stellate rather than bilobate. As wear proceeds, the buccal enamel islands first assume a bell-shaped outline, while the lingual ones remain five rayed, but later the lingual element becomes progressively more rounded and like the buccal column. Figure 6 indicates the appearance of the enamel islands in their various stages of attrition. The cheek teeth of the holotype are illustrated in Plate 5. Measurements of the upper molars are given in Tables 9–11.

Table 12 gives measurements for the overall lengths of the premolar and molar series and the ratios between them. The average ratio in the uppers is .57 compared with about .53 in *Potamochoerus*. The difference is almost entirely accounted for by the relatively greater length of the third premolar in the fossil. Table 13 shows the lengths of the individual teeth expressed as percentages of the overall length of the premolar/molar series: the proportional enlargement of the third premolar is obvious. Table 14 compares the maximum breadth of each tooth with the breadth of the second molar, which is a convenient standard for comparative purposes. Length/breadth ratios have already been given in Table 3.

Upper Milk Dentition

Only one small fragment of a juvenile right maxilla is preserved (KP 222). It

TABLE 12. *NYANZACHOERUS PATTERSONI* LENGTHS OF PREMOLAR AND MOLAR SERIES

Specimen No. (KP)	Stage of Wear	P^2–P^4	M^1–M^3	P^2–M^3	P^2–P^4 / M^1–M^3
		Upper Dentition			
244 left	Very early (subadult)	49.8	–	–	
" right		49.5	–	–	
225	Early (adult)	–	102.0	–	
239 left	Early to moderate	51.9	95.2	147.0	.54
" right		51.6	94.5	146.0	.55
201	Moderate	50.5	101.5	152.0	.49
264 left	Very advanced	68.0	99.1	(162e)	.69
" right		68.0	96.0	161.6	.71
Mean		55.6	98.1	153.7	.60
S.D.		7.876	2.987	6.904	

Specimen No. (KP)	Stage of Wear	P_2–P_4	M_1–M_3	P_2–M_3	P_2–P_4 / M_1–M_3
		Lower Dentition			
213	Very early	(52e)	97.9	(150e)	(.53e)
256	Early	–	106.4	–	–
239 left	Early to moderate	57.4	94.0	151.4	.61
" right		55.5	94.5	153.0	.59
263	Moderate	(54e)	97.0	(151e)	(.56e)
240	Moderate	(c57)	(c96)	(c153)	(c.60)
258	Moderate	–	(c99)	–	–
264	Moderately advanced	69	105	174	.66
219 left	Very advanced	62.1	102.7	164.8	.58
" right		63.3	102.4	165.7	.62
Mean		59.8	100.0	158.6	.59
S.D.		5.567	1.462	8.793	

TABLE 13. LENGTH OF EACH CHEEK TOOTH AS A PERCENTAGE OF LENGTH OF THE SERIES P2–M3 IN *POTAMOCHOERUS* AND *NYANZACHOERUS*

UPPER DENTITIONS	P^2	P^3	P^4	M^1	M^2	M^3
Potamochoerus porcus	9.5	12.6	12.4	16.2	21.0	28.3
Nyanzachoerus pattersoni	7.8	15.3	12.3	13.6	19.1	32.0
N. tulotos	10.0	16.2	13.2	14.8	18.9	26.9
N. plicatus	6.1	13.1	10.6	10.6	20.5	39.1

LOWER DENTITIONS	P_2	P_3	P_4	M_1	M_2	M_3
Potamochoerus porcus	5.3	10.8	14.1	14.9	21.7	33.2
Nyanzachoerus kanamensis	6.0	17.2	13.0	15.0	18.6	30.2
N. pattersoni	6.6	16.0	14.0	12.5	16.9	34.0
N. tulotos	9.6	17.6	15.5	13.0	17.4	26.9
N. plicatus	5.7	13.1	12.2	10.8	18.2	40.0

TABLE 14. BREADTH OF EACH CHEEK TOOTH AS A PERCENTAGE OF THE BREADTH OF THE SECOND MOLAR IN *POTAMOCHOERUS* AND *NYANZACHOERUS*

UPPER DENTITIONS	P^2	P^3	P^4	M^1	M^2	M^3
Potamochoerus porcus	31	50	64	78	100	100
Nyanzachoerus pattersoni	29	78	89	75	100	124
N. tulotos	38	81	95	77	100	100
N. plicatus	25	69	76	c72	100	126

LOWER DENTITIONS	P_2	P_3	P_4	M_1	M_2	M_3
Potamochoerus porcus	30	45	60	74	100	100
Nyanzachoerus kanamensis	30	75	83	c74	100	109
N. pattersoni	34	97	96	69	100	120
N. tulotos	38	97	99	76	100	108
N. plicatus	38	89	90	90	100	125

consists of the dm^4 in fairly advanced wear, and the anterior two-thirds of the M^1. This specimen occludes well with the portion of juvenile mandible KP 221, and could well have come from the same individual. The unerupted large P^4 can be seen in the alveolus below the dm^4. The milk molar is essentially similar to that of *Potamochoerus* of approximately the same dental age, although the tooth in the fossil is somewhat longer as a result of the slight enlargement of the posterior cingulum. The permanent M^1 in the fossil is typical of *Nyanzachoerus*. The measurements are given in Table 15.

The Lower Dentition

The lower dentition is not complete in any of the specimens but the relationships of the teeth are best seen in the mandible of the holotype (Pl. 2). The cheek teeth are damaged in the mandible of the holotype and badly damaged in that of the paratype; they are present in the mandible of an old individual (KP 219), but the canine area is badly damaged and the incisors are lost. In the holotype there is a diastema of 48 mm between the front of the root of P_2 and the back of the canine; the distance from P_2 to the back of I_2 is 72 mm; the lower canine is intact and there is no diastema between it and I_3. The canines are broken in the mandibles of the paratype and of the old individual but one is present in a juvenile jaw in which the premolars are unerupted (KP 266). The milk molars occur in fragments of a pair of mandibular rami (KP 221) and the milk incisors are also present, but the canine-bearing area of the jaw is missing. Cheek teeth are preserved in several other incomplete mandibular rami. Table 16 gives the observed ranges of size and average measurements.

TABLE 15. DIMENSIONS OF JUVENILE UPPER TEETH IN *NYANZACHOERUS PATTERSONI* AND *POTAMOCHOERUS*

				Height	
		Length	Breadth	Anterior	Posterior
Potamochoerus	dm^4	13.5	11.5	5 +	4.5+
KP 221	"	15.5	12.4	5.5+	5.5+
Potamochoerus	M^1	16	12.5	8.5+	8 +
KP 221	"	15.5+ (20e)	16	12.5+	–

TABLE 16. AVERAGE DIMENSIONS OF LOWER CHEEK TEETH OF *NYANZACHOERUS PATTERSONI* COMPARED WITH *N. KANAMENSIS*

		N. pattersoni			*N. kanamensis*		
		Range	*N**	S.D.*	Mean	Holotype	Paratype
P_2	length (L)	10.4 – 10.7	2		10.6	c10	
	breadth (B)	7.2	2		7.2	c 6	
	L/B	1.45– 1.48			1.47	c 1.6	
P_3	length	24.0 – 27.1	4	1.279	25.7	28.9	
	breadth	19.3 – 21.7	4	0.960	20.3	15.1	
	L/B	1.24– 1.30			1.26	1.91	
P_4	length	21.0 – 23.4	6	0.800	22.5	21.6	
	breadth	18.9 – 21.8	6	1.284	20.5	16.8	
	L/B	1.07– 1.19			1.11	1.29	
M_1	length	18.3 – 21.9	8	1.193	20.2	c25	
	breadth	13.2 – 16.5	7	0.953	14.2	c15	
	L/B	1.10– 1.58			1.39	c 1.7	
M_2	length	24.5 – 29.7	11	1.262	27.6	31.0	28.0
	breadth	17.7 – 22.8	10	1.537	21.1	20.2	19.7
	L/B	1.19– 1.39			1.32	1.53	1.42
M_3	length	49.6 – 59.2	13	2.785	54.7	50.5	51.0
	breadth	22.8 – 28.6	11	1.801	25.1	22.0	23.2
	L/B	1.97– 2.35			2.17	2.28	2.24
$P_2 - P_4$		52.1 – 69.0	7	5.567	59.0	c60.5	
$M_1 - M_3$		94.0 –106.4	8	4.462	100.0	106.5	
$P_2 - M_3$		150.0 –174.0	7	8.793	158.6	167.0	
$\frac{P_2 - P_4}{M_1 - M_3}$		0.53 – 0.66	7		0.59	0.56	

* *N* denotes the number of specimens in the sample; *S.D.* is the standard deviation

As is the case with the upper cheek teeth, the lowers are structurally very similar to those of *Potamochoerus* and likewise differ mainly in the more columnar nature of the paired pillars in the molars and in the greater hypsodonty and enlargement of the premolars (Pls. 6, 8, 9). In *Potamochoerus* the third molar normally terminates in a pair of pillars that may be poorly developed or may be almost as well developed as the second pair, but only rarely is there a median pillar at the back of the tooth. In *Nyanzachoerus* the third pair of pillars is well developed and there is a terminal median pillar on the talonid.

Lower Incisors

The lower incisors are preserved only in the mandible of the holotype and have been described fully in the account of that specimen. The measurements are given in Table 17.

Lower Canines

There is a substantial size difference in the canines of the sexes and they also differ slightly in shape. The female canines are fully developed in the holotype mandible, and the left canine can be seen in the alveolus in the incomplete mandible KP 240; an isolated tip of a right canine (KP 224) matches that of the holotype. The cross section is almost heart-shaped near the base, becoming more triangular towards the tip. The back of the tooth has a broad shallow groove that disappears as the surface becomes flattened by attrition. The wear facet is oriented in the vertical plane, as it is in *Hylochoerus*, but does not show the slight backward slope from the dorsal to the ventral edge that is seen in *Phacochoerus*. The male canines, seen broken off in the paratype mandible and in the old mandible KP 219, are similar in cross section shape but 50 per cent larger. The respective cross sections are illustrated, natural size, in Figure 5 and the dimensions are given in Table 18. The posterior face is free of enamel, but the two lateral faces are covered with thin enamel, weakly grooved longitudinally, and with fine transverse striations that give a reticulate appearance to the enamel; it may be remarked that this finely reticulate enamel is also observed in the incisors and cheek teeth and is therefore of assistance in the diagnosis of teeth of *Nyanzachoerus*. The canines of the male are directed somewhat more laterally than those of the female and they were probably 10–15 cm long beyond the jawbone. The lower canines in the male appear to have open roots, whereas those of the female seem to be partly closed.

Table 17. *Nyanzachoerus pattersoni* dimensions of lower incisors

	I_1	I_2	I_3
Holotype skull KP 239			
Transverse (length)	9.2	11.1	11.2
Anteroposterior (breadth)	11.6	11.4	9.6
Height	18.6	25.0	15.0+

The Premolars

P_2 is preserved complete in the holotype, and somewhat worn in the male jaw KP 219. By contrast with the enlarged premolar behind it, it is a rather small tooth consisting of a low stout cone with a distinct posterior ridge, a small secondary posterior cusp, and a poorly developed cingulum. *Potamochoerus* normally has simpler and narrower teeth, comprising a single cone only, though a posterior cusp is sometimes present, together with anterior and posterior cingula.

P_3 is a robust tooth with a strong main cone (protoconid) and a moderately strong posterior cingulum with a small posterior cone rising from it; the cingulum and its cone rise one-half to two-thirds the height of the main cone. The tip of the main cone is centred over the front part of the posterior root, giving the cone an asymmetrical profile with a backward slant. This is even more marked in the longer and narrower P_3 of *N. kanamensis*. In the latter species there is also a very small anterior cusp that has not been observed in the specimens of *N. pattersoni*, although there is a very weak anterior cingulum in both species. Measurements are given in Table 20.

P_4 is also a stout tooth, with a conical protoconid, well-developed posterior cingulum and a posterior cusp three-quarters the height of the main cone. There is also a less massive anterior cingulum rising almost to half the height of the main cone. The protoconid is ridged anteriorly and posteriorly, the ridge lying slightly towards the lingual side of the centre line. In *N. kanamensis* the anterior cingulum is a little weaker and the whole tooth is proportion-

Table 18. *Nyanzachoerus pattersoni* dimensions of lower canines

Specimen No. (KP)		Position measured	Maximum	Minimum	Length
239	left	At alveolus border	21	12.7	45.0+
"	right	At alveolus border	23	13.4	45.5+
240		Within alveolus	21.7	15.7	–
264	left	Within alveolus	33.7	24.9	–
"	right	Within alveolus	34.7	24.7	–
219		Within alveolus	31.0	22.0	–

TABLE 19. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER P_2

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
239		Roots only	(c10)	(c8.5)	–
263		Socket	(c 6)	–	–
219	left	Moderate	10.7	7.2	6.5+
"	right	Moderate	10.4	7.2	6.5+

ally narrower than in *N. pattersoni*. The posterior foveae are more distinct in *N. kanamensis* than in *N. pattersoni*. Measurements are given in Table 21.

The Lower Molars

The molars are structurally very like those of *Potamochoerus*, but the cusps are more distinctly columnar and there is relatively more dentine in the enamel islands. In most of the specimens M_1 is worn to dentine, but the pattern can be clearly seen in two specimens that have milk teeth (KP 221 and 266) and also in the left mandible KP 213, in which M_3 is still in the process of eruption. Both M_1 and M_2 have two pairs of lateral pillars, a single median column, and anterior and posterior cingula. M_3 has three pairs of lateral pillars, separated by single median columns and a stout talonid pillar at the back. In the mandible KP 256 the back of the talonid has two smaller terminal pillars and a very small median pillar, forming an incipient extra pair of laterals. Several of the teeth have a small basal pillar on the

TABLE 20. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER P_3

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
213		Almost unworn	24.0	19.3	25.2
239		Roots only	(23.5e)	(16.0e)	
263		Early	25.0	19.5	18.7+
219	left	Well worn	27.1	21.7	19.4+
"	right		26.8	20.6	15.5+
Mean			25.7	20.3	
S.D.			1.279	0.960	

TABLE 21. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER P_4

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
213		Very early	21.0	19.1	22.0
255		Moderate	22.4	22	(14.5e)
256		Moderate	22.7	19.9	17.5+
239		Root only	(c20.5)	(c16)	–
263		Moderate	22.4	18.9	19.0+
219	left	Very advanced	23.4	21.8	6.5+
"	right		23.3	21.5	5.5+
Mean			22.5	20.5	
S.D.			0.800	1.284	

TABLE 22. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER M_1

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
221	left	Just beginning	21.5	13.9	14
"	right		21.9	13.9	14.5
228		Very slight	19.3	13.9	15.1
205		Slight	19.8	13.5	11.5+
266		Moderate	20.9	13.2	3.5+
213		Advanced	20.6	15.3	8.0+
263		Extreme	18.3	16.0	d
219		Extreme	19.0	(16.5e)	d
Mean			20.2	14.2	
S.D.			1.193	0.953	

lingual side of the talonid, and there is also a tendency for two or three small basal pillars to develop between the pairs of lateral columns. The anterior cingulum is thin but extends more than half the height of the anterior pair of pillars. Measurements are given in Tables 22–24. The lateral pillars are divided by three grooves, an axial one that is relatively weak and a stronger anterior and posterior pair. As a result, they wear into a complex trilobed pattern, consisting of an individual outer lobe, clearly separated off from a double inner lobe. With advancing wear, the outer lobe elongates so that in moderately advanced wear the lateral element is approximately the same length as the double inner lobe length and its shape becomes rather bell-like. The stages are illustrated in Figure 6 and actual examples are seen in Plate 5.

The Lower Milk Dentition

Two specimens, KP 221 and 266, display some of the milk dentition and have the first molars preserved so that assignment to the species is not in doubt, and they also possess the characteristic enamel. The more juvenile is KP 221, which consists of several pieces of mandible and two small skull fragments. The mandibular remains comprise the front of the symphysis with five

TABLE 23. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER M_2

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
220		Early	27.7	21.1	19.0+
266		Early	28.3	17.7	16.5+
213		Moderately early	28.2	20.2	15.1+
260		Moderate	26.8	20.2	
255		Moderate	29.7	22.8	10.5+
256		Moderate	28.7	21.4	10.4+
239		Root only	(c25)	(c18)	
263		Advanced	28.0	21.8	7.5+
240		Advanced	27.2	20.2	8.5+
219	left	Extreme	27.8	(23e)	2 +
"	right		27.1	22.7	3 +
259		Extreme	24.5	(c24)	d
Mean			27.6	21.1	11.5+
S.D.			1.262	1.537	

TABLE 24. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER M_3

Specimen No. (KP)	Stage of wear	Length	Breadth		Height	
			Anterior	Talon	Anterior	Maximum
213	Incompletely erupted	49.6	(22.5e)	–	19.2	23
256	Early	59.2	25.1	20.7	17+	19
239 left	Moderately early	53.6	22.8	20.0	18+	18.5+
" right		52.9	22.8	20.2	17.5+	18+
263	Moderate	50.3	24.8	20.2	12.3+	13.5
240 left	Moderate	55.0	24.0	18.6	11+	12.5+
" right		54.2	23.8	18.3	10+	12.5+
258	Moderate	52.7	25.1	20.1	13.5+	15.0+
264 left	Moderate	56.2	26.3	21.4	11.5+	13.5+
" right		58.5	(26+)	22.9	14.0+	14.5+
219 left	Very advanced	56.4	28.6	22.7	3+	4.5+
" right		57.0	27.9	22.5	4.5+	6+
259	Extreme	55.2	24.7	20.8	5	5+
Mean		54.7	25.1	20.7		
S.D.		2.785	1.801			

incisors; portions of mandibular rami containing the left dm_{2-4} and M_1 and the right dm_{3-4} and M_1, together with two small pieces of the lower border of the angle of the jaw. The first and second incisors are very similar in structure to those of *Potamochoerus* of similar age but a good deal longer; dI_3 in the fossil is a small distorted peg and is clearly not normal. The milk molars are structurally similar to those of *Potomachoerus* but are larger. However, dm_2 is as long as dm_3 and about twice as long as the dm_2 in *Potamochoerus;* it is astonishingly like a miniature of the adult P_3. Dm_2 is slightly broader than dm_3. Comparative measurements are given in Table 25 and the milk teeth are shown in Plate 11. In a *Hylochoerus* skull of comparable dental age, the angle of the mandible already shows the characteristic broadened border. In the fossil fragments, as in the adult specimens already described, this broadening is absent and the margin is no wider than the body of the bone.

Specimen KP 266 is part of a left mandibular ramus broken anteriorly and exposing the young permanent canine in early growth; the jaw is broken behind the partly worn M_2. At this early stage of development the posterior face of the canine is very slightly convex and lacks the groove characteristic of more mature tusks. In other respects it resembles the adult tusks. The dm_3 and dm_4 have been lost *post mortem* but the worn remnant of dm_2 is still in position. The tips of the main cone and cingulum crest of the permanent P_4 are emerging from the crypt. M_1 is in fairly advanced wear and M_2 in moderately early wear. The permanent teeth are very characteristic and make identification certain.

Postcranial Material

The vertebrae associated with the holotype have been described above. In addition there is a group of limb bones, numbered KP 215, which was found with tooth fragments sufficient to identify the species as *N. pattersoni.* This collection includes a left tibia, left fourth metatarsal, and some phalanges. Two other bones, numbered KP 243, are, respectively, a right tibia and a right third metatarsal of similar size and character, which may also be regarded as belonging to the same species. However, in the account that follows

TABLE 25. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER MILK DENTITION

		KP 221			
		left	right	KP 266	Juvenile *Potamochoerus*
dI_1	Transverse	4.3	4.3	–	3.5
	Anteroposterior	4.6	4.6	–	4.0
	Height	8.5+	8.5+	–	9.5
dI_2	Transverse	5.6	5.2	–	4.4
	Anteroposterior	5.3	5.5	–	5.3
	Height	14.0+	13.5+	–	13.0
dI_3	Transverse	–	2.7	–	2.8
	Anteroposterior	–	2.9	–	2.8
	Height	–	2.0	–	4.0
C	Maximum	–	–	13.0	–
	Minimum	–	–	7.0	–
dm_2	Length	10.4	–	10.4	6.7
	Breadth	6.4	–	5.2	3.3
	Height	9.5+	–	4.5+	4.7+
dm_3	Length	10.4	10.4	gap 28.0	9.8
	Breadth	6.2	6.2		5.1
	Height	8.0+	8.0		8.2+
dm_4	Length	22.2	21.9		20.4
	Breadth	10.3	10.2		9.0
	Height	5.0+	4.0+		6.8+
M_1	Length	21.5	21.9	20.9	18.2
	Breadth	13.9	19.9	13.2	11.2
	Height	14	14.5	3.5+	9.8
M_3	Length	–	–	28.3	–
	Breadth	–	–	17.7	–
	Height	–	–	16.5	–

only the associated material from KP 215 will be discussed. Measurements are given in Tables 26 and 27 and the specimens are shown in Plate 12.

Tibia

The tibia is very slightly larger than that of an average adult *Hylochoerus* female and could be matched fairly closely in an adult male. The morphology is also very similar in detail. The tuberosity at the upper part of the crest is proportionately not quite as broad as in *Hylochoerus*, and the groove for the middle patellar ligament is a little deeper, although not as deep as in *Potamochoerus* and *Phacochoerus*. The sulcus between the tuberosity and the lateral condyle is very like that of *Hylochoerus* in being wide and open laterally, whereas in both *Potamochoerus* and *Phacochoerus* the sulcus is narrowed by an anterior extension of the lateral condyle. The distal end is slightly broader across the malleoli than is the case in the three living species, both by comparison with the anterior-posterior dimension and also relative to the breadth across the proximal condyles; however, the differences are very slight. This widening of the distal end is not accompanied by a greater robustness of the shaft, for the medial lateral dimen-

Table 26. Measurements on limb bones of *Nyanzachoerus pattersoni* (KP 215) compared with those of living African suidae

Actual measurements in mm

	Nyanzachoerus	*Hylochoerus*	*Phacochoerus*	*Potamochoerus*
TIBIA				
length	238.0	221.0	204.0	173.0
proximal breadth	65.5	65.0	51.7	49.4
distal breadth	40.4	37.3	30.3	29.0
TALUS				
length	55.5	51.8	40.5	40.8
breadth—proximal	33.4	31.9	22.8	22.9
—distal	32.8	32.7	23.8	23.2
CALCANEUM				
length	108.0	102.1	78.8	76.0
breadth at sustentaculum	26.7	26.7	21.2	18.2
a/p diameter at sustentaculum	26.6	27.9	22.1	22.1
METATARSAL IV				
length	105.0	82.7	84.8	71.9
shaft breadth	19.7	20.6	14.9	13.1
shaft thickness (a/p)	14.0	13.7	10.7	10.4
PHALANGES—PES				
III P_1 length	46.6	42.8	37.3	32.3
prox. breadth	25.8	20.2	16.9	15.0
IV P_1 length	46.5	42.5	37.1	31.9
prox. breadth	24.3	20.5	16.6	15.3
V P_1 length	31.4	25.6	22.6	20.5
prox. breadth	14.6	13.8	10.1	9.8
PHALANGES—MANUS				
III P_1 length	44.1	43.2	37.1	31.7
prox. breadth	26.7	22.2	16.7	15.0
III P_2 length	33.1	32.4	22.7	21.1
prox. breadth	24.7	21.7	15.7	16.6
IV P_2 length	30.4	32.5	22.2	20.9
prox. breadth	25.4	21.1	15.7	14.7
IV P_3 length	35.5	33.6	25.5	26.3
prox. breadth	25.3	23.3	18.4	15.9

sions of the shaft, as compared with the overall length of the tibia, have the same proportion as in the bushpig and warthog and the bone is thus not quite as stout as in *Hylochoerus*.

Tarsal Bones

Articulating with the left tibia are the left talus, calcaneum, cuboid, and navicular.

The talus is somewhat larger than that of the forest hog and slightly more elongated. It is, however, not as narrow as in *Phacochoerus* or *Potamochoerus*, and its proportions are intermediate between those of the forest hog and the two other extant species.

The cuboid is a little damaged. It is more compressed than in the bushpig or warthog, but not as much so as in the forest hog, its morphology being intermediate between *Potamochoerus* and *Hylo-*

TABLE 27. RELATIVE PROPORTIONS OF LIMB BONES OF *NYANZACHOERUS PATTERSONI* (KP 215) AND THOSE OF LIVING AFRICAN SUIDAE

Proportions calculated relative to the length of the tibia as 100

	Nyanzachoerus	*Hylochoerus*	*Phacochoerus*	*Potamochoerus*
TIBIA				
length	100.	100.	100.	100.
proximal breadth	27.5	29.3	25.3	27.6
distal breadth	16.9	16.9	14.7	16.8
TALUS				
length	23.3	23.3	19.8	23.4
breadth—proximal	14.0	14.1	11.2	13.2
—distal	13.7	14.7	11.7	13.4
CALCANEUM				
length	45.2	46.1	38.6	43.9
breadth at sustentaculum	11.2	12.2	10.4	10.5
a/p diameter at sustentaculum	11.2	12.6	10.8	12.8
METATARSAL IV				
length	44.0	32.3	41.6	41.5
shaft breadth	8.3	9.3	7.3	7.6
shaft thickness (a/p)	5.9	6.2	5.2	6.0
PHALANGES—PES				
III P_1 length	19.6	19.3	18.3	18.7
prox. breadth	11.3	9.1	8.3	8.6
IV P_1 length	19.5	19.2	18.2	18.4
prox. breadth	10.2	9.2	8.1	8.8
V P_1 length	13.2	11.6	11.1	11.8
prox. breadth	6.1	6.2	4.9	5.7
PHALANGES—MANUS				
III P_1 length	18.7	19.5	18.2	18.4
prox. breadth	10.4	10.0	8.2	8.7
III P_2 length	13.9	14.6	11.1	12.2
prox. breadth	10.3	10.2	7.7	9.6
IV P_2 length	12.8	14.7	10.8	12.1
prox. breadth	10.7	9.5	7.7	8.5
IV P_3 length	14.9	15.2	12.4	15.2
prox. breadth	10.6	10.5	9.0	9.2

choerus in most of the details that can be seen. The navicular is also less compressed than in the forest hog and differs slightly in the size, shape, and angle of the lower facets; that for the external cuneiform is nearly equidimensional, as in the warthog. Otherwise the morphology is closest to that of *Hylochoerus*.

The calcaneum is longer than that of *Hylochoerus* but less robust so that its proportions are more like those of the bushpig. The articular facet on the lower surface of the sustentaculum is fairly smooth, as in *Potamochoerus*, but is rather wider and more equidimensional than in any of the living forms.

Other Bones of the Pes

The foot is represented by seven bones. The distal end of a left third metatarsal articulates with the first (proximal) phalanx; the left fourth metatarsal articulates with its first phalanx; and the distal end of the left fifth metatarsal is associated with its first phalanx. In addition there is the first phalanx of the fifth digit of the right side.

The left fourth metatarsal is 20 per cent longer than the corresponding bone in *Hylochoerus* but its shaft is not significantly stouter. The bone is thus, like that of the warthog, relatively long and slender and very different from the much stouter metatarsal of *Hylochoerus.* Another point in which it differs from the *Hylochoerus* metatarsal and resembles that of *Phacochoerus* is the ratio of width to anteroposterior thickness of the shaft: in *Hylochoerus* the shaft is rather flat, its width being approximately one and a half times its thickness, whereas in both the fossil and in *Phacochoerus* the disparity between the two diameters is rather less. The plantar projection is broken in the fossil and the general form of the proximal articular surface is otherwise *Potamochoerus*-like, but not very distinctive. There are no very characteristic features of the distal end, except that the articular facets are relatively a little wider than in the forest hog or the other living species.

The first phalanges of the third and fourth digits are differently proportioned from those of the three living species, in which the phalanges are rather similar. In length and in the dorsoventral dimensions of the proximal end of these phalanges the fossil is 10 per cent bigger than in the living *Hylochoerus;* however, the lateral-medial dimension is 20 per cent greater, so that the toes are proportionally wider (or are relatively shorter and stubbier). The first phalanges of the fifth digit, however, are proportioned like those of the bushpig and are relatively longer than the corresponding ones in the forest hog, although the differences are small.

Bones of the Manus

Of the front foot are preserved only phalanges for digits three and four of the right side. In the third digit both the first and second phalanges are intact; in the fourth digit, the first phalanx lacks the distal half, but the second and third phalanges are entire. In length they are very close to the corresponding bones in the forest hog but, as with the hind foot, the phalanges are wider, so that it would be equally true to say that they are relatively shorter or more compressed. Apart from the effect of this anteroposterior compression on the proportions, there are no significant differences that warrant comment, although *Phacochoerus* is least like the fossil phalanges in proportions. The terminal phalanx of *Potamochoerus* is decidedly narrower than that of the fossil; its articular region resembles that of *Hylochoerus.* However, the fossil phalanx has a thin "splayed out" border or flange on the anteromedial side, rather like that of *Potamochoerus.* In addition the second phalanx in digit three is relatively long, being 75 per cent of the length of the first phalanx; *Hylochoerus* gives the same ratio, whereas in *Phacochoerus* the corresponding value is only 60 per cent.

Unfortunately the material is not sufficient to give a full picture of the structure of either the fore or the hind limb of *Nyanzachoerus.* A few points of interest, however, emerge from a comparison with the extant African species. Of these *Phacochoerus* and *Hylochoerus* are of most interest. The limbs of the former show a number of cursorial adaptations: the humerus and femur are fairly short and the manus and pes rather narrow and elongated. This is shown in the narrow talus, the long slim metapodials and the proportions of the phalanges, the first being long and the second and third relatively short. In *Hylochoerus* the gait is less digitigrade and the foot broader and more spreading, in adaptation to locomotion on rather soft or even marshy ground. The proximal limb segments are long, the metapodials broad but not particularly thick anteroposteriorly and the disproportion between first and second phalanges is less.

Unfortunately no femur of *Nyanzachoerus* is known. However, the fourth metatarsal is 44 per cent of the length of the tibia, as compared with 41.6 per cent in *Phacochoerus*. It seems more reasonable to interpret this as meaning that the tibia is not particularly elongated and the femur therefore not correspondingly shortened, rather than as implying metapodials even more specialised than those of *Phacochoerus*. There is nothing in the rest of the limb bones known at present that would warrant the latter conclusion. However, even if the femur were not shortened, there are a few points in which the limbs differ from those of *Hylochoerus* and show some similarity to those of *Phacochoerus*, for instance, the elongation and narrowness of the metatarsals and the somewhat compressed tarsal bones.

Without more complete material it is difficult to draw any very positive conclusions about the limbs of *Nyanzachoerus*. It does, however, seem clear that while *Nyanzachoerus* may not have possessed such cursorial adaptations as are characteristic of *Phacochoerus*, it did not have the broad spreading hylochoerine type of foot and its limbs were not specially adapted to locomotion on soft ground.

Nyanzachoerus plicatus sp. nov.*

Text-figures 7–9; Plates 13–18

Hylochoerus Hopwood, 1931: 133.
Mesochoerus paiceae Leakey, 1958 (in part): 13.

Diagnosis. A species of *Nyanzachoerus* larger than the extant *Hylochoerus*. Third molars only slightly hypsodont; larger and more elongated than those of *N. pattersoni* and *N. kanamensis*. Upper third molars with three pairs of lateral pillars and talon pillar; length about twice breadth. Lower third molars with three pairs of lateral pillars and posterior complex; length about two and two-thirds times breadth. Premolars relatively less enlarged than those of *N. pattersoni*, with premolar series (P2–P4) approximately 40–50 per cent of the length of the molar series; P_4 about one-third the length of M_3. Enamel on molars more infolded than in *N. pattersoni* or *N kanamensis*, giving a complex pattern to the enamel islands produced by wear, particularly in M^3. Upper canines relatively small, devoid of enamel, flattened oval in section, and forming roots very early.

Holotype. KNM–KP 251: associated partial skull and damaged mandible.

Paratypes. KNM–KP 252: three upper canine teeth found with the holotype but not belonging to it. KNM–KP 262: associated pieces of mandible and skull. KNM–KP 257: portion of skull with cheek teeth.

Locality. Kanapoi, northwestern Kenya.

Horizon. Kanapoi sediments; probably Upper Pliocene.

REFERRED SPECIMENS

KNM–KP 235: parts of mandible with LM_3, broken RP_4, and pieces of lower canines; isolated LM^3 and fragment of RM^3; parts of the pelvis; third cervical vertebra. KP 254: isolated RM_3. KP 269: two parts of mandibular rami with milk teeth. KP 203: half of upper canine. KP 206: incomplete RM^2. KP 253: isolated RM^3. KP 225: isolated, damaged RM^3, and back portion of matching LM^3.

DESCRIPTION

The Holotype Skull and Mandible

The holotype (KNM–KP 251) comprises a badly damaged partial skull, found with a damaged mandible, and also associated with a pair of canines and some canine fragments (KNM–KP 252). The fragments could belong to the skull, but sufficient of the tusks are preserved in the holotype to make it clear that the more complete canines cannot have come from the skull

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* *N. plicatus* has been referred to in several preliminary faunal lists as *Nyanzachoerus* species "B."

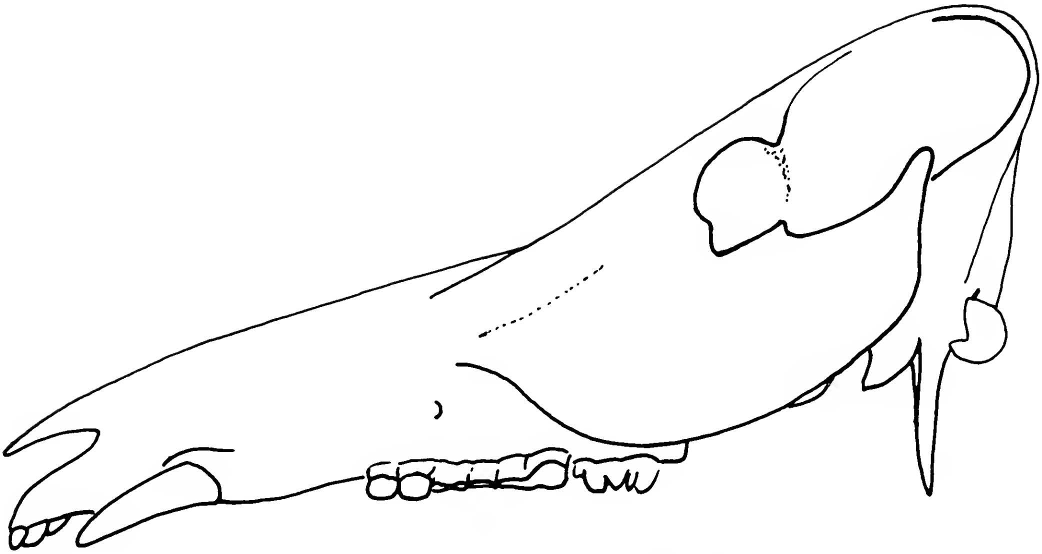

Figure 7. Attempted reconstruction of the skull of *Nyanzachaerus plicatus*. × ¼.

itself. These canines undoubtedly belong to the same species and are cited as paratypes.

The skull—if it can be dignified by such a designation—consists mainly of the snout from a point 7 cm behind the supraorbital foramina to the front of the canine fossae. The right side is very badly damaged, but the left side shows the lacrimal area and maxillary part of the beginning of the zygomatic arch (Pl. 13). A partial and very tentative restoration, based on all the material available and especially on the holotype and the third paratype, is given in Figure 7.

The lacrimal and supra-orbital foramina and a very small part of the margin of the orbit are preserved on the left side. The arrangement of the foramina is phacochoeroid; the lacrimal foramina are situated very close to the margin of the orbit and the supra-orbital foramen is virtually at the same level. In *Hylochoerus* the supra-orbital foramen lies further forward, distinctly anterior to the lacrimal foramina, and the latter lie slightly further in front of the orbit, so that the distance between the infra-orbital and supra-orbital foramina is much less than in *Phacochoerus*. This distance is no more than 10 cm in a big skull of *Hylochoerus* as against 15 cm for *Phacochoerus;* in the fossil skull, this distance is almost 20 cm, indicating that the cranium has the same sort of backward elevation as does that of *Phacochoerus*. In *Phacochoerus* this is achieved by elongation at the level of the lacrimal and jugal. In the fossil, the lower margin of the lacrimal is not complete, but the preserved portion of the suture with the jugal measures just over 5 cm in front of the orbit. In a large *Hylochoerus* the suture is no longer than 3.5 cm, so it would appear that in the fossil skull elongation has taken place in the same area as in *Phacochoerus*. In the snout region, however, the fossil skull is very different. There is no distinct preorbital constriction; the snout runs forward from the level of the infra-orbital foramen without any significant increase in width, and the nasal sutures are virtually parallel throughout their length. In this the resemblance is closer to *Hylochoerus* than to *Phacochoerus*. The contour of the snout, as it would appear in transverse section, is highly characteristic and cannot

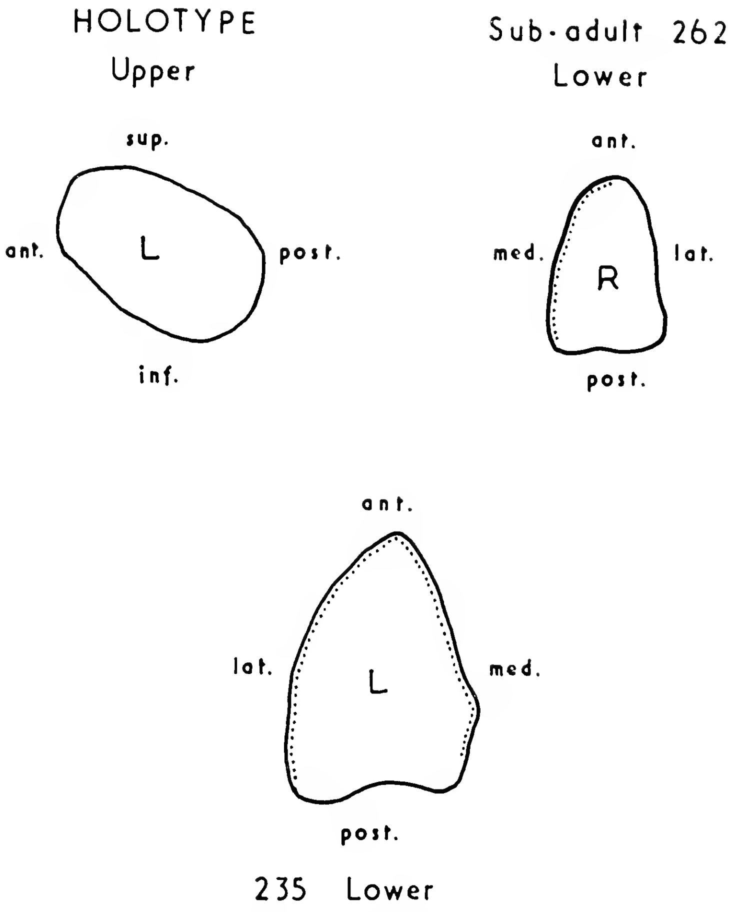

Figure 8. Sections through upper and lower canines of *Nyanzachaerus plicatus*, near the border of the alveolus. The dotted line indicates the zone covered with enamel. Nat. size. Abbreviations as in Fig. 5.

be matched in any of the extant African species. From the nasomaxillary suture ventrally, the maxillae slope inwards very slightly; at the level of the suture the bone is slightly inflated on either side to form a convex shoulder. These shoulders run backwards and would be continuous with a pair of conspicuous lateral ridges, forming the margins of the skull table just in front of the orbits, were they not interrupted in their course by the very well marked preorbital sulci passing down from the dorsal surface of the skull to the sides of the snout. The nasals, although flattened towards the midline, curve downwards then outwards to meet the "shoulders" in a smooth curve. The whole conformation of the snout is, in fact, like an elongated and narrowed version of that of *Nyanzachoerus pattersoni.*

On the sides of the snout, the flare of the zygoma starts just behind the infra-orbital foramen but very little of it is preserved. The bony flange at the base of the canine is large but less laterally directed than in *Phacochoerus* or *Hylochoerus*, and the basal part of the canine alveolus runs almost parallel with the axis of the skull. Between the canines, the palate shows a rather more marked medial groove than

TABLE 28. MEASUREMENTS ON SKULLS OF *NYANZACHOERUS PLICATUS*

	KP 251	KP 257	KP 262
Facial length	380e		
Nasal breadth	57	c45	
Muzzle breadth	46		
Ocular breadth	130e		124
Interorbital width	116e		100e
Frontal breadth	140e		146
Bizygomatic breadth		c280–300	
Orbital height		c140–150	
Posterior platal breadth		36	
Anterior palatal breadth		53	
Postcanine breadth	c60		
Precanine breadth	c115		
Length of premolar series		left 42.5 right c46	
Length of molar series		right 116	

does that of *Hylochoerus*, flanked by ridges that are separated from the canine flanges by the usual shallow blood vessel channel.

The left canine is broken at about the original alveolar margin and its root remains in the socket; it is flattened oval in cross section, slightly narrower lingually than on the outer side, and flattened above and below (Fig. 8). The curvature indicates that the tooth emerged almost parallel to the palatal plane at an angle of about 45° to the axis of the skull. The broken cross section shows no pulp cavity. The right canine is broken well below the alveolar margin, is of similar form, and still fails to show any pulp cavity. It is thus apparent that the canines have closed roots. This is one of the important diagnostic features of the species and is possibly also a general feature of the genus *Nyanzachoerus*. A few measurements are given in Table 28.

The associated mandible has lost the incisor/canine area, the left ascending ramus, and the right ramus behind the fourth premolar, although the right third molar is preserved, embedded in an isolated fragment of alveolar bone. The front of the mandible is narrow as befits the skull; it could only have contained relatively slender canines. The symphysis was probably 120–130 mm long. In profile the outer surface of the symphysis is almost straight and its lower corner lies well below the general level of the bottom of the corpus of the mandible, which curves down to it from a point below the fourth premolar (Pl. 14). This curvature is rather more marked than in *Hylochoerus*, and the symphysis is proportionally distinctly longer. The symphysis is fairly deeply scooped out on the inner surface and laterally compressed.

The left and right third premolars are in moderately advanced wear and the third molars are in fairly advanced wear (Pl. 18). The left fourth premolar and left second molar are worn to the dentine; the left first molar is broken away and the right fourth premolar badly damaged. Some measurements are given in Table 29.

P_3. The third premolar is a stout tooth and the main cone forms the full width of the crown. There is a fairly narrow posterior cingulum with a small cingular cusp, originally perhaps two-thirds the height of the crown. There is a very small anterior cingulum cusp.

M_3. The third molar shows the existence of three pairs of lateral columns, separated by unpaired median columns and a talon complex of three or four columns. The outer walls of the paired columns are stout and broadly curved, coalescing at the base of the crown without forming a marked cingulum, but the laterals were probably well separated in the upper part of the crown. The worn surfaces of the lateral pillars have a bilobed "cottage loaf" shape, the outer lobe being larger than the axial one. The median columns are irregular in outline.

The First Paratype

From the same locality as the holotype comes a pair of complete upper canines matching exactly those of the skull; there

TABLE 29. DIMENSIONS OF LOWER CHEEK TEETH OF *NYANZACHOERUS PLICATUS*

Specimen No. (KP)	Stage of Wear	Length (L)	Breadth (B)	Height	L/B
P_2					
235	Roots	9.0	7.0	–	
P_3					
235 left	Roots	25.0	16.5	–	
″ right		21.0	16.0	–	
251 left	Moderately	23.0	17.0	15.0+	1.35
″ right	advanced	23.2	16.2	15.0+	1.43
P_4					
235 left	Roots only	21.5	16.5	–	
″ right	damaged	22.5	17.0	–	
251 left	Very advanced	21.4	16.7	c3+	1.28
″ right		19.0	17.0	c17	c1.12
M_1					
235 left	Roots	19.0	19.0	–	
251 left	Broken	19.0	–	–	–
M_2					
235	Roots	27.5	22.0	–	
262	Incomplete	c38	20.3	13+	c1.90
251 left	Very advanced	26	c20	–	c1.30
M_3					
254	Almost unworn	c77	29.0	30.5	2.65
262	Moderately early	c74	24.3	26.5+	3.03
235	Moderate	68.5	28.0	25.0+	2.44
Specimen KP 251					
Length of premolar series		c56	Length of molar series		112
Specimen KP 235					
Length of premolar series		c55	Length of molar series		c115

is also a small section of root of another upper canine (KNM–KP 252; Pl. 14). The canines measure respectively 159 and 155 mm from tip to root and at the widest part the maximum and minimum diameters are 31.5 × 22.0 mm and 30.9 × 21.7 mm (Table 30). The roots are completely closed. There is no enamel remaining on the teeth, even at the tips, but it is not impossible that a little enamel may have been present in the juvenile stage. Both canines show a broad wear facet on the anterior lower face. This facet truncates the curved edge of the tooth and produces a straight upper edge that would have been approximately perpendicular to the axis of the skull. As we judge from the orientation of the tusks in the holotype skull, the facet itself does not appear to be quite vertical but seems to slope slightly backwards and downwards. A sloping wear could be produced only if there were a

TABLE 30. DIMENSIONS OF UPPER CANINES OF *NYANZACHOERUS PLICATUS*

Specimen No. (KP)	Maximum Diameter	Minimum Diameter
251 left	27.0	21.0
″ right	29.5	20.0
252 left	31.5	22.0
″ right	30.9	21.7
262	26.0	21.0
235 left	34.5	23.5

Table 31. Dimensions of lower incisors and canines of *Nyanzachoerus plicatus* (Specimen KP 262)

		Length	Breadth
I_1	(root)	9.0	13.0
I_2	(root)	7.5	14.0
I_3	(root)	7.0	12.0
C_1	(in alveolus)		
	left	21.0	15.5
	right	22.0	15.5

strong propalinal component in the jaw action, of a type unknown elsewhere. It seems more likely that there has been some distortion in the holotype skull and that in fact the facet had the usual vertical orientation. The lower canines must therefore have flared outwards and upwards so that the tips were not quite vertical but sloped slightly outwards. Closed rooted canines have been recorded hitherto only in "*Promesochoerus mukiri*" Leakey (1965), but it is believed that *Nyanzachoerus pattersoni* also had upper canines with closed or nearly closed roots.

The Second Paratype

A number of closely associated fragments represent pieces of a skull and mandible of a very young adult (KNM–KP 262; Pl. 15). The fragments include a piece of left maxilla showing the canine with its characteristic shape. There is also a piece of the left parietal broken along the midline but including the upper rim of the orbit, the supra-orbital foramen, and part of the parietal crest behind the postorbital processes; it is thus possible to estimate the interorbital width as about 100 mm as compared with 116 mm for an estimate made on the older holotype skull. The upper rim of the orbit lies a trifle below the surface of the skull roof, which is almost flat, very much as in *Hylochoerus* and contrasting with the raised orbits of *Phacochoerus*. The parietal crest behind the orbit, however, runs sharply towards the axis of the skull, almost at 45°, very much as in *Phacochoerus*, and it would appear that the braincase was shortened in the same way as in the warthog. The parietal constriction must have been narrow.

There is a rather flattened mandibular symphysis containing the roots of the incisors, the root of the left canine, and the right canine lacking only the tip (Pl. 15A) (Table 31). The morphology of the symphysis matches that of the holotype mandible. The lower canines are unlike the usual sharp triangular lower canines of the suids and resemble the upper canines in general outline but are anteriorly a little tapered and posteriorly flattened or slightly grooved. Enamel is visible only on the upper surface and is weakly rugose and very thin. The canine, like the upper tusks, is more forwardly directed than those of either *Hylochoerus* or *Phacochoerus*. The roots are still open but might have closed later in life.

A portion of the right mandibular ramus contains the second molar, damaged anteriorly, and the third molar, damaged posteriorly but with the impression of the back of the tooth visible in the bone (Pl. 15D, E). Dimensions are given in Table 29. Both in size and in structure the third molar corresponds to that of the holotype. Each of the paired columns is divided into a lateral and an axial element separated by well-marked anterior and posterior grooves. The lateral element is bounded by the broadly curved outer wall of the pillar, which is fairly smooth and has thick enamel. The inner element has a rather crenulated or irregular axial wall. The anterior lingual pillar has its posterior axial corner nearly isolated by a deep vertical groove, almost giving the appearance of an extra median pillar (this feature is also apparent in specimen KP 254). The anterior buccal pillar has a smilar vertical groove, nearly isolating an anterior lobe that resembles an eccentric anterior pillar. The second molar is rather elongate, having a strong shelflike posterior cingulum that produces a trefoil-shaped enamel

TABLE 32. DIMENSIONS OF UPPER CHEEK TEETH OF *NYANZACHOERUS PLICATUS*

	Specimen No. (KP)		Stage of Wear	Length (L)	Breadth (B)	Height	L/B
P²	257		Early	10.5	6.7	6.0	1.57
P³							
	257	left	Moderate	22.5	18.0	14.0+	1.25
	"	right		22.5	18.2	14.5+	1.23
P⁴							
	257	left	Moderate	18.4	19.8	14.0+	0.93
	"	right		18.2	20.3	14.5+	0.90
M¹							
	257	left	Very advanced	18.5	c19	3.0+	c0.98
	"	right		18.0	c19	2.5+	c0.95
M²							
	262		Moderate	39.0	26.7	16.0+	1.46
	206		Moderate (Very weathered)	37.6	c27	12.0+	c1.4
	257	left	Advanced	32.1	25.5	7.0+	1.26
	"	right		32.8	26.2	7.5+	1.25
M³							
	225	right	Early	68.0	c30	31.0	c2.25
	235	left	Moderate	63.5	31.5	25.0+	2.01
	257	left	Moderate	66.6	35.7	20.0+	1.86
	"	right		67.8	35.2	21.5+	1.92
	253		Moderately advanced	71.5	33.2	21.5+	2.15
Specimen KP 257							
	Length of premolar series			c46			
	Length of molar series			117			

island. The form of the pillars corresponds closely with those of the third molar.

An upper right second molar in early wear occludes perfectly with the lower teeth and provides a firm link between upper and lower tooth characters (Pl. 15 D, E). The lateral wall of the paired pillars is not as long as on the lower teeth, with the consequence that the axial element of the structure is longer than the lateral one. The lingual pillars have a decided and persistent stellate form, whereas the buccal pillars are more bell-shaped with an irregular axial wall. There is a strong posterior cingulum, like that in the lower second molar, and also a broad symmetrical anterior cingulum. The median pillar is irregular. Dimensions are given in Table 32.

The Third Paratype

This specimen comprises part of a skull, broken anteriorly immediately in front of the premolars, and posteriorly close to the supra-orbital foramina and through the back of the palate (KP 257; Pl. 13). The zygomatic arches are also lost. All the cheek teeth are preserved except for the right P².

The general morphology of the frontal and lacrimal areas corresponds well with the holotype. The muzzle is obviously narrow and has the same cross section as the holotype. At the same level of the zygoma the same sort of lateral "shoulders" are present. The beginning of the zygomatic arch lies high above the palatal plane, and the maxilla above M² is hollowed so that the lower edge of the arch is sharply defined. This resembles in some respects the condition in female warthogs. Below this rather high beginning of the flare, the zygoma descends to a low point above the middle of M^3, quite unlike any of the living African suids. The rest of the zygoma looks as if it were more hylochoerine than phacochoerine, and the basal portion expands laterally so much as to suggest that a zygomatic protuberance or knob must have been present, although too much is missing for this to be certain. The profile of the skull from the frontals towards the occiput must have resembled *Phacochoerus* to some extent, although the elevation of the cranium was not as exaggerated; the front of the snout did not droop in the warthog fashion and was relatively longer than in *Phacochoerus*. Some dimensions are given in Table 28 and a tentative restoration in Figure 7.

The elevation of the skull is reflected in the contours of the pterygoid and sphenoid areas above the back of the palate. The nasal passage is curiously narrowed above the third molar, possibly because the tooth is very wide and its roots restrict the space available. The palatine notch is not visible but must have been well behind the back of the third molar. The main foramina are level with the middle of M^3.

The upper dentition (Pl. 16) agrees excellently with the features seen in the M^2 of KP 262. The RP^3 is twisted into a position at right angles to its normal orientation, but the left one is in the normal position. The second premolar has also been twisted out of the normal orientation, but to a lesser degree. Measurements are given in Table 32.

P^2. The second premolar is a very small tooth. It is relatively broad with a central cone the full width of the crown; there are anterior and posterior ridges and possibly a secondary cone towards the back of the crown.

P^3. The third premolar has a stout main cusp with a moderately strong anterior cingulum on the anterolingual side. On the back of the tooth is a narrow high cingulum and there is a rounded postero-internal cusp.

P^4. This tooth is almost square and is built in the *Potamochoerus* fashion with a pair of buccal cones (paracone and metacone), apparently not widely separated and uniting into an island which, at least at this stage of wear, maintains a notch on the axial side. The lingual cone (protocone) is transversely narrower than the buccal cones, and produces an irregularly shaped enamel island similar to the buccal columns in the third molar, but laterally more compressed. There are moderate anterior and weak posterior cingula.

The M^1 are worn to dentine and no features can be distinguished.

M^2 is in advanced wear and the pattern is difficult to decipher, but there is nothing visible that conflicts with the details shown in the less worn tooth described in the second paratype.

M^3. The third molars are wide anteriorly and taper progressively towards the talon. There are three pairs of lateral pillars separated by single median pillars and there is a stout central talon pillar. Accessory columns rise from the base of the tooth between the second and third pairs of pillars on both sides and between the first and second pairs on the buccal side. The shape of the enamel islands is closely similar to that in the second molar KP 262 described above. A feature of the dentition which deserves comment is the rather marked upward taper from the base of the molars towards the crown; the occlusal width is thus 20 per cent narrower than the base in this specimen. The measurements are given in Table 32 and the teeth are illustrated in Plate 16.

Referred Specimens

A small assemblage of associated material, all numbered KP 235, very probably belonged to a single individual. There is an almost complete upper left third molar, in early wear, a piece of the right upper third molar, two parts of the mandible and pieces of both lower tusks, parts of the pelvis, a third cervical vertebra, and small fragments of skull and other bones.

The upper left third molar fits perfectly with the third molar of the mandible, so that there is no doubt about the identity. It matches closely in dimensions and structure the corresponding tooth in the skull KP 257. It has been sectioned half way down and the pattern is shown in Figure 9; photographs are given in Plate 17 and dimensions in Table 32. The other fragment represents the back half of the corresponding upper right molar.

The mandible has only two teeth reasonably well preserved. The left ramus is broken anteriorly and also behind the third molar, which is intact; the roots of P_2–M_2 are present. The right ramus is only a fragment, broken behind P_4, has the roots of P_3, the socket for a small P_2, and some of the socket for the canine. The third molar matches in structure the third molar in the second paratype, but the enamel is smoother and the convolutions in the axial region are less complex. It is illustrated in Plate 18 and the dimensions are given in Table 29. The P_4 in the right ramus fragment, undoubtedly of the same individual, lacks much of the lingual side. There is a fairly stout main cone, with a steep broad ridge extending to a rather pustulate anterior cingulum. There is a high posterior cingulum, bearing a stout cusp. A very large mandibular foramen is shown on the anterior part of the jaw fragment, lying below a point about 3 cm in front of the P_2 socket.

The canine fragments belong to a pair of lower tusks, the larger piece being 11 cm long and, as we judge by the slight curvature, is from the left side. Its cross section is subtriangular, with the upper and lower faces gently curved and the apex bluntly rounded; the posterior face is slightly hollowed (see Fig. 8). The maximum diameter near the base is 34.5 mm and the transverse dimension 23.5 mm. Thin enamel is present on both the upper and the lower surfaces. In this respect it appears to differ from the juvenile tusks in the symphysis of KP 262, in which enamel is visible only on the upper surfaces, although it may well have been present on the lower surface in later life.

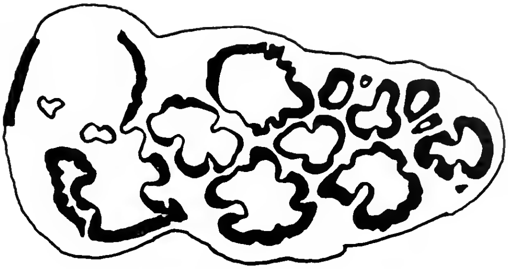

Figure 9. Enamel pattern on sectioned surface of isolated upper left third molar of *Nyanzachoerus plicatus* (see also Pl. 17). Nat. size.

The two incomplete pelvic bones correspond in general morphology to those of *Hylochoerus* but are 20 per cent longer. The third cervical vertebra also agrees reasonably well with *Hylochoerus* in general form but is a good deal larger, perhaps by 15–20 per cent.

Four isolated upper molar teeth, or fragments, are also assigned to this species. One (KP 253) is a complete upper right third molar in moderate wear, corresponding very closely with the molars in skull KP 257, although a little larger (see Table 32; Pl. 17). Two upper third molars in early wear are numbered KP 225 and belong to a single individual. The RM^3, although damaged, is very similar to the upper molar KP 235, both in morphology and in dimensions (Table 32). Only the back half of the LM^3 is preserved. There is also a very rolled and weathered right upper second molar (KP 206) that can be assigned to the species as it corresponds to the same tooth in the skull KP 257.

An unworn right lower third molar (KP 254) lacks the front part of the first pair of pillars. When complete it was slightly larger than KP 262 but it displays the same structure. The talon shows a number of

Table 33. Measurements on possible lower milk dentition of *Nyanzachoerus plicatus* (KP 269)

	Length	Breadth	Height
Ldm$_3$	11.2	6.4	4.6+
Rdm$_3$	10.8	6.3	4.6+
Ldm$_4$	24.8	10.9	3.5+
Rdm$_4$	24.8	10.9	3.5+
RM$_1$	28.0 (23.0 at base)	16.8	14.5+

small accessory columns extending from one-third to one-half the height of the crown (Pl. 17).

The tip of a gently curved isolated canine (KP 203) has a flattened oval cross section and measures near the broken base 29.5 mm by 20.0 mm; the length from the damaged tip to the broken base is 10 cm. There is no enamel. On the inner side of the tip is a small wear facet. The curvature of the tooth matches that in the isolated canine referred to *N. plicatus* and the dimensions are similar. Although there are slight differences in the cross section, it seems probable that the tooth should be assigned to that species.

Possible Lower Milk Dentition

Two parts of the rami of a mandible (KP 269) possess on the left side dm$_3$ and dm$_4$ and on the right side dm$_{3-4}$ and M$_1$; there is also a fragment of LM$_1$; P$_3$ and P$_4$ are visible in the crypt on each side and they are not yet fully formed. Two fragments of an unerupted and incompletely formed M$_2$ were recovered and presumably came from the crypt. The form of the pillars and of the anterior cingulum in the M$_2$ makes it clear that the specimen does not belong to *N. pattersoni*. There is no known *N. plicatus* second molar in early wear available for comparison, but the structure of the anterior part of the M$_2$ is so like that of the unworn M$_3$ that it is reasonable to assign this milk dentition to *N. plicatus*.

The dm$_3$ differs from that of *N. pattersoni* in possessing a slightly stronger posterior cingulum on the lingual side, in being a little longer than the corresponding tooth in *N. pattersoni*, and in having wider lateral pillars. The M$_1$ is considerably longer than the M$_1$ of *N. pattersoni*, the extra length being in part due to elongation of the lateral pillars, in part to strong development of a posterior cingulum. The enamel figures are like those of adult teeth which have been assigned to *N. plicatus*, the lateral pillars being rather more folded than in *N. pattersoni*. Measurements are given in Table 33.

DISCUSSION

Although there can be no doubt that the material representing the species *plicatus* is very different from that assigned to *Nyanzachoerus pattersoni*, there is also the possibility that it belongs to a distinct genus. The third and fourth premolars are less enlarged than is the case in *N. pattersoni*, but they are nevertheless enlarged relative to *Sus* or *Potamochoerus*, as will be demonstrated later in this account. The lower canines are very similar to those of *N. pattersoni*. The material available is not sufficient to show whether there is any marked sexual dimorphism in *plicatus*, but the third paratype skull suggests that there was at least a fair degree of zygomatic inflation. The snout, though longer and thinner than that of *N. pattersoni*, shows the same general conformation, and the degree of elevation of the braincase is similar. The upper canines are oval in cross section, show no signs of enamel and have a very small pulp cavity; root formation clearly occurred early, possibly even earlier than in *N. pattersoni*. The teeth are constructed in a manner generally similar to those of *N. pattersoni*, and the main difference lies in the enlargement of the third molar and in the greater degree of complexity of the folding of the enamel in the molars, which provides the basis for the specific name. Although more complete material may make it possible to show that a different genus is represented, at the present time it seems reasonable to assign *plicatus* to the genus *Nyanzachoerus*.

It now transpires that a tooth of *N. plicatus* has been known for some time but could not be recognised. It is an upper right third molar from the Chiwondo Beds, near Lake Nyasa, Malawi, and it was described by Hopwood in 1931 as the lower third molar of a large *Hylochoerus* (BMNH M 14121). Leakey (1958) considered that it was probably an upper third molar of *Mesochoerus paiceae* (the upper dentition of which is not certainly known). The specimen has all the features found in the third paratype but is a little more robust, and the talon is broader and somewhat more complex. It is cracked and weathered and there seems to have been some slight expansion of the crown as a result of wedging by mineral growth, so that the original dimensions may have been a millimetre or two less than the present length of 73.5 mm and maximum anterior breadth of 37.0 mm. The tooth is moderately well worn and the present maximum height, at the talon, is 21 mm, but it is clear that the intact crown was only about 30 mm high. The same upward taper is seen as in the Kanapoi material and the specific identity is not in doubt.

THE NEW *NYANZACHOERUS* FROM LOTHAGAM

Nyanzachoerus tulotos sp. nov.*

Text-figure 10; Plates 19–25

Diagnosis. A species of *Nyanzachoerus* about the size of the extant *Hylochoerus*, but more robust. Both upper and lower first premolars present; third and fourth premolars large, P^4 approximately as broad as M^3. Third molars relatively low-crowned and composed of only two pairs of lateral cusps, together with a small talon or talonid. In both upper and lower jaws, the premolar series P2–P4 is over 70 per cent of the length of the molar series; P$_4$ is more than half as long as M$_3$. Diastema from lower canine to P$_2$ about three quarters the length of the premolar series P$_2$–P$_4$. In the male the preorbital ridges are strongly marked; the maxillary flanges around the canines, and the nasopremaxillary thickenings, are large, the former rising to the level of the dorsal surface of the snout. Skull table broad but lightly built, in striking contrast to the heavy muzzle region. Zygomatic protuberances of moderate size and, while considerably expanded laterally, not deep dorsoventrally; viewed from the side they are not significantly deeper near the posterior than near the anterior end, and the lower margin is approximately horizontal.

Holotype. KNM–LT 316; an almost complete skull, regarded as male.

Paratype. KNM–LT 302; incomplete left and right mandibular rami, regarded as male. KNM–LT 287: damaged mandible, including symphysis and lower canines, regarded as male. KNM–LT 295: mandible of adult with symphysis damaged but showing very small lower canines, together with a loose incisor, regarded as female.

Locality. Lothagam, northwestern Kenya.

Horizon. Lower part of deltaic series (Unit 1, Member B), Lothagam sediments; probably Middle to Upper Pliocene.

Remarks. As was indicated in the introduction, and shown diagrammatically in Figure 2, the fossil suid material has come from two zones in the deltaic series of Unit 1. The most complete specimens, and the best range of material, came from Member B, below the red marker and tuff marker; these are regarded as the "typical" *Nyanzachoerus tulotos*, and the account that follows is based on this material only. The specimens from Member C show some differences and they will be discussed

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* *N. tulotos* has been referred to in several preliminary faunal lists as *Nyanzachoerus* species "C."

separately and the measurements will be shown separately in the relevant tables.

REFERRED SPECIMENS FROM UNIT 1, MEMBER B

KNM–LT 282: isolated, unerupted LM_3. LT 283: isolated, damaged M_3. LT 288: much crushed mandibular symphysis and right ramus, including canines and roots of two incisors, damaged remains of premolars and heavily damaged molars. LT 290: several isolated teeth, not belonging to the same individual, comprising LP_4, tip of right lower canine, two damaged RM^3, and a fragment of maxilla with RP^3 and RP^4. LT 291: right mandibular ramus with stump of canine, RP_2–M_1 and the stump of RM_2. LT 300: right mandibular ramus with RP_3–M_2 and the anterior part of M_3; the two premolars are badly damaged. LT 301: damaged fragments, including LP_3, LP_4, RP_4, remains of LM_3 and RM_3, a fragment of lower canine. LT 303: left mandibular ramus with LP_4, LM_3 and roots of LM_1 and LM_2. LT 305: damaged right mandibular ramus with base of canine, roots of RP_2 and RP_3, and anterior part of RM_3. LT 319: isolated unerupted M^3. LT 321: isolated RM^3.

DESCRIPTION

The Holotype Skull

Specimen KNM–LT 316 consists of a skull, somewhat cracked and crushed dorsoventrally but almost complete. The only parts missing are the greater part of the occiput, together with the posterior regions of the skull table and left zygoma, and the tips of the nasals. The incisors, canines, and RP^1 are missing but all the other cheek teeth are present.

The skull belongs to a young adult, with the third molars fully erupted but not much worn. It is of moderate size, with an estimated vertex length of 425 mm, which is about the size of a large *Hylochoerus* skull, although the fossil is wider and more robust (Table 34). The presence of very large maxillary flanges whose dorsal wings extend almost as high as the snout, together with corresponding thickenings on the muzzle at the nasopremaxillary suture, is at once reminiscent of the condition in a male bushpig. It is because of these features that the skull is regarded as belonging to a male. There are, however, differences in detail from the condition in the bushpig; the dorsal wings of the very elongated maxillary flanges are situated almost directly above the canine alveoli, instead of somewhat behind the tusks, and they rise almost vertically without a significant backward rake. The flanges more closely resemble a hypertrophied version of the relatively small ones that occur in *Hylochoerus* than they do those of the bushpig and are, indeed, very like those of *Sus strozzi.* Another resemblance to *Hylochoerus* is the distinct bulge on the premaxilla in front of the flanges, which lies between the tendons of the levator rostri and dilator naris lateralis muscles. In the bushpig, with its very small rhinarium, these tendons lie closer together and the vertical surface of the premaxilla is almost flat.

Behind the maxillary flanges, the muzzle shows only a slight constriction at the level of the pre-orbital foramina. Although there has been some crushing and distortion in this region, it is clear that the upper surface of the muzzle was slightly convex and that rounded "shoulders" separated this from the more vertical side walls. As they pass backwards, the shoulders become more distinct and are continuous with pre-orbital ridges of the same sort as occur in *Nyanzachoerus pattersoni,* but they are much larger in the Lothagam species.

The whole posterior region of the skull is extremely broad. The width across the zygomata is three-quarters of the basilar length, and the maximal width across the frontals is almost 40 per cent of the total length of the skull. The supra-orbital foramina lie just anterior to the orbits; at this level the enlarged pre-orbital ridges

TABLE 34. MEASUREMENTS ON HOLOTYPE SKULL OF *NYANZACHOERUS TULOTOS* COMPARED WITH *HYLOCHOERUS MEINERTZHAGENI*

	Holotype	*Hylochoerus*
	LT 316	MA 1 H 1
Vertex length	425e	428
Basilar length	402	375
Bizygomatic breadth	295	246
Greatest breadth across nasals	63	56.5
Breadth of muzzle between infraorbital foramina	50	71
Parietal constriction	88e	96
Breadth across postorbital processes	166	125
Height of top of orbit above palatal plane left	92	115
right	103	
Palatal length	316	283
Breadth of palate		
between M^3–M^3	36	46
between P^2–P^2	38	59
Palatine notch position*	46	83
Palatine notch width	23	40.5
Precanine breadth across premaxillae	90	74
Breadth between back of I^3–I^3	77	51.5
Diastema C–P^1	11	–
C–P^2	39	35
Length of premolar series P^1–P^4	93	–
P^2–P^4	63.5	24.5
Length of molar series	90	77

* Distance from anterior back of palatine notch to line joining boundary between M^2 and M^3

terminate and the surface of the skull, from the orbits back, is smooth and gently concave, very much as in *Phacochoerus*. The orbits, however, are not raised above the level of the skull table, but, as in *Hylochoerus*, lie slightly lower than the parietal crest. The latter slopes gently upwards and it is clear that, as in *Hylochoerus*, the parietal crest was the highest point of the skull.

The zygomata originate on the muzzle at the level of P^4 and from this point flare outwards sharply, very much like an exaggerated version of *Hylochoerus*. Below and just behind the orbit, the jugal is expanded laterally and thickened dorsoventrally to form a zygomatic protuberance that, although smaller than that of *Nyanzachoerus pattersoni*, is both larger and more posteriorly situated than the zygomatic thickening on *Hylochoerus*. The surface of the bone is not very well preserved, but it certainly cannot have been as rugose as in the zygoma of *Hylochoerus*. It therefore seems improbable that any extensive zygomatic wart was present, although there may have been some thickening of the skin overlying the protuberance.

Although the occiput is damaged, sufficient of the temporalis attachment is present to show that this muscle must have been of approximately hylochoerine proportions. The shape of the orbits has been much distorted by crushing but one distinctive feature is preserved, to wit, that in front of the postorbital process the upper margin is dilated and projects slightly to overhang the actual eye socket. This must have given the eyes, in life, an unusually deep-set appearance.

The curiously "lumpy" appearance of the skull, and also of the teeth, forms the basis for the specific name, derived from the Greek (τυλωτός) meaning a knob, lump, or callous.

The character of the canine alveoli, small with large maxillary flanges, together with the unreduced upper incisors, gives the anterior part of the palate a somewhat potamochoeroid aspect. The snout, however, is much less specialized as a digging organ than in the bushpig and tapers gently from the margin of the canine alveolus to the anterior end, instead of being narrow and parallel sided. There is very little widening of the palate at the level of the canines, and the blood vessel grooves therefore run an almost parallel course from the anterior to the posterior palatal foramina. The palatine notch is very similar to that of *Potamochoerus*: it does not lie far behind the third molars and the posterior edge of the palatines bends upwards sharply beneath the nasal passage. The bullae resemble those of *N. pattersoni*, being laterally compressed and ending anteroventrally in a sharp point, but they are relatively larger. The glenoids are only slightly raised above the palatal plane and are wide from front to back—both of which facts indicate that the jaw movement was not a specialised sideways grinding action. The lower surface of the zygoma is flat and extremely broad, but the surface preservation is not good enough to permit the limits of the masseter origin to be made out.

Although none of the incisors is preserved, the alveoli show that three pairs were present and that they were unequal in size. Both *Hylochoerus* and *Phacochoerus* retain only one pair of permanent upper incisors. The canines, too, are represented only by alveoli, but these show that the tusks must have been small and much flattened dorsoventrally, and they probably rooted early. Details of the tooth structures are given later in the section on the upper dentition.

The First Paratype Mandible

Specimen KNM–LT 302 comprises portions of right and left mandibular rami. The right ramus includes P_3–M_3 and the left one has P_2–M_1, together with some remnants of the canine. The relatively large size of the tusk suggests that the jaw belonged to a male, and in both size and morphological characteristics the specimen agrees very well with the type skull.

The corpus of the mandible is rather heavy, its thickness at the level of P_4/M_1 being about 42 mm. Just sufficient of the right ramus is preserved to show that behind M_3 the inner margin of the bone curves abruptly outwards; this is to be expected if the bone forming the angle was light, as in *N. pattersoni*. Nothing of the symphysis is preserved and the portion of the root of the canine that remains is much damaged. The latter, however, is sufficient to show that the maximal diameter of the tusk within the aveolus cannot have been less than 20 mm and was probably rather more. The dimensions of the teeth are included in the appropriate tables and the jaw is illustrated in Plates 20 and 22.

The Second Paratype Mandible

Specimen KNM–LT 287 is a somewhat damaged mandible, including the symphysis and lower canines, and is considered to belong to a male. The jaw is rather crushed, the anterior margin is eroded, and of the incisors only some fragments of the central pair remain. On the right, the ramus is preserved to a level a little behind the third molar, but of the cheek teeth only P_1–P_3 and a damaged P_4 remain; the molars have been broken away and only traces of the roots exist. On the left, the ramus extends only to the level of P_4; P_1 has been broken off at the alveolar margin; P_2 is present, together with the much cracked P_3 (Pl. 20).

The preserved second and third premolars agree very closely with those of the first paratype; the length of the cheek tooth series and the thickness of the jaw are similar. There can be little doubt that the two belong to the same species, and the size of the canines in the present specimen suggests that it too is a male. Although the cheek teeth are much damaged, this specimen complements the first paratype and provides information about the characters of the symphysial region, missing in the latter.

A little more of the posterior part of the jaw is present in this specimen than in the first paratype and this shows that, as indicated in the latter, the thick corpus narrows very rapidly behind the tooth row, where the masseter and pterygoideus muscles are inserted. The preserved part of the lower margin of the angle, although ridged in relation to these muscle insertions, is very slender, exactly as in the jaws of the species of *Nyanzachoerus* from Kanapoi.

The symphysis is elongated. It extends back to the level of the anterior root of P_3 and its length, measured along the curved ventral surface, is approximately 150 mm.

The general shape is roughly similar to that of the bushpig but the constriction behind the canines is less marked and the anterior end of the jaw is more pointed, so that between the canines the bone forms a pointed extension and the incisors do not lie virtually in a straight line, as they do in the bushpig. This accords well with the tapering snout region in the type skull. The anterior mental foramina lie behind the level of the posterior end of the canine alveoli, and, in front of them, the bone extends for at least 40 mm. This is in contrast to the bushpig, where the central region is truncated, the incisors lie almost in line, and the distance between the anterior mental foramina and the alveoli of the central incisors is consequently very short. The insertion of the protractor muscle of the lower lip in the fossil is extremely like that of the bushpig, and, at the posterior margin of the symphysis, the insertions of the geniohyoideus and genioglossus are clearly marked. They are deeply inset just above the lower border of the posterior wall of the symphysis exactly as they are in the bushpig. The dorsal aspect of the symphysis is also distinctly potamochoeroid, with the same differences as noted above, the constriction behind the canines being a little less marked and the margin in front of the canines more pointed.

The Third Paratype Jaw

Specimen KNM–LT 295 is the mandible of an adult with very small canines, regarded consequently as belonging to a female; associated with it is an isolated left central incisor. The jaw is broken off on either side a little behind the third molars and the anterior part of the symphysis is missing, but it is otherwise complete (Pl. 20). The incisors are missing, except for the root of the right I_1, and the canines, first premolars, and left second premolar are broken off at the alveolar margin. The other cheek teeth are present on both sides (Pl. 23) and their measurements are included in the relevant tables.

A very peculiar feature of the mandible (KNM–LT 295) is the asymmetry of the jaw. On the left side the rising curve of the ascending ramus is approximately 9 cm behind the back of the third molar. On the right side the corresponding point is only 3.5 cm behind the third molar, so that the whole jaw is shortened on this side, although the third molars are equidistant from the symphysis. There is no possibility that this is the result of post-mortem distortion, as is attested by the normality of the muscle impressions. It is thus clear that the ascending ramus was much foreshortened. It would be expected that such malformation would have effects on the jaw movement, and hence on the teeth. Contrary to this expectation, the teeth are worn in a completely normal manner, indicating either that the mandibular condyle was nevertheless in a normal position (which is difficult to imagine), or that there were compensating distortions in the skull.

This specimen differs from the second paratype jaw mainly in the small size of the canine, the maximal diameter being 14.8 mm as compared with 22.5 mm in the latter. It is this feature that is taken to indicate that specimen LT 295 should be identified as belonging to a female. The fact that the cheek teeth in this specimen are, in general, rather small should not be regarded as characteristic of females. As may be seen from Table 40, there are other specimens in which the canines are very small, but the dimensions of the cheek teeth are not below the mean values.

Specimen LT 295 shows the usual heavy, thickened rami, thinning away sharply behind the third molars. Presumably in relation to the small canines, the whole symphysial region, although of the same general form as that of the second paratype, is much shorter. Although the anterior margin is missing, the presence of one central incisor showing the enamel line makes it possible to estimate the length of the symphysis with considerable confi-

TABLE 35. *NYANZACHOERUS TULOTOS* DIMENSIONS OF UPPER INCISORS

Specimen No. (LT)	Tooth	Transverse (length)	Anteroposterior (breadth)	Height
295	RI^1	21.5	10.8	16.0+
326	RI^1	21.3	10.5	12.8+
316	LI^1 alveolus	18.8	15.0	–
	RI^1 alveolus	18.2	14.6	–
	LI^2 alveolus	20.8	11.4	–
	RI^2 alveolus	20.2	11.5	–
	LI^3 alveolus	19.4	c10.6	–
	RI^3 alveolus	18.6	12.6	–

dence. It must have measured approximately 105 mm, as compared with 150 mm in the second paratype. The anterior mental foramina lie further forward than in the male jaw, being situated approximately at the level of the anterior margin of the canine alveolus, instead of slightly behind the posterior margin. The origins of the geniohyoid and genioglossus muscles, as in the male, are strongly marked and deeply inset, like those of the bushpig.

The Upper Dentition

Only a single upper incisor tooth, belonging to specimen LT 295, is known from the lower deltaic beds. This is a left central incisor; its general form is very much like that of the bushpig, but on the mesial two-thirds of the lingual face there is a low cingulum. An almost identical right upper incisor tooth (LT 326) occurs in the upper deltaic beds. Alveoli are present in the holotype and their measurements, together with those of the two actual teeth, are given in Table 35.

No upper canines are known but the dimensions of the alveoli of the type skull (given in Table 36) indicate that they cannot have been very large. The flattened oval shape has already been mentioned. A canine found with the holotype is almost round in cross section and does not fit the skull.

TABLE 36. *NYANZACHOERUS TULOTOS* DIMENSIONS OF UPPER CANINES

Specimen No. (LT)	Position	Maximum	Minimum
316	Left alveolus	41.5	29.0
	Right alveolus	40.7	34.0

P^1 and P^2 are known only from the type skull. P^1 is present only on the left side. It is a small elongated tooth with an ill-defined main cusp and a posterolingual cingulum. It lies midway between the canine and the second premolar, separated from each by a short diastema. On the right, an alveolus is present in the corresponding position.

P^2 is a small, elongated tooth, composed of a rather low main cusp surrounded by a cingulum to which it is linked by rather poorly defined anterior and posterior crests. At the posterior end, the cingulum extends lingually and a small fovea intervenes between it and the main cusp: the outline of the tooth is thus subtriangular. Although there is considerable wear on the more posterior teeth of the type skull, P^1 and P^2 are almost unworn and they cannot have been of much functional value.

P^3 is a large tooth, almost as broad as it is long (Table 37). In the type specimen the large main cusp is almost circular in cross section and is surrounded by a much crenulated cingulum. The cingulum is broadest at the antero- and posterolingual margins and thins away on the outer surface over the large buccal root. In the referred specimen (LT 290) the cingulum is not quite so well developed; it is absent

TABLE 37. *NYANZACHOERUS TULOTOS* DIMENSIONS OF UPPER PREMOLARS

FROM MEMBER B

	Specimen No. (LT)		Stage of Wear	Length	Breadth	Height
P^1						
	316	left	Slight	12.1	6.4	5.9
	"	right	Alveolus	16.5	7.8	–
P^2						
	316	left	Slight	15.2	10.5	c8
	"	right		15.4	10.8	c8
P^3						
	290		Moderate	24.8	22.0	14.5+
	316	left	Moderately heavy	24.5	23.7	c16 +
	"	right		24.5	23.0	c17 +
P^4						
	290		Moderate	20.6	25.0	13.2+
	316	left	Moderately heavy	19.8	28.5	14.3+
	"	right		19.9	26.4	14.6+

FROM MEMBER C

	Specimen No. (LT)	Stage of Wear	Length	Breadth	Height
P^3					
	310	Early	29.4	29.3	20.6
	313	Moderate	31.0	31e	17.5e+
P^4					
	310	Moderate	22.7	28.0	15.0+
	313	Moderately heavy	22.5	30.8	10.6+

on the whole of the buccal surface and thins away in the centre of the lingual surface.

P^4 is also large. The main cusp is transversely elongated and the tooth is broader than it is long. Anteriorly and posteriorly a crenulated cingulum embraces the main cusp but thins away on the buccal and lingual faces, so that the main cusp accounts for the whole width of the base of the tooth. In the referred specimen, LT 290, the cingulum is smaller. Towards the apex the main cusp divides into the separate lingual and buccal elements typical of nyanzachoerine fourth premolars. In the more heavily worn type specimen these have fused to give a single wear facet, which on the buccal side is a smooth semicircle but lingually is irregularly folded where it contacts the cingulum. Dimensions of premolars are given in Table 37.

The first and second molars are known only from the type specimen (Table 38). M^1 is heavily worn but clearly consisted of the usual anterior and posterior pairs of cusps. A small median element may well have been present but the tooth is so heavily worn that it is no longer distinct.

M^2 is a large tooth with a crown composed of anterior and posterior pairs of cusps and anterior and posterior cingular complexes. A small median cusp has almost fused with the posterior cusps. The outlines of the wear facets on the main cusps are roughly circular with some slight irregularities towards the centre of the tooth, where they contact the median element.

TABLE 38. *NYANZACHOERUS TULOTOS* DIMENSIONS OF UPPER FIRST AND SECOND MOLARS

FROM MEMBER B					
Specimen No. (LT)		Stage of Wear	Length	Breadth	Height
M^1					
316	left	Heavy	23.0	22.0	9.3+
"	right		21.8	21.3	8.0+
M^2					
316	left	Moderate	28.6	28.9	11.5+
"	right		28.7	27.2	11.9+

FROM MEMBER C				
Specimen No. (LT)	Stage of Wear	Length	Breadth	Height
M^1				
310	Moderate	23.3	21.6	6.5+
313	Very heavy	26.3	24.5	6.3+
M^2				
293	Moderate	31.3e	27.2	12.5+
313	Moderate	35.6	31.8	7.5+

M^3 is a rather low-crowned tooth, very similar in structure to that of *Potamochoerus.* Two main pairs of cusps are separated by a lower, rather ill-defined median cusp. Anteriorly there is a cingular complex and posteriorly the talon is formed by a single terminal cusp, together with a few ill-defined auxiliary cusplets on the posterobuccal face. In none of the specimens is the wear on the cusps very heavy, but in the type and in the damaged specimen, LT 283, it is enough to expose the form of the pillars. These are stout and very like those of *Potamochoerus* with an infolded rosette form, but the folding is more strongly marked than in the bushpig, especially on the lingual cusps. Dimensions are given in Table 39.

The Lower Dentition

The lower incisors are represented by only a few root stumps and alveoli in the

TABLE 39. *NYANZACHOERUS TULOTOS* DIMENSIONS OF UPPER THIRD MOLARS

FROM MEMBER B							
				Breadth		Height	
Specimen No. (LT)		Stage of wear	Length	Anterior	Talon	Anterior	Maximum
319		Unworn	45.0	31.5e	15.2	19.0e	19.0
321		Early	43.0	28.6	14.8	18.0+	18.0+
290B		Early	40.0e	29.0	14.6	16.0+	18.5
290A		Moderate	41.0e	26.7	15.8	11.5+	11.5
316	left	Moderate	41.5e	27.0	22.8	16.1+	16.1+
"	right	Moderate	38.0	27.4	23.2	16.0+	16.0+
283		Heavy	39.4	c27	21.6	–	–
Mean			41.2	28.6	14.8		
S.D.			2.172	1.637			

FROM MEMBER C						
			Breadth		Height	
Specimen No. (LT)	Stage of Wear	Length	Anterior	Talon	Anterior	Maximum
326	Unerupted	45.5e	31.5e	–	19.5	19.5
286	Early	46.1	32.0	17.1	16.6+	21.1
324	Moderately early	42.3	29.5	15.5	19.5+	19.5+
313	Moderate	48.8	33.7	19.5	15.0+	17.3+
293	Moderate	44.3	30.5	15.0	16.8+	18.2+
307	Moderately heavy	45.6	31.5	15.7	13.3+	14.0+
Mean		45.4	31.5	16.6		
S.D.		1.961	1.295			

TABLE 40. *NYANZACHOERUS TULOTOS* DIMENSIONS OF LOWER CANINES

Specimen No. (LT)	Position	Maximum	Minimum	Length
291	right alveolus	17.2	11.0	–
305	right	22.0	c17.5	?
295	right	c16.5	c14.0	?
290A	left	21.3	15.0	74+
287	left	23.2	21.5	c80
"	right	22.5	20.5	c78
288	left	24.0	22.0	c85
"	right	25.5	22.0	c91

second and third paratypes and in specimen LT 288. These indicate that I_1 and I_2 were large and I_3 a little smaller. As already mentioned, the front of the symphysis is somewhat pointed and the incisors do not lie in a straight line.

Canines are present in the second paratype and in specimens LT 288 and 305; LT 290 includes an isolated canine tip. Roots are preserved in the third paratype (LT 295) and in specimens LT 300 and 291. As can be seen from the measurements given in Table 40, the roots in the third paratype and in specimen LT 291 are considerably smaller than in the other specimens. As already noted, this is interpreted as sexual dimorphism, and the two specimens with the small canines are regarded as female. The small tusks are known only from the broken off stumps included in these two specimens, but complete examples of the larger, presumed male, tusks are preserved. As can be seen from Table 40, even these are relatively small, the largest of them (specimen LT 288) measuring only 91 mm from alveolus to tip along the curved outer margin and having a maximum diameter of 25.5 mm. The tusks are more rounded than those of the bushpig; both upper and lower faces are gently convex, and where the two meet anteriorly, they do so smoothly without any sharp crest. Both are covered with enamel that bears fine cross striations, but no enamel is present on the posterior face (Fig. 10). The tusks emerge from the jaw at much the same angle as those of *Potamochoerus* and the wear facets of the two also show some similarity. In *Phacochoerus* the wear facet is a single almost flat vertical surface that looks as though it were made by a single clean cut. In *Potamochoerus* the distal part of the facet is similar but proximally it curves outwards rather irregularly, as though hacked out by a number of individual cuts. This difference, of course, reflects the specialized sideways grinding of *Phacochoerus* and the more rotatory action of the *Potamochoerus* jaw. It is the back-and-forth component of the movement that is responsible for the basal excavation in the wear facet of the latter. In the fossil, the potamochoeroid basal excavation is present, but is distinctly less marked than in the extant bushpig. This is

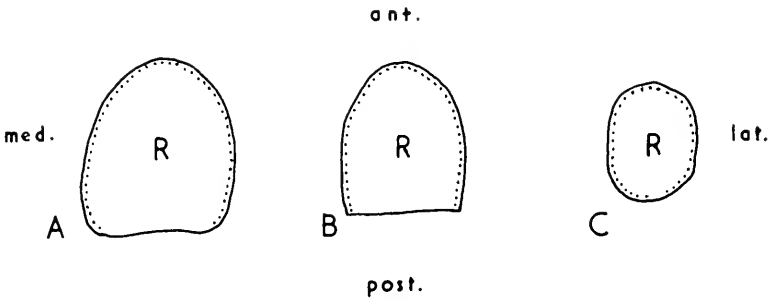


Figure 10. Sections of right lower canines of *Nyanzachoerus tulotos*. A is from the 2nd paratype (presumed male) and shows the shape of the alveolar border; B is the same tooth, 2 cm higher up, and shows the flat posterior wear facet. C is from the 3rd paratype (presumed female) and, although taken at the alveolar border, is close to the tip of the tooth and does not represent the final adult shape. Nat. size. Abbreviations as in Fig. 5.

TABLE 41. *NYANZACHOERUS TULOTOS* DIMENSIONS OF LOWER P_1

Specimen No. (LT)		Position	Length	Breadth	Height
291		root alveolus	c11.0	–	–
295	right	root alveolus	10.5	6.5	–
290A	left	broken	c11.0	c6.5	–
	right	moderate	10.1	6.0	5.5+

TABLE 42. *NYANZACHOERUS TULOTOS* DIMENSIONS OF LOWER P_2

Specimen No. (LT)		Stage of wear	Length	Breadth	Height
291		Slight	14.3	8.1	8.2
302	left	Slight	15.5	8.2	6.0+
295	left	Root	(14.5)	–	–
	right	Slight	15.0	7.6	6.0
287	left	Slight	15.3	8.8	7.0
	right		15.0	7.8	7.0
288	right	Root	(c14e)	(c8)	–
Mean			15.0	8.1	
S.D.			0.407	0.409	

in agreement with the characters of the glenoid in the type skull, which also suggests relatively unspecialized jaw action.

P_1 is present only in specimen LT 287 but broken off root stumps in other specimens show that it was regularly present. It lies midway between the canines and P_2 and is approximately oval, with a low main cusp and an anterior crest. Measurements are given in Table 41.

P_2 is a small elongated tooth with a low central cusp, joined by anterior and posterior ridges to low cingula, the posterior one of which bears a low cingular cusp (Table 42).

P_3 is large, with a somewhat backwardly raked conical main cusp. Anteriorly this is linked by a crest to an anterior cingulum that rises to a small pointed cusp where it meets the crest. Posteriorly, there is a broader, higher cingulum, the apex of which forms a small posterior cusp. In the almost unworn specimen LT 291 this rises to about half the height of the main cusp. Early wear on this tooth produces a backwardly sloping facet. As a result the posterior cingular cusp soon becomes abraded and its wear facet unites with that of the main cusp. Dimensions appear in Table 43.

P_4 is a broad, roughly rectangular tooth, composed of a strong main cusp, with slightly crenulated anterior and posterior cingula. The posterior cingulum bears a small cusp rising to at least three-quarters of the height of the main cusp. Measurements are given in Table 44.

M_1 is relatively small (Table 45). It has the usual anterior and posterior pairs of

TABLE 43. *NYANZACHOERUS TULOTOS* DIMENSIONS OF LOWER P_3

Specimen No. (LT)		Stage of wear	Length	Breadth	Height
291		Slight	28.0	22.0	27.0
305		Root	(30.5e)	(25e)	–
302	left	Moderate	29.0	23.3	25.0
"	right		29.2	23.6	25.0+
295	left	Moderate	26.0	19.1	20.7+
"	right		24.2	17.8	19.7
287	left	Moderately heavy	c30.0	c22.0	24.5+
"	right		28.0	21.8	24.5
300		Moderately heavy	25.0	18.8e	16.0+
301		Heavy	24.3	20.4	19.0+
288	right	Heavy	c29.5	20.5+	10.0+
Mean			27.3	20.9	
S.D.			2.126	1.944	

TABLE 44. *NYANZACHOERUS TULOTOS* DIMENSIONS OF LOWER P_4

Specimen No. (LT)	Stage of wear	Length	Breadth	Height
291	Slight	22.3	22.3	25.2+
305	Moderate	25.6	22.2	21.8+
302 left	Moderate	25.6	23.3	17.5+
" right		25.2	23.2	16.4+
295 left	Moderate	22.0	20.0	16.0+
		23.4	19.4	15.6+
303 right	Moderate	22.7	21.4	19.5+
290A	Moderate	22.3	19.8	16.6+
287 right	Moderately heavy	c28.0	24.0	21.5+
300	Moderately heavy	24.6	19.7e	15.3+
301	Heavy	23.7	21.6	9.8+
288	Heavy	c23.8	(20.5+)	8.5+
Mean		24.1	21.5	
S.D.		1.701	1.551	

cusps, and in the less worn specimens a posterior cingulum and traces of a very small anterior one are visible. A small median element becomes united with the posterior cusps before wear has proceeded very far.

M_2 has the usual structure of a pair of anterior and a pair of posterior cusps, separated by a smaller median element. Anteriorly there is only a very weak, slightly crenulated cingulum and posteriorly a much larger cingular complex, with a large cingular cusp. The cusps wear to an irregular rosette pattern with the outer margin smooth and the axial margin slightly indented. Measurements are given in Table 46.

M_3 is low crowned. The body of the tooth is composed of two pairs of lateral cusps, separated by a small median. Behind these lies a talonid consisting of a median and a pair of small posterior cusps, together with one or more very small cusplets. There is a crenulated anterior cingular complex and in the spaces in front of and behind the second buccal cusps are a few small, irregular cusplets. An unerupted tooth (LT 282) has a crown height of 21.2 mm, which is just a little less than the anterior breadth (Table 47).

TABLE 45. *NYANZACHOERUS TULOTOS* DIMENSIONS OF LOWER M_1

Specimen No. (LT)	Stage of wear	Length	Breadth	Height
291	Moderately early	21.1	17.2	11.1+
305	Moderate	22.1	17.3	9.5e+
302 left	Moderate	20.9	17.6	9.3+
" right		21.6	17.4	8.2+
295 left	Advanced	20.0	15.3	7.8+
" right		19.1	15.6	7.0+
300	Advanced	18.1	15.4	7.5+
288	Extreme	18.5	(c16.0)	–
Mean		20.2	16.5	
S.D.		1.388	0.985	

TABLE 46. *NYANZACHOERUS TULOTOS* DIMENSIONS OF LOWER M$_2$

FROM MEMBER B

Specimen No. (LT)		Stage of wear	Length	Breadth	Height
291		Moderately early	–	22.5	15.7+
305		Moderately early	30.7	21.0	15.5+
302		Moderate	28.3	22.0	15.5+
295	left	Moderate	27.5	21.2	11.8+
"	right		27.0	20.3	11.7+
300		Advanced	26.0	22.3	9.3+
288		Extreme	23.0	c22.0	–
Mean			27.1	21.6	
S.D.			2.334	0.748	

FROM MEMBER C

Specimen No. (LT)	Stage of wear	Length	Breadth	Height
309	Roots	(30e)		
296	Early	26.7	20.3	15.5

Possible Referred Material

There are also a few other specimens in the collection from Member B that probably belong to *N. tulotos* but have not been included in the above account.

Specimen LT 306 consists of scraps of a skull and pieces of mandible. Recognisable are a left P^3 and P^4 in advanced wear and matching teeth of the right side, a well-worn LM^3 and a fragment of well-

TABLE 47. *NYANZACHOERUS TULOTOS* DIMENSIONS OF LOWER M$_3$

FROM MEMBER B

Specimen No. (LT)		Stage of wear	Length	Breadth		Height	
				Anterior	Talon	Anterior	Maximum
282		Unerupted	39.0	22.5	14.8	21.2	21.2
305		Moderately early	45.5e	24.3	–	19.0+	19.0+
302	right	Moderate	43.6	22.2	16.6	18.5+	18.5+
295	left	Moderate	41.0	23.5	18.7	17.0+	17.0+
	right		41.1	23.5	17.4	16.3+	16.3+
303		Moderate	36.7	22.5	13.7	13.0+	13.0+
287		Roots only	(47e)	–	–	–	–
300		Moderately advanced	43.0e	24.4	–	10.8+	–
288		Extreme	42.8	22.7	15.5	6.5+	7.0+
301		Extreme	c43.0	c24.5	c14.8	–	8.0+
Mean			41.7	23.3	15.9		
S.D.			2.496	0.866			

FROM MEMBER C

Specimen No. (LT)	Stage of wear	Length	Breadth		Height	
			Anterior	Talon	Anterior	Maximum
309	Moderate	48.8	24.0	19.5	19.0+	19.0+

TABLE 48. AVERAGE DIMENSIONS OF UPPER CHEEK TEETH OF *NYANZACHOERUS TULOTOS*

		FROM MEMBER B			FROM MEMBER C		
		Range		Mean	Range		Mean
P^1	length (L)	12.1	(1)*	12.1			
	breadth (B)	6.4		6.4			
	L/B	1.90		1.90			
P^2	length	15.2 –15.4	(2)	15.3			
	breadth	10.5 –10.8		10.7			
	L/B	1.42– 1.45		1.44			
P^3	length	24.5 –24.8	(3)	24.6	29.4 – 31.0	(2)	30.2
	breadth	22.0 –23.7		22.9	29.3 – 31.0		30.2
	L/B	1.03– 1.12		1.07	1.00		1.00
P^4	length	19.8 –20.6	(3)	20.1	22.5 – 22.7	(2)	22.6
	breadth	25.0 –28.5		26.6	28.0 – 30.8		29.4
	L/B	0.70– 0.83		0.76	0.73– 0.81		0.77
M^1	length	21.8 –23.0	(2)	22.4	23.3 – 26.3	(2)	24.8
	breadth	21.3 –22.0		21.7	21.6 – 24.5		23.1
	L/B	1.01– 1.04		1.03	1.07– 1.08		1.08
M^2	length	28.6 –27.8	(2)	28.7	31.3 – 35.6	(2)	33.5
	breadth	27.2 –28.9		28.1	27.2 – 31.8		29.5
	L/B	0.99– 1.05		1.03	1.12– 1.15		1.14
M^3	length	38.0 –45.0	(8)**	41.2	42.3 – 48.8	(6)**	45.4
	breadth	26.7 –31.5		28.2	29.5 – 33.7		31.5
	L/B	1.38– 1.53		1.46	1.43– 1.45		1.44
$P^2 - P^4$		62.0 –63.5	(2)	62.8	70	(1)	70
$M^1 - M^3$		88.0 –90.0	(2)	89.0	108.3	(1)	108.3
$\frac{P^2 - P^4}{M^1 - M^3}$		69 –72		71	65		65

* Figure in brackets indicates number of specimens in each case
** For standard deviations see Table 39

worn upper incisor, all of which could belong to a single individual. However, there is a lower RP_3 in fairly early wear and a fragment of the left side of the symphysial area with a root of LP_2 and part of a very small canine, like that in the third paratype, LT 295; these must belong to a younger individual.

Specimen LT 284 comprises two pieces of a mandible in an eroded condition and bearing only roots of some of the teeth. The larger piece belongs to the left side and is broken at the back of M_2 and anteriorly at the front of the canine. The general morphology is very like that of the second and third paratypes but the diastema between P_1 and P_2 is a little shorter. The canine has maximum and minimum dimensions within the alveolus of 24.5 mm and 19.5 mm respectively and has the shape usual in *N. tulotos.*

Specimen LT 292, which comes from the very bottom of the deltaic series, is an extremely weathered and fragile piece of a right mandibular ramus with a damaged RP_3 in moderate wear. It cannot be separated morphologically from other material belonging to *N. tulotos*, but its length of 29.9 mm and estimated breadth of not less than 24.0 mm are a little larger than usual.

SPECIMENS FROM UNIT I, MEMBER C

Material. KNM–LT 286: isolated, partially erupted RM^3. LT 293: right maxillary fragment with M^3 and damaged M^2. LT

TABLE 49. AVERAGE DIMENSIONS OF LOWER CHEEK TEETH OF *NYANZACHOERUS TULOTOS*

		Range	*N**	*S.D.**	Mean
P_1	length (L)	10.1 –11.0	2		10.5
	breadth (B)	6.0 – 6.5	2		6.2
	L/B	1.69			1.69
P_2	length	14.3 –15.5	5	0.407	15.0
	breadth	7.8 – 8.8	5	0.409	8.1
	L/B	1.74– 1.97			1.86
P_3	length	24.2 –30.0	10	2.126	27.3
	breadth	17.8 –23.6	9	1.946	20.9
	L/B	1.19– 1.44			1.31
P_4	length	22.0 –28.0	12	1.701	24.1
	breadth	19.4 –24.0	11	1.551	21.5
	L/B	1.00– 1.25			1.12
M_1	length	18.1 –22.1	8	1.388	20.2
	breadth	15.3 –17.6	7	0.985	16.5
	L/B	1.16– 1.31			1.23
M_2	length	23.0 –30.7	6	2.334	27.1
	breadth	20.3 –22.3	7	0.748	21.6
	L/B	1.05– 1.46			1.27
M_3	length	36.7 –45.5	9	2.496	41.7
	breadth	22.2 –24.5	9	0.866	23.3
	L/B	1.64– 1.97			1.80
$P_2 - P_4$		63.5 –76.0	8	4.716	69.2
$M_1 - M_3$		78.0 –98.0	7	6.439	89.3
$\frac{P_2 - P_4}{M^1 - M^3}$		0.74– 0.77	6		0.76

* *N* denotes the number of specimens in the sample; *S.D.* is the standard deviation

296: right mandibular fragment with M_2. LT 307: isolated moderately worn RM^3. LT 309: right mandibular fragment with M_3 and the roots of M_2. LT 310: left maxillary fragment with damaged P^3–M^1. LT 313: right maxillary fragment with P^3–M^3. LT 320: incomplete isolated LM^3. LT 324: fragment of maxilla with RM^3. LT 326: pieces of skull and teeth of juvenile with loose, damaged LM^2, and LM^3 (unerupted); also RI^1 in moderate wear.

Description. The foregoing account was based only on material recovered from Member B of the deltaic series. The material from Member C, above the "marker" beds, is essentially similar in structure but there may be slight differences in form and size. Comparison is made more difficult by the fact that lower teeth are commoner than uppers in the material from Member B, but the reverse is true for that from Member C. There are insufficient lower teeth for comparisons of dimensions to be meaningful, but the relative ranges and average sizes for the uppers are given in Table 48. It will be seen that the upper third molars are larger, on the average, by 4.2 mm in length and 2.0 mm in breadth, although there is some overlap in the ranges.

The only reasonably complete specimen from Member C, LT 313, has preserved all the teeth from RP^3 to RM^3 (Pl. 24), each of which is larger than in the holotype skull; the molar series is 18–20 mm longer, a difference of 20 per cent. Morphologically, however, the teeth are very similar, although the premolars have smaller cingula than those of the type, agreeing in this respect with those of the referred specimen LT 290. The same is true of the third and fourth premolars preserved in LT 310. On the other hand, the beautifully preserved RM^3 in early wear (LT 324) from Member C is very closely comparable with LT 319 from the lower member. Dimensions for individual teeth have been given in the appropriate tables.

There are not enough lower cheek teeth from Member C for meaningful statistical comparisons to be made. However, average dimensions from lower cheek teeth from Member B are given in Table 49. The largest lower third molar from Member C (LT 309) is 48.8 mm long, which is about the length to be expected for a lower molar to match the uppers of LT 313 (Table 47). Apart from its larger size, however, the only point in which this lower molar differs in any way from the specimens from Member B is that, although the front of the tooth is no higher crowned, the cusps of the talonid are a trifle more hypsodont.

Although the material from Member C is too scanty to justify any definite conclusions, it does suggest that during the time represented by the deposition of the entire deltaic series of Unit 1, some increases in size were taking place.

THE SPECIES OF *NYANZACHOERUS*

The Four Species from East Africa

The skull characters of *Nyanzachoerus kanamensis* are not known and the skull material of *N. plicatus* is rather incomplete, although the latter exhibits features consistent with the general characteristics of the excellent skull material of *N. pattersoni* and *N. tulotos*. The skulls show some primitive features, such as the early rooting of the upper canines and the rather low-crowned cheek teeth; but they also display highly specialised characters, such as the enlarged premolars and the lateral expansion of the zygomatic arch. It is reasonable to suppose that this complex has had a fairly long geological history and diverged from the other African suid stocks well down in the Pliocene.

TABLE 50. AVERAGE MEASUREMENTS OF UPPER TEETH IN FOUR SPECIES OF *NYANZACHOERUS*

	Kanam M^3	*pattersoni*	*tulotos*	*plicatus*
P^1				
length (L)			12.1	
breadth (B)			6.4	
L/B			1.90	
P^2				
length		12.1	15.3	10.5
breadth		7.4	10.7	6.7
L/B		1.64	1.44	1.57
P^3				
length		23.7	24.6	22.5
breadth		19.8	22.9	18.1
L/B		1.22	1.07	1.24
P^4				
length		19.1	20.1	18.3
breadth		22.4	26.6	20.0
L/B		0.86	0.76	0.92
M^1				
length		21.2	22.4	18.3
breadth		18.8	21.7	c19
L/B		1.13	1.03	c1.0
M^2				
length		29.7	28.7	35.4
breadth		24.9	28.1	26.3
L/B		1.22	1.03	1.34
M^3				
length	42.5	49.8	40.8	67.5
breadth	28.1	31.2	28.1	33.1
L/B	1.51	1.60	1.45	2.03
P^2 – P^4		55.6	60.0*	51.3
M^1 – M^3		98.1	91.9	121.2
P^2 – M^3		153.7	151.9*	172.5
$\frac{P^2 - P^4}{M^1 - M^3}$		.60	.65	.42

* Excluding P^1

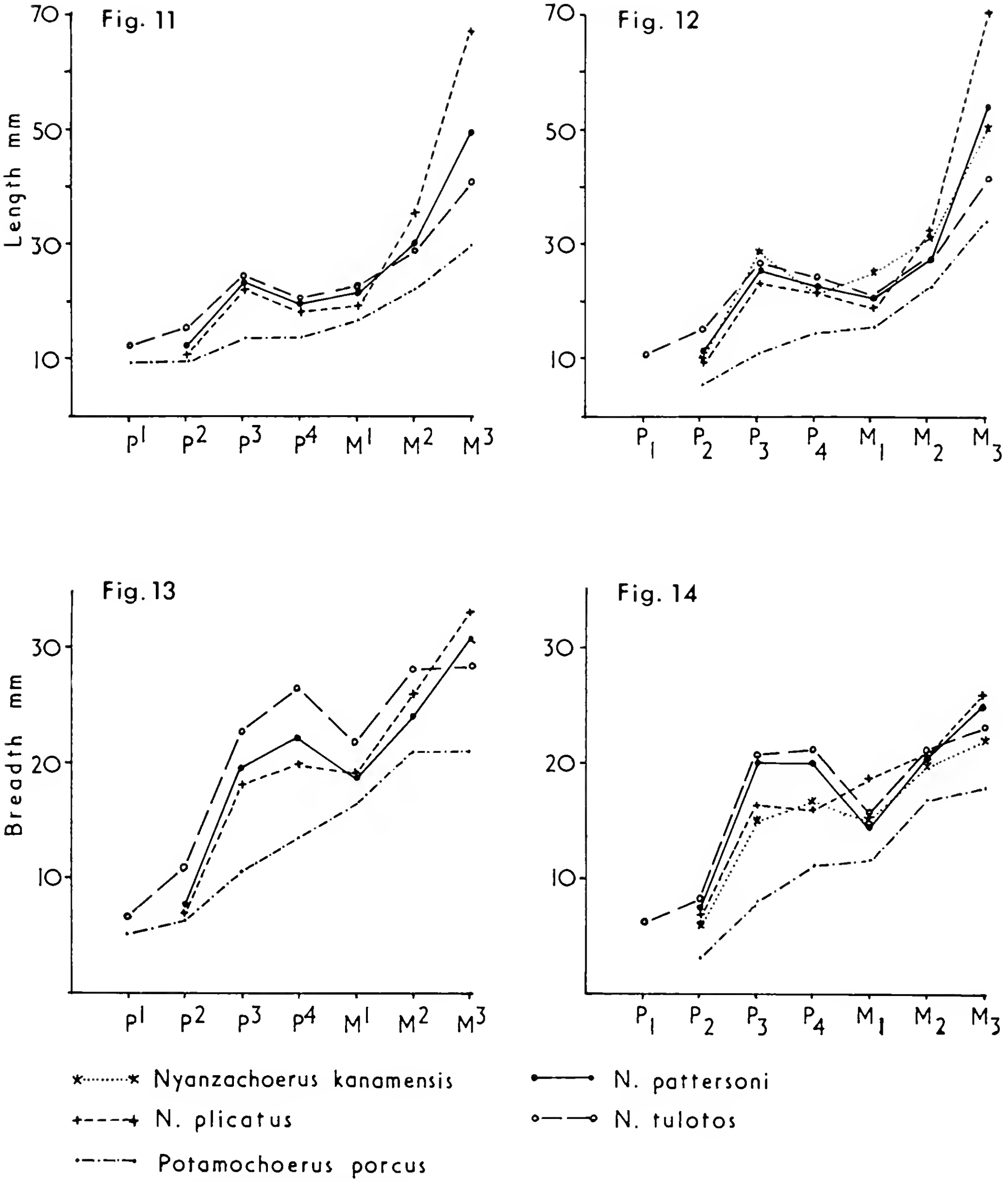
The proportions of the cheek teeth differ in the four species and an examination of these differences is useful. Tables 50 and 51 summarize the average dimensions of the upper and lower premolars and molars, and these data are presented diagrammatically in Figures 11–14 in comparison

Table 51. Average measurements of lower cheek teeth in four species of *Nyanzachoerus*

	kanamensis				
	holotype	paratype	*pattersoni*	*tulotos*	*plicatus*
P_1					
length (L)				10.5	
breadth (B)				6.2	
L/B				1.69	
P_2					
length	c10		10.6	15.0	c10
breadth	c 6		7.2	8.1	c 8
L/B	c 1.6		1.48	1.86	c 1.25
P_3					
length	28.9		25.7	27.3	23.1
breadth	15.1		20.3	20.9	16.6
L/B	1.91		1.26	1.31	1.39
P_4					
length	21.6		22.5	24.1	21.4
breadth	16.8		20.5	21.5	16.7
L/B	1.29		1.11	1.12	1.28
M_1					
length	c25		20.2	20.2	c19
breadth	c15		14.2	16.5	c19
L/B	c 1.7		1.39	1.23	c 1.0
M_2					
length	31.0	28.0	27.6	27.1	c32
breadth	20.2	19.7	21.1	21.6	c21.1
L/B	1.53	1.42	1.32	1.27	c 1.5
M_3					
length	50.5	51.0	54.7	41.7	70.6
breadth	22.0	23.2	25.1	23.3	26.4
L/B	2.28	2.24	2.17	1.80	2.68
$P_2 - P_4$	c60.5		59.0	66.4*	54.5
$M_1 - M_3$	106.5		100.0	89.0	121.6
$P_2 - M_3$	c167.5		158.0	155.4*	176.1
$\frac{P_2 - P_4}{M_1 - M_3}$	.56		.59	.75	.45

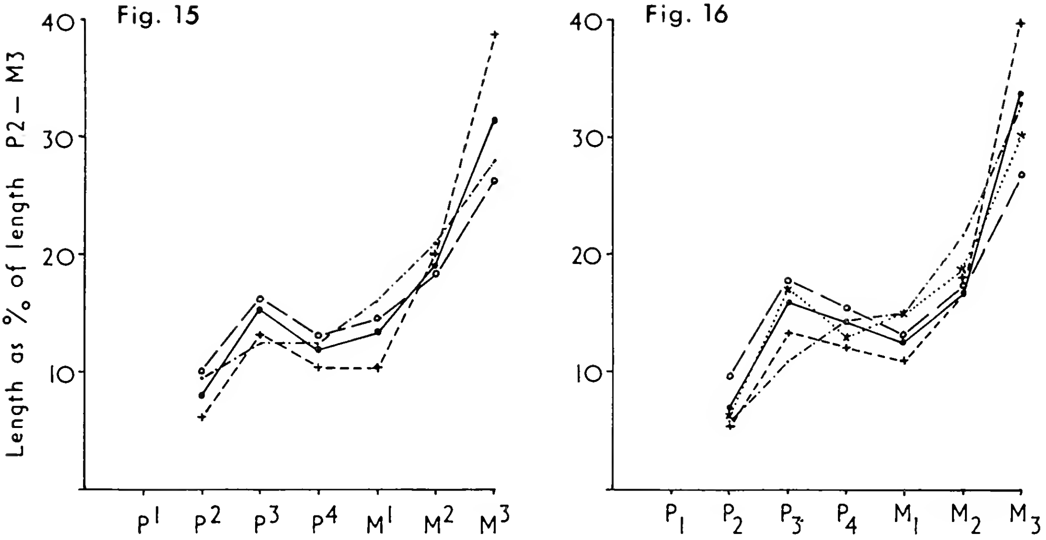
* Excluding P_1

with corresponding averages for *Potamochoerus*. It will be noted that in the bushpig there is a more or less steady increase in length and breadth of the successive premolars and molars. All four of the *Nyanzachoerus* species show substantial relative elongation of the third premolar and broadening of both the third and the fourth premolars. The similarity of these trends, in comparison with a more normal suid, provides additional confirmation that the four species almost certainly belong to a single genus. Figures 15 and 16 present the data given in Table 13, in which the length of each tooth is expressed as a percentage of the total length of the premolar/molar series. This serves to emphasize the lengthening of the third premolar. Figures 17 and 18 show the data given in Table 14, in which the breadth of each tooth has been related to the breadth of the second molar as a reference standard; this is actually a

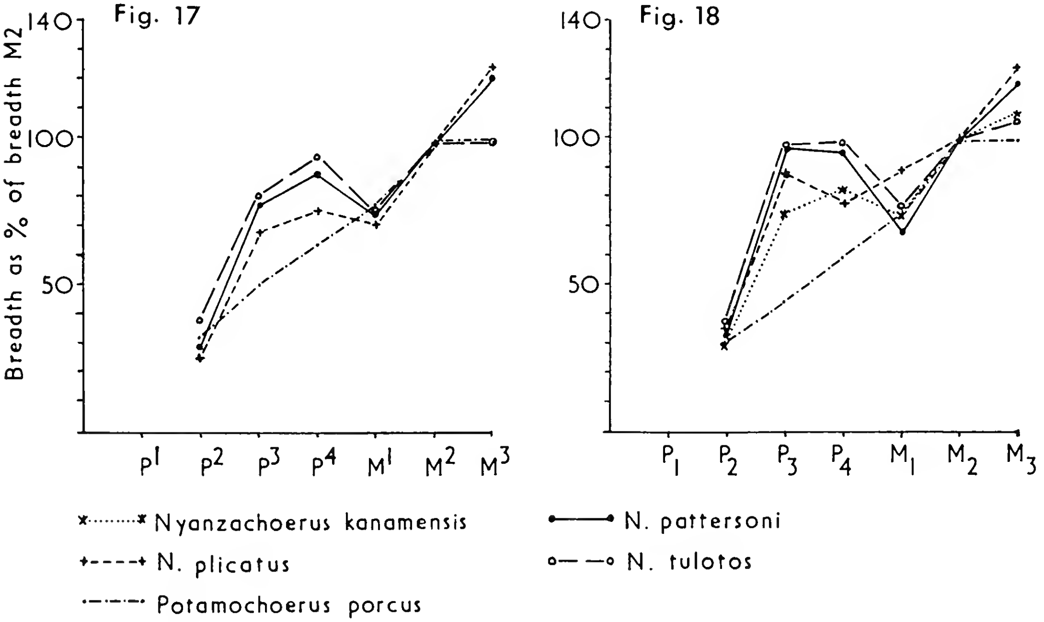


Figures 11–14. Graphs showing the variation in length and in breadth for each cheek tooth in different species of *Nyanzachoerus*, compared with *Potamochoerus porcus*. Figs. 11 and 12 show length and Figs. 13 and 14 show breadths. Figs. 11 and 13 represent the upper dentition and Figs. 12 and 14 the lower dentition.

useful practical aid in specific identification. The relative broadening of the fourth permolar is shown to be greater than that of the third premolar, as compared with the condition found in *Potamochoerus*. These diagrams also show the relative roles of the various teeth within the dentitions, indicating for *N. plicatus* a



Figures 15, 16. Graphs showing, for different species of *Nyanzachoerus* and for *Potamochoerus porcus*, the length of each cheek tooth expressed as a percentage of the total length of the series from second premolar to third molar, inclusive. Fig. 15 is for the upper dention and Fig. 16 for the lower dentition.



Figures 17, 18. Graphs showing, for different species of *Nyanzachoerus* and *Potamochoerus porcus*, the breadth of each tooth expressed as a percentage of the breadth of the second molar. Fig. 17 is for the upper dentition and Fig. 18 for the lower dentition.

considerable emphasis on the third molars and diminished weighting on the premolars; *N. tulotos* is very conservative in the molar teeth and the relative importance of the premolars is great; *N. pattersoni* has its premolars proportionally as well developed as in *N. tulotos* but the third molar is also enlarged; *N. kanamensis* is fairly similar to *N. pattersoni* but the teeth are less robust.

A possible interpretation of the dental evidence would be to suggest that a smaller and less specialised version of *N. tulotos*, with elongate but less robust premolars, might be a suitable common ancestor. *N. tulotos* itself has developed further premolar enlargement. *N. kanamensis* has not strengthened the premolars very much from this hypothetical ancestor but has elongated the third molars to a moderate degree. *N. pattersoni* has done the same, but has also developed stouter premolars. *N. plicatus*, following a somewhat different trend, has enlarged the third molar substantially and is in the process of secondary reduction of the previously enlarged premolars. However, such a relationship is still very speculative.

Probable *Nyanzachoerus* from North Africa

Material from two sites in North Africa has been referred to the Indian genus *Sivachoerus*, primarily because of enlargement of the third and fourth premolars which, at that time, was a feature known only from the Siwalik fossils. However, these specimens exhibit a number of differences in morphology from the Indian material and conform to the characteristics of the East African *Nyanzachoerus*. It is thus much more likely that they belong to this African genus, although further study of the original specimens is needed before they can be placed with assurance.

In 1936, H. Tobien described a small collection of suid material from the Wadi Natrun in Egypt and referred it to *Sivachoerus giganteus* (Falconer and Cautley). The general age of this deposit is supposedly Middle to Upper Pliocene, but there is some uncertainty about the relative dating as the total fauna has not been described. The material comprised a good part of a skull, with the palate almost complete, most of the muzzle and the parietal area, but lacking the occiput and zygomatic arches; the cheek teeth were much damaged, except for the left second and third molars. There also occur, though apparently from a different collection, an isolated right lower canine and isolated LP^3, RP^3, RP^4, LM^3 and RM_3. The skull was originally in the Geologisch-Paläontologisches Institut of the University in Freiburg, and the other specimens belonged to the Institut für Paläontologie und Historische Geologie in Munich, but they cannot now be found and are presumed to have been lost or destroyed during World War II.

Measurements are given by Tobien for the teeth, including the second and third molars of the skull, but not for the skull itself. By approximate scaling from the illustrations, the original (intact) palatal length was about 260–270 mm; the corresponding basilar length would be in the vicinity of 350–370 mm. Also by estimation from the photographs, the length of the cheek tooth series P^2–M^3 was approximately 145–155 mm. There is no indication of the presence of an upper P^1. The bony bosses surrounding the canines were only moderately developed, and, although Tobien regarded the skull as male, it might well be female. The general morphology accords fairly well with that of the holotype of *Nyanzachoerus plicatus* and is similar also to the male paratype of *N. pattersoni*, but narrower and less massive. The parietal area is not nearly as broad as in *N. tulotos*. The second and third molars of the skull have a general resemblance to those of *N. tulotos*, but the M^2 and M^3 together are longer than P^2–M^1 inclusive, which is quite unlike that species and more like the condition found in *N. plicatus*. There is thus a suspicion that the skull might represent an ancestral form of the latter. The upper and lower third molars would accord with this view. They are less like those of *N. tulotos* in being a little higher crowned and in having a more compact structure; the upper molar has a much wider talonid and is less triangular. These features would also be expected in an ancestral *N. plicatus.*

The isolated third and fourth premolars are somewhat larger than those of *N. plicatus* but are very similar in structure, lacking the "wrap around" cingula of *N. tulotos.* However, Tobien's drawings show —and he mentions in the text—strong enamel ribs on the inner (lingual) face of the main cusp, a feature seen only weakly in typical teeth of the four described species of *Nyanzachoerus.* However, there is an undescribed specimen from the Lukeino Beds in the Lake Baringo area of Kenya very similar to the Wadi Natrun material and also displaying ribbing of the upper premolar. This ribbing is supposedly typical of *Sivachoerus* and was perhaps the strongest argument for placing the material in that genus. In discussing the skull, Tobien points to a number of differences between it and the type material from India. For example, the cranial vault of *Sivachoerus* is rounded in *Sus*-like fashion, whereas in *Nyanzachoerus* it is flattened; Tobien ascribes the flattened parietal area in the Wadi Natrun skull to crushing, but it would now seem to have been inherent. He notes that the Indian genus is extremely narrow across the temporals, whereas in the Wadi Natrun fossil this region is very broad (as is typical of *Nyanzachoerus*). Another difference is in the palate, which in *Sivachoerus* has a considerable prolongation behind the third molars, but this is not the case in the fossil skull or in *Nyanzachoerus.* There is thus very little reason to maintain the generic reference of this material to *Sivachoerus.* As the Indian material does not show the zygomatic inflation so marked in *Nyanzachoerus*, as well as differing in other ways as mentioned above, it seems very unlikely that the two genera are synonymous.

Further North African material was referred to *Sivachoerus* cf. *giganteus* by Leonardi (1952), on the basis of a moderately complete skull from Sahabi in Sirtica, north-central Libya (see Appendix I). The specimen is now in the collections of the Instituto di Geologia e Paleontologia of the university in Rome, but the lower jaw described by Leonardi as a new species, *Sivachoerus syrticus*, is missing and is believed to have been destroyed during World War II. Although Leonardi's description of the skull is sound, there is a discrepancy between the dimensions given for the individual cheek teeth and the figure of 136 mm quoted for the length of the series P^2–M^3. Our measurements confirm Leonardi's individual measurements and give the length of the series as 156.5 mm on the right side and 159.5 on the left side. More complete data are given in Appendix I. The general morphology of the skull is very like the female holotype of *Nyanzachoerus pattersoni*, but the zygomatic arches flare outwards a little more and the area below the orbits is flattened. Morphologically the cheek teeth are intermediate between those of *N. pattersoni* and *N. plicatus*, but the enamel folding in the second and third molars approaches the latter more closely. It is considered that it most probably represents a form ancestral to *N. plicatus.* There is good agreement between the Sahabi specimen and the third molars from Wadi Natrun.

The lower jaw from Sahabi, now unfortunately missing, was described by Leonardi as a new species, *Sivachoerus sirticus.* He separated it from the skull on account of both the massiveness of the mandible and the presence of P_1, whereas P^1 was absent from the upper dentition. He also reports that the states of fossilization are different. In both the presence of P_1 and the general morphology of the jaw and teeth, this specimen comes close to *Nyanzachoerus tulotos*, although the symphysis is substantially longer in the Sahabi jaw; the back of the symphysis is below the back of P_3, whereas in *N. tulotos* it lies below the front of P_3. The M_2 is decidedly wider than in any of the *N. tulotos* material and M_3 is a little wider. The length of the series P_2–M_3 is given as 143 mm, which is shorter than the smallest of the Lothagam *N. tulotos* specimens. There are thus some important differences, and, as the lower teeth are rather less diagnostic than the uppers, it would be premature to suggest that *syrticus* and *tulotos* are conspecific; however, it is virtually certain that the Sahabi jaw belongs to *Nyanzachoerus*, and it may now be regarded as a distinct species, *N. syrticus* (Leonardi).

Despite the apparent improbability of there being two different species at Sahabi, one represented by a skull and the other by a lower jaw, Leonardi's reasoning is sound and must be upheld, particularly in view of the possession or lack of the first premolar. The skull appears to belong to a form similar to that from Wadi Natrun and possibly to be ancestral to *N. plicatus*, whereas the lower jaw apparently belongs to a form closer to *N. tulotos* and perhaps ancestral to it.

FUNCTIONAL ASPECTS OF *NYANZACHOERUS*

The specimens of *Nyanzachoerus pattersoni* and *N. tulotos* that have been described provide so much information about the architecture of the skull and mandible that it seems worth while attempting some analysis in functional terms. For *Nyanzachoerus plicatus*, however, the material is inadequate. As *N. pattersoni* is the species about which we have most information, it will be convenient to discuss it first and then proceed to a consideration of *N. tulotos*.

(i) *Nyanzachoerus pattersoni*

In dealing with skull architecture, an analysis of the mechanics of jaw action is important and leads to deductions about possible feeding habits. It is necessary to deal separately with the cheek teeth and with characters of the snout and incisor teeth in so far as they affect feeding methods. In the very omnivorous bushpig, rooting in the ground is a regular method of searching for food and this is reflected in the narrow snout, shovel-like symphysial region and large incisors. The forest hog and warthog are more restricted in their feeding habits, the latter feeding from choice on grass and the former on softer dicotyledonous plants. Although both can dig, neither does so as extensively as does the bushpig, and in both the snout is broader and less pointed and the incisor teeth show some reduction. In the forest hog the rhinarium is very large and rather ill-adapted for digging, but vertical wear on the tips of the lower incisors suggests that they, rather than the rhinarium, constitute the main digging organ.

In *Nyanzachoerus pattersoni*, the snout is relatively narrow, although less shovel-like than in the bushpig, and the incisor teeth are large. The wear on the tips of the teeth is such as could have been made by chewing against the upper incisors, rather than by digging. The animal therefore probably rooted in the ground as the bushpig does, but, since its adaptations to this habit are less marked, digging was probably not as important to *N. pattersoni* as it is to the bushpig.

In the extant pigs, as might be expected from their diets, the cheek teeth of the warthog are the most specialised and those of the bushpig the least specialised for grinding; the same is true of their jaw movements. In the bushpig the jaw action is mainly a simple crushing with a slight rotatory movement in which the sideways component is not much more important than the fore-and-aft motion. In the forest hog the sideways component of the movement predominates, while in the warthog the movement is almost exclusively sideways and the fore-and-aft component is negligible. These differences are reflected in the character of the glenoid, which is a narrow, almost flat bar in the warthog and is wider and slightly more concave in the other two species: it is also shown in the relative size of the temporalis muscle, which is responsible for pulling the jaw backwards.

The size of the temporalis relative to the superficial masseter may be expressed in terms of the lengths of their origins on the skull. If the temporalis is measured from the tip of the postorbital process to the posterior end of the temporal crest, then the ratio of this to the length of the masseter insertion along the lower margin of the zygoma gives a measure of the relative importance of the temporalis muscle; this, in turn, is a measure of the relative importance of the back-and-forth component of the jaw action. For the extant species the temporalis:masseter ratios are about 90 per cent for bushpig, 65–70 per cent for forest hog, and less than 50 per cent for warthog.

The cheek teeth of *N. pattersoni* are only slightly hypsodont, and, although ultimately they are abraded to a flat surface, in early wear stages some similarity to the wear on *Hylochoerus* teeth is apparent. In no specimen can the lengths of both masseter and temporalis origins be measured, but in the female skull, the restoration necessary to provide these measurements can be made with a fair degree of confidence. Working from the restoration, maximum and minimum estimates for the temporalis:masseter ratio are 78 per cent and 65 per cent. Both values are well above the figures for warthog, possibly a little more than is typical of *Hylochoerus* but distinctly below those for bushpig. This, together with the slightly narrowed glenoid suggest that, as in *Hylochoerus*, there has been some reduction in the importance of the fore-and-aft component in the jaw movement.

The character of the posterior margin of the angle of the mandible remains to be considered. This resembles the potamochoeroid condition and the angle lacks the widening found in both *Hylochoerus* and *Phacochoerus*. As explained elsewhere (Ewer, 1970) this widening is interpretable as an adaptation to withstand the strains produced when the superficial masseter and internal pterygoideus muscles contract alternately rather than synchronously, in the manner required to produce an efficient sideways grinding action. Its absence in *Nyanzachoerus pattersoni* shows that although there has been some elaboration in the third molars, increasing the surface area and the lasting power of the dental battery, specialisation in the pattern of muscular contraction involved in chewing has not yet occurred—or at least must be at such an early stage that skeletal adaptations to the complex asynchronous contraction sequence have not yet been acquired.

It has been argued elsewhere (Ewer, 1960) that, on general grounds, one would expect elaboration of the teeth to lead the way in evolution, and specialisation of jaw action to follow only when the teeth have reached a stage of complexity making the sideways grinding action "worth while." The adaptational syndrome shown in *N. pattersoni* appears to be in accord with this view. In terms of feeding habit, the characters of the skull and jaws of *N. pattersoni* appear to imply a diet in which roots and tubers are less, and green vegetation correspondingly more, important than they are in the bushpig; the degree of grinding ability shown, however, does not appear sufficient to cope with a diet in which abrasive grasses predominate, as they do in that of the warthog. The adaptations shown in the dentition and chewing mechanism thus appear to be related to an increasing dependence on browsing or grazing on surface vegetation, which requires efficient trituration, and a corresponding decrease in the importance of soft bulbs and tubers, which must be dug up but require relatively little grinding.

It is not, however, these characteristics of dentition and jaw muscles that constitute the most striking feature in the *Nyanzachoerus pattersoni* material but rather the structure of the zygoma. The variability in the development of the zygomatic knobs has been described and has been interpreted here as resulting from sexual dimorphism. If we assume this to be correct, the significance of the knobs still requires elucidation. Their position and their greater development in the male than in the female at once invite comparison with the zygomatic warts of *Phacochoerus*. In the earlier paper (Ewer, 1958) it was suggested that although these warts may have originated with a protective function, their present degree of elaboration is explicable only if they act as display organs. Geist (1966) has expressed the same opinion.

Mammalian offensive threats are most commonly derived from intention movements of attack (Ewer, 1968). This automatically produces a "weapon threat," in which the opponent is given a view of the organs to be used in the attack that may follow. The warthog's method of fighting, described by Frädrich (1965), makes it virtually certain that the function of the warts is to increase the intimidatory effect of a threat display. In fighting, warthogs adopt a forehead-to-forehead pushing technique, very similar to the type of contest characteristic of the horned and antlered artiodactyls. The broadness of the forehead makes a pushing contest of this type possible even in the absence of locking horns or antlers; the large upper tusks, too, may help to compensate for this lack and may also act as holding organs, ensuring that the contestants' heads do not slip apart. In the narrow-headed, short-tusked bushpig, the danger of slipping is minimised by the animals turning their heads slightly sideways, so that they cross snouts, instead of making a symmetrical forehead-to-forehead contact. In the warthog, it is thus the broad forehead, rather than the tusks, that constitutes the main weapon. The intention movement for warthog fighting is therefore to face the opponent and lower the snout, so that this "weapon" is displayed. The zygomatic warts are so placed as to be visible to the opponent and have the effect of increasing the apparent width of the head, which is equivalent to making their possessor appear more dangerous.

In *Nyanzachoerus pattersoni,* the broad forehead suggests that fighting must have been of the warthog type and the zygomatic knobs, like the warts of *Phacochoerus*, are so placed as to increase the width of the head displayed to an opponent in the "ready for action" position. The most plausible suggestion as to their function is therefore that they constitute display organs, used in intraspecific contests between males.

In *Phacochoerus* the zygoma underlying the wart is somewhat inflated and there is a roughened area directly beneath the wart. The knobs of *Nyanzachoerus*, on the other hand, show no such roughening and one must therefore conclude that in life they were not surmounted by any specialised epidermal thickening. Selective pressure for increasingly impressive threat would thus appear to have produced the same effect in the two cases by rather different means. In *Nyanzachoerus* head width is increased by bony outgrowths, in *Phacochoerus* the same result is attained by epidermal thickenings. The latter would appear to be the more satisfactory arrangement, since not only are warts lighter than bony knobs (even though the latter are hollowed out inside) but their growth does not increase the demand for calcium, and any damage to them is likely to have much less serious consequences than would an injury to bone.

Geist (1966) makes a further point with reference to the horned and antlered artiodactyls. In some species these weapons show sustained positive allometric growth, and, even after maturity is reached, the age of an animal is manifested in the relative size of the horns or antlers. In other cases this is much less marked and once the adult body proportions are attained, there is little further change. Geist relates this difference to differences in the social organisation of the various species. The same considerations would apply to the zygomatic protuberances of *Nyanzachoerus.* Thus, if sufficient material becomes available, it is possible that the growth characteristics of the zygomatic protuberances may ultimately provide the basis for deductions about social life.

Two final points may be made. In living species visual displays are not usually important in the behavior of animals that are nocturnal or that live in dense cover; the knobs of *Nyanzachoerus* therefore suggest that this species was probably diurnal and lived in terrain that was at least moderately open. Secondly, it should be noted that in extant mammals, fights between males are normally intraspecific and members of a different species are not molested. One might therefore expect that if zygomatic knobs were evolved in other species sympatric with *Nyanzachoerus pattersoni,* these would have some visible differences, making it easy for the animals to tell a conspecific male from one belonging to another species. Although one might expect such differences to take the form of differences in the shape of the knobs, it should be remembered that even similar knobs would appear different in life, if surmounted by hair tufts of different colours.

(ii) *Nyanzachoerus tulotos*

As far as the characters of the dentition and feeding methods go, interpretation of the skull of *Nyanzachoerus tulotos* presents no particular difficulties. The incisor region of the snout is essentially similar to that of *N. pattersoni,* but possibly a little more elongated. The snout was almost certainly an efficient digging organ, although not as highly specialised for this function as that of the bushpig. The cheek teeth resemble those of *N. pattersoni* but are more primitive, the third molars being short-crowned and less elongated. The characteristics of the glenoid, of the mandibular angle, and of the wear facet on the lower canine suggest a relatively primitive jaw movement, without the development of a specialised sideways grinding action. It would thus seem that *N. tulotos,* like *N. pattersoni,* was a mixed feeder in the process of becoming adapted to a more abrasive diet requiring efficient trituration with the cheek teeth. *N. tulotos,* however, is at an earlier stage and its masticatory adaptations are less advanced.

It is, however, in interpreting those characteristics of the skull of *N. tulotos* that are not related to feeding that problems arise. The anterior and posterior parts of the skull are sharply contrasting. The muzzle, with its enlarged maxillary flanges, premaxillary thickenings, and thick preorbital ridges, is heavily built and rugged. The broad frontal and parietal region, on the other hand, is devoid of any bony ridges or protuberances: its unusual width is produced by overhanging flanges of the frontals and parietals that are thin and delicate by comparison with the muzzle region. The thickening along the line of the parietal and occipital crests characteristic of *Hylochoerus* is completely absent. All this suggests that *N. tulotos* probably fought by pushing with the snout, rather than the forehead, more after the manner of the bushpig than the warthog or forest hog. If it adopted the bushpig snout-crossing tactic, then the preorbital ridges and premaxillary thickenings would have acted as anti-slip devices, preventing the opponent's snout from slipping either upwards cranially or downwards rostrally.

The ease with which a frontal fighting technique may lead to the evolution of structures increasing the effectiveness of frontal threat has already been discussed in relation to *Nyanzachoerus pattersoni.* The same consideration would apply here and the zygomatic protuberances of *N.*

tulotos, like those of *N. pattersoni*, can be interpreted as threat organs. The characters of the frontal and parietal region of the skull of *N. tulotos*, however, suggest a further possibility. The widening of the skull table does not appear to relate to a forehead pushing-fighting technique and it is certainly not the result of any enlargement of the braincase. It therefore seems possible that the widening of the forehead, as well as the zygomatic exaggeration, is an adaptation whose function is to increase the intimidatory effect of frontal threat.

It is, of course, possible that once a broad forehead has been evolved, a transition to a forehead contact in fighting might follow. With this technique, the combatants go over directly from threat to attack in a symmetrical manner and there is less chance of their heads slipping apart than in the snout pushing technique, which requires the opponents, as they meet, to turn their heads to opposite sides so as to cross snouts. Slipping apart of snouts, of course, involves the danger of a slash with the sharp lower tusks. The primary function of the maxillary flanges appears to be to protect the tendons of the snout muscles against a wound of this sort.

If snout pushing is replaced by a forehead to forehead contact in fighting, then a new set of selective pressures comes into operation: thickening and strengthening of the forehead becomes a desideratum and possibly also the production of ridges to minimize the chance of slipping. In fact, the broad forehead, which began as a deceptive intimidatory device, must be converted into a genuine weapon. At the same time, the importance of the maxillary flanges and the thickening on the muzzle declines. One might therefore expect to find the evolution of the fighting forehead accompanied by reduction in the fighting adaptations of the snout.

It does not, of course, follow that forehead contact is always secondary and must necessarily be derived from a snout-crossing fighting technique nor that all lineages have followed the same evolutionary course. If a frontal technique is adopted then the forehead, if it is not too rounded, rather than the muzzle, might become the main contact area right from the start. One would not, however, expect that the inherently more effective forehead contact would ever be replaced subsequently by snout-crossing.

Unfortunately, in none of the specimens of *N. pattersoni* is the vertex of the skull well preserved. It is therefore not possible to say whether adaptations increasing the efficiency of the forehead fighting had been evolved in this species. It is, however, clear that the muzzle is much less specialised for snout-crossing than that of *N. tulotos*, and it is tempting to regard the smaller maxillary flanges and preorbital ridges of *N. pattersoni* as being secondarily reduced, rather than merely less developed than those of the latter. Such a view is in accord with the more advanced characteristics of the dentition of *N. pattersoni*. While we do not wish to suggest that *N. tulotos* is itself directly ancestral to *N. pattersoni*, they do appear to represent two closely related species, one of which is more primitive than the other in its fighting technique and associated structural adaptations, as well as in its dentition and feeding adaptations.

OTHER SUID REMAINS FROM KANAPOI

Nyanzachoerus sp.

There are three specimens that seem to belong to *Nyanzachoerus* but which are difficult to place. Although the teeth are closer to those of *N. pattersoni* than to those of *N. plicatus*, they cannot be matched exactly by any of the other material that has been assigned to these species. The specimens may be considered individually.

KNM–KP 218 comprises fragments of a left mandible in which the bone is much blackened and unlike nearly all the other

TABLE 52. DIMENSIONS OF TEETH OF *NYANZACHOERUS* SP. IN MANDIBLE FRAGMENT KP 218

Tooth	Length	Breadth	Height
LP_3	20.0	13.8	13 +
LP_4	21.6	15.4	14.7+
LM_3	32.7+(c50)	21.5+(c25)	20 +

TABLE 53. DIMENSIONS OF UPPER TEETH OF *NYANZACHOERUS* SP.

Specimen No.	Tooth	Length	Breadth	Height
KP 214	LP^3	21.4	18.5	11.5+
"	LP^4	17.8	19.0	11.5+
KP 211	RP^3	18.7	17.5	8.5+
"	RP^4	16.3	19.5	9.0+

material from Kanapoi in this respect. By contrast, the teeth are grey, whereas many of the other Kanapoi teeth are black, so there exists a possibility that the specimen was not in place but was derived from some other deposit in the vicinity. Preserved are LP_3 and LP_4 in moderate wear, a little worn LM_3 lacking the anterior pillars, a fragment of an M_2, and a small piece of canine. Measurements are given in Table 52. Although the M_3 is essentially similar to the corresponding tooth in *N. pattersoni,* the two premolars are a good deal narrower than in any of the undoubted *N. pattersoni* material; however, the LP_3 is shorter than the LP_4, contrary to the situation in all the other known *Nyanzachoerus* material, and particularly unlike *N. kanamensis.* Nevertheless, P_3 is larger than in normal suid dentitions, where it is usually only about 60–70 per cent of the size of P_4. The scrap of M_2 is not very helpful but its structure is not readily matched in any genus other than *Nyanzachoerus.* The canine fragment also shows clearly the rather U-shaped cross section typical of this genus. The evidence thus points towards the assignment of the specimen to *Nyanzachoerus;* its specific status is problematical but it is not impossible that it may be an unusual variant of *N. pattersoni.*

KNM–KP 214 is a fragment of left maxilla retaining the fairly well worn LP^3 and LP^4. Measurements are given in Table 53. Morphologically these teeth are very similar to the corresponding molars in the holotype skull of *N. pattersoni,* but the cingulum development in the LP^3 is weaker and the shape of the crown suggests that the teeth were originally less hypsodont than in the holotype. The P^3 is at the lower limit of size and P^4 is narrower than in any known specimen of *N. pattersoni.* These features are like those of the lower teeth in KNM–KP 218 and similar conclusions apply to it.

KNM–KP 211 is a piece of right maxilla with very worn RP^3 and RP^4, the crowns of which are almost patternless. The dimensions are smaller than those of KP 214 (see Table 53), but the relative size of the P^3 suggests that the specimen may belong to a small *Nyanzachoerus;* its reference is problematical.

Genus *NOTOCHOERUS* Broom 1925

Notochoerus cf. *capensis*

Notochoerus capensis Broom, 1925: 307, text-fig.

Remarks. The status of *Notochoerus capensis* will be discussed elsewhere and some comments on the differences between that species and the Kaiso *Notochoerus euilus* have been given (Cooke and Coryndon, 1970). Accordingly, it is not proposed to repeat here the full details and synonymy relating to this giant extinct pig, especially as there is uncertainty about the proper specific designation for the Kanapoi material. An undescribed partial skull from the lower Omo beds exhibits some of the features seen in the Kanapoi material and this specimen is tentatively regarded as *Notochoerus* cf. *capensis,* as is also the bulk of the material from Laetolil described by Dietrich (1942) as *Hylochoerus euilus.* The Omo skull is a good deal smaller than the Kanapoi form and it is unlikely that the two are specifically identical. In all probability the Kanapoi form belongs to a new species but the specimens are not considered adequate as type material, despite the novel features they display.

Material. KNM–KP 226: incomplete mandible, retaining RP_3 and imperfect RM_3. KP 241: much damaged mandible with RP_3. KP 242: skull fragments associated with KP 241. KP 267A: fragment of lower jaw with LM_3. KP 267B: fragment of lower jaw with RP_3 and RP_4. KP 267C: left upper canine, lacking the tip. KP 210: fragment of lower jaw with rolled and damaged RM_3.

DESCRIPTION

Specimen KNM–KP 226 consists of the greater part of a mandible, which is exceptionally massive. The symphysial area is well preserved but the two rami are severely crushed and the back of the mandible is missing. On the right side the outline of a good deal of M_3 is still visible, broken off at the talon, but the only tooth which is intact is the right P_3. This latter tooth is 22 mm long, 14 mm wide, and 8 mm high. It seems to consist of a single stout cone and has no anterior cingulum; the back is broken and it cannot be determined whether a cingulum was present or not, but there is no sign of any posterior cone. The socket for the fourth premolar is fairly small and the entire premolar series was no more than 42 mm long. The first and second molars together occupied about 37 mm, and the third molar exceeded 75 mm in length.

The symphysis extends back almost as far as the front of the third premolar and is exceptionally long, measuring 186 mm from the front of the jaw between the sockets for the large central incisors. The distance from the front of the mandible to the estimated position of the back of the third molar is 355 mm, and it is estimated that the length of the entire mandible must have been in the vicinity of 50 cm (compared with 35 cm for a very large *Hylochoerus*). The front of the mandible flares outwards and the width at the back of the canines, as preserved, is 175 mm and was probably a little greater; this is almost double the width in a male *Hylochoerus*. The general shape of the symphysis is similar to *Hylochoerus* or *Phacochoerus*, but all six incisors were retained and the front of the jaw is even less curved than in the forest hog. The angle at the back of the symphysis lies a little below the lower border of the rami and the profile is thus more phacochoerine than hylochoerine. The sockets for the incisors are filled with matrix. The central incisors are compressed and are flanked by much larger and more equidimensional teeth. There is no socket for a lateral incisor on the right side and only a small one on the left. The left canine is still in place, although broken off in line with the incisors. It has an almost U-shaped or rounded triangular transverse section with the greatest diameter 39 mm and the transverse diameter 27 mm. A detached piece of this canine is also associated with the jaw and it shows a trace of the bottom of an anterior wear facet. The jaw is illustrated in Plate 26.

Specimen KP 241 is a much damaged mandible without any cheek teeth except the right P_3 (Pl. 26). This tooth consists of a stout main cone, a very minute anterior cusp, and a fairly narrow posterior cingulum. The socket for a small P_2 is present. The canines are exposed in cross section in the broken symphysial area and are a little larger than those in the other specimen (Pl. 26; Figure 19). The symphysis was about 185–190 mm long, but does not seem to have been quite as wide across the canines as is the case in KP 226. A fragment of the back of the RM_3 is preserved in a detached portion of the mandible that does not quite join the remainder. It is in advanced wear and shows the back of the last pair of lateral pillars and a complex of six enamel islands forming the talonid.

The third fragment of lower jaw, KP

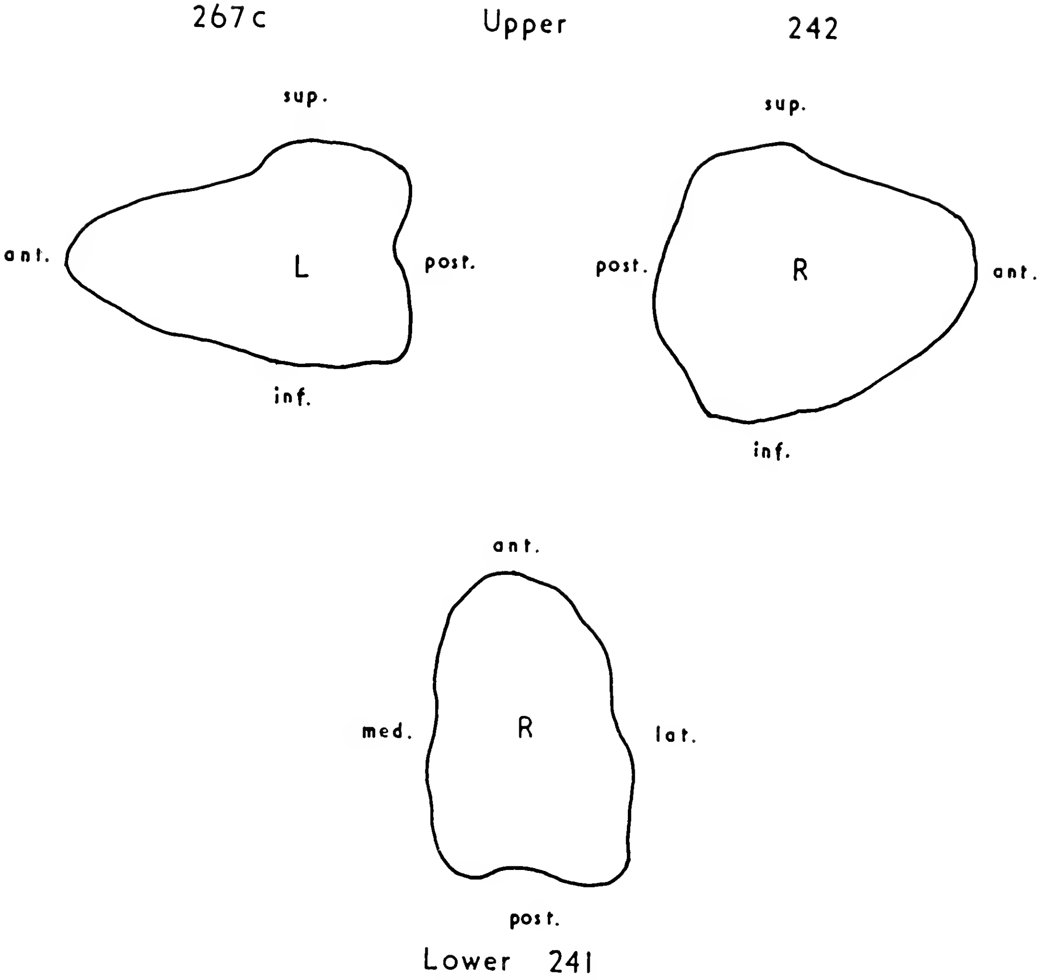


Figure 19. Sections of upper and lower canines referred to *Notochoerus* cf. *copensis* from Kanapoi. Nat. size. Abbreviations as in Fig. 5.

267A, matches the other specimens in contour and massiveness but has only the LM$_3$ preserved. This is in very advanced wear and its dimensions are 82 mm long, 29 mm broad and 8–9 mm high. The tooth originally had three well-developed pairs of lateral pillars, a weaker pair behind them, and a complex of four or five pillars in the talonid. Accessory columns existed at the base between the lateral pillars on the buccal side. As far as can be determined, there was only a single median pillar between successive pairs of laterals. The tooth is illustrated in Plate 26.

There is also a fragment, KP 267B, containing the right P$_3$ and P$_4$. P$_3$ is 22 mm long, 13.5 mm broad, and 13.5 mm high. It is a little narrower than the two corresponding teeth in the other jaw. There is no sign of an anterior cusp and the posterior cingulum is small. P$_4$, which is heavily worn, is 19 mm long and 16 mm broad. It appears to have consisted only of a single stout cone. With it was associated a large upper canine with the tip missing (KP 267C). The length, measured in a straight line across the arc, is 27 cm. At the base the tusk is 47 mm by 32 mm, while at the broken tip its dimensions are 38 mm by 22 mm. In cross section it tends to be trapezoidal with the posterior face perpendicular to the broad lower face, a narrow dorsal face parallel to the lower one, and a sloping anterior face; it is shown in Figure 19. This cross section, which might be described as a highly distorted bell-shape, is characteristic of upper canines from other sites that have been ascribed to *Notochoerus;* in some of these the "bell-shape" is more marked.

Specimen KP 210 consists of a fragment of right mandible with a rolled and damaged third molar preserved. The tooth is 81 mm long and 28 mm broad anteriorly. There are three well-developed pairs of lateral pillars, separated by single median columns, a much weaker fourth pair of lateral pillars, and a complex of three pillars in the talonid. The pattern in wear is very like that of lower teeth from Omo that have been assigned to *Notochoerus euilus*, but the Kanapoi specimen is more robust and the fourth pair of lateral pillars is much weaker. The talon is little worn and the original crown height can be estimated as about 30 mm.

Associated directly with the mandible KP 241, and numbered KP 242, is a collection of small skull fragments. It has been possible to assemble only a few pieces, but these include most of the front of the palate with the bases of the canines, and also a detached large bony knob from the zygoma. The front of the palate was shaped very much like that of *Hylochoerus*, but about half as big again, and the canines themselves and the bony flanges around their bases are proportionally larger than in the forest hog. The canines are rounded triangular or subtrapezoidal in shape and the dimensions of the right canine in the alveolus are: transverse diameter—42 mm, dorso-ventral—36.5 mm. A similar shape is seen in canines of *Notochoerus euilus* in a skull from Omo (not yet described), and the morphology of the palate is also similar except that the canines are directed slightly more forwards in the Kanapoi than in the Omo specimen. The Kanapoi fragments also show that the anterior cheek teeth are less reduced than in the Omo species.

The bony knob mentioned above represents a protuberance on the zygomatic arch, rather different in nature from the expanded zygoma of *Nyanzachoerus.* It is almost cylindrical in form, expanding slightly near the broken base where it joined the more normal part of the zygoma; the other end is rounded and slightly rugose. It could, perhaps, best be described as thimble-shaped. The "height" (lateral extent) is 118 mm, and the diameter of the subtriangular cylinder is 85–95 mm. A very similar, but smaller, protrusion occurs on the zygoma of an undescribed skull from Omo, also provisionally referred to *Notochoerus* cf. *capensis.* The Kanapoi "knob" and the Omo skull are shown in Plate 27.

DISCUSSION

This collection, unsatisfactory as it is, establishes the existence of a very large suid with some distinctive characteristics, apart from its absolute size. The form of the mandible is hylochoerine or phacochoerine, with a long symphysis. The lower incisors have a normal complement of six, but show reduction in size both in the central and in the outer lateral pairs. The large lower canines are U-shaped to subtriangular in cross section and the upper canines are trapezoidal to a squashed bell-shape in cross section. The premolars are reduced, with P_2 very small and the whole premolar series only about half the length of M_3 alone, M_3 itself being about half of the total length of the cheek tooth series. The cheek teeth, although large, are apparently small in relation to the great size of the skull, bearing about the relationship seen in *Hylochoerus.* A large cylindrical protuberance occurs on the zygoma, possibly restricted to male animals.

Notochoerus cf. *euilus*

Hylochoerus euilus Hopwood, 1926: 21, text-fig. 7, pl. 2, figs. 7–10.
Notochoerus euilus Leakey, 1958 (in part): 31.
Notochoerus euilus Cooke and Coryndon, 1970: 147, pl. 7, figs. 7–10.

Remarks. The status of the type material of Hopwood's species from Kaiso has been considered elsewhere (Cooke and Coryndon, 1970). The lower molars are fairly elongate but relatively narrow, measuring about 65–75 mm by 25 mm, and are not very much higher crowned than their width. They normally have four pairs of laterals in the lower third molars, plus a small talonid or talonid complex. The lateral pillars are well separated for most of their height and they wear to produce enamel islands with a dumbbell or distorted H-shape, becoming collar-stud-shaped in advanced wear. Similar teeth occur plentifully in the lower part of the Omo beds, but are undescribed, and are associated with mandibles, upper dentitions, and a skull. The lower and upper canines are similar in general structure to those described above for the *N.* cf. *capensis* material from Kanapoi; the presumed *euilus* skull lacks the zygomatic knobs and differs in other respects from the Omo skull regarded as cf. *capensis.*

DESCRIPTION

One incomplete lower third molar KNM–KP 245, does not fit well with the material ascribed to *Notochoerus* cf. *capensis* above, but agrees well with the material from the lower Omo beds regarded as belonging to *N. euilus.* As preserved, the specimen is 44.5 mm long and it was probably near 65 mm when complete. It is 25 mm broad at the base of the crown and the height is 29 mm on the little worn posterior column and may have been as much as 35 mm when intact.

Another specimen, KP 209, is a chemically corroded fragment of a lower third molar showing characteristics similar to those of the Omo *N. euilus.*

Also in the Kanapoi collection are a rather slender left lower canine (KP 248) and the broken tip of a similar tusk (KP 224). The almost complete specimen is 128 mm in length from the tip to the broken root area; the greatest diameter at the base is 23 mm and transversely is 17.5 mm. There is a wear facet on the upper 4 cm of the tusk. All three sides of the triangular tooth are coated with enamel that is thickest on the buccal side. There is a fairly deep posterior groove in the complete specimen, but this groove is shallower in the broken tip of KP 224. While it is not impossible that these tusks belonged to a variety of *Nyanzachoerus,* it is difficult to place them at the present time.

OTHER SUID REMAINS FROM LOTHAGAM

Nyanzachoerus sp.

Two specimens, one from below the "marker" horizon in Unit 1 and one from a level towards the top of Member C, are difficult to place within the known range of *Nyanzachoerus tulotos,* although it is not completely impossible that they may belong to variants of that species.

Specimen KNM–LT 318, from the lower horizon, consists of parts of the two mandibular rami. The left is broken behind LM_3 and through the symphysis a little in front of the root of LP_2, exposing the canine; part of the right corpus joins the back of the left posterior border of the symphysis and is broken off behind RM_2. On the left side, only M_3 is preserved, although damaged anteriorly, but the roots of the other teeth are still present, broken off at the alveolar margin. On the right side, part of the battered crown of P_3 remains, as well as the extremely worn RM_2. The RP_3 is a little larger than the biggest specimen assigned to *N. tulotos* and seems to have

TABLE 54. MEASUREMENTS ON MANDIBLE LT 318 FROM UNIT 1, MEMBER B

Tooth	Description	Length	Breadth	Height
LP_2	Roots only	17.0	10.0	–
LP_3	Roots only	34.0	28.5	–
RP_3	Damaged crown	28.7 + (31e)	23.7 + (24e)	10.0+
LP_4	Roots only	31.5	31.0	–
RP_4	Roots only	32.5	32.5	–
LM_1	Roots only	21.5	22.0	–
RM_1	Roots only	20.0	21.6	–
LM_2	Roots only	27.0	24.5	–
RM_2	Very worn crown	24.7	21.6	dentine
LM_3	Damaged crown	39.5	23 e	10.8+

only a very weak anterior cingulum. The RP_4 is shown by the roots to have been substantially longer than any of the other known specimens, but it is also very much wider so that the crown must have been more or less equidimensional. By contrast, the LM_3 is particularly small, lying at the lower limit of size for *N. tulotos*. The canine is of moderate size, with a maximum diameter of 25.0 mm and a minimum of 20.3 mm, and its shape is subtriangular like that of *N. tulotos*. Dimensions for the cheek teeth and the roots are given in Table 54 and the specimen is shown in Plate 28. Although it is possible that splaying of the roots could have the effect of exaggerating the apparent size of the missing crowns of the premolars, the appearance of the jaw suggests that the specimen belongs to a different species showing further premolar enlargement beyond that displayed in *N. tulotos*.

Specimen LT 299, from Member C, is an isolated left P_3 in moderate wear. The dimensions are: length 29.6 mm, breadth 24.7 mm, and height 20.3 mm. Like the corresponding tooth in the mandible from the lower horizon, it differs from normal *N. tulotos* in being broader and in having only a very faint anterior cingulum and no anterior cingular cusp.

Nyanzachoerus cf. *pattersoni*

Five specimens from Lothagam seem to belong to a *Nyanzachoerus* different from *N. tulotos* but close to *N. pattersoni*. Two are from the upper part and three from the lower part of Unit 1.

UNIT 1, MEMBER B

KNM–LT 312: a piece of right mandibular ramus with pieces of P_4, M_1 and M_2, the dimensions of which are very close to those of LT 294 (below), as is also the morphology of the tooth fragments that remain. This specimen is recorded as coming from the very base of the deltaic series, although it is a surface find and its provenance is not certain.

LT 294: a piece of left mandibular ramus with P_4 and M_2 intact, but only the roots of M_1 (Pl. 29). The teeth are very little worn and show the typical features of *Nyanzachoerus*. The LP_4 is 22.6 mm long, 17.3 mm broad, and 22.5 mm high. Although it is almost the same size as the P_4 in the type of *N. kanamensis*, and thus narrower than is usual in *N. pattersoni*, it is morphologically much closer to the latter species. The LM_2 is much shorter than in *N. kanamensis* but agrees very well with *N. pattersoni*; its length is 26.8 mm, breadth 20.0 mm, and height as preserved 15.5 mm. The specimen probably represents an early *N. pattersoni*.

LT 304: a fragment of left maxilla with roots of parts of P_3 and M_2, part of an extremely worn M_1, and the buccal half of P_4. The general morphology of the pieces of maxilla, which show the beginning of the zygoma, and also the size and form of the tooth roots and enamel remnants, resemble the corresponding parts of the holotype skull of *N. pattersoni*. Identification is very uncertain.

UNIT 1, MEMBER C

LT 285: two associated specimens are an upper right M^2 in fairly advanced wear, and a piece of left mandibular ramus with most of P_4 and the three molar teeth; M_1 is worn to dentine only and M_2 has some enamel remaining. The dimensions are given in Table 55 and the ramus is shown in Plate 29. The teeth are near the upper range of size variation for *N. pattersoni*, but the morphology is typical and there can be very little doubt about the identification.

TABLE 55. DIMENSIONS OF TEETH OF SPECIMEN LT 285 REFERRED TO *NYANZACHOERUS* CF. *PATTERSONI*

Tooth	Stage of wear	Length	Breadth	Height
RM^2	Advanced	30.0	27.8	8.0+
LP_4	Fairly advanced	–	21.3	12.0+
LM_1	Extreme	16.8+	c16	dentine
LM_2	Very advanced	29.7	23.0	8.0+
LM_3	Moderately advanced	57.2	26.0	15.3+

Nyanzachoerus plicatus

Three specimens from the upper part of the Lothagam succession are assigned to this characteristic Kanapoi species. Two are from the uppermost part of Unit 1, Member C, higher than any of the *N. tulotos* material; one specimen comes from the fluviatile deposits of Unit 3, well above the intrusive basalt (see Fig. 2).

TOP OF DELTAIC SERIES (MEMBER C)

KNM–LT 311: this is an isolated upper third molar in early wear, damaged anteriorly so that the front buccal pillar is lost and the lingual pillar is only partially preserved. The present length is 57 mm and is estimated as having been close to 70 mm when the tooth was intact; the breadth is 34.1 mm and the height of the little worn second lateral pillar on the buccal side is 26.5 mm and that of the unworn third lateral pillar on the lingual side is 27.6 mm. The form and structure of the tooth is characteristic of the species, but it is a little broader and slightly less hypsodont than the typical Kanapoi material.

TABLE 56. MEASUREMENTS ON DAMAGED TEETH LT 308 FROM TOP OF UNIT 1, MEMBER C REFERRED TO *NYANZACHOERUS PLICATUS*

Tooth	Length	Breadth	Height
RP_3	29.0	21.0e	24.5+
RP_4	25.8	14.5 + (c22)	20.5+
RM^2	34.1	24.0	12.0+
left lower canine	maximum 39.0	minimum 27.0	

KNM–LT 308: this collection apparently represents the remnants of a disrupted skull and comprises a piece of lower left canine, an imperfect RP_3, the buccal half of RP_4, an incomplete RM^2, and a scrap of RM^3. The dimensions are given in Table 56. The lower premolars are larger and broader than in the Kanapoi specimens, but otherwise agreement is good.

FLUVIATILE SERIES (UNIT 3)

Specimen KNM–LT 298 is the front part of an upper LM^3, broken behind the second pair of lateral pillars, but retaining the second median pillar. The lateral pillars are a little more tapered and smoother than in the Kanapoi material and lack the dentate "paramolars" displayed in the other specimens of *N. plicatus*. In this respect they are thus somewhat more like the third molars of *N. pattersoni*, but a great deal larger; the resemblance to *N. plicatus* is otherwise close. The present length is 43.5 mm and cannot have been less than 60–65 mm even if allowance is made only for a modest talon complex; the anterior breadth is 32.9 mm and the height of the unworn anterior pillars is 33.2 mm.

Suidae indet.

Two specimens from Member B of Unit 1 do not seem to belong to *Nyanzachoerus* and are difficult to place.

Specimen KNM–LT 317 is a right upper canine, found with the holotype skull of *Nyanzachoerus tulotos* but it does not fit the alveoli in the skull. It is curved fairly strongly in the horizontal plane and is truncated diagonally by a large wear facet (Pl. 29). The tooth is 12.5 cm long, as preserved, and tapers towards a fairly narrow root. The cross section is almost circular and below the worn facet measured 28.5 mm anteroposteriorly and 27.0 mm dorsoventrally. On the lower surface are the remnants of a band of thick, grooved enamel and there are also remnants of enamel on the upper surface. There is no indication of the inset lateral enamel ridge-bands characteristic of *Potamochoerus*.

Specimen KNM–LT 314 is a left upper third molar, completely unworn but fully formed. It displays the simple basic pattern found in *Sus* or *Potamochoerus*. There are small accessory pillars between the first and second pair of laterals, single on the lingual and multiple on the buccal side. There is a fairly well-developed stout talon pillar. The molar is rather more triangular in outline than that of *Potamochoerus* and more like the form seen in *Sus* and *Nyanzachoerus*. The length is 33.1 mm and the breadth is 22.3 mm anteriorly, 19.2 mm at the second pair of laterals, and 14.5 mm at the talon. The unworn pillars are approximately 14.5–15.0 mm high, but the base of the enamel is damaged and exact measurement is not possible. The pillars are individually rather more separate and distinct than in typical *Sus*, in fact resembling *Nyanzachoerus* more closely in this respect. In the absence of more adequate material it seems best to refer the teeth for the present to an unknown unspecialized suid.

Notochoerus cf. *euilus*

Two specimens from the fluviatile series (Unit 3) seem to belong to *Notochoerus*. One of these, KNM–LT 327, is from the highest horizon and the other, KNM–LT 297, is from the lower part of this series at about the same horizon as the partial LM^3 of *Nyanzachoerus plicatus* (KNM–LT 298) described above. These three specimens are the only Suidae from Unit 3.

KNM–LT 297 is the back half of a LM$_3$. The length as preserved is 42.0 mm and it may originally have been 65–70 mm. The maximum breadth at the base is 23.3 mm and the height is 35 mm and could originally have been as much as 40 mm. In morphology it is very close to other material referred to *Notochoerus euilus*, although the columns are more tapered than is usual.

KNM–LT 327 is a fragment of the right mandibular ramus with a badly damaged M$_2$, the front half of M$_3$, and the posterior root area (Pl. 30). The second molar is very damaged but its length at the base was about 25 mm and the breadth approximately 19 or 20 mm. The length of the front part of the RM$_3$ is 46.0 mm, and it is estimated that the length of the entire tooth was close to 70 mm. The breadth of the crown is 22.8 mm anteriorly and 24.6 mm at the second pair of laterals; this width relationship has been noted characteristically in specimens from the lower Omo beds that have been assigned to *N. euilus*. The height, as preserved, is 12 mm and the crown is in fairly advanced wear. It can be matched closely in both dimensions and enamel pattern with correspondingly worn teeth from Omo.

Specimen from an Unknown Locality

One specimen collected from the Lothagam area consists of two lower teeth (an LM$_2$ and an incomplete LM$_3$) that are very characteristic examples of *Notochoerus euilus* and can be matched closely with material from the lower Omo beds. They are numbered KNM–LT 289. They were found at an old camp site, known as "Robbins' Camp," which was used by the Harvard expedition; there is no means of determining where they came from originally, except that they were probably collected somewhere in the general region. This may be an indication that a patch of Omo beds (or their equivalent) exists in the neighborhood and has escaped attention.

SUID REMAINS FROM EKORA

At Ekora (see Fig. 1) the upper Kanapoi beds are capped by lava and this is overlain by a moderate thickness of sediments, conveniently termed the Ekora beds. Only a very few suid remains have come from this area, and they include a few teeth of *Phacochoerus* that were not *in situ* and may well have been derived from younger deposits. The upper Kanapoi beds yielded a very small number of fragments (KNM–EK 270) and there is only one specimen from the Ekora beds proper (KNM–EK 271).

Nyanzachoerus cf. *pattersoni*

KNM–EK 270 comprises a few pieces from the upper Kanapoi beds. There is a piece of mandible with RP^4 and part of RM^1; two loose incisors, an LI_2 and an RI_3; and an LM^3 that had not yet erupted but was probably completely formed. Measurements on the cheek teeth are given in Table 57. The structure and morphology of the teeth agree with those of *N. pattersoni*, but the LM^3 is lower crowned and not as "compact" as in the type material. It is therefore not identified with certainty at the specific level.

TABLE 57. MEASUREMENTS ON TEETH FROM THE UPPER KANAPOI AT EKORA REFERRED TO *NYANZACHOERUS* CF. *PATTERSONI*
(EK 270)

Tooth	Length	Breadth	Height
RP^4	18.1	25.2	21.0+
RM^1	20.0e	?	10 +
LM^3 unworn	42.7	28.5 anterior	18.5
		16.3 talon	15.0

Nyanzachoerus cf. *plicatus*

KNM–EK 271, the only suid from the Ekora beds, is an LM_3, damaged both anteriorly and posteriorly. Despite this fact, it is structurally so like known material of *N. plicatus* that there can be very little doubt about the identification. It is illustrated in Plate 30.

AGE AND CORRELATION

The Harvard Expedition Localities

In the three areas studied by the Harvard University expeditions, some age relationships could be determined by field evidence. The Kanapoi beds lie directly below a basalt that can be traced through to the Ekora locality, and the Ekora beds lie above the basalt. The basalt was believed to be a lava flow, although the possibility that it might be a sill cannot be totally excluded. Determinations of age showed a scatter from 2.5 to 2.9 million years, with a mean of about 2.7 million years. The faunal evidence is strongly against such a date, and, until further data on the basalt are available, these determinations are not accepted as definitive of the age of the sediments themselves.[1]

The Lothagam locality is isolated and cannot be tied in stratigraphically to the Ekora and Kanapoi areas. The Lothagam sequence is complex, comprising a lower unit of deltaic deposits, a middle unit of lacustrine beds, and an upper unit of fluvial origin. An intrusive basalt occurs at the contact between the deltaic sequence and the lake beds, and its age of 3.71 ±

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[1] Re-determination on fresh specimens gives an age close to 4.0 million years.

0.23 million years provides a minimum age for the entire sedimentary succession (see Fig. 2).

The distribution of the Suidae at these localities has been given in Table 1. Although the fossil pigs appear to provide a useful basis for correlation, consideration must be given to the possibility that the faunal differences between the various deposits could be the result of ecological factors. However, both *Nyanzachoerus plicatus* and *N. pattersoni* are now known to occur at a number of other localities in East Africa, often together, and *N. plicatus* is found at Lothagam, in the upper horizons, as well as at Kanapoi and Ekora. These facts suggest that ecological differences were at most only of secondary significance.

Although a *Nyanzachoerus* that might be *N. pattersoni* does occur in the deltaic beds of Unit 1 at Lothagam, it is rare and most probably represents an early or ancestral form of the typical Kanapoi species. *N. plicatus* has not been found in the lower part of Unit 1 and is very rare in the upper part of that unit. On the other hand, one of the three specimens of suid from the fluvial beds (Unit 3) is *N. plicatus*, and the other two are *Notochoerus* cf. *euilus*, which is common in the lower part of the Omo beds (see below). *Nyanzachoerus tulotos* has not been found at Kanapoi or at Ekora, and it seems likely that it had become extinct by the time those beds were laid down. The "best fit" correlation from the suid material alone would place the fluvial beds (Unit 3) at Lothagam as approximately coeval with the Kanapoi beds, although perhaps slightly younger and possibly as young as the Ekora beds. If the Kanapoi equivalent lay in the upper part of the unfossiliferous lake beds (Unit 2), the suid distribution would be satisfied. Although the total fauna has not yet been worked out, similar general conclusions have been reached from a study of the Proboscidea by Maglio (1970), except that he suggests closer equivalence between the Kanapoi beds and Unit 3 at Lothagam.

Other East African Deposits

The Olduvai succession is already well known and the fauna has been reviewed by Leakey (1965). Several horizons within the sequence have been dated radiometrically. A basalt that was formerly regarded as the base of the deposits has an age of 1.9 million years, but Hay (1967) has designated it as the Basalt Member of Bed I and suggests that the lower sediments to the west of the Fifth Fault might be older than the Basalt Member in the east. However, little is known of the mammalian fauna in the western area. *Nyanzachoerus* has not been reported from Olduvai and the various peculiar Suidae from Bed I are so far not known from other localities. The specimen that Leakey (1965) tentatively referred to *Notochoerus* cf. *euilus* from Bed I is most probably a juvenile of a different form found at Omo. The typical suid *Mesochoerus olduvaiensis* is represented in the upper part of Bed II and possesses elongate and moderately hypsodont third molars; in the lower part of Bed II the molars are a little lower crowned and shorter, and in Bed I there are a few specimens that cannot be separated from the advanced stages of *Mesochoerus limnetes* (= *M. heseloni* Leakey = *Omochoerus heseloni* of Arambourg) from the upper part of the Omo sequence.

The Omo Beds are known, as a result of recent studies, to have a thickness of more than 1700 feet, within which a number of distinctive tuff horizons have been recognized (Arambourg, Chavaillon, and Coppens, 1967; Howell, 1968). A fairly high tuff, originally designated "H," has been dated at 1.81–1.87 million years, which is close to the age of the *nuee ardente* above the basalt at Olduvai (1.70–1.76 m.y.). Tuff "D," near the middle of the Omo succession, has a date of 2.37–2.56 ± 0.12 million years, and the next-to-lowest tuff "B" has been dated provisionally at 3.75

± 0.20 million years. A tentative interpretation of the faunal succession has been given by Arambourg, Chavaillon, and Coppens (1968) and much of the suid material has been studied independently by one of the present authors. *Mesochoerus limnetes* seems to undergo progressive increase in the length of the third molars, as well as in their complexity, and there is reason to suspect that *M. limnetes* and *M. olduvaiensis* may represent a true lineage, the changes being consistent with the radiometric correlations. Below tuff "C" there occurs abundant material referred to the Kaiso species *Notochoerus euilus* (see Cooke and Coryndon, 1970), but above this horizon the typical large suid is *Notochoerus scotti,* the third molars of which become very elongate and hypsodont in the higher levels. *N. euilus* is characteristic of two sites known as "Brown Sands" and "White Sands" (Howell, 1969), which lie well north of the "Type" area (see Fig. 1) but which are regarded as correlatives of a zone between tuffs "B" and "C." Their age is estimated as close to 3 million years. A *Nyanzachoerus* occurs at both these localities but the material is scanty and it is not certain whether it is *N. pattersoni* or *N. kanamensis.* No specimens have been found that could represent *N. plicatus.*

An isolated locality in the northern part of the Omo area was found and worked by Mr. Richard Leakey and his party, and was designated "Yellow Sands" (see Fig. 1). The sediments are capped by a basalt that has been dated, by a single determination, as 4.05 ± 0.20 million years (see Howell, 1968). Both *Nyanzachoerus pattersoni* and *N. plicatus* have been identified from this deposit, but no other Suidae were noted in the material recovered. This suggests a close equivalent in age between "Yellow Sands" and the Kanapoi deposit, a view supported by the proboscidean material (Maglio, 1970). The absence of *N. plicatus* at "Brown Sands" and "White Sands" suggests that the Ekora beds are older, and they are regarded here as probably about coeval with tuffs "A" and "B" near the base of the Omo beds in the Type area. Provided that the Omo age determinations are correct—and they are both numerous and consistent—these faunal affinities are very strongly against acceptance of the 2.9 m.y. age of the Kanapoi basalt as indicative of the age of the Kanapoi and Ekora sediments.

Nyanzachoerus has also been found at a number of other localities in East Africa, including the type material from Kanam. The fauna of the Kaiso Formation in Uganda has been discussed at some length by Cooke and Coryndon (1970), who recognized two main mammalian assemblages from horizons near the bottom and near the top of the 2,000-foot thickness of sediments; these were termed respectively the "Earlier Kaiso" and the "Later Kaiso" assemblages. *Nyanzachoerus* inseparable from *N. kanamensis* occurs in the "Later Kaiso," but specimens from the lower horizons may now be recognized as having a closer resemblance to *N. pattersoni* (which was not known at the time the Kaiso study was undertaken). The general faunal affinities suggest broad equivalence of the "Later Kaiso" with the middle part of the Omo sequence and of the "Earlier Kaiso" with the base of the Omo deposits.

Sediments in the vicinity of the Kazinga Channel and in the northeastern corner of Lake Edward have been regarded as belonging to the Kaiso Formation, although the detailed stratigraphic relations have not been worked out. Material recently discovered by Dr. W. W. Krommenhoek in the area (personal communication) includes a few specimens representing both *Nyanzachoerus pattersoni* and *N. plicatus,* thus providing yet another paired occurrence of the two species, as at Kanapoi and "Yellow Sands." A roughly similar age is thus indicated for the particular horizons from which these fossils came.

As far as the age of the Kanam deposit is concerned, some uncertainties exist. The occurrence of *Nyanzachoerus kanamensis* and *Equus* sp. might be taken to imply correlation with the "Later Kaiso." However, Proboscidea of "Earlier Kaiso" and Kanapoi affinities occur at Kanam as well. Preliminary restudy of the material suggests that two different ages may be represented in the Kanam collections, which do not come from a single site. The correlation of the Kanam beds is thus somewhat problematical at the moment.

In the areas west and north of Lake Baringo, systematic mapping by parties from Bedford College (London University) under the direction of Professor B. C. King and Dr. W. W. Bishop has resulted in the discovery of a number of sedimentary formations within a long sequence of lavas and associated rocks. The youngest major group of sediments was named the Chemeron Beds (McCall, Baker, and Walsh, 1967) and was described briefly by Martyn (1967). The sediments are more than 700 feet thick in the centre of the main basin and rest on the Kaparaina Basalts which, in turn, overlie trachytic lavas dated at 5 million years (Bishop, personal communication). A second basin in the same area contains the Kipcherere Beds, which are probably broadly equivalent to the Chemeron Beds. These deposits have yielded only a few mammalian fossils, one of which is a hominid temporal (Tobias, 1967), but the fragmentary remains include two specimens of *Nyanzachoerus pattersoni* and one undetermined fragment that may represent a different *Nyanzachoerus*. The basal parts of the Chemeron and Kipcherere beds, from which these fossils came, thus seem to be broadly equivalent in age to the Kanapoi beds.

Below the Kaparaina Basalts in this region is another sedimentary group known as the Lukeino Beds. These deposits rest on an eroded surface of the Kabarnet Trachytes, which are dated as 7 million years old (Bishop, personal communication). The only suid specimen from the Lukeino Beds is a fragment of skull with much of the palate and most of the cheek teeth. It is clearly a *Nyanzachoerus*, resembling *N. tulotos* in some respects but differing from the Lothagam material in having smaller third and fourth premolars, stronger folding in the main cusps of the molars, and an M^3 that is relatively more enlarged as compared with M^1 and M^2. These characters suggest a form allied to *N. tulotos* but in some respects less specialized and in others modified in a direction towards *N. plicatus*. There are thus apparent resemblances to the Wadi Natrun "*Sivachoerus*" and the Sahabi skull, so that the age may be similar. The Lukeino Beds lie well below another small sedimentary unit called the Kaperyon beds, which do not contain fossil suids but have yielded proboscidean remains which Maglio (1970) equates with the lower beds at Lothagam.

Central and North African Deposits

The occurrence of *Nyanzachoerus* in the Chiwondo Beds of Malawi has already been mentioned (p. 193 above). The specimen is clearly *N. plicatus* and there can be little doubt that the horizon from which it came must be close in age to the Kanapoi beds. This horizon is low down in the Chiwondo Beds, the greater part of which are probably somewhere within the time span of the lower Omo beds. The fauna of the Chiwondo Beds was discussed briefly by Coryndon (1966) and a full account by John Mawby is in the press (personal communication). The giant suid *Notochoerus capensis* is a notable element, together with primitive proboscideans.

In the Lake Chad area, on the southern side of the Sahara, an australopithecine cranium was recovered from one locality in a complex of deposits (Coppens, 1961). A preliminary faunal analysis was made by Coppens (1967) and several stages were recognized for the first time. *Notochoerus capensis* occurs in association with proboscidians resembling those at the base

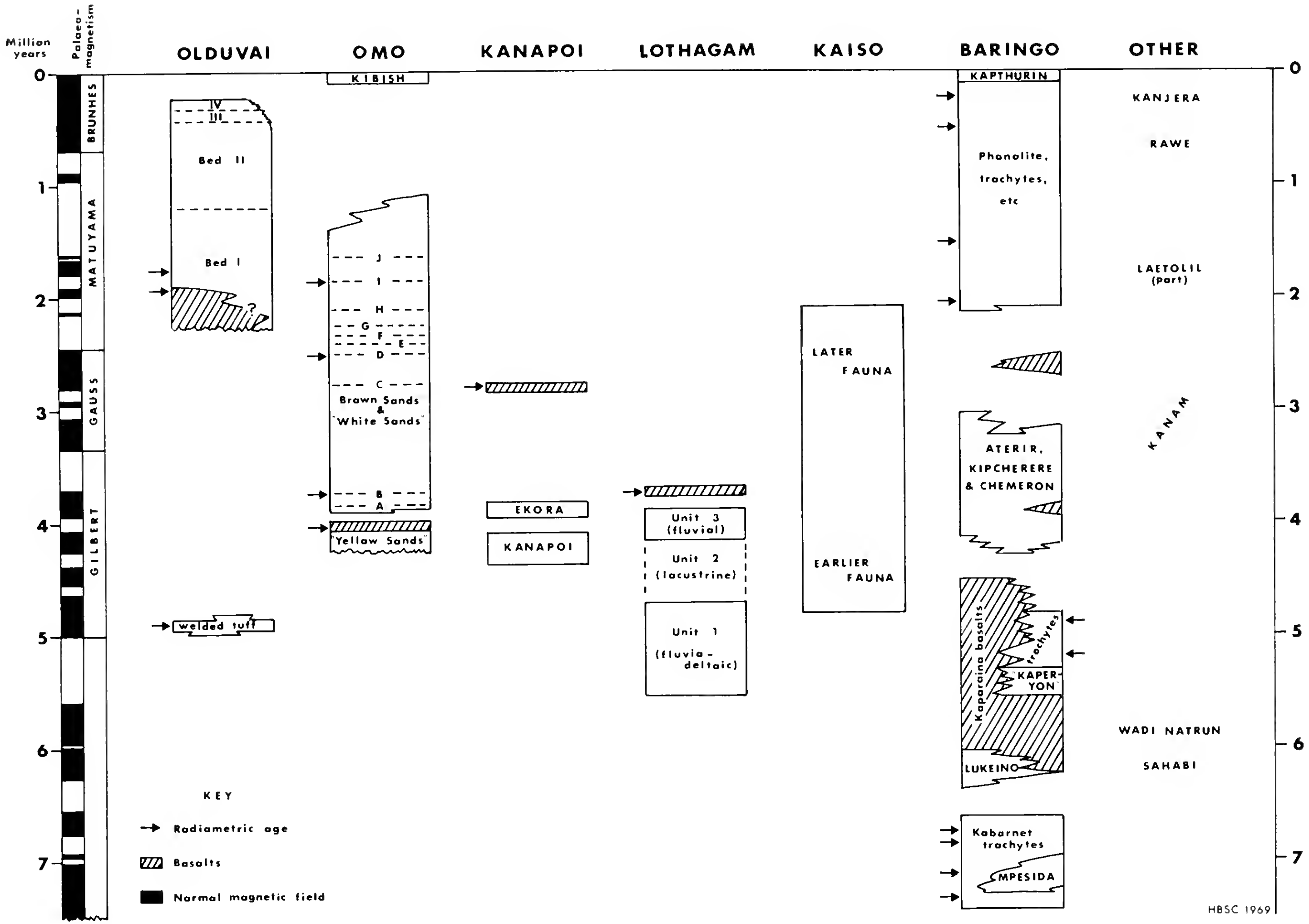

Figure 20. Provisional correlation of Pliocene-Pleistocene deposits in East and North Africa, based primarily on the Suidae. Radiometric dates are shown and are used as controls where possible. The date for the Kanapoi basalt (which lies between the Kanapoi and Ekora sediments) does not accord with the palaeontological evidence and is regarded as anomalous. The sequence for the Baringo area is based on preliminary data supplied by Dr. W. W. Bishop, but the section presented here is a composite one and prepared by the present authors.

of the Omo sequence; a *Nyanzachoerus* has now also been recognized (Coppens, personal communication). As far as can be determined the whole complex ranges over about the span of the Omo beds, but the published data do not allow of more exact correlation of individual sites at the present time.

Until further Sahabi suid material is discovered, and more details are available regarding the whole fauna, the age relations of this site are somewhat uncertain. The lower jaw from Sahabi, *Nyanzachoerus syrticus*, could very well be ancestral to *N. tulotos* from Lothagam, and this suggests a slightly greater antiquity for the North African locality. The skull might represent a form ancestral to *N. plicatus* and there are resemblances to the material from Wadi Natrun and from Lukeino. It therefore seems best for the moment to regard the Sahabi, Wadi Natrun, and Lukeino deposits as roughly equivalent in age and probably a little older than the base of the Lothagam sequence.

The age relations inferred above are set out in tabular form in Figure 20. The conclusions reached are based mainly on the Suidae, and proper correlation must depend on fuller evaluation of the total faunas from each of the sites. It now seems clear that all the deposits that have yielded material assigned to *Nyanzachoerus* are generally older than 3 million years. Although there is not yet agreement on a definition of the base of the Pleistocene, 2.5 million years is a reasonable limit and few authorities have proposed as much as 3 million years. It thus seems reasonable to regard *Nyanzachoerus* as essentially a Pliocene genus. Its earlier Pliocene history is as yet unknown, but new localities are being found and further material is coming to light that may soon clarify existing problems regarding the origin and phylogeny of this genus. Clearly *Nyanzachoerus* is useful for correlation purposes, with a known range from the southern Sahara to Malawi, and it is hoped that the correlations here suggested may assist in the evaluation of relative ages for the important hominid fossils that are being found in increasing numbers in many of these deposits.

ACKNOWLEDGMENTS

The material that forms the basis for this account was collected by expeditions from the Museum of Comparative Zoology, Harvard University, supported by National Science Foundation grants GP 1188 and GA 425 to Professor Bryan Patterson. The specimens themselves are the property of the National Museum Centre for Prehistory and Palaeontology, Nairobi, and we are deeply indebted to Dr. L. S. B. Leakey and to Professor Patterson for making the material available to us for study and description. We are grateful to the Trustees of the National Museum for the provision of working space and to the entire staff of the Centre for invaluable assistance and hospitality. Mrs. S. C. Coryndon (now Mrs. Savage) provided material help, as well as critical comment and helpful discussion. A number of individuals, including Dr. Leakey, Professor Patterson, Professor C. Arambourg, Yves Coppens, V. J. Maglio, John Mawby, Dr. F. Clark Howell, and Dr. W. W. Bishop have made available to us unpublished material and data for which we are most appreciative. A particular debt is owed to the Wenner-Gren Foundation for Anthropological Research, New York, for financial support without which this study could not have been undertaken, as well as to its Director of Research, Mrs. Lita Osmundsen, for her help and encouragement. The Wenner-Gren Foundation has also furnished a generous grant towards the cost of publication of this paper.

APPENDIX I

NOTES ON *NYANZACHOERUS* SKULL FROM SAHABI

This skull was described by Leonardi (1952) as *Sivachoerus* cf. *giganteus* Falc.

& Cautl. It was found by Professor Carlo Petrocchi at Sahabi, in Sirtica, north-central Libya and is now in the collections of the Instituto di Geologia e Paleontologia of the Universita degli Studi in Rome; thanks are due to Dr. Carmelo Petronio for making it available for study.

The skull is dorsoventrally crushed and the cranium was apparently lost by erosion before recovery; the dorsal area has been filled with a grey cementlike plaster and further restoration would be difficult. The snout is long and narrow and the nasals are gently arched. The nasals may overhang the maxillae slightly but the curve is smooth and not abrupt as it is in *Potamochoerus.* The nasals are almost parallel sided, with only a limited amount of expansion above the front of the canines. The canine flanges are very small, like those of a female *Potamochoerus* but without any vertical wings. The canines are small and almost circular in cross section, with the anteroposterior dimension at the alveolar border 17.5–18.5 mm and the vertical dimension 14.5–15.0 mm. The tips have been lost since Leonardi photographed the specimen but the illustrations indicate that they were very like those of the female holotype of *Nyanzachoerus pattersoni.* In the middle of the broken surface is a small pulp cavity, like that seen in *N. plicatus*, but the canines are not as flattened as in that species. The palate is wider in front of the canines (78.5 mm) than behind them, reaching a minimum of 59 mm just in front of P^2.

The zygomatic arches begin above P^4 and emerge gently at about 30° to the axis of the skull. They then turn to 40°–45° and curve smoothly back almost parallel to the axis at the widest part. Below the orbits the front of the zygoma is rather plate-like and less hollowed than in *N. tulotos* or *N. pattersoni*; this area is not as flat as is inferred for *N. plicatus.* The whole jugal area is thickened laterally and the inner wall of the zygoma is nearly vertical. The inflated portion is hollow and it is crushed on the right side. The outer border droops almost to the palatal plane, thus descending farther than in *N. tulotos.* On the inner side the root of the zygoma extends back as far as the front part of M^3. The ventral surface is almost horizontal and represents a broad area of muscle attachment.

The premaxilla is long and bluntly pointed, as in *Potamochoerus* and in *Nyanzachoerus pattersoni*, and it lacks the truncated tip seen in *N. tulotos.* All six incisors were present in life, but the left I^3 is now missing. I^1 and I^2 are of normal size and are similar in structure, with a simple inner cingulum ridge that encloses a shallow fossette. I^1 is slightly shorter and stouter than I^2 (18 mm by 12.3 mm as against 20 mm by 12.0 mm). I^3 is separated by a gap of almost 10 mm and is a small tooth (10.7 mm by 6.3 mm) that stands erect and looks rather like a miniature canine; the socket on the left side suggests that this is normal. There is a short diastema to the canine and a longer one to P^2. No sign of P^1 exists on either side.

The cheek teeth are in a very bad state, with the enamel pitted and corroded. P^2 is present on the right side, but broken off at the roots on the left. It is a small, simple tooth with a longitudinal median ridge. P^3 is conical, drawn obliquely backwards and inwards, so that the tip lies two-thirds of the way back and lingual to the mid line. There is a small antero-internal cingulum and a larger postero-internal cingulum, the latter almost constituting a low cusp. The outer enamel appears to have been smooth, but the inner side is furrowed either naturally or as a result of erosion. P^4 had a moderately high crown and the main cone is divided into two near the tip. This bifid cone is separated by a transverse fissure from the protocone so that two islands develop with wear. There seems to have been an anterior cingulum ridge almost three-quarters of the height of the main cone and a similar, but smaller, posterior cingulum.

M^1 has been damaged on the left side. On the right it has the two anterior elements

TABLE 58. MEASUREMENTS ON SKULL OF SAHABI *NYANZACHOERUS*

Vertex length	c450	
Basilar length	c400	
Bizygomatic breadth	245	
Greatest breadth across nasals	45–50	
Frontal breadth	c120	
Palatal length	325e	
Width of palate		
between M^3–M^3	29	
between P^2–P^2	38	
Breadth across maxilla outside M^3–M^3	92	
Breadth of maxillae behind inferior border of canines	c105	
Breadth of premaxillae in front of canines	86	
Distance I^3–P^2	95	
Diastema C–P^2	54	
Length premolar series	left 53.5	right 52.0
Length molar series	106.0	104.5
Length P^2–M^3	159.5	156.5

TABLE 59. MEASUREMENTS OF CHEEK TEETH IN SKULL OF SAHABI *NYANZACHOERUS*

Tooth	Length	Breadth	Height
LP^2	root 13.5	root 8.5	–
LP^3	21.5	20.7	21.0
LP^1	18.2	24.1	18.5+
LM^1	gap 21.0	–	–
LM^2	33.3	24.3	18.5+
LM^3	57.0	34.0	27.0
LP^2–P^1	53.5		
LM^1–M^3	106.0		
RP^2	12.3	8.2	7.0+
RP^3	19.0	19.6	21.0
RP^4	17.6	23.6	17.5+
RM^1	21.2	18.8	c5.0+
RM^2	31.7	–	–
RM^3	54.0e	31.5	28.0
RP^2–P^4	52.0		
RM^1–M^3	104.5		

already united into a single island, with a wavy edge. The posterior islands are damaged but it can be seen that the outer one is roughly bell-shaped and the lingual one is more complex. M^2 is badly weathered on the left side of the skull and the right one is damaged externally. The antero-internal column has an island consisting of a rounded lateral element, separated by a constriction from a flattened median element, and another constriction separates this from an axial element; the whole island looks like a concertinaed bell. The antero-external island has a more normal bell shape. The posterior columns are in early wear but conform to the typical *Nyanzachoerus* form. M^3 is almost unworn but the structure of the columns agrees with that seen in the second molars. The maximum crown height of M^3 is almost 28 mm which is slightly less than its anterior basal breadth. It is smaller than any of the corresponding teeth of *N. plicatus* from Kanapoi but the morphology of the tooth, as well as the wear pattern of the islands in M^2 and M^3 is closer to that species than to the other known forms.

Measurements on the skull are given in Table 58 and on the individual cheek teeth in Table 59.

Although the dorsal surface and the occiput of this skull are damaged, it is clear that the temporal-frontal area was broad, as in all the other skulls assigned to *Nyanzachoerus* and unlike the narrow area in *Sivachoerus*. The back of the palate is about level with the back of M^3, as in other specimens of *Nyanzachoerus*, whereas *Sivachoerus* shows a marked elongation of the back of the palate. There is thus no valid reason to continue to assign the Sahabi skull to the Indian genus and it is here regarded as a species of *Nyanzachoerus*.

As far as skull size is concerned, the Sahabi specimen is comparable with the other known species of *Nyanzachoerus*. Compared with *N. tulotos*, the frontal breadth is smaller and the Sahabi skull lacks the lumpy appearance of the Lothagam holotype; the zygomatic arches are generally similar in form, but they droop more and are not as wide in the Sahabi skull; the third molars are substantially larger and the premolars much less robust than in *N. tulotos*; P^1 is clearly absent in the Sahabi

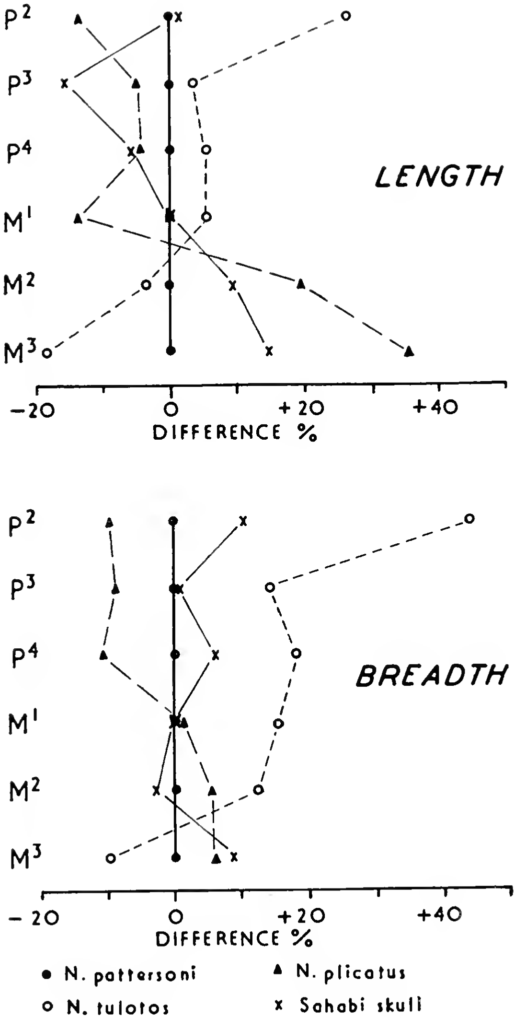

Figure 21. Length (top) and breadth (bottom) of upper cheek teeth in three species of *Nyanzachaerus*, and in the Sahabi skull, expressed as percentage differences relative to the corresponding dimension in *N. pattersoni*. A + shows a larger dimension and a− shows a smaller dimension.

species. Compared with *N. pattersoni*, the morphology of the skull is generally similar, and the canines are of a size comparable to those of the female holotype; the shape of the zygomatic arches is rather different, even from those of the female; the premolars are somewhat smaller and the third molars longer, broader, and with more complex enamel structure; the incisors are more specialized in the Sahabi skull; both species lack P^1.

It is less easy to compare the skull morphology with that of *N. plicatus*, which is known only from fragmentary material, but where the Sahabi skull differs in morphology from the other species, similar points of difference are found in a more advanced stage in *N. plicatus*. Both in *N. plicatus* and in the Sahabi skull the third and fourth premolars are relatively smaller and the second and third molars relatively larger than in *N. pattersoni*. The enamel folding in the second and third molars resembles that in *N. plicatus*, but the complexities are less developed. The canines of the Sahabi skull are intermediate between those of *N. pattersoni* and *N. plicatus*. The unusual incisors cannot be matched, but these teeth are unknown in *N. plicatus*.

Clearly the Sahabi skull must be excluded from close affinity with *N. tulotos*, not only because of the absence of P^1 but also because of important differences in the teeth. In dental characters, as well as in general morphology, it is intermediate between *N. pattersoni* and *N. plicatus*. The premolars are as broad as in the former, but their length is reduced as in the latter. The third molars are both broader and longer than in *N. pattersoni*, but not as enlarged as in *N. plicatus*, and their morphology is closer to the latter. On balance, the Sahabi skull forms a very reasonable ancestor for *N. plicatus* of Kanapoi, having diverged in this direction from an earlier stock which gave rise to the whole *Nyanzachoerus* complex. It is difficult to decide whether the resemblances require it to be placed within the species *plicatus* as an early representative, or whether the differences demand that the Sahabi skull receive a different specific name. The problem would be resolved if the skull of *N. plicatus* were better known. Accordingly it is felt that it is better to leave the matter open at this stage and to designate the Sahabi skull as *Nyanzachoerus* sp. (cf. early *plicatus*).

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Plate 1. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**, **C**. Dorsal, right lateral, and palatal views of the holotype (female) skull, KNM-KP 239, from Kanapoi. × 1/4.

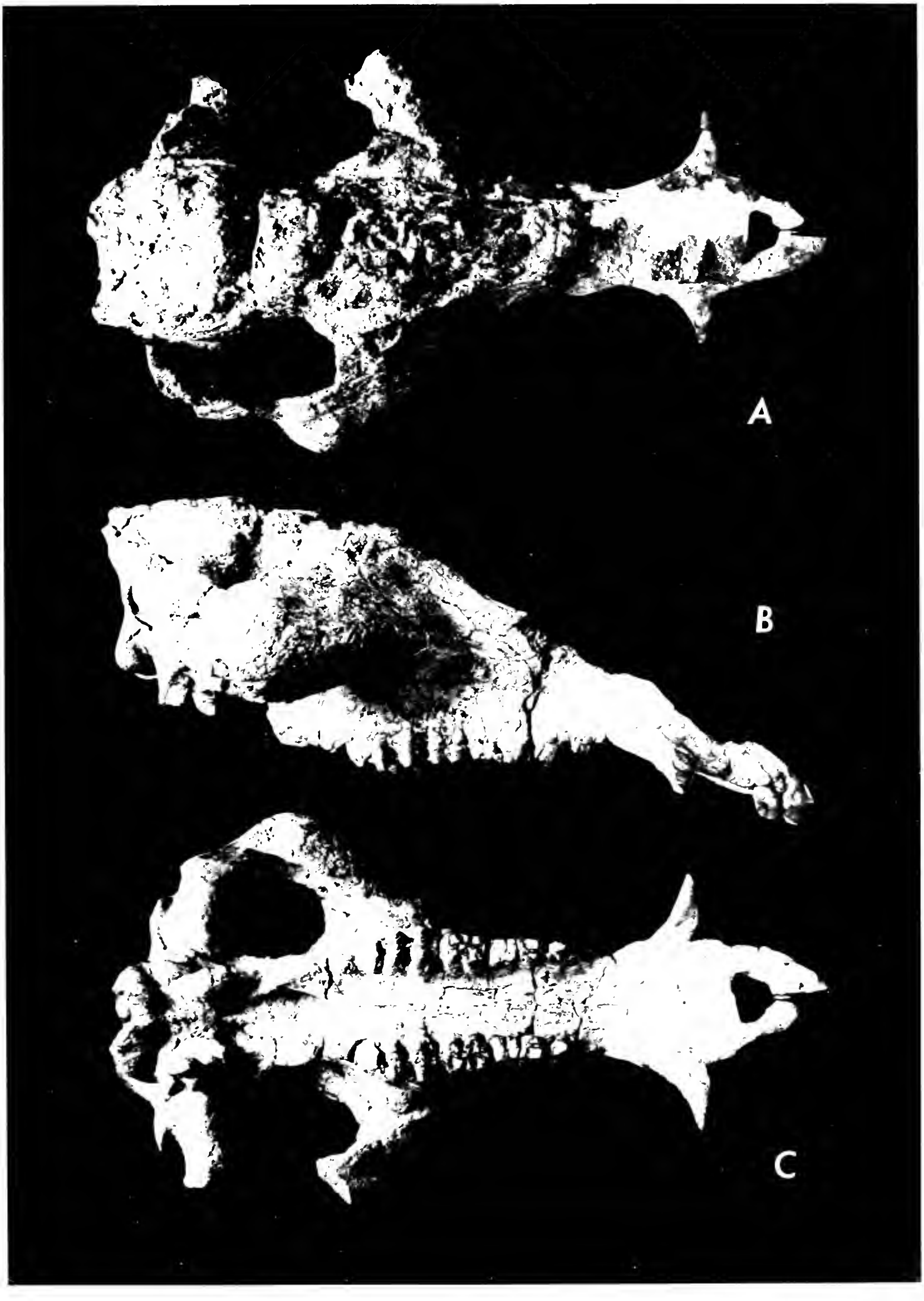

A
B
C

Plate 2. *Nyanzachaerus pattersoni* sp. nov. **A**, **B**. Occlusal and left lateral views of mandible of the holotype, KNM-KP 239. × ¼. **C**. Dorsal view of paratype (male) skull, KNM-KP 264. × ¼.


A
B
C

Plate 3. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Right lateral and palatal views of paratype (male) skull, KNM-KP 264, from Kanapoi. × ¼.

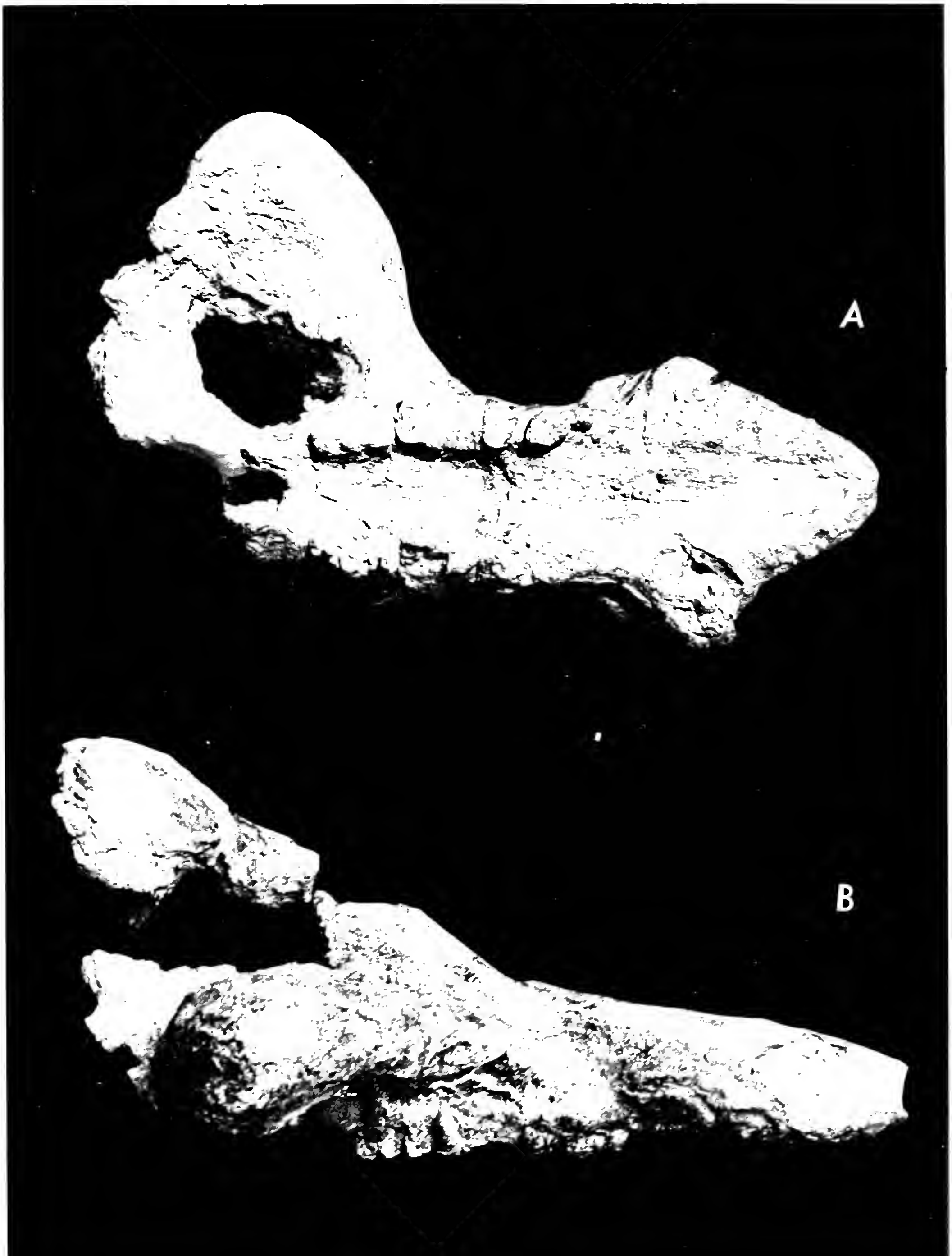

A
B

Plate 4. *Nyanzachaerus pattersoni* sp. nov. **A**, **B**. Occlusal and left lateral views of the massive mandible of the paratype, KNM-KP 264. × ¼. **C**. Crown view of left lower third molar of paratype, KNM-KP 264. Natural size. **D**, **E**. Occlusal and right lateral views of mandible of an old individual, KNM-KP 219, from Kanapoi. (See also Pl. 8). × ¼.

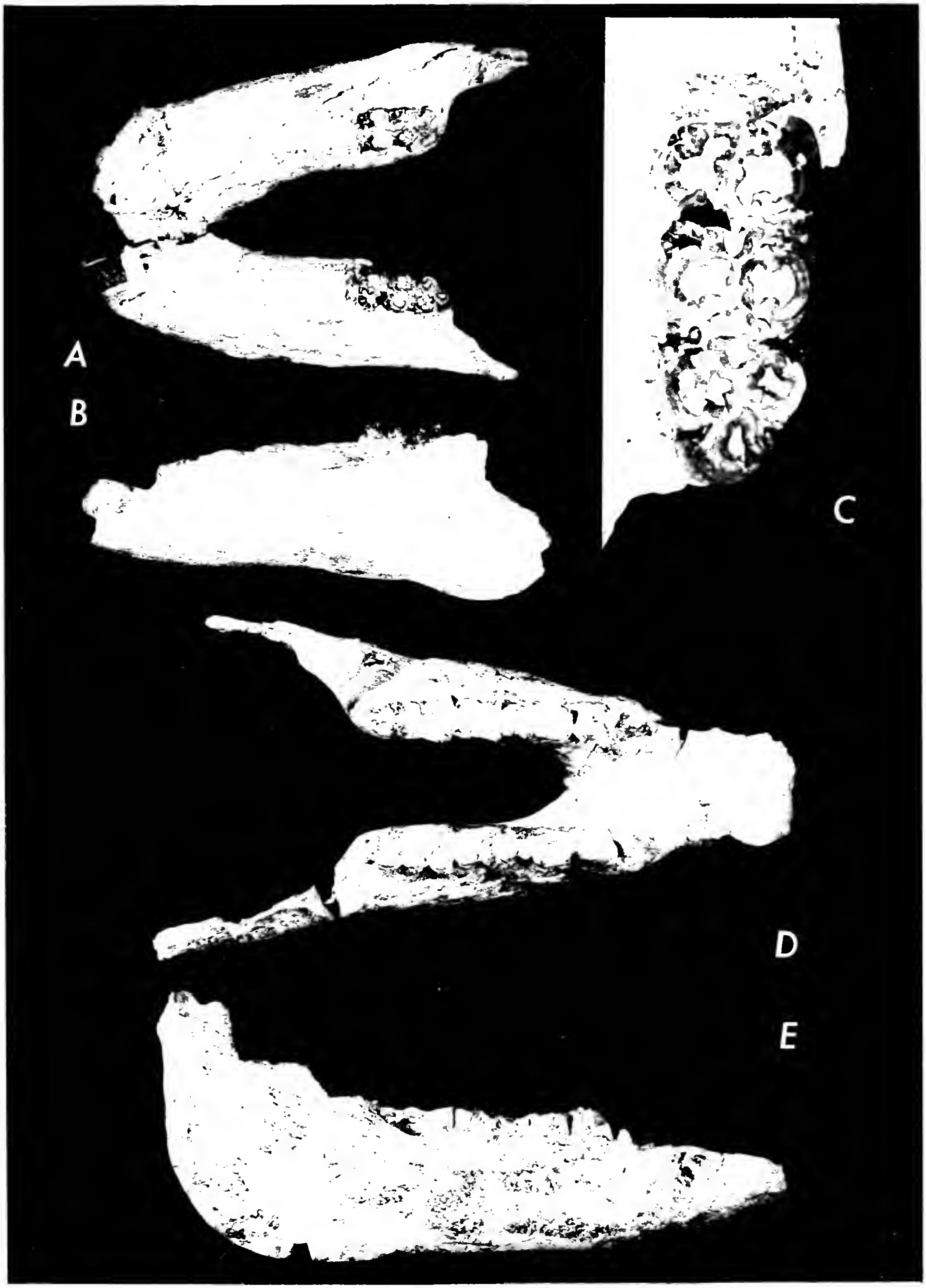

A
B
C
D
E

Plate 5. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Occlusal and right lateral views of upper cheek teeth in the holotype skull, KNM-KP 239. Natural size.

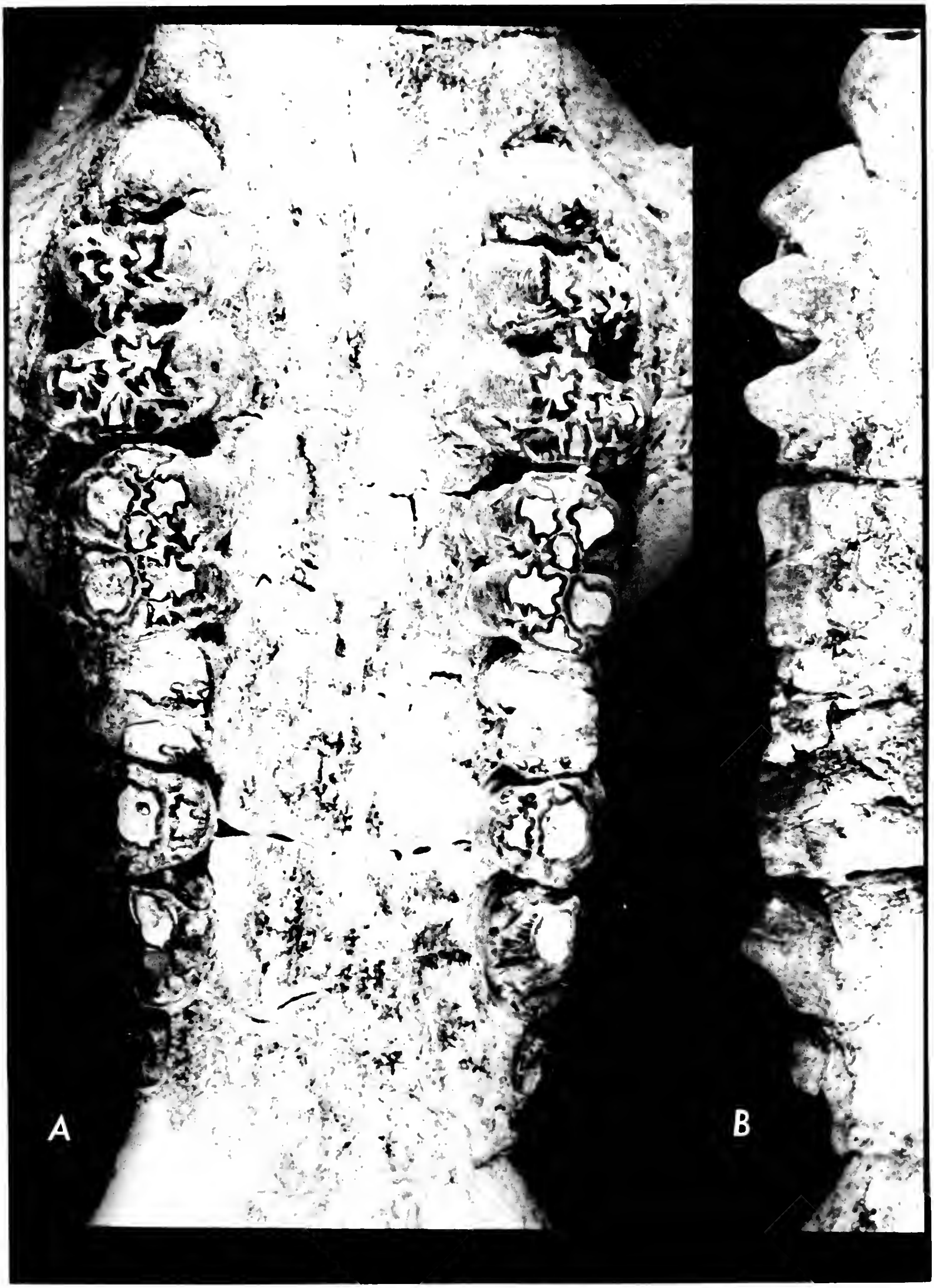

A
B

Plate 6. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Occlusal and left outer lateral views of lower cheek teeth in the holotype mandible, KNM-KP 239. Nat. size.


A
B

Plate 7. *Nyanzachoerus pattersoni* sp. nov. Palate and well-worn, damaged cheek teeth in the skull of the paratype, KNM-KP 264. Nat. size.

Plate 8. *Nyanzachoerus pattersoni* sp. nov. Occlusal view of well-worn cheek teeth in the mandible of an old individual, KNM-KP 219 (see also Pl. 4). Nat. size.

Plate 9. *Nyanzachaerus pattersoni* sp. nov. **A**, **B**. Occlusal and inner lateral views of the left lower cheek teeth in mandibular ramus of a subadult individual, KNM-KP 213. Nat. size. **C**, **D**. Occlusal and inner lateral views of left lower cheek teeth of an adult individual, KNM-KP 263. Nat. size.


A
B
C
D

Plate 10. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Right lateral and palatal views of the skull of an immature (sub-adult) individual with M^3 unerupted, KNM-KP 244. × ¼. **C**, **D**. Outer right lateral and palatal views of cheek teeth in the immature skull shown in A and B above. Nat. size.

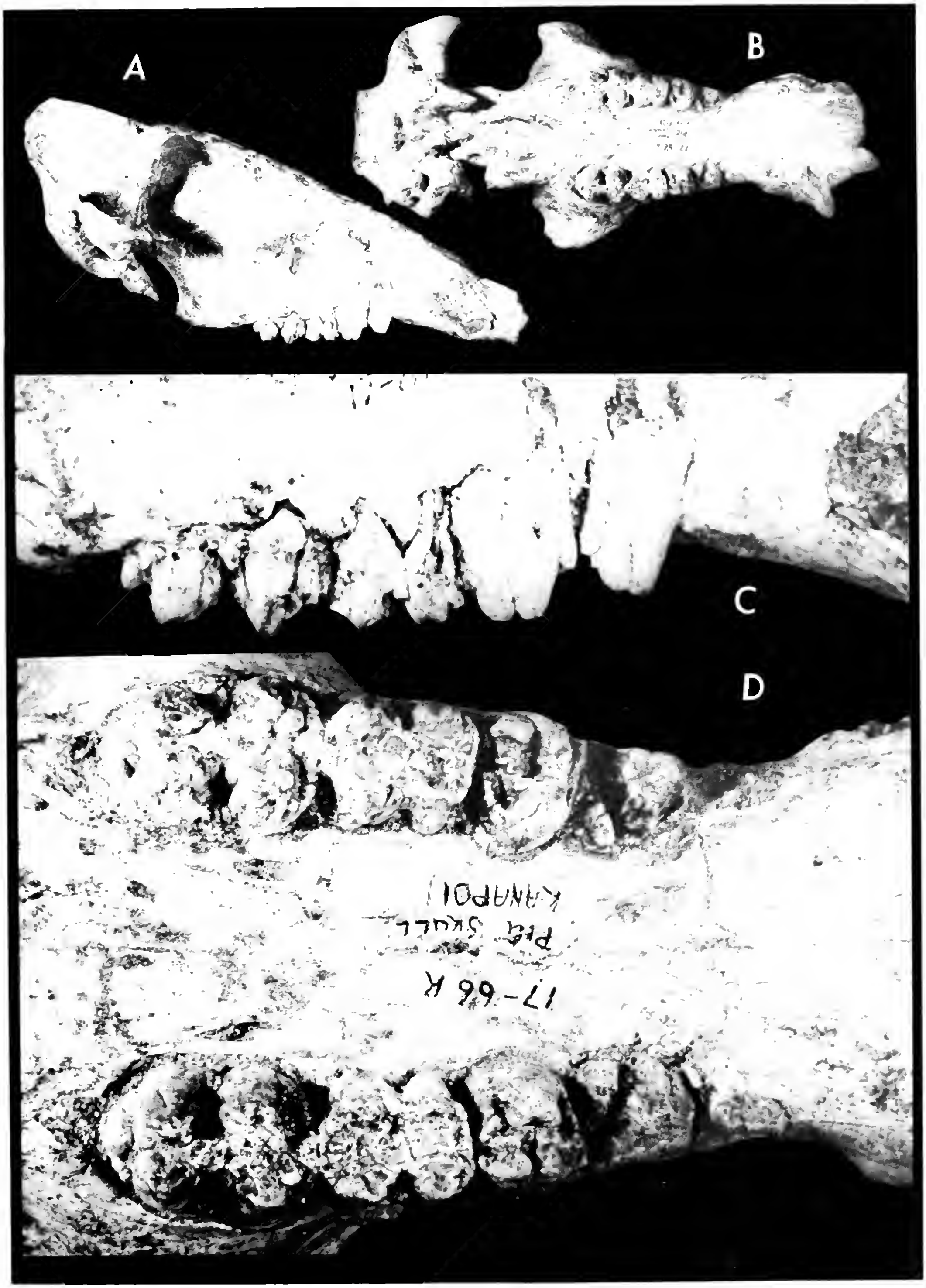
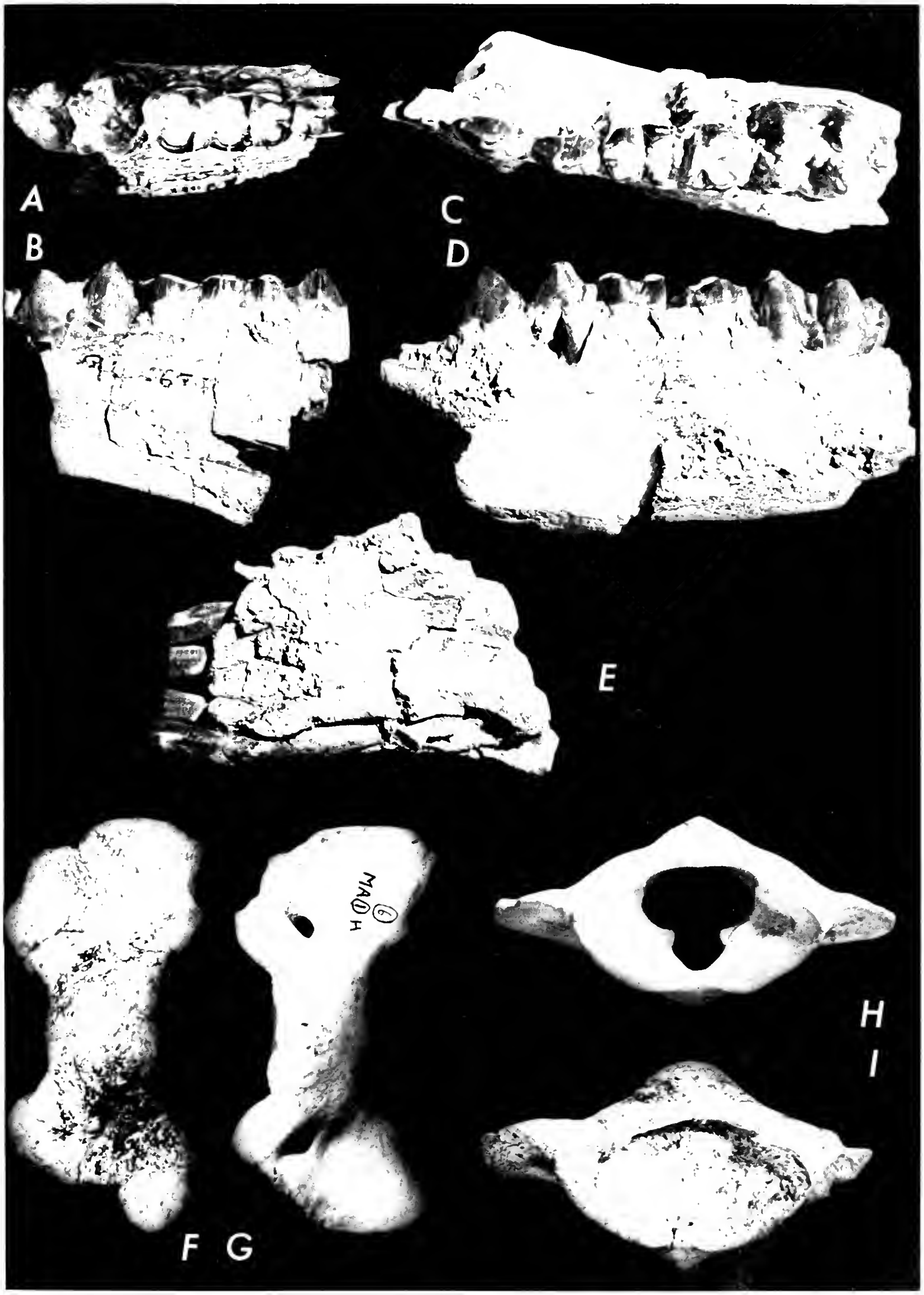

A
B
C
D
17-66 K
PIG SKULL
KANAPOI!

Plate 11. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Occlusal and inner lateral views of piece of juvenile right mandibular ramus, KNM-KP 221 with dm_{3-4} and M_1. Nat. size. **C**, **D**. Occlusal and inner lateral views of portion of juvenile left mandibular ramus, KNM-KP 221, with dm_{2-4} and M_1. Nat. size. **E**. Dorsal view of symphysis of juvenile mandible, KNM-KP 221 with LdI_{1-2}, RdI_{1-3}. Nat. size. **F**, **G**. Dorsal view of atlas of the holotype (F) compared with the atlas of *Hylochoerus* (G). × ½. **H**, **I**. Anterior view of atlas vertebra of the holotype (I) compared with that of *Hylochoerus* (H). × ½.


A
C
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E
F
G
H
I

Plate 12. *Nyanzachoerus pattersoni* sp. nov. Associated limb bones, KNM-KP 215. In the centre is the left tibia (A), below which are the matching calcaneum (B), talus (C), cuboid (D), and navicular (E). To the right are bones of the pes; the complete left fourth metatarsal (F) and its matching first phalanx (G), are flanked by the distal end of the metatarsal (H) and proximal phalanx (I), and the distal end of the left fifth metatarsal (J) and its first phalanx (K). L is the first phalanx of the fifth digit of the right side. To the left of the tibia are bones of the right manus. M and N are the first and second phalanges of the third digit. O, P, Q are the three phalanges of the fourth digit; the proximal end of the first phalanx (O) is missing. × ½.


A
M
O
F
P
N
H
J
Q
I
K
G
L
B
C
D
E

Plate 13. *Nyanzachoerus plicatus* sp. nov. **A**, **B**. Dorsal and left lateral views of holotype skull, KNM-KP 251, from Kanapoi. × ¼. **C**, **D**, **E**. Dorsal, palatal and left lateral views of third paratype skull, KNM-KP 257. × ¼.

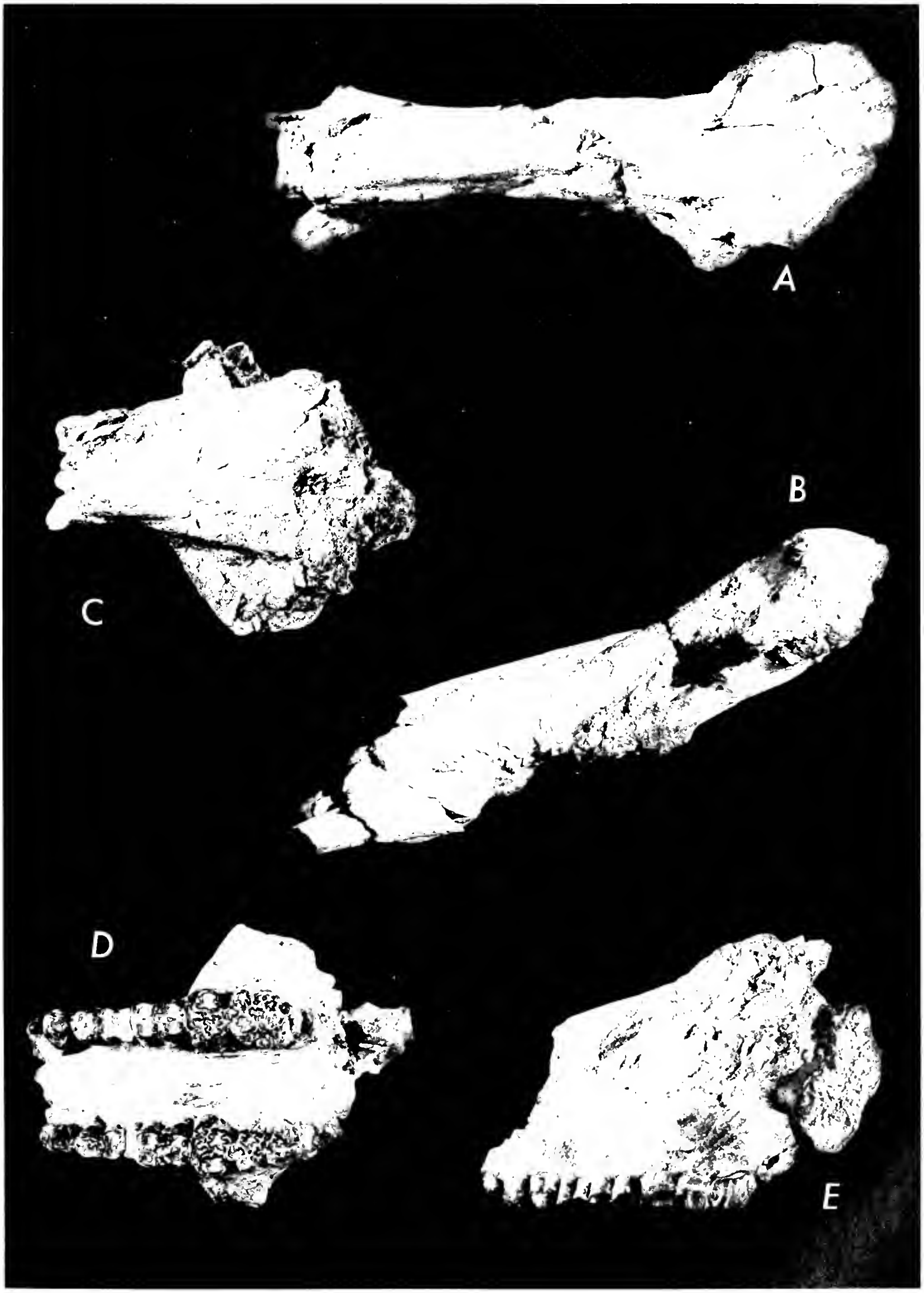
A
B
C
D
E

Plate 14. *Nyanzachoerus plicatus* sp. nov. **A**, **B**. Occlusal and left lateral views of mandible of the holotype, KNM-KP 251. × ¼. **C**. Tip of isolated left upper canine, KNM-KP 203. × ½. **D**. Pair of upper canines and root fragment of a third upper canine, found with the holotype but not belonging to it; cited as first paratypes of the species, KNM-KP 232. × ½.

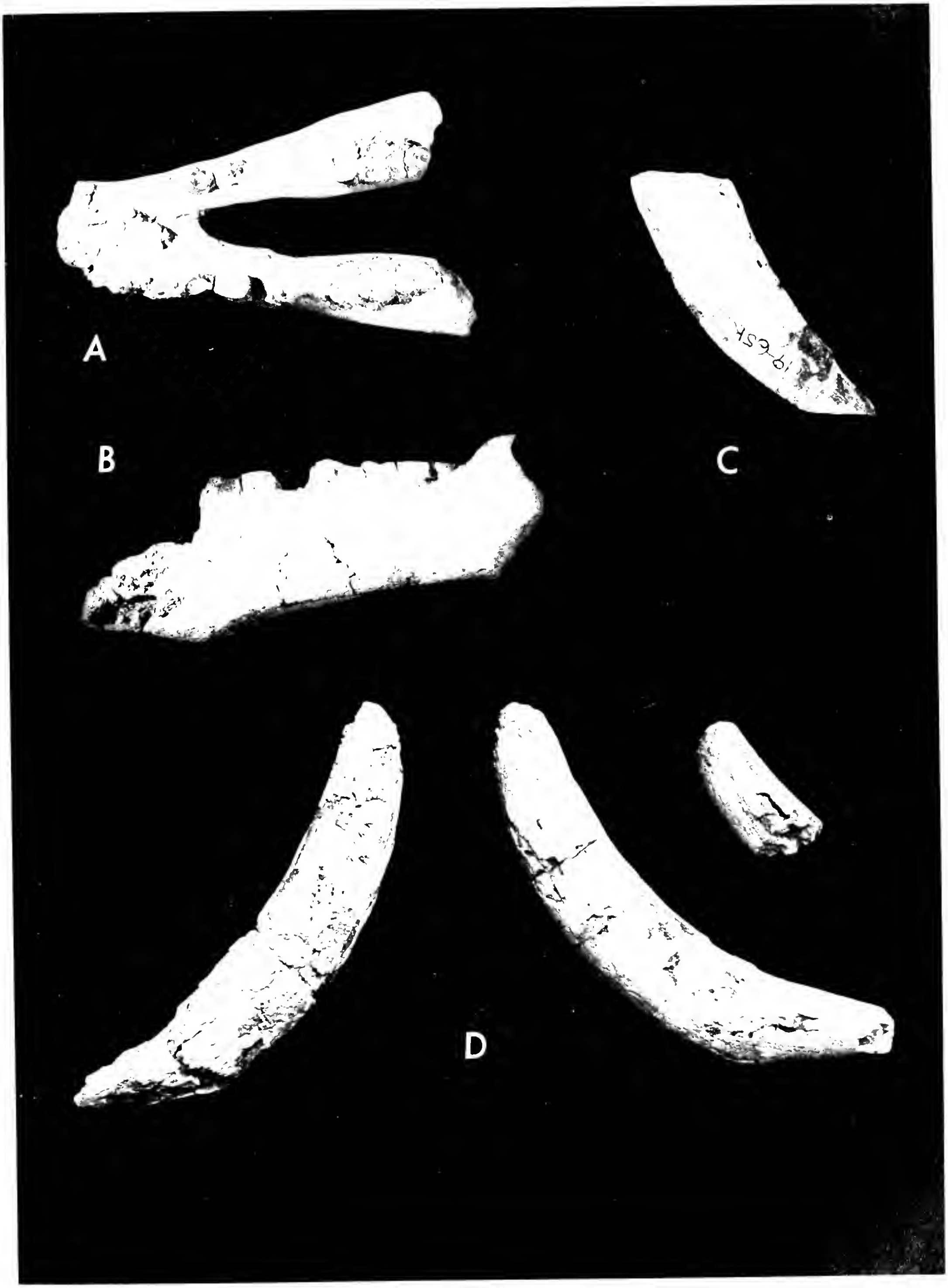
A
B
C
19-65K
D

Plate 15. *Nyanzachoerus plicatus* sp. nov. Associated pieces of second paratype, KNM-KP 262. **A**, **B**. Outer lateral and crown views of upper right second molar. Nat. size. **C**, **D**. Dorsal and ventral views of slightly crushed symphysis with right canine well preserved. × ½. **E**, **F**. Occlusal and inner lateral views of piece of right mandibular ramus with half of M_2 and complete M_3 in early wear. Nat. size.

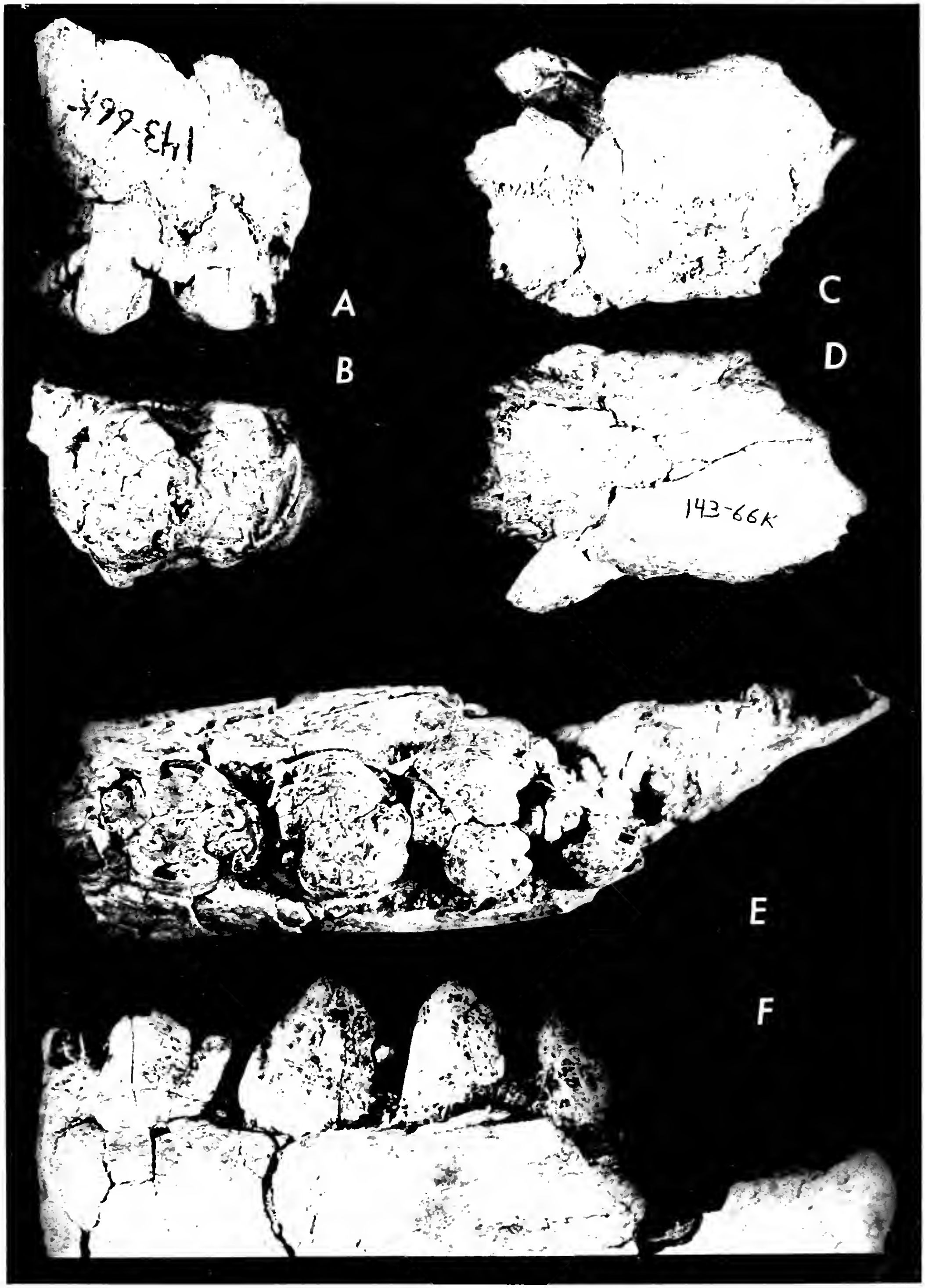
143-66K
A
C
B
D
143-66K
E
F

Plate 16. *Nyanzachoerus plicatus* sp. nov. Palate and cheek teeth of third paratype, KNM-KP 257. Nat. size.

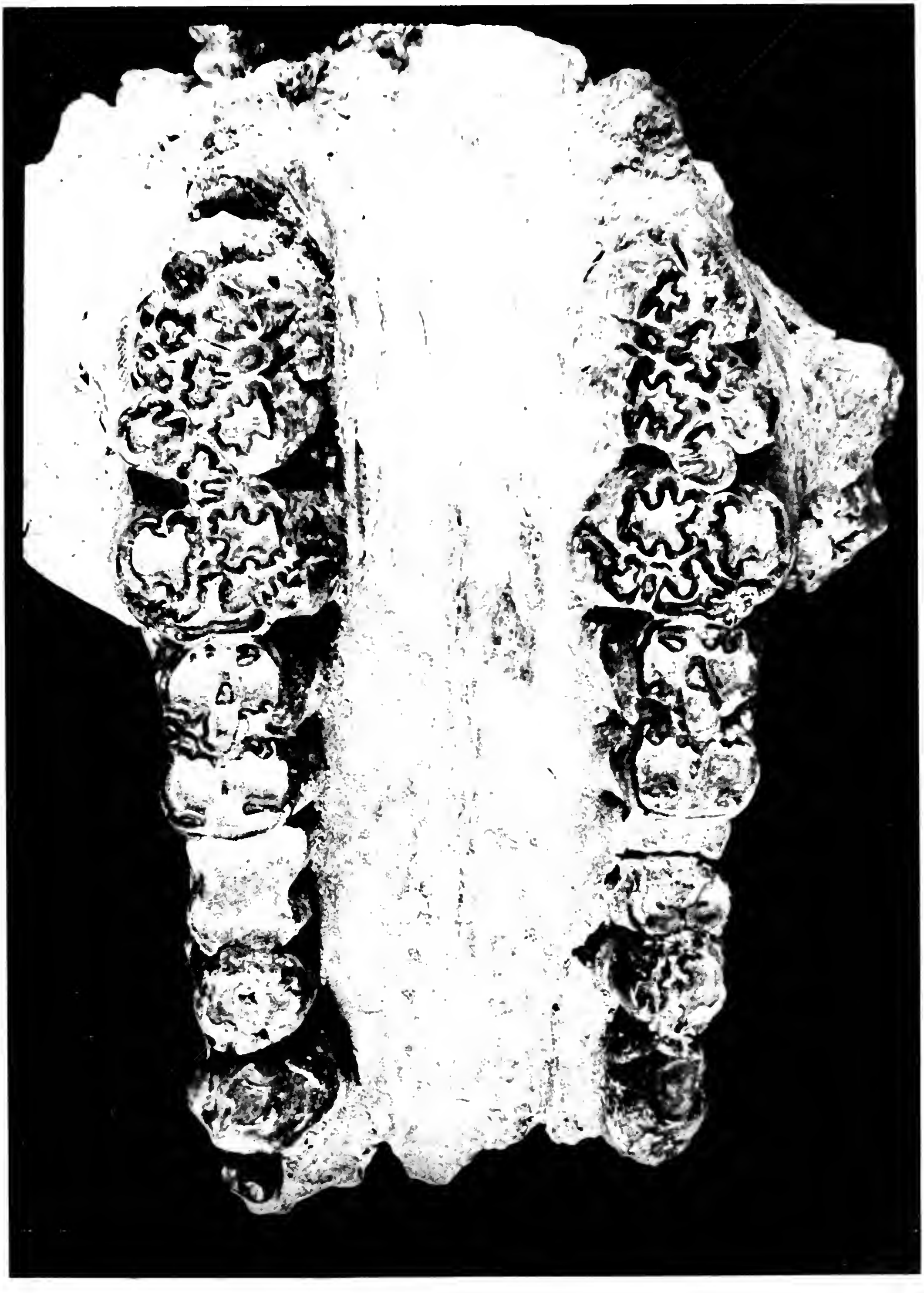

Plate 17. *Nyanzachoerus plicatus* sp. nov. **A**, **B**. Occlusal and inner lateral views of little worn upper right third molar, KNM-KP 225. **C**, **D**. Occlusal and outer lateral views of little worn upper left third molar, KNM-KP 225, found with A, B above. **E**, **F**. Crown view of slightly worn upper left third molar, KNM-KP 235, and view of sectioned surface (F) half way down the height of the crown. **G**, **H**. Crown and inner lateral views of upper right third molar, KNM-KP 253. **I**, **J**. Inner lateral and occlusal views of incomplete unworn lower right third molar, KNM-KP 254. All nat. size.

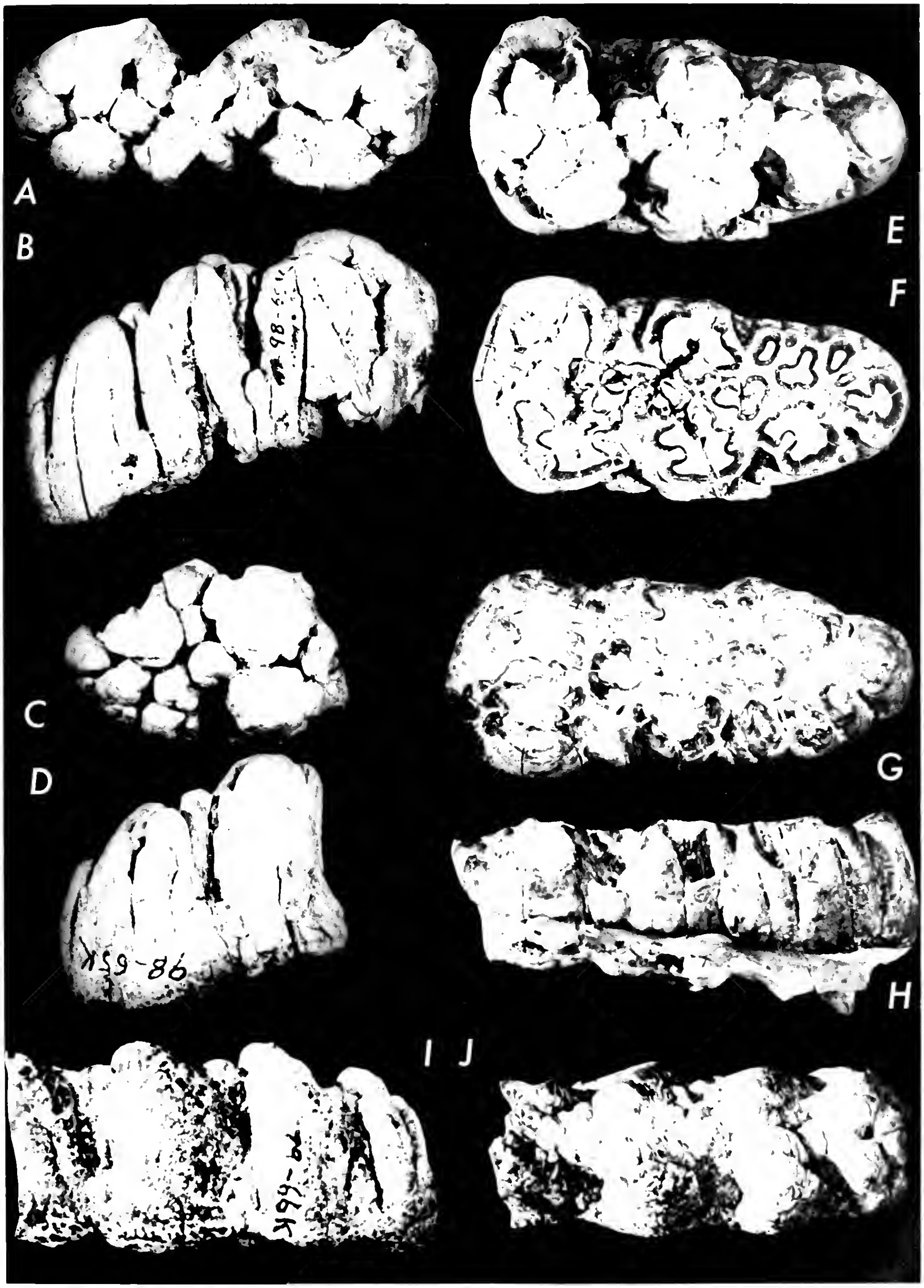
A
B
C
D
98-65K
E
F
G
H
I
J
98-66K

Plate 18. *Nyanzachoerus plicatus* sp. nov. **A**. Crown view of left lower cheek teeth in the mandible of the holotype, KNM-KP 251. **B**. Occlusal view of left mandibular ramus with LM$_3$ intact and roots of the other cheek teeth, KNM-KP 235. **C**. Occlusal view of fragment of right mandibular ramus of the same individual as B, showing the damaged RP$_4$, KNM-KP 235. **D**. Outer lateral view of the third molar in B. Note: B–D are associated with the upper molar shown in Plate 17 E, F.


A
D
B
C

Plate 19. *Nyanzachaerus tulotos* sp. nov. **A**, **B**. Dorsal and palatal views of holotype skull, KNM-LT 316, from Lothagam, regarded as male. × ¼.

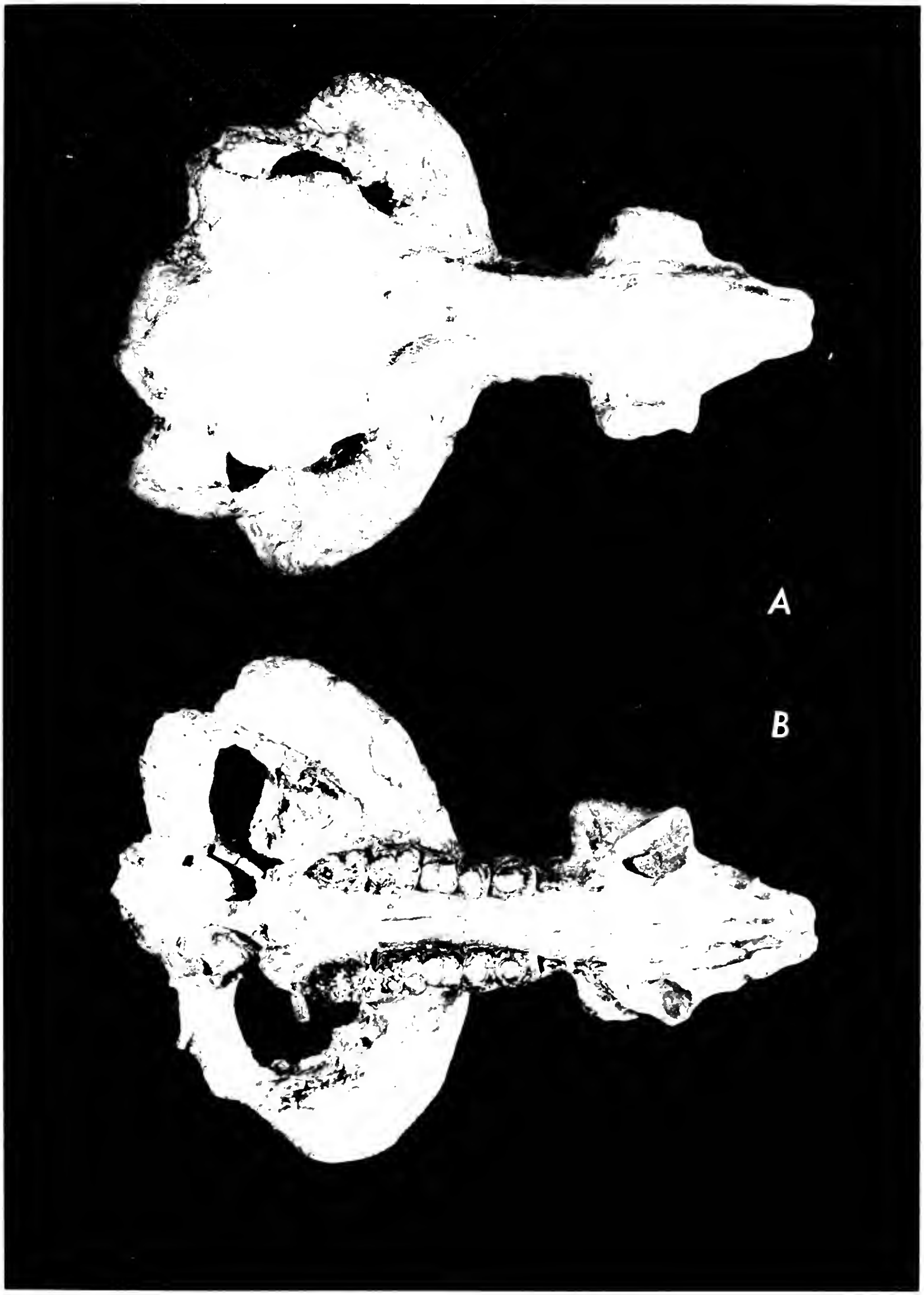
A
B

Plate 20. *Nyanzachoerus tulotos* sp. nov. **A**. Left lateral view of holotype skull, KNM-LT 316. **B**. Occlusal view of incomplete mandible of first paratype, LT 302, regarded as male. **C**, **D**. Occlusal and right lateral views of damaged mandible of second paratype, LT 287, regarded as male. **E**, **F**. Occlusal and left lateral views of mandible of third paratype, LT 295, regarded as female. All ¼ nat. size.

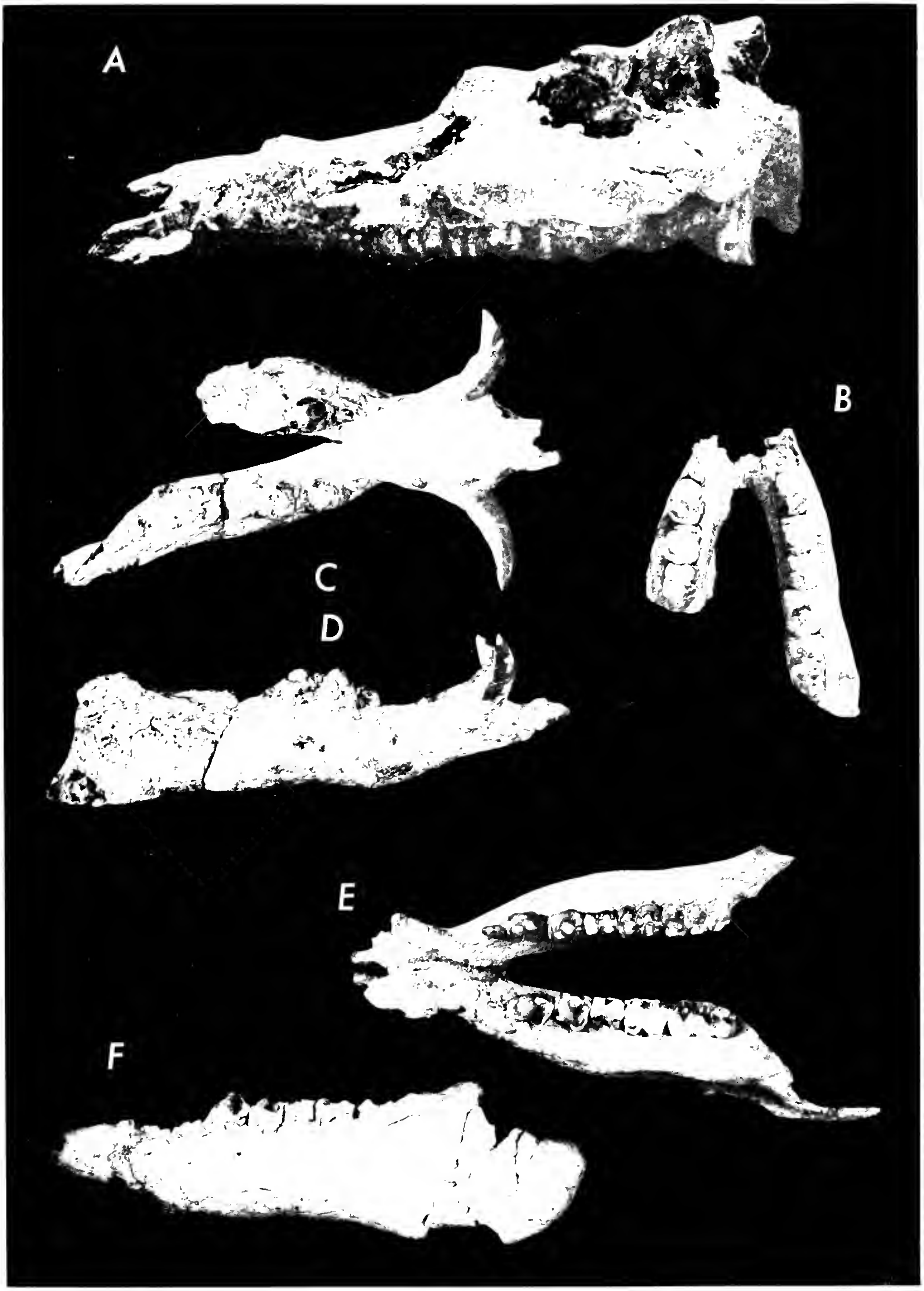
A
B
C
D
E
F

Plate 21. *Nyanzachoerus tulotos* sp. nov. Palate and cheek teeth of holotype (KNM-LT 316). Nat. size.

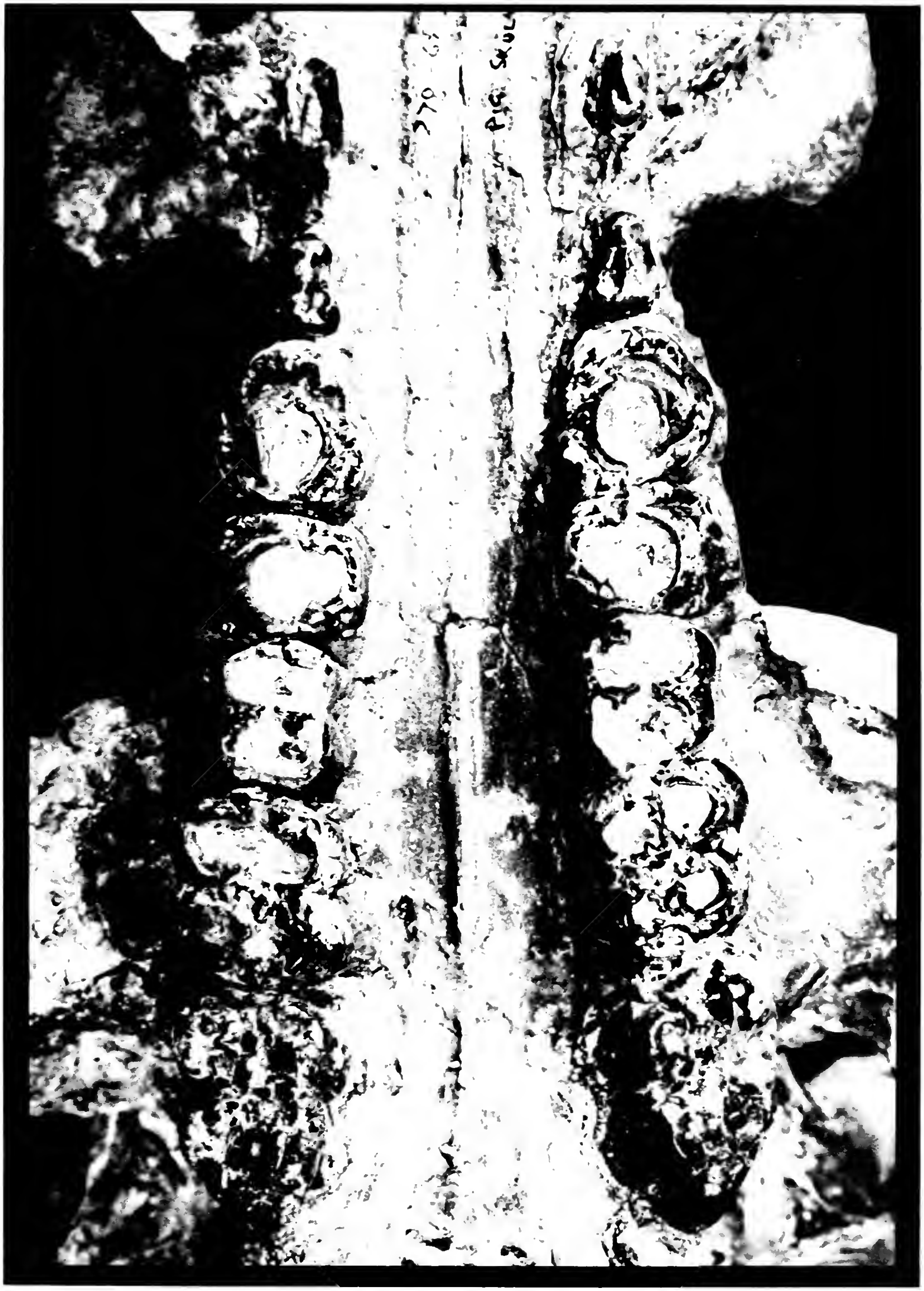

Plate 22. *Nyanzachoerus tulotos* sp. nov. **A**. Occlusal view of lower cheek in the mandible of the first paratype, KNM-LT 302. **B**. Outer lateral view of left lower cheek teeth in A. **C**. Inner lateral view of right lower cheek teeth in A. All nat. size.


A
204-67K
204-67K
B
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Plate 23. *Nyanzachoerus tulotos* sp. nov. Occlusal view of lower cheek teeth in mandible of the third paratype, KNM-LT 295. Nat. size.

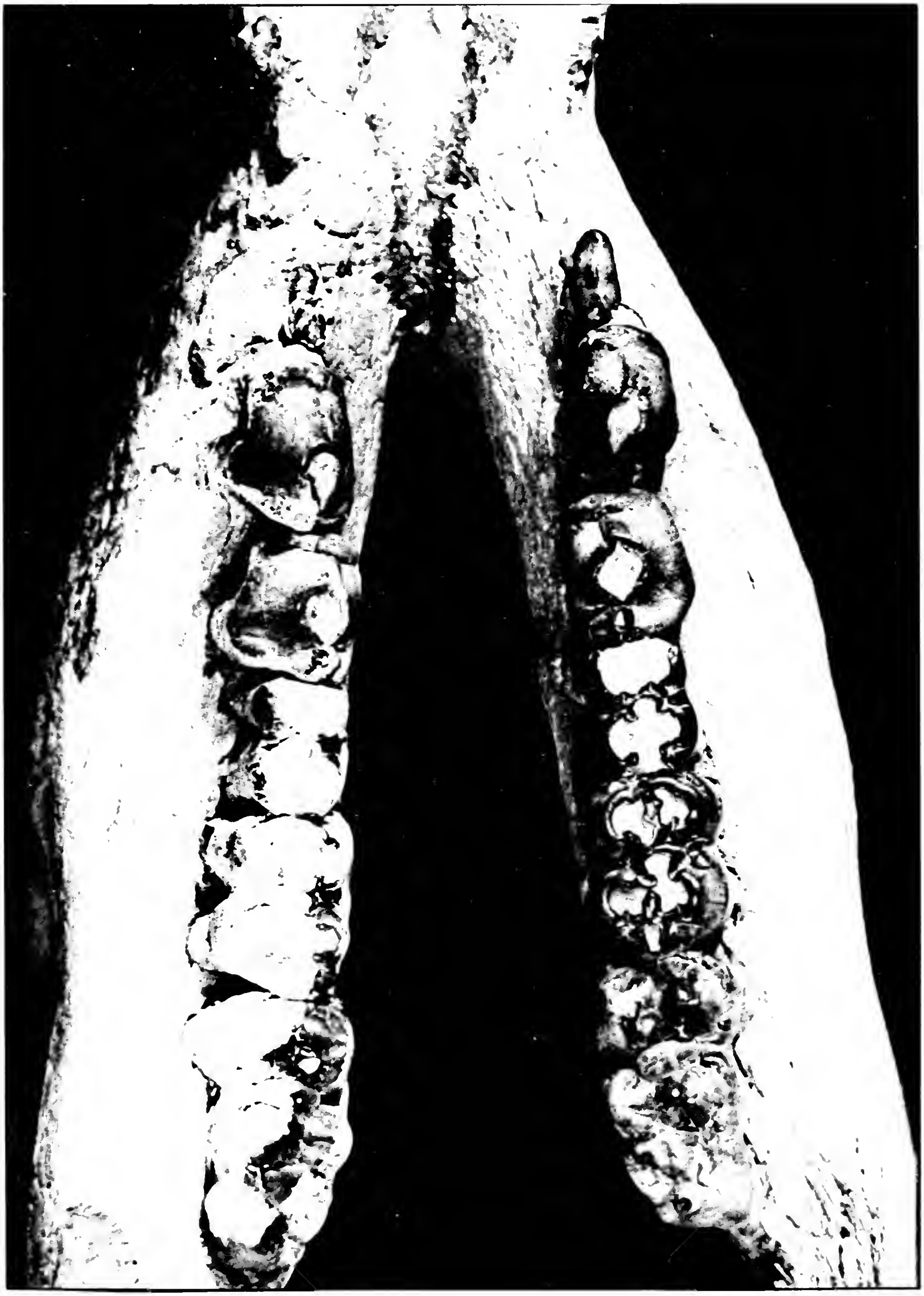
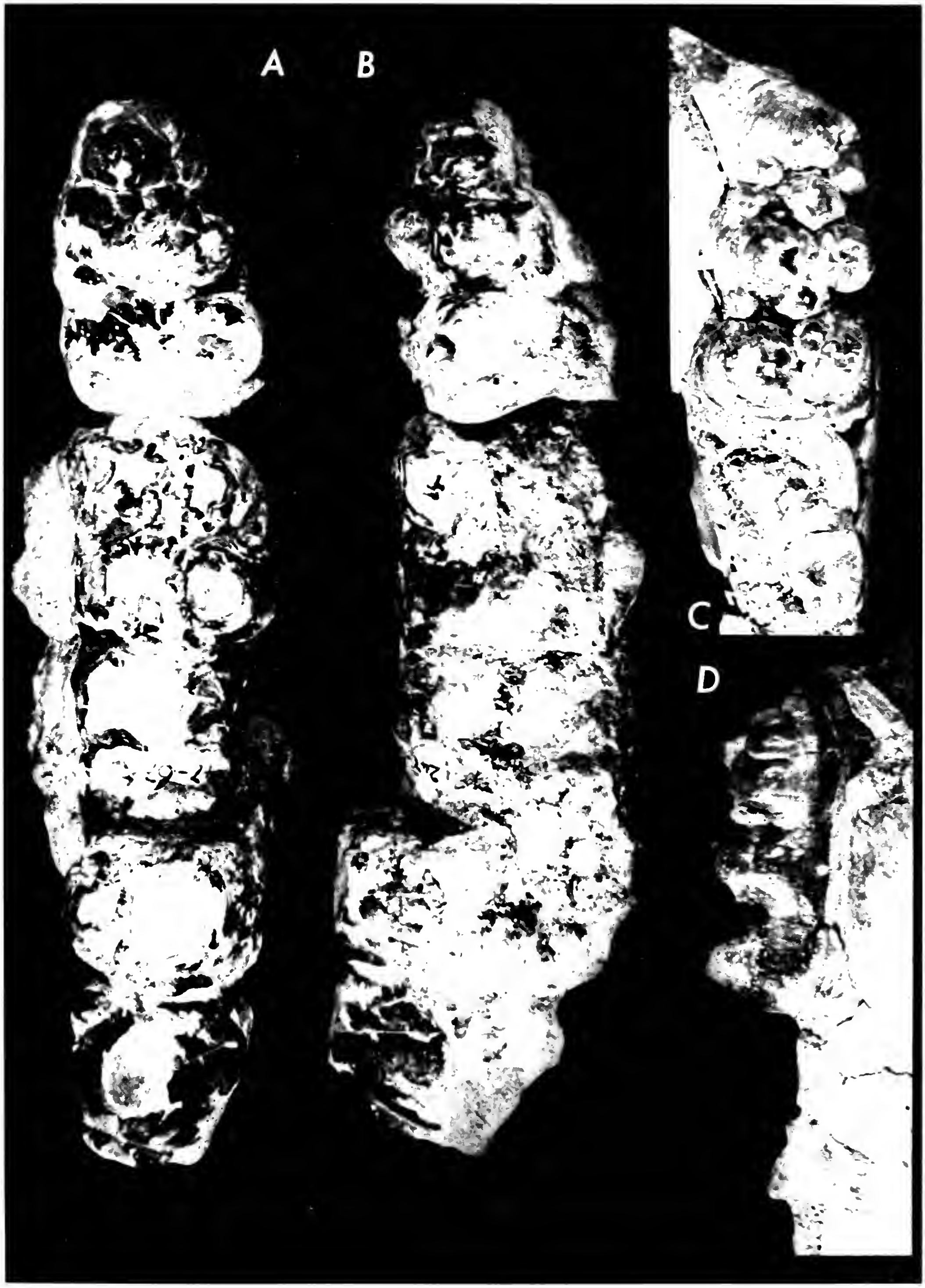


Plate 24. *Nyanzachoerus tulotos* sp. nov. **A**, **B**. Occlusal and outer lateral views of right maxillary fragment with upper cheek teeth of large individual, KNM-LT 313, from Member C of Unit 1 at Lothagam. **C**, **D**. Occlusal and inner lateral views of piece of right mandibular ramus with RM$_3$ and roots of RM$_2$ (KNM-LT 309). All nat. size.


A
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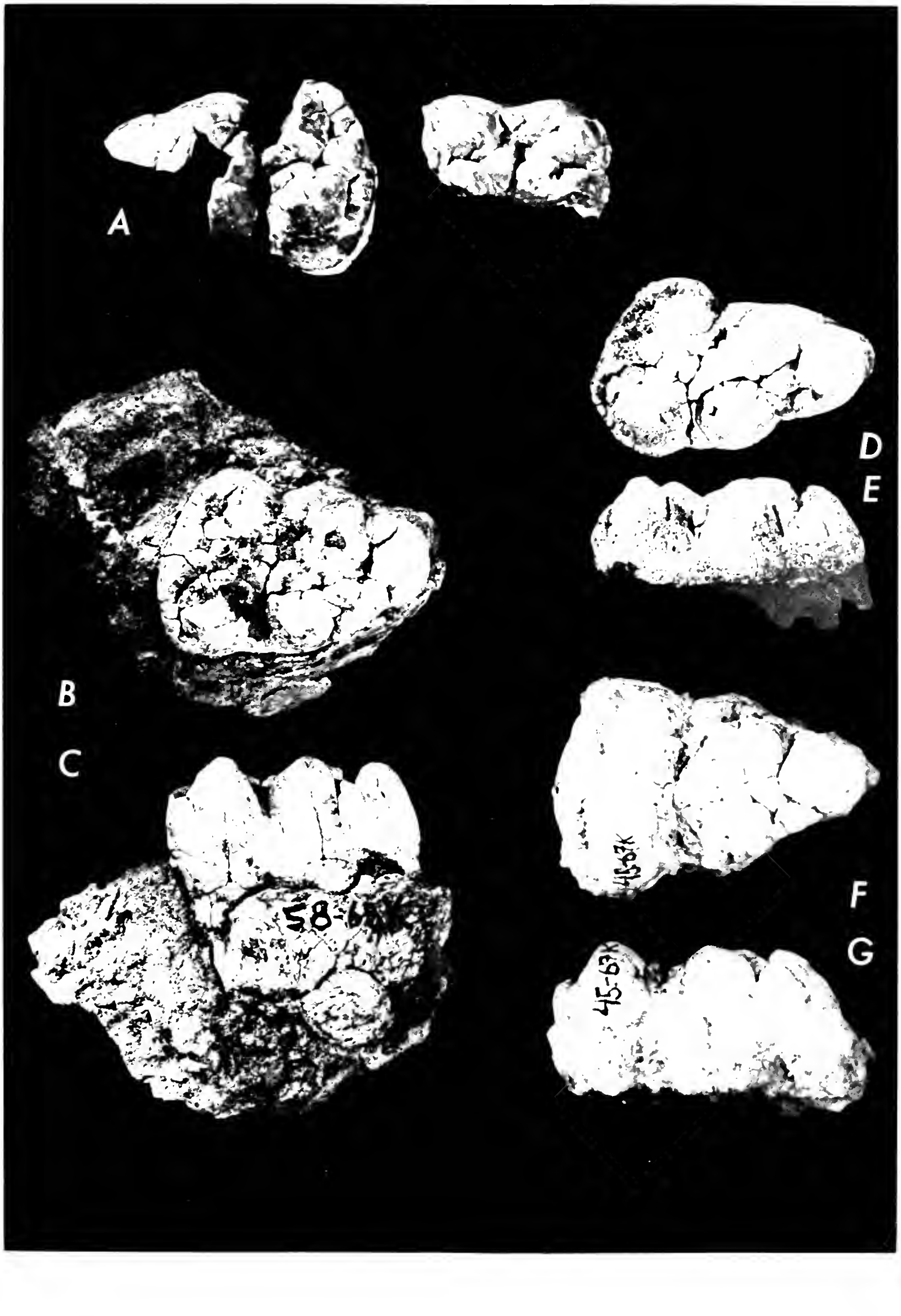
C
D

Plate 25. *Nyanzachoerus tulotos* sp. nov. **A**. Incomplete, unworn LM^3 and LM^2 (KNM-LT 326) from an uncertain horizon within Unit 1 at Lothagam. **B**, **C**. Crown and outer lateral views of RM^3 in fragment of maxilla (KNM-LT 324) from Member C of Unit 1 at Lothagam. **D**, **E**. Crown and inner lateral views of unworn RM^3 (KNM-LT 321) from Member B of Unit 1 at Lothagam. **F**, **G**. Crown and inner lateral view of little worn RM^3 (KNM-LT 286), from Member C of Unit 1 at Lothagam.


A
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C
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E
F
G
58-
45-63K
45-63K

Plate 26. *Notochoerus* cf. *capensis* Broom. **A, B**. Occlusal and right lateral views of damaged mandible, KNM-KP 226, from Kanapoi. × ¼. **C, D**. Occlusal and right lateral views of incomplete mandible, KNM-KP 241. × ¼. **E**. Crown view of rather rolled piece of right mandible with RM$_3$ in moderately early wear, KNM-KP 210, from Kanapoi. Nat. size. **F**. Crown view of well-worn LM$_3$ from piece of left mandible, KNM-KP 267A, from Kanapoi. Nat. size.


A
B
C
D
E
F

Plate 27. *Notochoerus* cf. *capensis* Broom. **A.** Inferior view of left upper canine, KNM-KP 267C, from Kanapoi. × ½. **B**. Dorsal view of two pieces of the snout of a disrupted skull, KNM-KP 242, associated with the mandible shown in Plate 26 C, D and with the zygomatic "knobs" in C and D below. The flange surrounding the base of the left canine is at the top and the premaxilla is at the right. × ¼. **C**, **D**. Lateral and (?) dorsal views of hollow bony zygomatic "knob" from the disrupted skull, KNM-KP 242. × ½. **E**. Palatal view of incomplete skull from the locality at Omo known as "White Sands," to show a zygomatic protuberance ("knob") similar to, but smaller than, the one from Kanapoi shown in C, D. × ¼.

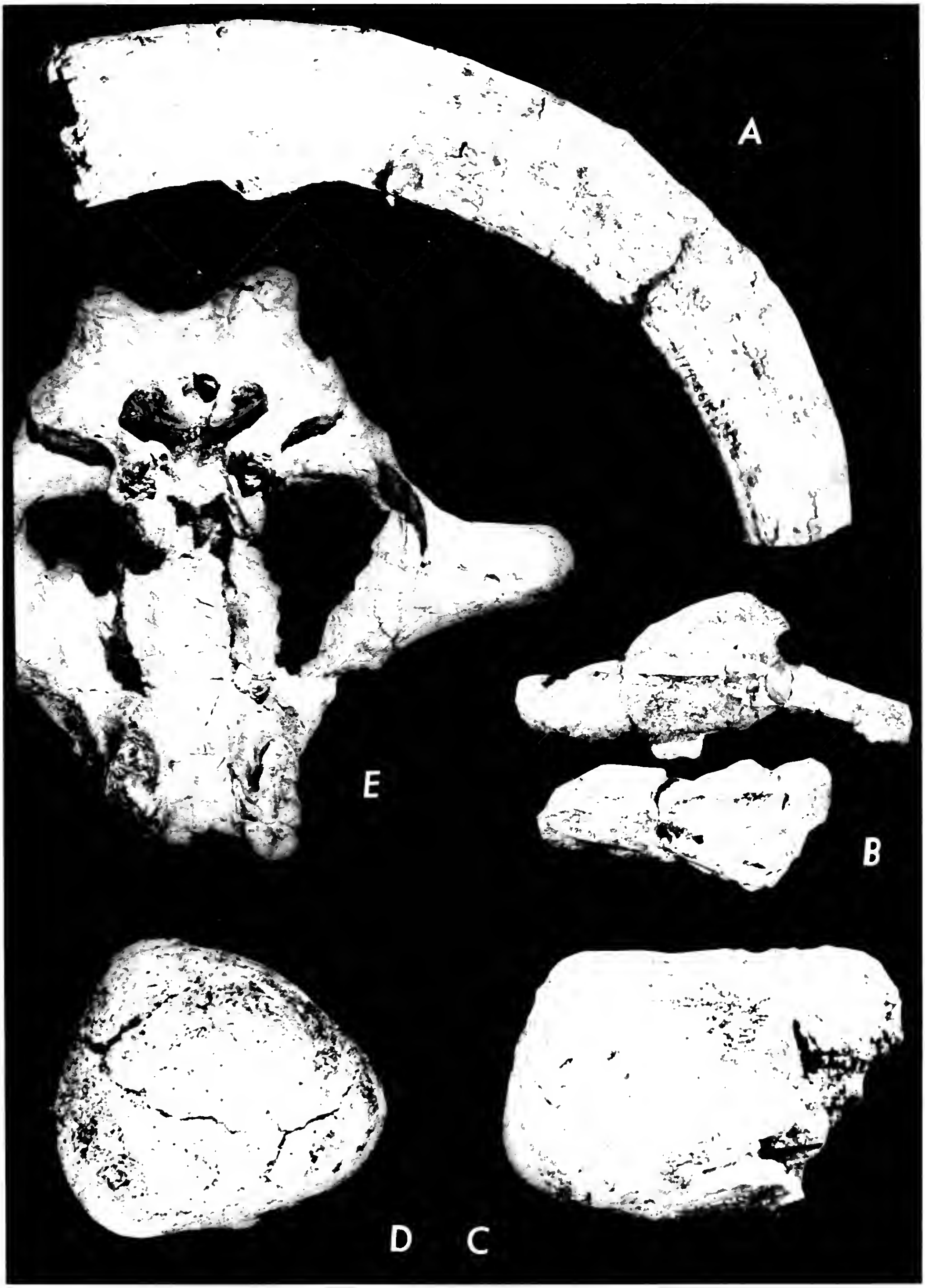
A
E
B
D
C

Plate 28. *Nyanzachoerus* sp. Occlusal view of mandible from Lothagam, KNM-LT 318, with much enlarged roots of P_3 and P_4 and remains of small LM_3. Nat. size.

Plate 29. **A**. *Nyanzachoerus* cf. *pattersoni*. Occlusal view of piece of left mandibular ramus with LP$_4$ (damaged) to LM$_3$ (KNM-LT 285) from Member C of Unit 1 at Lothagam. **B**. *Nyanzachoerus* cf. *pattersoni*. Occlusal view of RM^2 associated with the mandible in A above (KNM-LT 285). **C**, **D**. *Nyanzachoerus* cf. *pattersoni*. Occlusal and outer lateral views of fragment of mandible with LP$_4$ and LM$_2$ (KNM-LT 294). **E**, **F**. Suid *indet.* Occlusal and inner lateral views of unworn LM^3 from Lothagam (KNM-LT 314). **G**. Suid *indet.* Dorsal view of right upper canine (KNM-LT 317) found at Lothagam with the holotype skull of *Nyanzachoerus tulotos*. All nat. size.

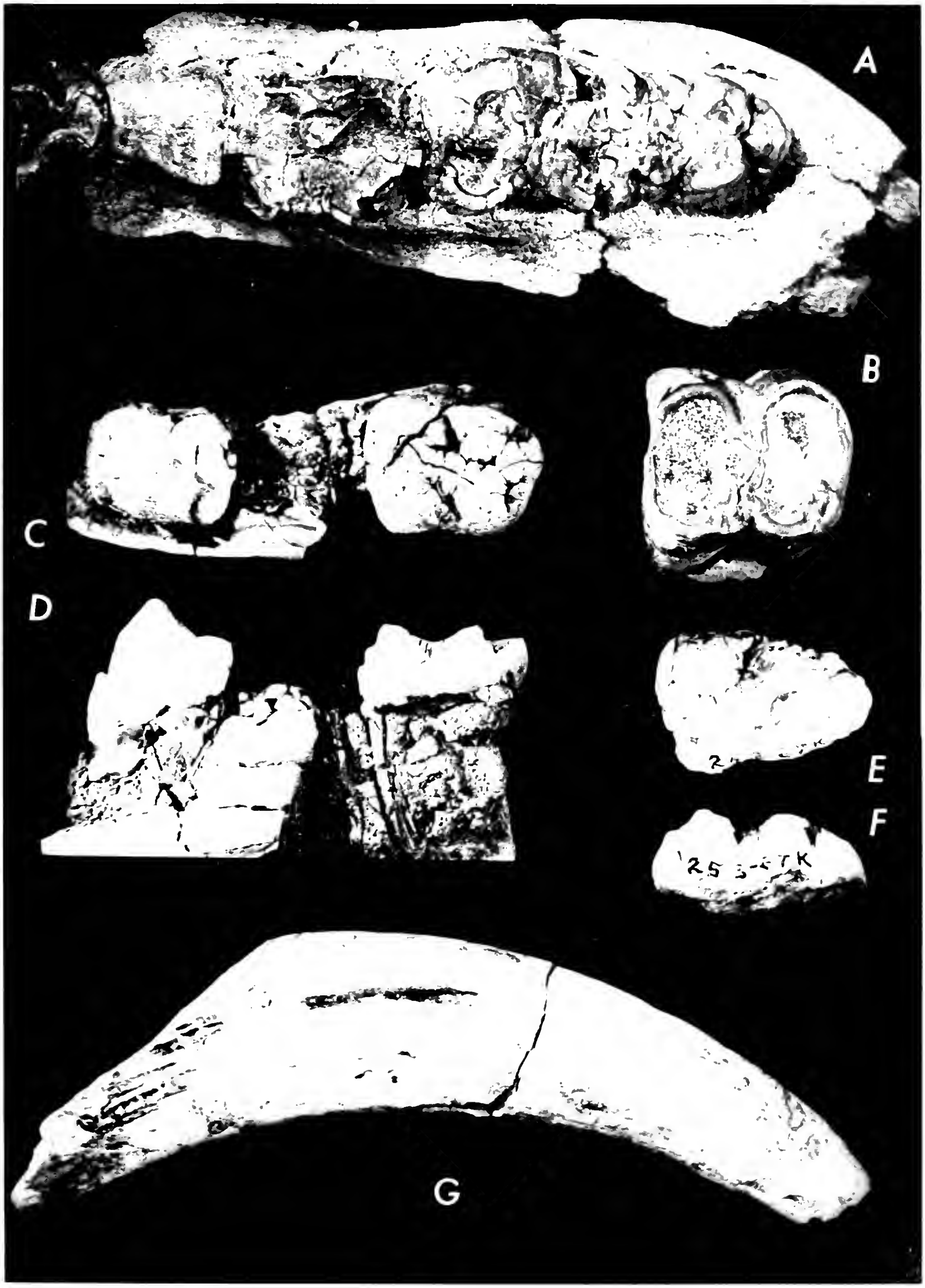
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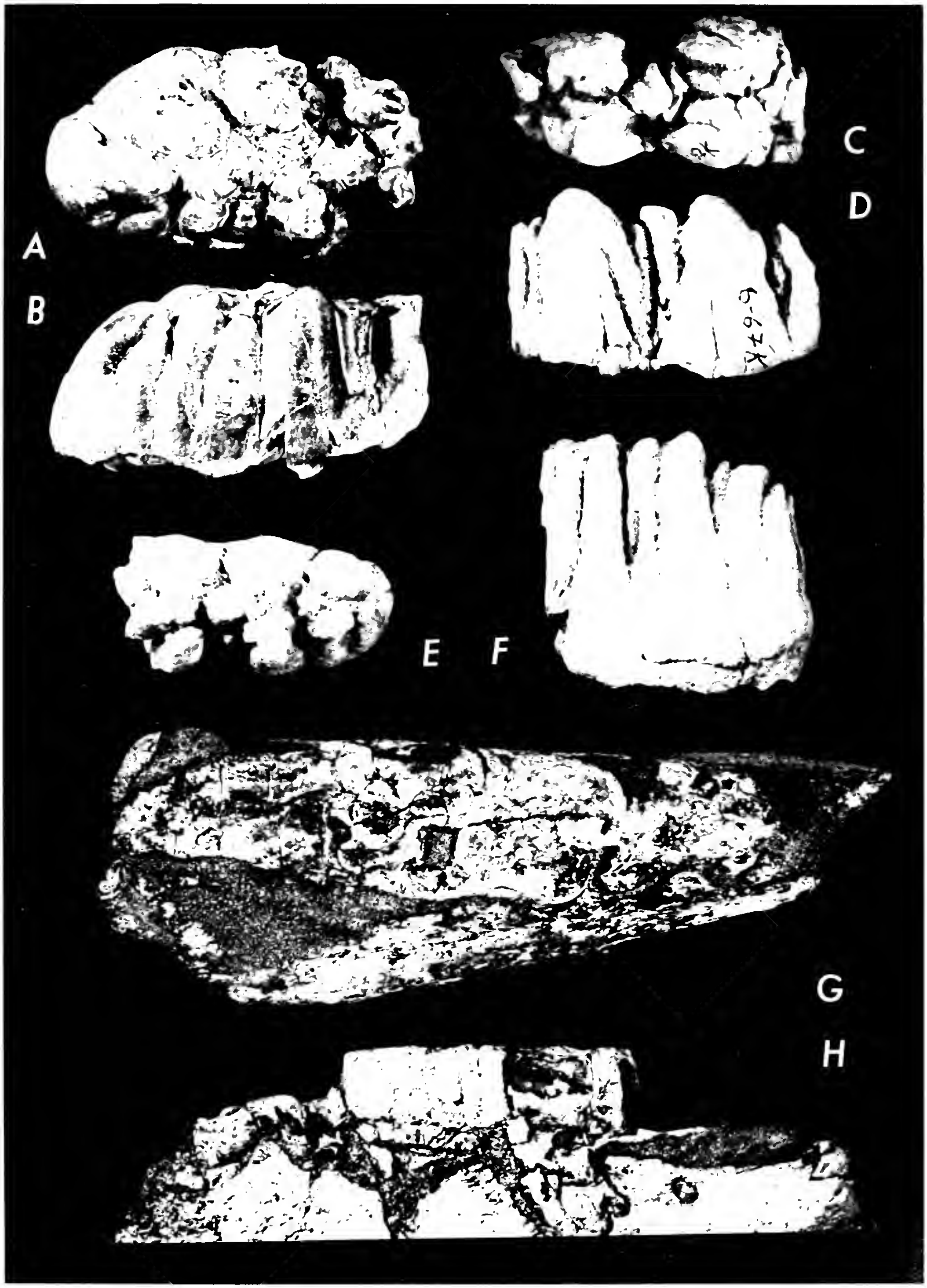
Plate 30. **A**, **B**. *Nyanzachoerus plicatus*. Crown and outer lateral views of upper LM^3 (KNM-LT 311) from near the top of Member C of Unit 1 at Lothagam. **C**, **D**. *Nyanzachoerus* cf. *plicatus*. Crown and inner lateral views of incomplete LM$_3$ from Ekora (KNM-EK 271). **E**, **F**. cf. *Notochoerus euilus*. Occlusal and inner lateral views of LM$_3$ (KNM-LT 297) from Unit 3 at Lothagam. **G**, **H**. *Notochoerus* cf. *euilus*. Occlusal and lateral views of piece of mandible with damaged well-worn RM$_2$ and incomplete RM$_3$ (KNM-LT 327) from the upper part of Unit 3 at Lothagam. All nat. size.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B
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D
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H

Bulletin OF THE Museum of Comparative Zoology

Biology and Evolution of the *Atlapetes schistaceus* Species-Group (Aves: Emberizinae)

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VOLUME 143, NUMBER 4
27 JUNE 1972

Authors preparing manuscripts for the *Bulletin of the Museum of Comparative Zoology* or *Breviora* should send for the current Information and Instruction Sheet available from Ms Penelope Packard, Editor, Publications Office, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

BIOLOGY AND EVOLUTION OF THE *ATLAPETES SCHISTACEUS* SPECIES-GROUP (AVES: EMBERIZINAE)

RAYMOND A. PAYNTER, JR.

ABSTRACT

Atlapetes schistaceus, *nationi*, *leucopterus*, *albiceps*, *pallidiceps*, and *rufigenis*, ranging in the subtropical and temperate zones of the high Andes from Colombia to Peru, form a species-group. The six species are thought to have originated in the Pleistocene. The present distribution of *A. schistaceus* closely approximates the presumed location of lowland forest refugia during warm-dry interglacial periods. The remaining five species appear to have had their origins in small moist pockets, also during warm-dry interglacial periods, within the high Andes of Ecuador and Peru, either as derivatives of ancestral *schistaceus* or of more recently arisen species within the species-group.

INTRODUCTION

Atlapetes, a genus of secretive brush-inhabiting emberizines, occurs at high elevations from the northern Mexican plateau southward through Middle America to northern South America, east to southeastern Venezuela and immediately adjacent Brazil, and south through the Andes to southern Peru, Bolivia, and northwestern Argentina. Twenty-two species of *Atlapetes* are currently recognized (Paynter, 1970: 190–206), seventeen of these occur in the northern Andes between northern Colombia and southern Ecuador.

Within the genus there are six species, viz., *schistaceus*, *nationi*, *leucopterus*, *albiceps*, *pallidiceps*, and *rufigenis*, which are morphologically similar and which appear to be more closely related to one another than to other members of the genus. The six species might be considered as comprising a superspecies, but until more is known of the apparent partial sympatry of several forms it seems better to treat them simply as the "*A. schistaceus* species-group." The group is distributed from northern Colombia and western Venezuela south to southern Peru, with particularly complex and interesting distributional patterns in southern Ecuador and northern Peru (Fig. 1). However, as is true of most species of *Atlapetes*, the ranges of these birds are known only in broad outlines and there are very few published accounts of any aspects of their biology.

Because a meaningful analysis of the origin and evolution of such an assemblage is difficult without knowledge of the living birds, it was decided to study the species-group in Ecuador, where, of the six species, only *rufigenis* fails to occur. In June 1965 David W. Norton went to Loja, the southernmost province of Ecuador, in order to reconnoiter localities where the various species could be studied. Norton found *leucopterus* at Cruzpamba on the Río Celica and *albiceps* at Yamana in the upper Casanga Valley, as well as other species of the genus not relevant to the present paper. My field work began in October. We had planned to spend the three months of the first field season working northward from the southern border of the country, becoming familiar with the species and mapping their distribution.

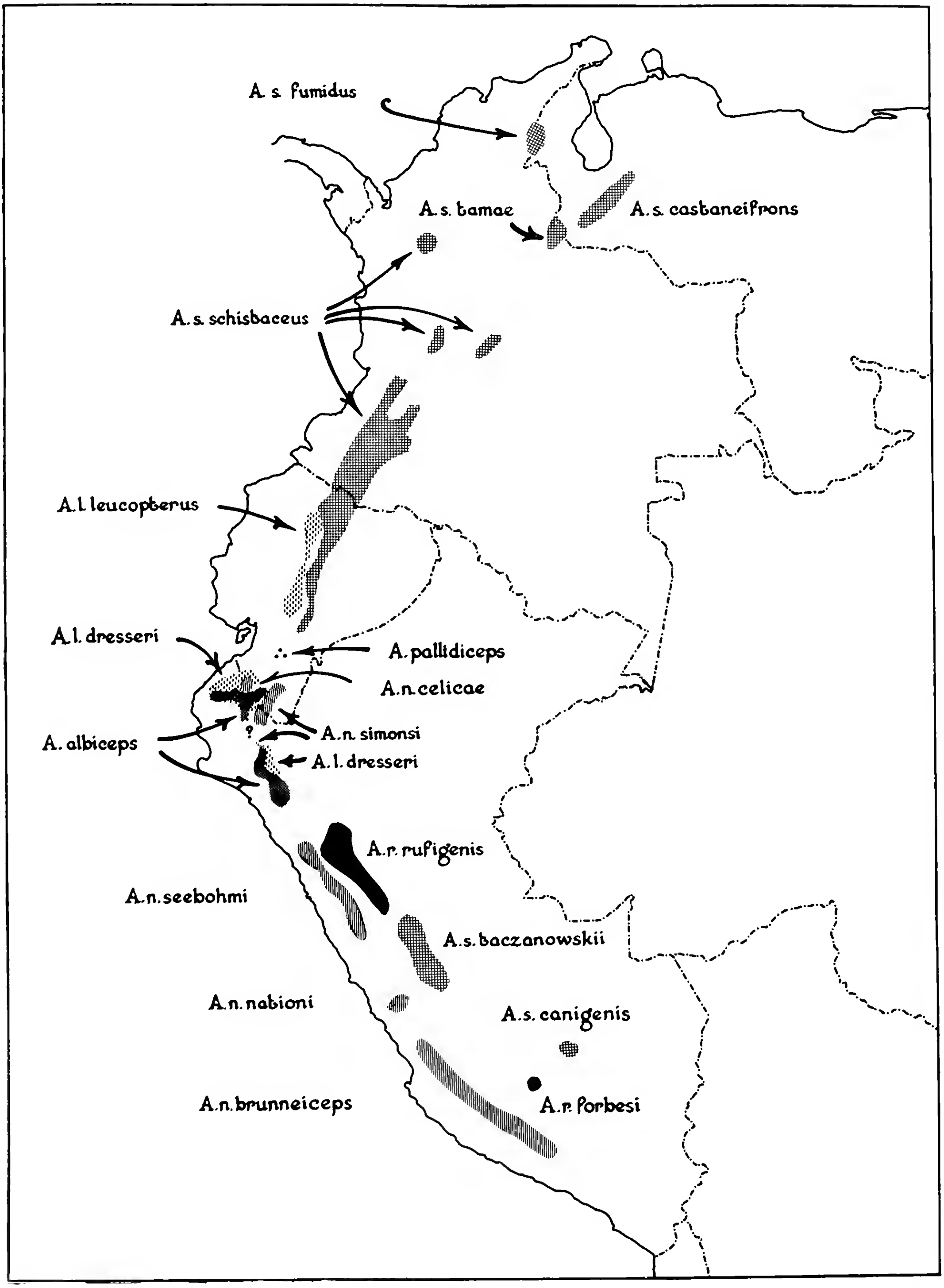

FIGURE 1. Distribution of the *Atlapetes schistaceus* species-group.

More detailed studies of their biology and distribution were scheduled for future seasons. By early November we had reached Las Palmas, a settlement in the valley of the Río Paute, east of Cuenca, Azuay. Here our party was attacked by a band of villagers, resulting in almost fatal injuries and causing abandonment of plans for further field work.

I was fortunate in having been able to observe four of the six species of the group, viz., *nationi*, *leucopterus*, *albiceps*, and *pallidiceps*. Although these observations were hardly more than an introduction to the living birds, they do provide a better insight into the complexities of the species-group than was available heretofore.

ACKNOWLEDGMENTS

For permitting me to borrow or examine specimens in their care, or for providing me with unpublished data and other courtesies, I am grateful to James Bond of the Academy of Natural Sciences of Philadelphia; Dean Amadon and Charles E. O'Brien of the American Museum of Natural History; John W. Hardy of Occidental College; Kenneth E. Stager of the Los Angeles County Museum of Natural History; George H. Lowery, Jr. of Louisiana State University; Emmet R. Blake of the Field Museum of Natural History; Gustavo Orcés V. of the Escuela Politecnica Nacional, Quito; François Vuilleumier of the University of Massachusetts, Boston; Ernst Sutter of the Museum d'Histoire naturelle Bâle; and Manuel Plenge of Lima. I am also greatly indebted to David W. Norton, a skilled observer and amiable companion, and to my wife, Elizabeth, whose brief taste of field work ended in a harrowing and tragic experience.

Jürgen Haffer, Ernst Mayr, and François Vuilleumier read the manuscript and offered suggestions for its improvement.

Support was received from the National Science Foundation through Grant GB-4210.

DISTRIBUTION, HABITS, AND MORPHOLOGY

Atlapetes schistaceus

Range. *A. schistaceus* has the most extensive range of the six forms within the species-group (Fig. 1). It occurs in the northernmost extensions of the Andes in the Sierra de Perijá of northeastern Colombia and northwestern Venezuela and as far east as the Cordillera de Mérida of western Venezuela.

One race, *fumidus*, is known only from the northern portion of the Sierra de Perijá. It may be isolated there because of the generally lower elevation of the southern part of the cordillera. However, the race is the least distinctive of the six recognized and I suspect that gene flow between *fumidus* and nearby races is facilitated by the presence of yet undiscovered semi-isolated populations in the small areas with altitudes in excess of 2,000 m that form an irregular chain through the southern half of the Sierra de Perijá. Another race, *castaneifrons*, occurs in Venezuela from eastern Táchira northeast to Trujillo and apparently is separated from *tamae*, the form of western Táchira and adjacent Santander, Colombia, by the arid valley of the Río Torbes, a known barrier to other birds (Vuilleumier, 1971).

Although the records are sparse and spotty, the species seems to be found at higher elevations on both the eastern and western slopes of all three Andean ranges in Colombia (de Schauensee, 1951; Phelps and Phelps, Jr., 1963). There are, however, large segments in each cordillera from which the species has not been recorded. Presumably the mountains are too low here for the species to occur, with the result that there are probably several isolated populations as, for example, on Nudo Paramillo in Antioquia.

In Ecuador the species is known from numerous records on the eastern slope south to Tungurahua, but south of here there exist only two records, one from the

TABLE 1. COMPARATIVE MEASUREMENTS OF *A. SCHISTACEUS* SUBSPECIES.

		Wing (flat)				Tail				Culmen (fr. base)			
Race	Sex	N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD
fumidus[1]	♂	14	71.2–77.7	74.5 mm		14	73.2–82.8	78.6 mm		14	14.2–15.2	14.8 mm	
castaneifrons[2]	♂	3	73–77	75.0	2.0	3	76–81	78.3	2.5	2	16	16.0	
tamae[3]	♂	?	74–78			?	79–82						
schistaceus[2]	♂	3	73–84	78.6	5.4	4	73–87	80.0	6.6	4	14–15	14.3	0.5
taczanowskii[2]	♂	4	78–81	79.0	1.4	4	82–84	83.5	1.0	4	15–17	15.6	1.0
canigenis[4]	♂	1	76			1	78			1	15.5		
fumidus[1]	♀	16	66.4–72.9	69.9		16	69.7–78.0	78.0		15	14.3–15.8	14.8	
castaneifrons[2]	♀	5	68–74	70.4	2.3	5	69–77	72.8	3.5	5	14–17	15.8	1.3
tamae[3]	♀	?	73–74			?	76–78						
schistaceus[2]	♀	7	77–83	79.4	2.0	7	78–85	80.8	1.5	7	14–16	15.4	0.5
taczanowskii[2]	♀	3	71–77	74.3	2.9	3	75–81	77.3	3.2	3	16–17	16.3	0.6
canigenis[4]	♀	1	72			1	72			1	15		

[1] Wetmore and Phelps, Jr., 1953: 13–14.
[2] Original data.
[3] Hellmayr, 1938: 404.
[4] Chapman, 1919: 330.

upper Río Upano (Chapman, 1926), which apparently is in Zamora near the border of Chimborazo, and one from Las Palmas, northeastern Azuay (specimen in Moore Collection, Occidental College). On the western slope the species barely enters Ecuador. One specimen has been taken on "the road to Nanegal," northern Pichincha (Chapman, 1926) and one from a short distance farther north at Intag [= Intac], southwestern Imbabura (Berlepsch, 1912).

An 800-km break in the distribution occurs between southern Ecuador and northern Peru with the species (race *taczanowskii*) reappearing in Huánuco and Junín, again on the eastern slope of the Andes. Its southern limit appears to be the Urubamba Valley, central Cuzco (race *canigenis*). It has not been recorded between Junín and Cuzco. This wide gap is probably an artifact attributable to the absence of observers, although a smaller discontinuity almost certainly exists owing to the presence of the arid valley of the Río Apurimac.

A. schistaceus is a high altitude form, ranging from 1,850 m to as high as 3,750 m, with the majority of records from about 2,500 to 3,000 m. There are insufficient data to detect any geographic variation in altitudinal range.

Habitat. Most authors (e. g., Chapman, 1917, 1919, 1921, 1926; and de Schauensee, 1951, 1964) describe the species as occurring in the subtropical and humid temperate zones. The only specific indications of its habitat seem to be those of Wetmore and Phelps, Jr. (1953), who mention the northernmost race (*fumidus*) as occurring in woodlands, and Zimmer (1930), who describes a Peruvian race as being found on the ground under bushes and in other shady places.

Habits. Except for a brief comment by Zimmer (1930) that the species scratches on the ground in the manner of towhees (*Pipilo*), there is no information about the living bird.

Morphological variation. In spite of the species' extended range and the existence of several major discontinuities, there appear to be no significant differences between the various named populations in wing, tail, or bill lengths (Table 1). The data suggest that the races *schistaceus* and *taczanowskii* might be larger than northern

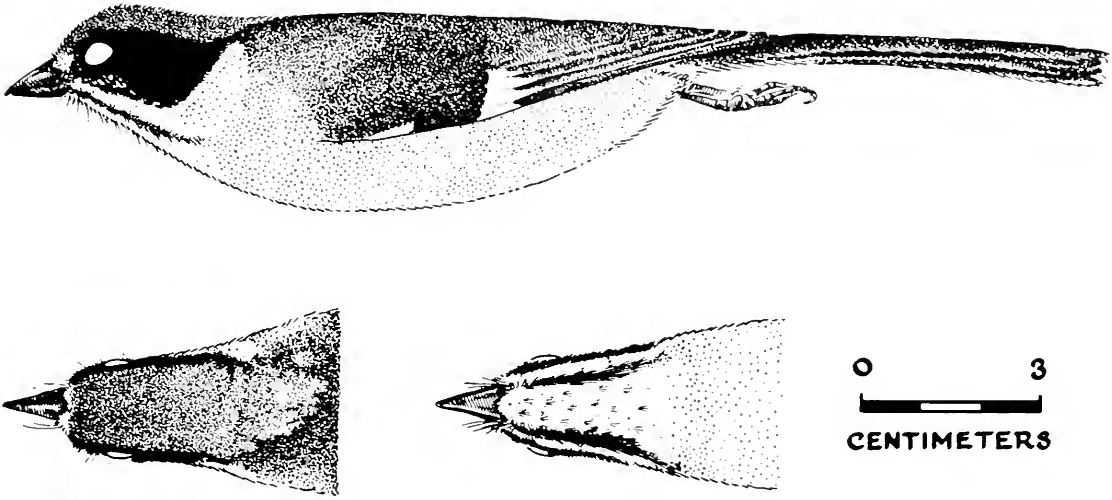

FIGURE 2. *Atlapetes s. schistaceus.* Oyacachi (2,500 m), Pichincha, Ecuador. ♀. MCZ 139,387.

Andean populations, but there are too few measurements to be certain. The species does, however, exhibit moderate sexual dimorphism in size. On the other hand, there is no sexual dimorphism in color and pattern but there is considerable geographic variation in these characters; these differences have been used in describing the six recognized races.

Nominate *schistaceus* (Fig. 2), which ranges through the Colombian Andes, except in the northeast, is characterized by a sooty, nearly black, back and black tail. The pileum is dark chestnut with a narrow area of black over the bill. The lore is extensively white and the side of the head is black with slightly lighter auriculars and a broad grayish white malar streak extending to the neck. The mystacal streak is broad and long. The throat is grayish white with an admixture of black feathers; the breast, abdomen, and sides are dark gray, lightening somewhat toward the mid-line. At times the portion of the upper breast adjacent to the throat patch is somewhat scalloped by black tips to the feathers. A conspicuous white alar speculum, varying moderately in size, characterizes the black wing. The concealed bend of the wing is white and occasionally there is a restricted area of white on the exposed base of the outer edge of the outermost primary.

A. s. tamae, which is not contiguous with nominate *schistaceus* or with *castaneifrons*, has a black back as well as tail. The crown and neck are a lighter chestnut than in the nominate form and there is only a faint trace of black above the bill. The sides of the head are black with no lightening in the auricular region; the lores are black or indistinctly dark gray. The malar streak is short and narrow, as is the mystacal streak. The throat is grayish white and sharply demarcated from the dark gray underparts, although there is still a tendency toward a lighter color on the abdomen. The wing is black with no speculum, but the concealed bend of the wing remains white.

A. s. castaneifrons, the form of western Venezuela, is similar to *tamae* except for lighter pileum and hindneck, a small white loral spot, and no trace of black over the bill. The malar streak is broader and whiter and the mystacal streak heavier. There is a tendency for the outer web of the outermost primary to be pale, reminiscent of the condition in the nominate form, and a faint suggestion of an alar speculum is evident in some specimens.

The race *fumidus,* from the northern Sierra de Perijá, is the least distinctive of the six subspecies. It is very similar to *castaneifrons* and differs from it in being less black dorsally and more uniformly gray on the breast and abdomen.

A. s. taczanowskii, the race isolated on the eastern slopes of central eastern Peru (Fig. 1), resembles *castaneifrons* except that its back is more sooty, there is no hint of a speculum or a white edge to the edge of the wing, and the lores are nearly white with the white extending to the sides of the forehead, accenting a pronounced area of black at the base of the bill.

The southernmost race, *canigenis* of the Cuzco region, differs from all other forms in lacking both the malar and mystacal streaks. Otherwise it is similar to *taczanowskii,* except that the lores are dark gray and the black at the base of the bill is replaced by dark gray, thus forming a gray band from eye to eye.

In summary, the main differences between the races are as follow. The pileum is darkest in nominate *schistaceus,* lighter in *tamae,* and is lightest, and similar, in *castaneifrons, fumidus, taczanowskii,* and *canigenis.* The alar speculum occurs only in nominate *schistaceus* but is faintly suggested in *castaneifrons.* White edging at the base of the outermost primary is found in some examples of *A. s. schistaceus,* and there is a tendency toward paleness on the web in some examples of *castaneifrons,* but in the remaining races the primaries are completely dark. Mystacal and malar streaks are found in various widths and lengths in five races but are entirely lacking in *canigenis.* Loral spots are pronounced in nominate *schistaceus,* very large in *taczanowskii,* small in *castaneifrons* and *fumidus,* nearly absent in *tamae,* and dark gray and concolor with the forehead in *canigenis.* The forehead is conspicuously black in *schistaceus,* very narrowly black in *tamae,* black with white edges in *taczanowskii,* gray in *canigenis,* and concolor with the crown in *castaneifrons* and *fumidus.*

Atlapetes nationi

Range. This species has an extensive range from southern Ecuador to southern Peru (Fig. 1). It is known from three localities in Loja, Ecuador, all of which are on the western slope of the Andes, although the type locality, which is the town of Loja, is nearly astride the continental divide. Presumably the Loja specimens were taken on the range to the west of the town, where Norton (personal communication) saw two birds at about 2,400 m in October 1965.

The next known occurrence of the species is some 200 km to the south in the Porculla Valley, east of Olmos, Lambayeque, Peru. The two specimens from here (Markl Collection, Basel Museum) are referable to *A. n. simonsi,* the race also occurring in Loja. The species reappears in Libertad and seems to have an interrupted range along the western slope south to Arequipa, southwestern Peru. There are two large distributional gaps on either side of the nominate race. The southern gap is probably an artifact, owing to the absence of collectors. The northern gap may be real; the marked difference between the races on either side suggests a broken distribution.

The type of the nominate form, which is lost, is said (Hellmayr, 1938) to have come from Ninarupa, Junín, which would place the species on the eastern slope. This is doubtless an error, as concluded by Koepcke (1958) and de Schauensee (1966).

A. nationi has been found at altitudes from 1,870 to 3,500 m.

Habitat. In contrast to *A. schistaceus,* the habitat requirements of *A. nationi* are well known, mainly through the work of Koepcke (1958; 1961; 1964), who describes it as inhabiting temperate brush and forests.

I observed the species in early October 5 km southeast of Gonzanamá at an altitude of 2,300 m. The area is subtropical, dry but not arid (small fields of sugar cane are grown without irrigation on the less steep slopes), with many fields and pastures. Areas unsuited for agriculture are heavily cut for firewood. The ridges, which have only a thin layer of soil and are drier than farther downslope, are covered with a low dense scrub about chest-high. *A. nationi simonsi* was found here. *A. torquatus*, a humid region form, was also noted in the area, but only in an isolated patch of woods about 7 m in height with a dark understory.

The locality where Norton observed *A. nationi* on 24 October is situated on the mountain between Loja and Catamayo. This is a vast region of apparently naturally occurring scrub similar to the small area where we found the species near Gonzanamá.

We did not find *A. n. simonsi* in woodland, in contrast to Koepcke's observations in Peru of *A. n. nationi*, *brunneiceps*, and *seebohmi*. It would seem that where *A. nationi* occurs in the temperate zone, as in most of Peru, it is a forest species but where it descends to the semi-arid subtropical zone, as does *A. n. simonsi*, it occurs in scrub, possibly because of the presence of *A. torquatus* in the wetter and taller woods. This will be considered more fully in a subsequent study of *A. torquatus*.

Habits. Eight specimens were collected near Gonzanamá over a period of several days. All were taken from small flocks; four specimens are known with certainty to have come from flocks consisting of but three birds. They were very secretive, generally keeping low in the dense brush but frequently uttering a loud metallic "seep seep." It is of interest that, in contrast to my experience, Koepcke (1958) describes the call in Peru as consisting of a single soft "zieh," although she does note that in the breeding season the song is strong and loud.

When birds were flushed and forced to fly from one clump of brush to another, their wings made a noticeable noise. Koepcke (1964) mentions the bird's habit of raising its tail but, although we often heard individuals scratching among dry leaves, we never glimpsed them on the ground.

There were no indications of breeding; presumably the breeding season is during the rains, as has been noted in Peru (Koepcke, 1958).

Food. Two stomachs were preserved. One contained a large dipterid, the body of an unidentifiable large insect, a few small seeds, and some grit. The other had finely ground bits of chitin, fragments of seeds, and a considerable quantity of grit. Most of the latter was bright reddish brown; a few particles were clear quartz.

Peruvian specimens examined by Koepcke (1958) had fed on few insects but had eaten fruit and plant material, none of which occurred in the Gonzanamá material. I imagine that these differences in food are related to the season in which the specimens were collected, rather than to any fundamental differences in diet.

Morphological variation. Although the data are scanty, there appears to be a general increase in size, particularly in weight, from north to south (Table 2). On the other hand, regional differences in color and pattern are pronounced.

A. n. simonsi (Fig. 3), which is known from the type and one other specimen collected at (=near?) Loja (Chapman, 1921), from eight specimens taken by us near Gonzanamá and from two specimens from the Porculla Valley, Lambayeque (Markl Collection, Basel Museum), is dark sooty gray on the back and wings, with a nearly black tail. It is lighter than any race of *A. schistaceus*, but not markedly different. The pileum is light chestnut, very closely resembling the head color in *A. s. castaneifrons*. The feathers over the nares are black. There is a dirty white supraloral spot and the side of

TABLE 2. COMPARATIVE MEASUREMENTS OF *A. NATIONI* SUBSPECIES.

Race	Sex	Wing (flat)				Tail				Culmen (fr. base)				Weight			
		N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD
simonsi[1]	♂	3	75–79	77.3 mm	2.1	3	75–81	77.3 mm	3.2	3	15–16	15.6 mm	.6	3	31.2–33.1	32.1	.9
celicae[2]	♂	1	68.5			1	63 (worn)			1	16						
seebohmi[3]	♂	?	74–81			?	80–87			?	15–16						
nationi[1]	♂	1	82			1	80			1	19			2[4]	41.5–43.4	42.5	
simonsi[1]	♀	2	71–75	73.0		1	73			2	15–16	15.5		4	27.1–37.1	31.4	4.2
seebohmi[3]	♀	?	74–76			?	75–77			?	14–15						
nationi[1]	♀	1	83			1	76			1	19			2[4]	40.5–41.0	40.8	
brunneiceps[5]	?	?	81–87			?	78–87			?	15–16.5			3[6]	38.3–43.1	40.2	.3

[1] Original data.
[2] Chapman, 1925: 7.
[3] Hellmayr, 1938: 402.
[4] Koepcke, 1958: 179.
[5] Hellmayr, 1938: 412; measurements not divided by sex.
[6] Koepcke, 1958: 180; 2 ♀, 1? ♂.

the head is black, lightening slightly in the auricular region. Below, the bird is white from throat to abdomen, with a band of gray across the breast which pales considerably in the center. There is a wash of buffy on the lower abdomen which intensifies on the crissum. The flanks and sides are dark gray. The very light colored venter is the most distinctive character distinguishing *simonsi* from all races of *A. schistaceus.* There are broad black mystacal stripes and a black line at the base of the mandible. The malar stripe is white, merging into the white of the throat. The outer web of the ninth primary is white and the outer half of the outer web of the eighth primary is gray.

A. n. celicae, which is known only from the type that is said to have been taken at Celica, only about 65 km west of Gonzanamá, offers a problem. It very closely resembles *simonsi* except that its wing is much smaller (Table 2) and it has a narrow dark area above the nares, a character tending toward the very dark forehead in *seebohmi.* It is slightly buffy on the chin, a feature not noted in any specimens of *simonsi* but which is a tendency toward the condition in nominate *nationi.* Chapman (1925; 1926), in contrasting this form with *simonsi,* remarked that the supraloral spot is obsolete, but I find it as prominent as in my series of *simonsi.*

In 1965 we searched extensively for this race in the vicinity of Celica (see Paynter, 1970: 197) but failed to find it. The type was said to have been collected at an altitude of 6,900 ft. However, Celica is considerably lower than this and it is probable that the bird was taken northeast of the town toward Mt. Guachanamá. We collected for several days near the village of Guachanamá (alt. 2,500 m), finding *A. rufinucha* common. Presumably this locality is too moist for *A. nationi.*

For the present, therefore, we must accept the race *celicae* although eventually it may be found to be an aberrant example of *simonsi.*

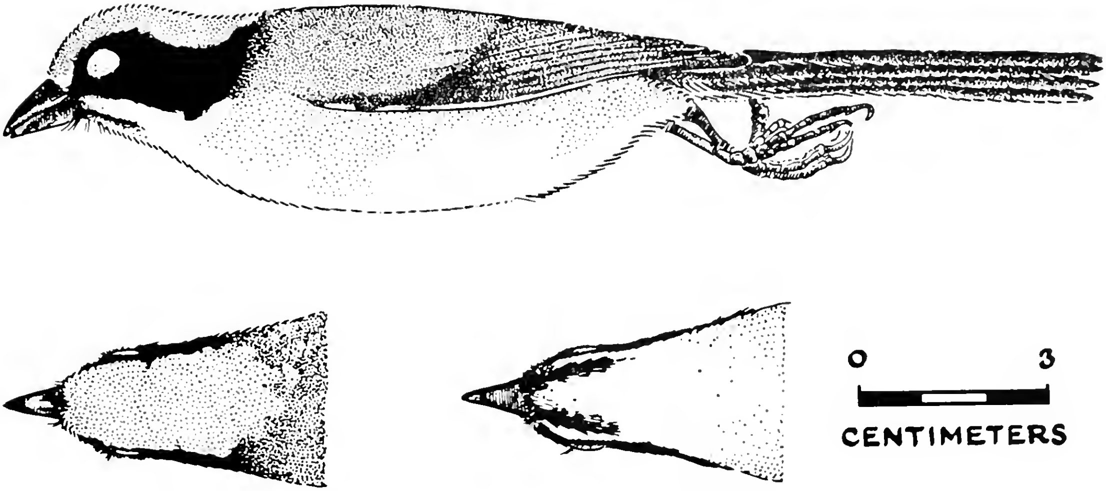

FIGURE 3. *Atlapetes nationi simonsi.* 5 km southeast Gonzanamá (2,300 m), Loja, Ecuador. ♂. MCZ 288,145.

A. n. seebohmi (Fig. 4), which ranges from Libertad to Ancash (Fig. 1) and which doubtless will be found to merge in the north with *simonsi*, but probably not in the south with nominate *nationi*, is closely similar to *simonsi*. Its back, wings, and tail are distinctly more olive gray, the breast band is broader and with only a slightly lighter area in the center, the crown is darker chestnut, and there is a broad band of black on the forehead. The gray edge to the eighth primary that is found in *simonsi* seems to be lacking in this form, but this feature is only evident in very fresh plumage in *simonsi* and I have seen no comparable specimens of *seebohmi*.

A. n. nationi (Fig. 5), which is known to occur only in a limited area to the east of Lima, differs fairly substantially from the preceding two forms in that instead of the pileum being chestnut it is reddish black, blending into the black of the sides of head

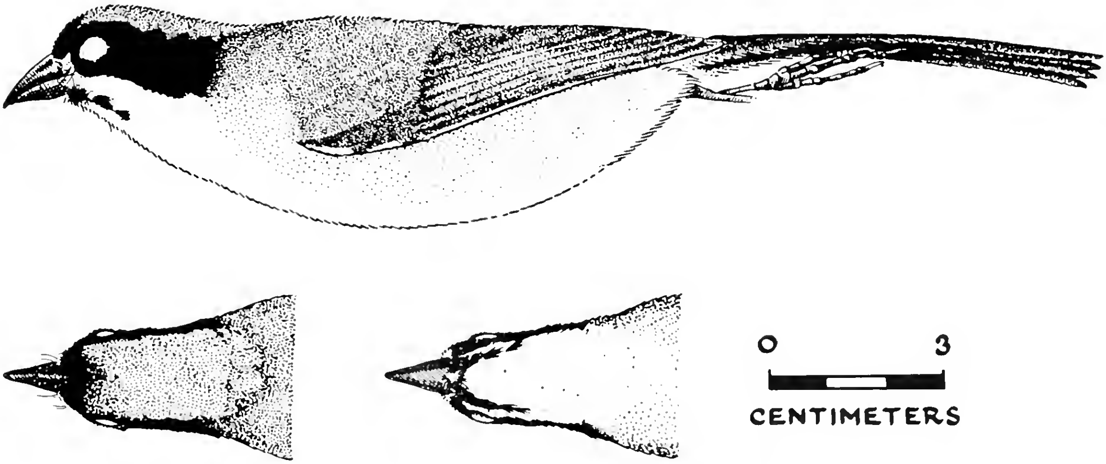

FIGURE 4. *Atlapetes nationi seebohmi.* Macate (alt. ?), Ancash, Peru. ♂. MCZ 287,193.

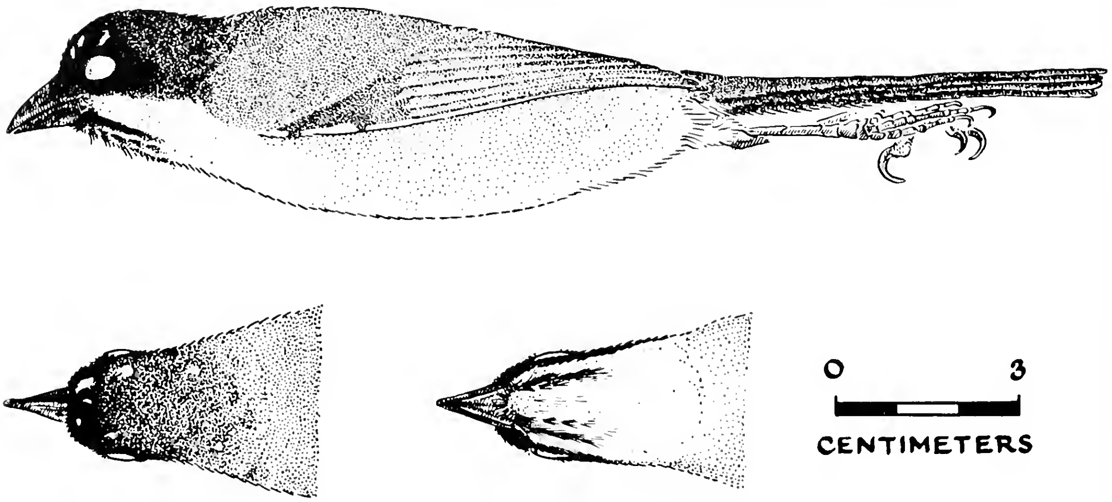

FIGURE 5. *Atlapetes n. nationi.* Canta (2,400 m), Obrajilla, Lima, Peru. ♂. MCZ 179,157.

and forehead. Scattered white feathers on the head appear quite frequently. The back is suffused with brown. The breast band is similar to that in *seebohmi* but the abdomen is dark buffy, paling in the center and where it meets the breast band, and darkening dorsally. The crissum is dark buff. The areas between the mystacal streaks and on both sides of them are washed with buff. The mystacal streaks are short but broad and without sharp borders, merging into a pronounced area of black at the base of the bill. The ninth primary again has a white outer web and the next two or three remiges have dark grayish outer borders.

The last race, *A. n. brunneiceps*, which has an extensive range from southern Lima province to Arequipa, resembles the nominate form except that it is lighter gray dorsally and the pileum and sides of the head are more brown, less reddish. The chin and malar region are more distinctly buffy. Scattered white feathers appear on the head as in *A. n. nationi.*

In summary, the three northern races are closely similar, differing mainly in the presence or absence of black on the forehead and in the depth of color of the breast band and pileum. The two southern races are heavier, and probably larger, than those of the north, have no chestnut on the pileum, and are distinctly rufous ventrally. They differ between themselves chiefly in dorsal coloration.

Atlapetes leucopterus

Range. A. leucopterus has a more restricted distribution than the previous two species, occurring on the western slopes of the Andes from northern Ecuador south to extreme northern Peru (Fig. 1). The northernmost recorded occurrence is "on the road to Nanegal," a classic source of material for local collectors near Quito. *A. schistaceus* has also been taken at this generalized locality, but whether the two species are sympatric or separated altitudinally is unknown.

There are a number of records from the vicinity of Quito, but the next known occurrence is 150 km south at Sinche, which is northeast of Guaranda in the province of Bolívar. The absence of records from intermediate points is almost certainly because the slopes in this region are not readily accessible to collectors. The species has been noted at several localities in the

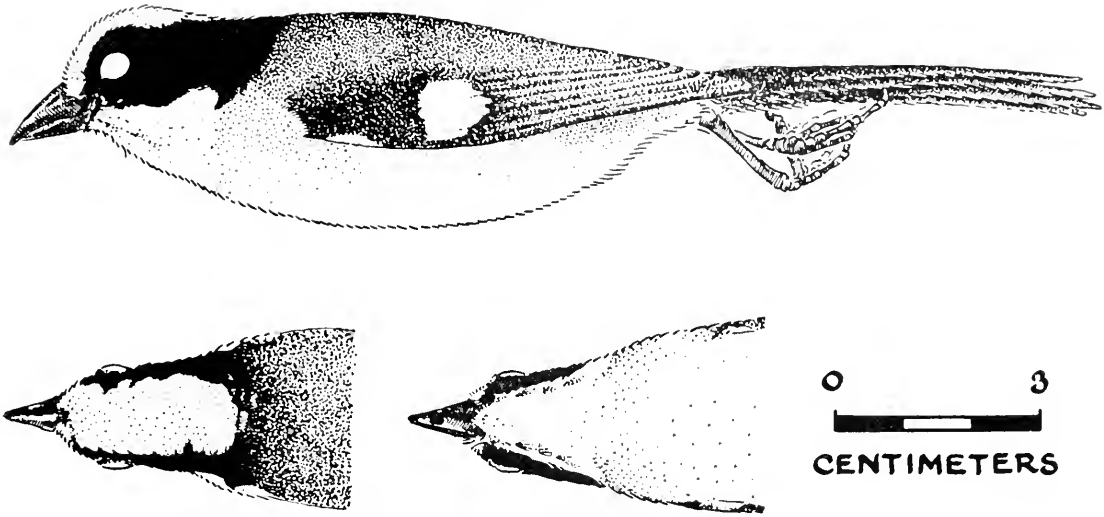

FIGURE 6. *Atlapetes l. leucopterus.* Valle Tumbaco (2,300 m), Pichincha, Ecuador. ♂. MCZ 288,135.

nearby Chimbo Valley in southwestern Chimborazo province, an area long accessible by train, but then there is another wide breach in the distribution, this time in excess of 200 km, with the species reappearing in southwestern Loja and in Piura and Lambayeque of adjacent northern Peru. Although the slopes are perhaps even more difficult to reach in southwestern Ecuador than farther north, there is a possibility that the southern distributional gap may be real and not the result of the vagaries of collectors. This seems probable because the birds from the southern limits of the range are morphologically very distinct from those on the other side of the presumed gap, i. e., those from central Ecuador, while those birds from northern Ecuador are indistinguishable from those of central Ecuador. The distance between the central and northern population samples is roughly the same as that between the central and southern samples, which suggests that the morphological distinctness of the southern population is the result of restricted gene flow.

In addition to the possible sympatry of this species with *A. schistaceus* north of Quito (see above) there are two other areas of interest. *A. l. dresseri* is known to be sympatric with *A. nationi simonsi* in the Porculla Valley, Lambayeque. Specimens in the Markl Collection (Basel Mus.) from the latter locality bear the annotation that the two species occur in the same flock. *A. l. dresseri* is also known to be sympatric, or at least parapatric, with *A. albiceps* in Piura in the somewhat isolated Cerros de la Brea in the vicinity of Sullana (specimens in Markl Collection and in Mus. Zool., Louisiana State Univ.).

The nominate form has an altitudinal range of from about 600 to 2,900 m, while *A. l. dresseri*, the southern race, has been found from 700 to 2,550 m.

Habitat. There seems to be no published description of the habitat. At Alamor, Loja, the only place where I have seen the species, it was found in viney thickets in an area of moderately moist subtropical vegetation.

Distributional records seem to indicate that while the species is found in the humid subtropics it may be most common in the arid subtropical zone. It also ranges into the arid temperate zone, at least in the vicinity of Quito.

Table 3. Comparative measurements of *A. leucopterus* subspecies.

Race	Sex	Wing (flat)				Tail				Culmen (fr. base)				Weight		
		N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean
leucopterus	♂	2	70–71	70.5		2	65–67	66.0		1	17					
dresseri	♂	1	68							2	14	14.0		2	20.7–22.7	21.4
leucopterus	♀	3	67–69	68.0	.71	3	62–65	63.0	1.73	3	16–17	16.7	.47			
dresseri	♀	1	65			1	63			2	14	14.0		1	26.1	

Habits. Again there seems to be no published description of the habits of this species. I observed a flock of three, or possibly more, birds for a brief time at Alamor. The birds were feeding in vines about two feet from the ground. Their white alar patches were very conspicuous and seemed to accent their quick movements as they searched the vegetation. This activity contrasted sharply with the slower, more deliberate, motions of a flock of *A. torquatus,* which was on the ground below, turning leaves with their bills and riffling the litter.

Food. One stomach, from a specimen collected at Alamor, was examined. Its food consisted entirely of ants. Interestingly, the grit it had consumed was mainly dark colored and rounded, in distinction to the bright and sharp fragments noted in *A. schistaceus* and *A. nationi.*

Morphological variation. A. leucopterus (Fig. 6) is essentially a small replica of *A. schistaceus* (in particular the nominate form, which has an alar patch) or of one of the brown-capped northern races of *A. nationi.*

The species has been divided into two races on the basis of color and pattern. I have seen little fresh-plumaged material of either race, but from limited measurements (Table 3) it appears that nominate *leucopterus,* the more northern form, may be larger. The length of the bill is almost certainly greater; the bill is proportionately more massive.

A. l. dresseri is also distinguished by an overall buffy tone. The white throat, chest, and abdomen are replaced by buffy white, the gray flanks are markedly buffy, and even the gray of the back has a foxy tone. In addition, the buffy white supraloral spots are larger in *dresseri* than in the nominate race and sometimes are so extensive they meet, forming a white forehead. In *A. l. leucopterus* a restricted area between the supraloral spots may be black or there are black feathers mixed with the chestnut, which extends forward from the

TABLE 4. COMPARATIVE MEASUREMENTS OF *A. RUFIGENIS* SUBSPECIES.

		Wing				Tail				Culmen (fr. base)			
Race	Sex	N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD
rufigenis	♂	6	86–98	90.5	3.98	5	89–98	91.6	3.65	6	18	18	
forbesi[1]	♂	4	77–81	80.5	2.89					1	16–17	16.25	.06
rufigenis	♀	1	92			1	95			1	19		
forbesi[1]	♀	1	74										

[1] Morrison, 1947.

crown. In *A. l. dresseri* there is always an extensive area of black on the fore-crown, a character not present in *A. l. leucopterus.* However, it is the variation in the extent of the black area that is particularly noteworthy. It ranges from a small area equal in size to the white postnasal band to complete coverage of the front half of the head. In the specimen taken at Alamor the black stripes which laterally border the chestnut crown in both races are so extensive that the chestnut is reduced to a triangular area with its slim apex in the center of the crown and its narrow base at the nape. All the specimens of *dresseri* that I have seen have white eye rings, whereas this character is lacking in nominate *leucopterus.* However, as in the variation in the amount of black on the head, the size of the eye ring varies enormously. It may be a narrow ring which contrasts with the black superciliary stripe and the near-black auriculars and circumocular region, or it may range up to a wide irregularly shaped ring that meets the supraloral spot, obliterating the black lores, and encroaching on the crown's lateral stripes, thus creating a bird whose cheeks are mainly white rather than black.

Mystacal streaks are characteristic of both races. They are indistinct in the nominate form but more pronounced in *dresseri,* although in the latter they vary in size and intensity.

In summary, *dresseri* is distinguished from nominate *leucopterus* by its smaller bill (and possibly wing and tail), more buffy coloration, black forehead, the presence of a white eye ring, and more pronounced mystacal stripes. *A. l. dresseri* exhibits unusually great variation in some of the characters that distinguish it from the nominate subspecies.

Atlapetes rufigenis

Range. Atlapetes rufigenis has a markedly restricted range. The species occurs in the highlands of northern Peru within the drainage system of the upper Río Marañón from Libertad and extreme southern Cajamarca south to Huánuco. There is then a breach in the distribution of about 650 km and the species reappears in Apurimac, where it is known from one locality in the valley of the Río Pampas, which is a tributary of the Río Apurimac.

Altitudinally the northern population has been found between 2,800 and 4,000 m but most records are from about 3,250 m. The southern population is known to occur at approximately 2,750 m.

Habitat. Zimmer (1930) reported collecting a single specimen of nominate *rufigenis* at Cullcui, Huánuco, from a jumble of vines and bushes that formed a semihumid oasis in an otherwise arid subtropical region. Morrison (1948) collected ten specimens of the southern form (*A. r. forbesi*) at Pomayaco in dense tangles in the humid temperate zone.

Habits. Morrison (1948) reported *A. r. forbesi* to be silent and very secretive. I have seen one specimen from Yánac, Ancash, which is said to have had moderately enlarged testes on 21 March.

Morphological variation. A. rufigenis is the largest member of the species group (Table 4). In color and pattern it is much

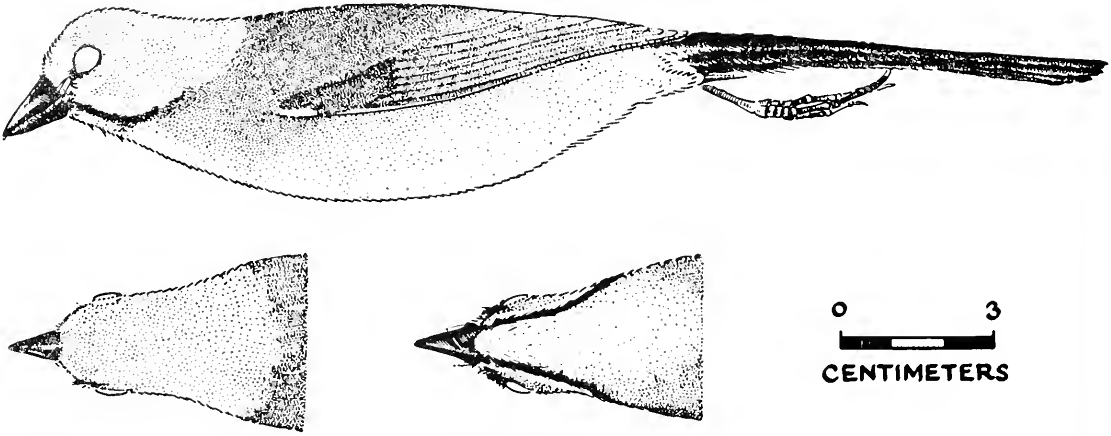

FIGURE 7. *Atlapetes r. rufigenis.* Yánac (3,700 m), Ancash, Peru. ♂. MCZ 179,163.

like *A. nationi seebohmi* or *A. n. simonsi,* except that the black on the sides of the head is either absent or reduced and replaced by the chestnut of the crown (Fig. 7).

In nominate *rufigenis* the lores are either white or gray and the supraloral region is buffy white. In some instances the pale supraloral areas almost meet above the bill. The sides of the head are concolor with the crown, except that in one of seven specimens examined there is an indistinct black eye ring and a few small black feathers in the auricular region. The outer edge of the outermost primary is a pale dirty gray which, while evident, does not sharply contrast with the rest of the wing, as it does, for example, in *A. n. simonsi.* The chestnut of the head is very similar to that in *A. n. simonsi,* while the color of the back, wings, and tail is nearly identical with that of *A. n. seebohmi.* Ventrally it most nearly resembles *A. n. simonsi,* which has a less distinct breast band than does *A. n. seebohmi,* but it differs from both taxa in having almost no trace of a buffy wash on the abdomen and crissum. The mystacal streaks are dark gray and are less prominent than in either *simonsi* or *seebohmi.*

I have not examined specimens of *A. r. forbesi,* the isolated southern form, but from the original description (Morrison, 1947) and the comments of Bond (1951) it is evident that its most noteworthy character is the presence of black on the forehead and in the circumocular area, which must make this race fairly similar to the northern forms of *A. nationi.*

Atlapetes albiceps

Range. The species is known from the western slopes of the Andes of southern Ecuador and northern Peru. There are records (Chapman, 1926, and specimens in MCZ and Basel Museum) from Paletillas, the Casanga Valley, and El Empalme in the southeastern part of the province of Loja, Ecuador, and a number of specimens have been collected in the Cerros de la Brea of adjacent Piura, Peru (Mus. Zool. Louisiana State Univ.; Basel Museum). Between here and eastern Lambayeque and western Cajamarca, from where there are several records, is a distance of about 200 km. The species is unknown between; presumably this gap will be filled when the area is better studied.

The vertical range is not readily determined because there are so few records with accurate altitudinal data. The species seems to occur from about 250 to 1,500 m. I have observed it at about 1,000 m in the Casanga Valley of Loja and ten specimens from the Cerros de la Brea, Piura, were taken between 580 and 800 m.

Habitat. We found the species at Yamana, near the upper end of the fairly arid subtropical Casanga Valley. My limited experience seems to indicate that the bird is not uniformly distributed in the valley but occurs only where there are patches of denser scrub. This observation recalls similar comments made by Zimmer (1930) regarding *A. rufigenis.* In the heavily cultivated and grazed Casanga Valley these scattered patches are confined to the edges of the valley in the vicinity of brooks descending from the mountains, where the terrain is too steep to be used for agricultural purposes. It seems likely that the species once was more widely distributed.

Habits. Five specimens were taken in mid-October at Yamana. They seem to have constituted a single flock. All were in fresh plumage and with small gonads. Norton obtained two birds at Yamana in early July. These specimens were in very worn plumage and they too had small gonads. A female collected forty years ago on 17 May "on the Porculla road," Lambayeque (specimen MCZ), is quite worn, particularly on the tail; it is noted on the label that the ovary was slightly enlarged. From these bits of evidence it may be assumed that breeding probably occurs around January or February when the rainy season is at its peak.

The birds at Yamana were very shy. Their thin, high-pitched "seep" was usually the first indication of the presence of the species in the undergrowth. They were extremely active and called often as they moved through the underbrush and vines. They were seen most often in close vicinity of a stream. Apparently they obtained water or grit in the mud along the banks, for several birds had muddy bills and feet when collected.

Food. The stomach contents of five specimens taken in October were examined. All contained whole small seeds and crushed larger seeds. Small quantities of ground-up insect material was found in four specimens. Only the leg of a hymenopteron, probably an ant, was identifiable. Considerable amounts of fine, sharp grit, predominately white or light colored, was present in all five specimens.

Morphological variation. A. albiceps differs from the four preceding species in having an extensively white forehead and (with the exception of the races *A. nationi nationi* and *A. n. brunneiceps*) in having a black rather than chestnut crown (Fig. 8). The white alar speculum immediately reminds one of *A. leucopterus,* or possibly of *A. s. schistaceus.*

There is a great deal of variation in the plumage of the head and throat of a series of six skins from Yamana and one from Lambayeque. The throats of two badly worn and heavily molting July specimens from Yamana are pure white but in the remaining five birds there are traces of mystacal streaks. These range from a single black feather to fairly pronounced, but unsymmetrical, streaks. In addition, one specimen has two dark feathers in the center of the throat.

The crowns of most specimens have scattered white filoplumes, particularly on the neck. A few white feathers at the edges of the black crown make for ragged borders on all specimens. One bird has a white feather in the center of the otherwise black nape and in the middle of the upper back. A single October specimen, presumably a young bird, is conspicuously brownish on the nape and reminiscent of *A. n. nationi.*

Birds in fresh plumage have a very thin white edge on the exposed base of the outer primary. The back is dark gray with a tawny wash, very similar to that of *A. nationi seebohmi.* The color of the venter is also extremely similar to that of *A. n. seebohmi.*

Measurements (Table 5) indicate that there is moderate sexual dimorphism in size (males larger) and that the tail is some-

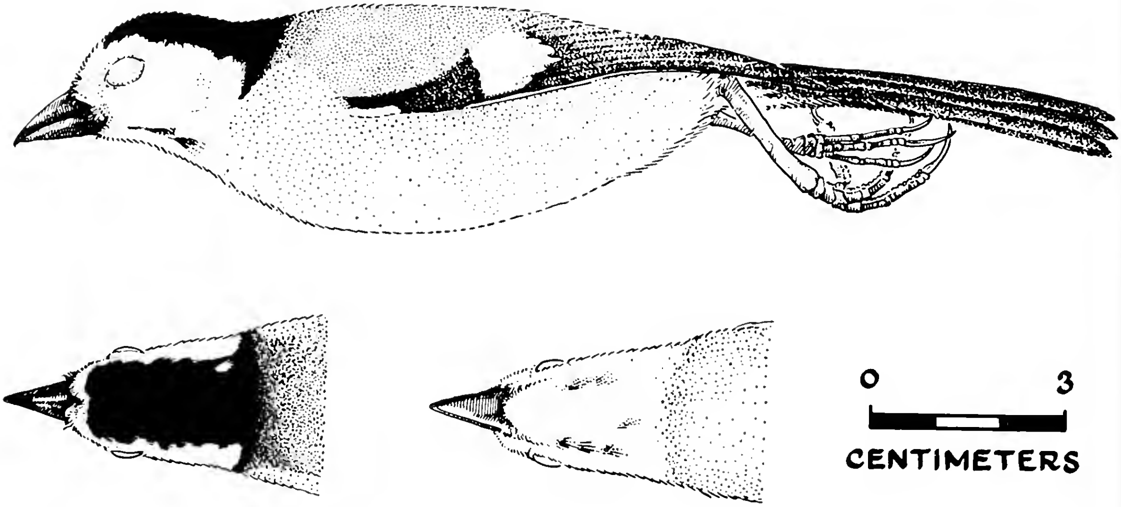

FIGURE 8. *Atlapetes albiceps.* Yamana (1,100 m), Casanga Valley, Loja, Ecuador. ♂. MCZ 288,116.

what shorter than the wing. These two characters are similar to the situation in *A. leucopterus.*

Atlapetes pallidiceps

Range. Atlapetes pallidiceps was described in 1900 by Sharpe from three specimens secured in May 1899 by the mammalogist P. O. Simons near Oña (1,900 m), Azuay, on the west side of the Andes of southern Ecuador. Hellmayr (1938), after examining the type series, reported that they had come from "Guishapa, Oña." Inquiries in the town of Oña in 1965 revealed no one with any knowledge of a locality by this name. Presumably "Guishapa" was an hacienda, now gone, or possibly the name was incorrectly transliterated from the Quechua, the suffix *shapa* or *chapa,* meaning "sentry," being common in placenames in the region.

In the 65 years following the discovery of the species additional specimens were taken at Girón (2,100 m) and in the Yungilla Valley (*ca.* 1,500 m), both in Azuay and within 35 km of Oña. However, in all, not more than 10 specimens were known to be in museums prior to 1965 (personal observation).

In early November 1965 we went to Oña in the hope of observing the species. The region is extremely arid with very little naturally occurring vegetation, and even this is extensively cut for firewood and primitive cultivation. After considerable searching for a locality that would appear to be a likely habitat for an *Atlapetes,* we found an isolated pocket, about 10 km northwest of Oña, with a few hectares of artificially irrigated fields interlaced with shrubs and low trees bordering a brook that feeds into the Río Leon, which is about one kilometer to the east and several hundred meters lower. Here we discovered the species to be fairly common, although difficult to observe.

TABLE 5. MEASUREMENTS OF *A. ALBICEPS.*

		N	Range	Mean	SD
Wing	♂	2	80–82	81.0	
	♀	3	77–81	78.3	2.31
Tail	♂	2	73–77	75.0	
	♀	3	70–72	71.3	1.16
Culmen (fr. base)	♂	3	17–18	17.3	.58
	♀	5	16–17	16.4	.55
Weight	♂	3	36.6–39.0	37.5	1.28
	♀	3	34.9–36.1	35.6	.64

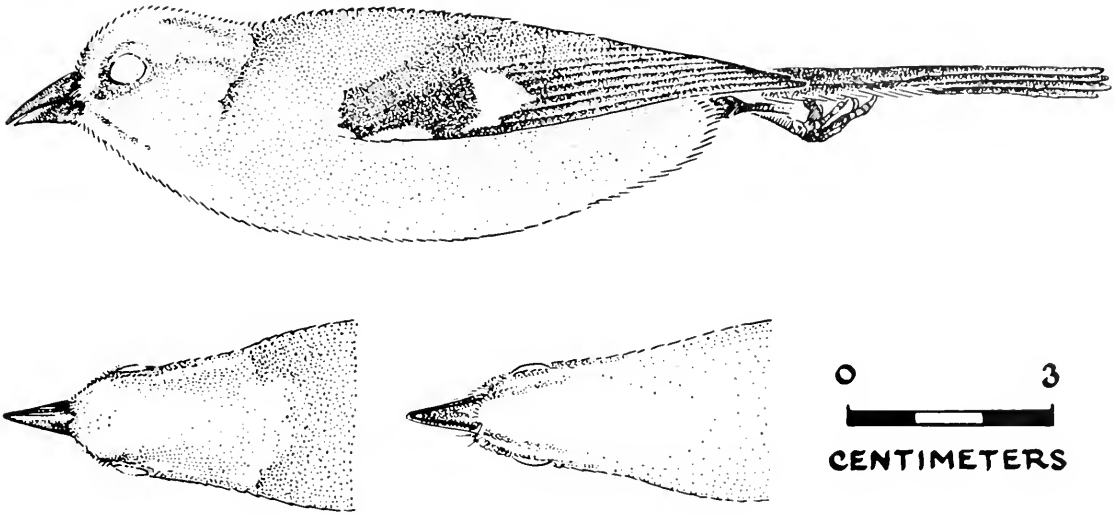

FIGURE 9. *Atlapetes pallidiceps.* 10 km north Oña (1,900 m), Azuay, Ecuador. ♀. MCZ 288,126.

The species is now known with certainty from three localities within an area no more than 35 km in diameter. It doubtless will be discovered beyond this restricted area, but I believe that it is almost a certainty that it is endemic to the valley of the upper Río Jubones and its tributaries. The presently known localities are on the Girón, Yungilla, and Leon rivers, all of which flow into the Jubones.

Habitat. We found the species in a small area of vegetation which stands as an oasis within the arid countryside. There was little thick undergrowth present, and the species occurred mainly in tree-sized acacias. It is not known whether the species normally frequents trees or is forced into them because of the absence of thickets.

Habits. Unlike other species of *Atlapetes*, we found *A. pallidiceps* to be arboreal to a great extent and, although shy, fairly conspicuous as it flew from tree to tree with its light-colored head appearing white against the foliage and sky. During our two days near Oña, a dozen specimens were obtained and others were sighted at least an equal number of times but were not collected. However, the species was seen only once in a flock as large as three birds; the balance of the observations were of single individuals, or less frequently, of pairs.

The call, a thin "seep," which was heard on several occasions, seemed unusually weak for a bird of this size and less metallic than in other *Atlapetes* with which I am familiar.

A single bird was glimpsed on the ground in an area in which scraggily coffee was grown under taller shade trees. The bird appeared to be turning dead leaves by means of its bill rather than its feet. I have noted this use of the bill in several other *Atlapetes* species; it is believed by Skutch (1954) to be characteristic of the genus.

Food. The stomachs of eight birds were examined. All contained a good deal of sand, which at times made up almost half of the material in a full stomach. The food material in nearly all cases was ground to an unrecognizable state. Insect remains were found in six stomachs, the relative quantity ranging from very little to roughly one-quarter of the recognizable material. Most birds had relatively large pieces of what appeared to be endosperm from a big seed. The outer coating was never attached to this material, and it seems likely that the seed was cracked before ingestion and the endosperm extracted in chunks. A few very small seeds (2 mm or less) of several types were also noted. A minute cocoon (5 × 2 mm) and a tiny (8 × 3 mm) larval coat of something like a fly larva were found in one specimen.

Morphology. A. pallidiceps is the most distinctive form of the species-group (Fig. 9), with its grayish white head and grayish olive back. However, when examined more closely, it appears merely to be a large version of *A. leucopterus dresseri* (particularly the variants in which there is a considerable amount of white circumocularly) in which the chestnut of the pileum has become grayish white and the black of the sides of the head has turned to dirty gray.

There is considerable variation in the color and markings of the crown and sides of the head in the 11 skins available to me (9 from near Oña, 2 from Yungilla). The area immediately above the bill is just slightly washed with tawny in a few specimens, but in others it is conspicuously rusty, and in one the whole center of the crown is also washed with this color. The dark lines in the crown and behind the eye are generally well delineated and separated by a pale line above the eye, but in some specimens darker feathers obscure the pale line, and in two birds the entire side of the head is dark. The crown ranges from dirty white to very pale brownish gray. The two specimens without pale and dark stripes on the sides of the head have the brownish gray of the back extended to the base of the pileum, thus restricting the pale area of the crown. The color of the back and rump varies slightly within the entire series but not so conspicuously as in the case of the head pattern and color. The amount and intensity of the tawny wash of the underparts varies. In some the wash is quite conspicuous on the throat, while in others it is entirely absent. In general this color is most intense in a band across the breast, while it is blended with gray on the flanks.

Table 6. Measurements of *A. pallidiceps*.

		N	Range	Mean	SD
Wing	♂	3	74–80	76.3	3.21
	♀	6	72–77	75.0	2.09
Tail	♂	3	70–81	75.3	5.01
	♀	6	74–81	75.8	2.64
Culmen (fr. base)	♂	3	17–18	17.3	.58
	♀	6	16–17	16.5	.55
Weight	♂	4	33.4–35.3	34.0	.86
	♀	6	28.7–32.8	31.2	1.53

A pale edge at the base of the outermost primary can be detected in a few specimens, but this trait is even less visible than in *A. albiceps.*

Mystacal streaks are evident in ten of the eleven skins examined. These are thin, faint, continuous lines restricted to the upper throat. They are not so conspicuous or so fragmented as in *A. albiceps.*

No sexual dimorphism is apparent in color, pattern, or linear measurements; the males may be slightly heavier (Table 6).

ORIGIN OF THE TAXA

In recent studies Haffer (e. g., 1967a, 1967b, 1969, 1970) has developed the convincing theory that the initial avifauna of the subtropical and humid temperate zones of the Andes was derived from that of the surrounding lowlands during the emergence of the Andes between the end of the Tertiary and beginning of the Pleistocene. And, further, that the multiplicity of present-day Andean taxa is the result of Pleistocene and post-Pleistocene climatic changes (cold-humid; warm-dry) and the associated changes in vegetation as well as altitudinal shifts in life zones, rather than because of orographic conditions. Although the geology and climatology of South America in the Pleistocene are known in no detail, thus making it impossible to determine with any precision the sequence and timing of the origins of the various taxa, the following appears to be a plausible reconstruction of the history of the *A. schistaceus* species-group based on Haffer's theory.

The genus *Atlapetes* ranges in the mountains from Mexico to Argentina, with the overwhelming majority of species present in the northern Andes. Most of these occur in the subtropical or humid temperate zones, generally in forests or on their edges. It is a reasonable assumption that the present center of abundance of the component species coincides with the area in which the genus arose, but this is of no importance in the discussion that follows. However, granting this as well as accepting Haffer's thesis, it also seems reasonable to postulate that the genus developed in the subtropical or the humid temperate zone and that the *A. schistaceus* species-group had its origin in the subtropical zone, the zone in which it most frequently occurs today.

The stock from which the *A. schistaceus* species complex arose probably ranged from the northernmost Andes south to the present limit of the group's distribution, or possibly as far south as Bolivia and northern Chile. This was probably during one or more glacial cool-moist periods when the subtropical zone occurred at altitudes from about 500 m up to roughly 1,200 m and the treeless páramo zone began at 2,000 m or even somewhat lower (Haffer, 1970). At this time the subtropical forests must have existed in an almost continuous belt around the three Andean ranges in the north, and on the east and west sides of the Andes farther south. The total area covered by the subtropical zone probably was vastly greater than that occupied today, even though its vertical range was more restricted.

With the advent of an interglacial warm-dry period, of which there were several, doubtless of varying degrees of intensity, the subtropical zone retreated from the foothills and eventually may have been restricted to elevations between roughly 1,500 and 2,800 m (Haffer, 1970). The subtropical zone existed, therefore, only on the higher mountains and thus was fragmented. In the region of southern Ecuador and northern Peru, where the Andes are on the average lower than elsewhere along the range and where deep valleys penetrate the mountains from both sides, the subtropical zone must have been particularly limited in area and much divided.

In conjunction with the upward movements in the life zones, owing to the warmer climate, there was also a radical change in precipitation and the type of vegetation it supported. According to Haffer (1967a; 1969), tropical forest largely disappeared from the Amazon basin and the northeastern lowlands and was confined to refuges, generally along the Andes. Presumably the lessened rainfall also affected the montane vegetation. Some areas that were high enough to support subtropical vegetation doubtless were covered by a nonforest type of growth. This would have been particularly true in the low area of southern Ecuador and northern Peru, a region of little rainfall even now. Here subtropical forest may have been entirely lacking, thus making a substantial breach in the distribution of any species dependent on this type of habitat.

Other major arid areas contributing to the fragmentation, restriction in range, and isolation of the avifauna of the subtropical forest were the upper valleys of the Cauca, Magdalena, Marañon, and Apurimac rivers. What occurred to the climate along the now arid coast of Peru and southern Ecuador during the warm-dry interglacials is unknown. Presumably the Humboldt Current existed then and affected the coastal and montane precipitation as it does now. If this is correct, it is probable that the treeless, and in places vegetationless, arid tropical zone extended higher on the western slopes of the Andes. The subtropical zone would, of course, have been correspondingly higher. It would also have been more restricted in extent than now because of the steepness of the mountains.

However, because the western slopes of the Andes of southern Ecuador and northern Peru derive their precipitation from winds coming off the Pacific, it seems likely that the subtropical zone here would have been less dry than, for example, the subtropical zone on the eastern slopes, which were above the dry, nonforested, areas of the Amazon basin. Pockets of fairly moist forest may have occurred on the western slopes wherever the Andes were high enough to deflect the moisture-laden westerly winds. Admittedly this is unproven and highly speculative, but the existence of such isolated pockets is strongly suggested when trying to account for the origin of certain species within the *A. schistaceus* complex.

A. schistaceus, a subtropical forest form that has a wider dispersal as well as greater vertical range than the five other species, exhibits a fragmented distribution (Fig. 1) that is explicable in light of the foregoing speculations. One of the most striking features of its present-day distribution is how closely this corresponds with the presumed locations along the Andes of interglacial forest refuges mapped by Haffer (1969, fig. 5).

In northeastern Colombia and adjacent Venezuela there is a group of subspecies (*fumidus*, *tamae*, and *castaneifrons*). Although the *group* is morphologically fairly distinct from other populations of *A. schistaceus*, the three races are weakly differentiated among themselves and probably were only recently and incompletely isolated from one another (see p. 299). The "Catatumbo" refuge occurred in this region.

The comparatively well-marked morphological differences between the group of three northern races and nominate *schistaceus* suggest that the distributional gap in the Eastern Andes of Colombia is real and relatively old. Similar gaps in this region are known for several species as, for example, the "coerebids" *Diglossa lafresnayii* and *D. humeralis* (Vuilleumier, 1969). The arid Chicamocha Valley cuts deeply into the eastern Andes (Haffer, 1967b) and possibly acts as a barrier to species of the humid forest today and probably did so in the interglacials. As now known, nominate *schistaceus* seems to have isolated populations at the northern ends of the western and central Andes (Fig. 1). The two western isolates correspond to the "Nechi" refuge and the eastern isolate to an unnamed and generalized refuge along both sides of the eastern cordillera. The three isolates do not appear to be morphologically separable from one another or from the main population of *A. s. schistaceus*, which suggests that isolation is incomplete or recent.

It will be noticed (Fig. 1) that nominate *schistaceus* ranges well south on the slopes of eastern Ecuador but only for a short distance on the western slopes. These distributional patterns closely approximate the boundaries of Haffer's (1969) "Choco" and "Napo" refuges, respectively.

The species next appears in Peru on the eastern slope, roughly between the upper Marañón and the Ucayali (the race *taczanowskii*), and then reappears south of the Apurimac (the race *canigenis*). Both of these areas are depicted by Haffer as interglacial forest refuges.

The absence of *A. schistaceus* from the subtropical slopes of southwestern Ecuador, from along the entire western side of the Peruvian Andes, from the mountains of southern Ecuador and northern Peru, and from large segments of eastern Peru, is a second very striking feature in the distribution of the species. It will be noted that these areas are those in which no forest refuges were present during interglacial periods (see Haffer, 1969, fig. 5). Furthermore, the western Andean slopes presently unoccupied by *A. schistaceus* are adjacent to the arid coastal strip that seems likely to have extended onto and well up the slopes during the interglacial periods; the distributional breach in the mountains of southern Ecuador and northern Peru is the area where subtropical forest was seemingly much restricted or absent at the same time; the distributional gaps in eastern Peru are in the vicinity of the arid valleys of the upper Marañón and Apurimac.

The presence of *A. schistaceus* where there were interglacial forest refuges, and the absence of the species where there were none, is certainly not coincidental. The only conclusion to be drawn is that the species was restricted to the refuges during one or more interglacial periods and that it has not been able to occupy subtropical forest that has developed since that time, either because of insufficient time or because of the presence of competitive species. The latter explanation seems to fit the evidence.

A. leucopterus and *A. nationi*, which occupy the western slopes from which *A. schistaceus* is absent, appear to be its counterparts to the north and south, respectively. Both species occur in habitats ranging from fairly arid scrub to moderately moist forest. This is a greater diversity than seems to be tolerated by *A. schistaceus* and may be because of their more varied evolutionary histories.

It appears that *A. leucopterus* arose as an isolate in western Ecuador during a warm-dry interglacial. It probably was derived from a population that was left behind in a less dry pocket on the slopes of the high mountains when, in the face of increasing aridity, *A. schistaceus* retreated to the moist Choco refuge. *A. leucopterus* would, then, have differentiated in a dryer habitat than that occupied by *A. schistaceus*. Later, as the climate became cooler but wetter, *A. leucopterus* was able to increase its range along with the expanding, but still relatively dry, subtropical forest. Later in the cycle it was able to accommodate to the change toward a more moist forest, a versatility still exhibited by the species. On the other hand, *A. schistaceus*, having arisen in moist forest and having taken refuge in moist forest during the interglacials, was unable to exploit a drier habitat, thus permitting *A. leucopterus* to move into the newly available habitat and to expand its range until it abutted the range of *A. schistaceus* in northern Ecuador. The fact that they are not known to be sympatric is doubtless evidence of the close relationship and similar habits of the two species.

A. leucopterus dresseri, the race of southern Ecuador and northern Peru, appears to be a recent derivative of the nominate form. It is phenotypically highly variable, which argues against this assumption because peripheral, newly formed, populations are genetically less variable than the parent population. However, *A. l. dresseri* may be the product of various colonizations of scattered subtropical forests that occurred during interglacials in the southern Ecuador–northern Peru area and that are now merging into a single population but have not yet achieved morphological uniformity.

A. pallidiceps, the species which while large and distinctive is essentially not very different from *A. leucopterus* (see p. 314), seems also to be a derivative of nominate *A. leucopterus*. Its occurrence in an isolated small valley doubtless prevented it from being absorbed into the population now constituting *A. l. dresseri*.

A. nationi, the species of the western slopes of the Peruvian Andes, probably originated in a manner similar to that of *A. leucopterus*. A likely site would be some place within the area of northern Peru now occupied by *A. n. seebohmi*. *A. n. simonsi*, and *A. n. celicae* if it is a valid subspecies, are only slightly differentiated from *A. n. seebohmi* and probably are recent derivatives of that form. Because these races are restricted to somewhat higher altitudes and are less adaptable to a variety of habitats than is *A. l. dresseri*, they may be more recent arrivals. The partial sympatry of *A. albiceps* (see below) further suggests this to be the case.

A. n. nationi and *A. n. brunneiceps*, two similar races that are abruptly and well differentiated from the three northern races of the species, seem to have been separated from the parent stock earlier. On the other hand, their distinctive characters (dark heads, brownish backs) could be the result of recent and minor genetic differences. *A. albiceps* may cast a light on this problem.

Immature *A. albiceps* is quite similar to nominate *A. nationi* and *A. n. brunneiceps.* The most conspicuous difference is that *A. albiceps* has a white alar speculum, a character entirely lacking in the species *nationi* and that immediately suggests affinity with *A. leucopterus.* Although conspicuous, the presence or absence of a wing patch is undoubtedly the result of a very small genetic difference. For example, nominate *A. schistaceus* has such a patch but its races do not. A similar situation is found in *A. rufinucha.* The race *latinuchus* has a speculum, whereas the other races lack it. Such a character can be of no value in determining specific affinities.

The presence of scattered white feathers on the heads of *A. n. nationi* and *A. n. brunneiceps* further suggests a tendency toward *A. albiceps.* It seems to me that *A. albiceps* was the earliest offshoot of *A. nationi* and that the dark-crowned races of *A. nationi,* with their scattered white feathers, are examples of an early stage of differentiation. In other words, in the process of differentiating, *A. albiceps* probably passed through a stage resembling that of *A. n. nationi* and *A. n. brunneiceps* and, given time, these two races may come to resemble *A. albiceps.*

The fact that *A. albiceps* regularly occupies a drier habitat than any other taxon within the group, with the exception of *A. pallidiceps,* may indicate that it entered northern Peru and southern Ecuador early, when the area was first recovering from a dry period. By having arrived early and having become well differentiated, the path was set for a second invasion of the parental form, *A. nationi.*

Only *A. rufigenis* remains to be considered. On geographical evidence alone one would postulate its derivation from *A. schistaceus.* The species is big and distinctive, but again the magnitude of the morphological differences probably does not reflect large genetic differences. As we have seen in *A. n. nationi* and *A. n. brunneiceps,* the loss of head pattern occurs readily. Size is an even more plastic character. Nominate *A. rufigenis* appears to have resulted from the isolation of a population of *A. schistaceus,* or its forerunner, in the arid upper Marañón valley. This could have occurred during a cold-dry interlude when *A. schistaceus* was retreating to the forest refuges on the Amazon slope. The valley is considerably lower than the surrounding mountains and could have served as a refugium. While there was little precipitation, the river may have supported ample vegetation for the continued existence of the bird. This would have been similar to the restricted habitat of *A. pallidiceps* nowadays.

It is less easy to account for the existence of the small isolated population *A. r. forbesi,* which is phenotypically quite similar to nominate *A. rufigenis.* I am, however, unable to picture a situation that would have allowed either taxon to have been derived from the other and that would not have involved resorption into *A. schistaceus.* I believe, instead, that this may be a situation where two peripheral isolates have responded morphologically to their isolation in a similar manner.

Perhaps one of the most interesting points revealed by this study is that while Haffer developed his theory of forested refugia to account for the origin of the varied avifauna of the tropical zone of the lower Andean slopes and adjacent lowlands, these refugia must have extended high in the Andes, at least to the subtropical zone, where they had an important role in differentiating various taxa within the *Atlapetes schistaceus* group (and doubtless among many species and genera yet to be studied). However, in addition to the large refugia extending from the tropical lowlands well up into the Andes, smaller refugia must have occurred in moist pockets at high altitudes, and it is these localized refugia that led to the differentiation of the less widely distributed taxa, such as *A. pallidiceps*, *A. leucopterus*, and *A. nationi*.

SUMMARY

Atlapetes schistaceus, *nationi*, *leucopterus*, *rufigenis*, *albiceps*, and *pallidiceps*, from the northern Andes, are believed to have arisen from a common ancestor during the Pleistocene. They form the *A. schistaceus* species-group.

A. schistaceus, the most widely distributed of the six species, has a disjunct distribution from Venezuela to eastern Ecuador and eastern Peru. It occurs in the subtropical and temperate zones at altitudes from 1,850 to 2,500 m. Six races are recognized. The present distribution closely approximates the assumed locations of interglacial forest refugia. The species apparently arose during a cool-wet glacial period and was restricted, one or more times, to the forest refugia during warm-dry intervals. It seems unable to expand into more recently available suitable habitats because of competition from related species.

A. nationi ranges on the western slopes from southern Ecuador to southern Peru, in the temperate and arid subtropical zones, at altitudes from 1,870 to 3,500 m. There are five races. The species appears to be the southwestern counterpart of *A. schistaceus*. It probably was derived from a population of ancestral *schistaceus* that was isolated in a moist pocket in northern Peru during a warm-dry period.

A. leucopterus occurs only on the western slopes from northern Ecuador to northern Peru in both the humid and arid subtropics and in the arid temperate zone, from 600 to 2,900 m. There are two well-differentiated races. The taxon seems to be the northern and central counterpart of *A. schistaceus* on the western slopes. Probably it was derived from an ancestral population left in a refuge in west-central Ecuador in a dry interval. The southern race is phenotypically highly variable and probably is a recent amalgam of isolated populations.

A. rufigenis is restricted to the eastern slope of Peru, in the drainage system of the Río Marañón and valley of Río Pampas. It occurs in the arid subtropical and humid temperate zone (a race in each) between 2,750 and 4,000 m. The species probably was formed from populations of *A. schistaceus*, or its forerunner, isolated in moist valleys during an interglacial period.

Monotypic *A. albiceps* occurs on the lower western slopes of southern Ecuador and northern Peru at altitudes between 250 to 1,500 m in the moderately arid subtropical zone. It is partially sympatric with *A. leucopterus* and *A. nationi*. It is fairly distinctive and is believed to have been an early derivative from *A. nationi*.

Monotypic *A. pallidiceps* is endemic to the arid valley of the upper Río Jubones of southeastern Ecuador, at altitudes from 1,500 to 2,100 m. Although superficially the most distinctive taxon of the species-group, it is believed to have been derived from nominate *A. leucopterus*.

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Bulletin OF THE
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Carboniferous Stem-Reptiles of the Family Romeriidae

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OR DISTRIBUTED BY THE
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BREVIORA 1952–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
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CARBONIFEROUS STEM-REPTILES OF THE FAMILY ROMERIIDAE

ROBERT L. CARROLL[1] AND DONALD BAIRD[2]

CONTENTS

ABSTRACT. The Family Romeriidae is ancestral to most, if not all, advanced reptilian groups. This family is known from the early Pennsylvanian to the early Permian. The species *Hylonomus lyelli* and *Paleothyris acadiana* are well represented among tree stump faunas in deposits of early and middle Pennsylvania age. Four additional species are known from individual but nearly complete specimens from Middle Pennsylvanian coal swamp deposits: *Cephalerpeton ventriarmatum*, Westphalian D of Mazon Creek, Illinois; *Anthracodromeus longipes* (new genus), latest Westphalian D of Linton, Ohio; and *Brouffia orientalis* and *Coelostegus prothales* (both new genera) from deposits of equivalent age from Nýřany, Czechoslovakia. Other members of this group are represented by less complete remains. Several distinct lineages may be recognized within this family, characterized by differences in patterns of the bones of the skull roof, the dentition, the number and configuration of the vertebrae, and the proportions of the limbs. The diversity within the group suggests the initial differentiation of the later, more specialized reptilian groups. All romeriids are small, insectivorous forms that apparently lived in a fairly wide range of terrestrial environments. The family was the most numerous and diverse in the Middle Pennsylvanian; by the early Permian the group was largely replaced by more specialized descendants.

INTRODUCTION

The earliest mammals are known primarily from very incomplete material—teeth and even fragments of teeth, edentulous jaws, and partial skulls. The relationship among the various groups of Mesozoic mammals is subject to continuing revision, and the specific ancestry of the Tertiary orders is equally contentious. Despite the much greater age of the relevant fossils, there is a surprisingly good record of the early reptiles. Fortunately, the best known group is the family Romeriidae, which is ancestral to most, if not all, higher reptilian taxa. Specimens have been described recently from the Lower Pennsylvanian of Joggins, Nova Scotia (Carroll, 1964), and the Middle Pennsylvanian of Florence, Nova Scotia (Carroll, 1969a). From these forms the basic anatomy of the family is well established. Numerous other genera can now be recognized as belonging to this group. They indicate a considerable range of variability in the patterns of the skull roof, the nature of the dentition, the shape of the vertebrae, and especially in limb proportions. The specializations seen within this group may presage the more significant adaptive changes that occurred within the early evolution of the higher reptilian

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lineages. It is therefore of considerable importance to describe the various romeriids in detail. At least a dozen genera are known, from the Lower Pennsylvanian to the Lower Permian of North America and Europe. For various reasons, it is more practical to consider the Pennsylvanian and Lower Permian genera separately. Only the earlier members of the group will be described in this paper.

The best known of the Pennsylvanian romeriids were discovered in upright tree stumps at Joggins and Florence, Nova Scotia. In these localities, romeriids are relatively common members of the fauna. Romeriids can also be recognized in the coal swamp localities of Linton, Ohio, and Nýřany, Czechoslovakia, and from Mazon Creek, Illinois. Here romeriids are very rare, with no more than a single specimen of any particular species being recognized. Several of the romeriids from these localities have been described previously, but their anatomy typically was not known in sufficient detail to establish their identity. New techniques of preparation and an increase in knowledge of other Paleozoic reptiles makes revision of these forms necessary.

Museum abbreviations. Specimens from various institutions are indicated by the following abbreviations: AMNH: American Museum of Natural History; BM(NH): British Museum (Natural History); ČGH: National Museum, Prague, Czechoslovakia; MB: Humboldt Museum, Berlin, German Democratic Republic; MCZ: Museum of Comparative Zoology, Harvard; MP: Mestké Museum Historicté, Pilzen, Czechoslovakia; YPM: Yale Peabody Museum.

ACKNOWLEDGMENTS

All of the specimens described in this paper were preserved, to a greater or lesser extent, as natural molds in coal shale or ironstone and have been studied by the use of latex casts. We are very grateful for permission to prepare and cast material from various institutions. Dr. and Mrs. James Brough were very kind in permitting the senior author to study specimens from Czechoslovakia that were in their possession, and for allowing additional casts to be made. Dr. A. Charig arranged for these casts to be prepared by the British Museum (Natural History), after obtaining permission from the museums in Prague and Pilzen, Czechoslovakia, from which they had originally been borrowed. Dr. J. T. Gregory, then of Yale University, permitted the junior author to prepare a cast of the type specimen of *Cephalerpeton ventriarmatum.* Dr. E. H. Colbert, then of the American Museum, allowed the type of *Anthracodromeus longipes* to be prepared with hydrochloric acid and cast in latex. Dr. H. Jaeger of the Humboldt Museum was very helpful in allowing the senior author to prepare casts of numerous specimens from the Carboniferous coal swamp fauna of North America and Europe. The specimens have been painstakingly drawn by Mrs. Pamela Gaskill. The photographs were prepared by David C. Stager. Several drafts of the manuscript were typed by Mrs. D. Alison. The work was supported by grants from the National Research Council of Canada, the American Philosophical Society, the Jeffries Wyman Fund of Harvard University, and the William Berryman Scott Research Fund of Princeton University.

SYSTEMATIC DESCRIPTIONS

Class *REPTILIA*
Subclass *ANAPSIDA*
Order **COTYLOSAURIA**
Suborder **CAPTORHINOMORPHA**
Family ROMERIIDAE
Genus *Cephalerpeton* Moodie, 1912: 349
Species *Cephalerpeton ventriarmatum* Moodie, 1912: 350

Holotype. Yale Peabody Museum No. 796. This is the only known specimen.

Horizon and locality. Mazon Creek, Grundy Co., Illinois. Francis Creek Shale above Morris (no. 2) Coal, Carbondale

Formation, Westphalian D, Middle Pennsylvanian.

Revised diagnosis. Romeriid captorhinomorph, known at present from a single, incomplete, immature specimen. Teeth of upper jaw much larger and fewer in number than in other romeriids. Sixteen teeth in maxilla, four "pre-canines," two "canines," and ten "cheek" teeth. Size of cheek teeth variable, with some larger than canines. Approximately 24 teeth in dentary, which are smaller than those in maxilla and alternate with them in length. Large teeth show labyrinthine plication of enamel. Palatal bones covered with shagreen of denticles. Longer denticles arranged in three rows radiating from basicranial articulation. Number of presacral vertebrae not established, 28 estimated. Tall neural spines, rectangular in outline. Neural arches suturally attached to centra. Intercentra large crescents, which may have been continued in cartilage to form complete rings. Scapulocoracoid ossified in three units. Humerus equal in length to five trunk vertebrae. Neither supinator process nor ectepicondylar ridge ossified. Ulna and radius two-thirds the length of the humerus.

Description. Like the Joggins romeriid *Hylonomus*, the Mazon Creek genus *Cephalerpeton* was originally described as a microsaur, and has repeatedly been cited as indicating that this group was ancestral to reptiles. In the initial description (1912 and 1916), Moodie compared the genus with a wide range of forms, most of which are now considered as temnospondyl labyrinthodonts, and placed it in the "microsaurian family Amphibamidae." This classification was followed by Hay (1929).

Gregory (1948) accepted Moodie's assignment of the genus to the Microsauria, but interpreted its anatomy as indicating reptilian affinities. Following Romer's (1950) re-evaluation of the microsaur concept, Gregory (1950) placed *Cephalerpeton* in the captorhinomorph family Protothyrididae [*sic*] (essentially synonymous with Romeriidae). Gregory's work very ably illustrated the basic anatomy of this genus. High-fidelity latex casts, however, provide sufficient additional detail to warrant a new drawing of the specimen (Fig. 1) and information from recently described romeriids from other localities suggests some modifications in his restoration of the skull. A revised reconstruction of the skull was published by Baird (1965, fig. 6), who first formally assigned the genus to the Romeriidae.

The remains include most of the skull, the first 23 presacral vertebrae, the pectoral girdle, fore limbs and the ventral scales. Outlines of the limbs can be seen in the matrix, indicating the extent of the soft tissue and the texture of the skin. The bone itself was represented by a very soft, claylike material that had been removed from the hard, ironstone matrix. The resulting cavities were cast with liquid latex, giving a detailed impression of the original structure (Baird, 1955).

Skull. The skull is preserved so as to expose the inside surface of the roofing bones and the ventral surface of the palate. None of the bones of the posterior margin of the skull roof are visible. The configuration of the supratemporal, tabular, and postparietal can be restored only by analogy with other romeriids. The parietals are present only in part, so that their extent must be judged from the configuration of the other parts of the skull. The cheek, outer portion of the skull roof, and snout are preserved so that the skull as a whole can be readily restored.

As restored (Fig. 2) the skull appears relatively deeper and shorter than in other romeriids. The very large circular orbit is slightly posterior to the middle of the skull. The nature of preservation precludes determination of the pattern of the sculpturing. The position of the sutures shown in the restoration is based almost entirely on their appearance in internal view. The configuration of the bones is close to that seen in other romeriid genera, although the pre- and postfrontals very nearly meet beneath the frontals. In dorsal view, how-

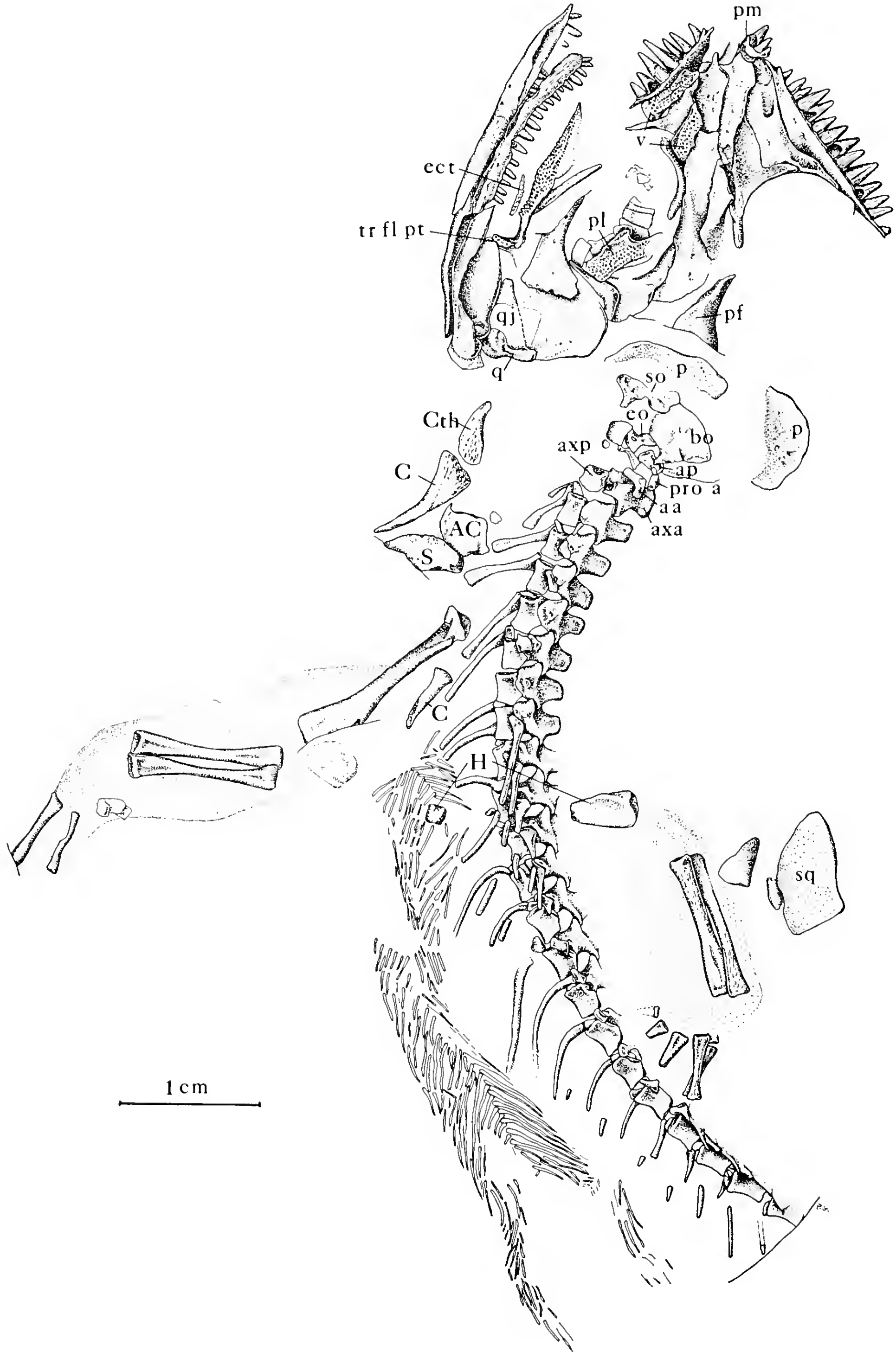


Figure 1. Skeleton of *Cephalerpeton ventriarmatum*. Type YPM 796. × 2. For abbreviations see page 325.

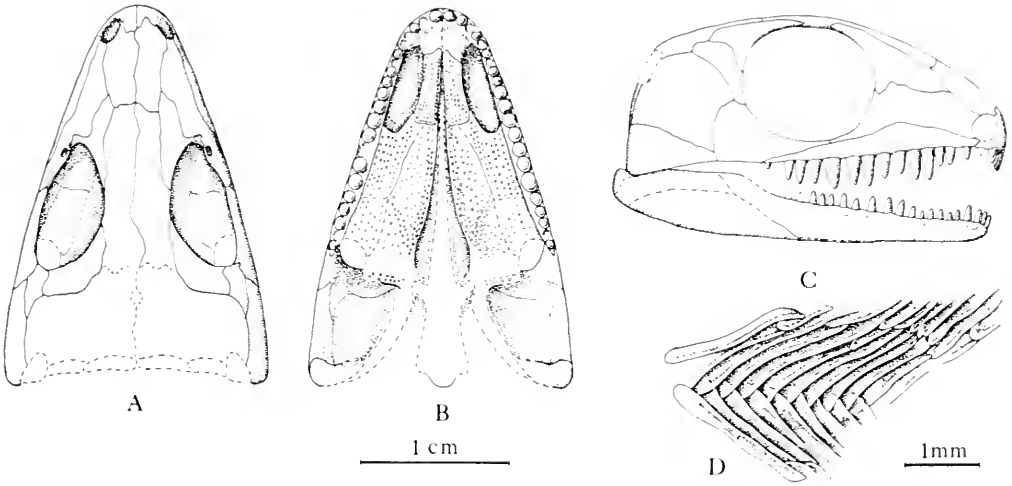


Figure 2. Restoration of skull of *Cephalerpeton ventriarmatum* in A. dorsal; B. palatal; and C. lateral views. × 2. D. Detail of ventral scales in ventral view (somewhat schematic). × 10.

ABBREVIATIONS

AXIAL SKELETON

a—articular
aa—atlas arch
ai—atlas intercentrum
ap—atlas pleurocentrum
axa—axis arch
axp—axis pleurocentrum
bo—basioccipital
d—dentary
ect—ectopterygoid
eo—exoccipital
f—frontal
j—jugal
l—lacrimal
m—maxilla
n—nasal
o—otic capsule
p—parietal
pf—postfrontal
pl—palatine
pm—premaxilla
po—postorbital
pp—postparietal
prf—prefrontal
proa—proatlas
ps—parasphenoid
pt—pterygoid
q—quadrate
qj—quadratojugal
sa—surangular
so—supraoccipital
sq—squamosal
SR—sacral rib
st—supratemporal
tr fl pt—transverse flange of pterygoid
v—vomer

APPENDICULAR SKELETON

A—Astragalus
AC—Anterior coracoid
C—Clavicle
Ca—Calcaneum
Cth—Cleithrum
F—Fibula
H—Humerus
I—Ilium
IC—Interclavicle
P—Pubis
S—Scapula
T—Tibia

ever, the frontals have fairly wide exposure above the orbits. One apparent difference from other genera is the great width of the parietals. This is not sufficiently well established to be strongly emphasized, however. A number of typical sclerotic plates can be seen in the right orbit. The most significant feature of the skull is the dentition. The entirety of the left maxilla is exposed. Fourteen teeth are in place with room for two others. This is far below the number in *Hylonomus* (36) or *Protorothyris* (30). Even *Romeria* has room for 21. Like these genera, the most anterior teeth (four in this genus) of *Cephalerpeton* are small, and the next two are large "canines." The remaining teeth are not uniformly small, but of large diameter and variable length. The sixth from the rear is the largest of all. All the teeth are conical and bluntly pointed. The largest show definite labyrinthine infolding at their bases. This feature indicates clearly that the presence or absence of plication of the enamel is not significant to the origin of reptiles. This feature apparently is related primarily to the size of the teeth. *Limnoscelis* and *Solenodonsaurus* have large teeth with labyrinthodont infolding. Most romeriids have small teeth that lack this feature. *Cephalerpeton* might be said to be the exception that proves the rule. The sixth, ninth, and twelfth teeth are deeply eroded at the base, preparatory to replacement.

The premaxillae are not well exposed. Their general configuration can be determined from the restoration of other parts of the skull. There was room for approximately five teeth. Two are present on the left side. They are longer than the most anterior maxilla teeth but smaller than the "canines." In an earlier restoration (Baird, 1965, fig. 6) *Cephalerpeton* is figured as having an overhanging premaxilla, as in *Romeria* and the captorhinids. The configuration of the remainder of the skull makes such a restoration unlikely.

Neither the parasphenoid nor any of the anterior portion of the braincase is preserved. Both vomers and the right palatine, as well as the medial portions of the right pterygoid and ectopterygoid, are present. From these bones the palate can be almost completely restored. The general pattern resembles that of other romeriids. As was noted by Gregory, the base of the transverse flange of the pterygoid is clearly visible. A very interesting feature is evident in the pattern of the denticles. They cover the vomers and palatine bones in uniform rows. Most of the pterygoid is covered as well, but not uniformly. The margin of the transverse flange is outlined in large denticles. The anterior surface is only sparsely covered. Those on the palatal ramus appear to be uniform, but close examination shows that those on the medial margin of the bone and those extending in a line running anterolaterally from the area of the basipterygoid articulation are slightly raised above their surroundings. This is evidently an early stage in the evolution of the distinct radiating ridges of denticles seen in *Paleothyris, Protorothyris*, and most members of other primitive reptilian groups.

Only the posterolateral portion of the right quadrate is preserved. The articulating surface resembles that of other small captorhinomorphs. The epipterygoids are not preserved.

Behind the skull can be seen elements of the rear of the braincase: supraoccipital, basioccipital, and exoccipital. None are sufficiently well exposed for detailed comparison with other early reptiles. All appear to follow the general pattern seen in other romeriids.

The anterior end of the left lower jaw is exposed in lateral view. The dentary is sculptured in a pattern of shallow irregular pits. The right lower jaw is seen in medial aspect. The most notable feature is the presence of a retroarticular process extending one or two millimeters behind the articulating surface. Eighteen teeth can be seen in the left dentary. There is room for approximately four more in this series. About two additional teeth were probably present at the rear of the jaw to correspond with those in the maxilla. A total of 24 teeth in the lower jaw is three more than the number suggested for the maxilla and premaxilla. The length of the teeth in the lower jaw alternates with that seen in the upper. The most anterior dentary teeth are short. The length increases to fit into a series of short teeth at the front of the maxilla. The length of successive teeth decreases to accommodate the long canine fangs and then increases behind them. This arrangement probably served as a very efficient device for holding and piercing the bodies of small invertebrates.

Postcranial skeleton. Twenty-three vertebrae are in position behind the skull. The greater number (25 or 26) suggested by Gregory apparently resulted from inclusion of some of the occipital elements among the cervical series. Nothing of the pelvic girdle or rear limb is preserved. In other romeriids, the last five or six pairs of trunk ribs are conspicuously shorter than are those further anterior. The last preserved rib (the 22nd) in *Cephalerpeton* is similar in size and shape to those just anterior to this short series. This would suggest approximately six more pairs. A count of 28 presacral vertebrae is intermediate between that observed in *Hylonomus* (26) and *Paleothyris* (32). Such a count is consistent with a constant head trunk ratio of approximately 1:3.1 in these three genera. (Two romeriid genera from Nýřany, Czechoslovakia, however, have a head trunk ratio of approximately 1:2.8.) The first two vertebrae are specialized cervicals, very similar to those described in *Paleothyris*. The right proatlas, seen more or less in its natural position, is a small oval bone. The atlas intercentrum is not recognizable. It may be represented by a small bone fragment below the right atlas arch. The atlas centrum can be seen just anterior to the right proatlas. It is a flat-ended cylinder, indented dorsally for the neural canal. It apparently incorporates the tissue that, in pelycosaurs, develops as a separate axis intercentrum. The paired atlas arches are small, L-shaped bones. They do not appear to have had very extensive areas of contact with the centrum. The area of attachment for the tuberculum of the first cervical rib is not preserved. The anterior margin of the axis centrum is not complete. This is the longest centrum in most primitive reptiles. Restoration of the remainder of the cervical region in *Cephalerpeton*, however, indicates that it is no longer than the immediately successive centra. The axis neural arch is very long and high. It is only suturally attached to the centrum, not fused as in other early reptiles. This is probably the result of the immaturity of this particular specimen.

The remaining trunk vertebrae follow a standard pattern. There are large, high-spined neural arches, suturally attached to cylindrical centra. The intercentra are fairly wide crescents. The anterior margin of the arch somewhat overlaps the anterior dorsal margin of the centrum, in a similar fashion, but to a lesser degree than that noted in *Gephyrostegus* (Carroll, 1970a). This feature suggests that the intercentra were probably continued in cartilage to form narrow cylinders.

No ribs are present in association with the atlas. They are present on all more posterior vertebrae. All are clearly double headed, but without the great degree of separation noted in *Seymouria*. The anterior ribs have flattened, but not expanded, blades, which extend posteriorly as well as ventrolaterally. More posteriorly, the shaft is cylindrical and extends primarily ventrally. The length increases to about the tenth rib and then decreases gradually as far as the last preserved presacral.

The pectoral girdle lies in the area of the third to fifth vertebrae. The interclavicle is not preserved. The right clavicle lies in essentially its natural position relative to the endochondral shoulder girdle. The left is posterior to the right humerus. The bones are small, with the blades well sculptured with radiating grooves. Near the right clavicle is another sculptured bone. It might conceivably be a displaced supratemporal, but it is considerably larger than that element in other romeriids. More probably it is the blade of the cleithrum. It is unusually large for this bone also but it is more or less in the correct area. It is sculptured in a similar manner to the clavicle.

Three elements of the endochondral shoulder girdle are preserved, two in the area of the clavicle, and the third at the distal end of the right humerus. Those near the clavicle are unquestionably the right scapula and anterior coracoid in almost their natural positions relative to one another (although upside down relative to the remainder of the skeleton). The entire girdle can be reconstructed according to the pattern of the pelycosaurs. The third element is not well enough preserved to establish its identity. It might be either the left procoracoid, or one of the posterior coracoids. These elements are very incompletely ossified, suggesting that *Cephalerpeton* was very immature. The dorsal end of the scapula is buried in the matrix. It must have been much more extensive both dorsally and anteriorly in the mature animal. A foramen pierces the bone just above the glenoid. The procoracoid is roughly circular in outline. The posterior margin is largely occupied by the anterior face of the glenoid. Beneath this structure is the coracoid foramen. The scapulocoracoid in most romeriids that have been described is preserved as a single ossification. The tripartite structure as seen in *Cephalerpeton* probably has no taxonomic significance. The presence of one or more coracoids in pelycosaurs, procolophonids, and other reptiles may have resulted from prolongation of the pattern of development seen originally only in immature animals.

The humerus, despite the incomplete ossification of the articulating surfaces, is the length of five trunk centra. It is a lightly built bone with the distal extremity expanded flatly. The entepicondylar foramen is an elongate opening. The ulna and radius are present in close association on both sides. As a result of the low degree of ossification they appear almost identical. They are approximately the length of four trunk vertebrae. The ends are almost equally expanded. The shaft of the ulna is slimmer than that of the radius. There is little, if any, ossification in the area of the carpals. There is one element that might be a distal, but could also be a fragment of a metacarpal or phalanx.

The largest metacarpal is almost half the length of the ulna or radius. Neither the digital nor phalangeal formula can be established. The elements present indicate that the hand was very long, as are all elements of the forelimb.

Skin and scales. The skin impressions along the forelimb have a slightly pebbly texture—rougher than the limb bones but smoother than the broken surface of the matrix. There is no evidence of discrete scales. An indication of epidermal scales would be expected in this type of preservation, if they were present in the animal. This suggests that this specimen of *Cephalerpeton* lacked epidermal scales. Some indication of dorsal dermal scales appears in the reptilelike anthracosaurs *Gephyrostegus* and *Eusauropleura.* Dermal scales are apparently lost early in reptilian evolution. Unfortunately, epidermal scales can only be recorded as impressions and this type of preservation is rare and apparently not reported in other Paleozoic reptiles. There is no record sufficiently early to indicate the time at which epidermal scales evolved. There may have been a period during which dermal scales were completely lost, but epidermal scales had not yet evolved.

The ventral dermal scales are preserved in this specimen of *Cephalerpeton.* The overall pattern is similar to that of other primitive reptiles: a series of overlapping scales forming a chevron pattern, the apex of which points anteriorly. The detailed configuration and pattern of overlap is somewhat difficult to see in either of the photographs (Plates I and II) or the draw-

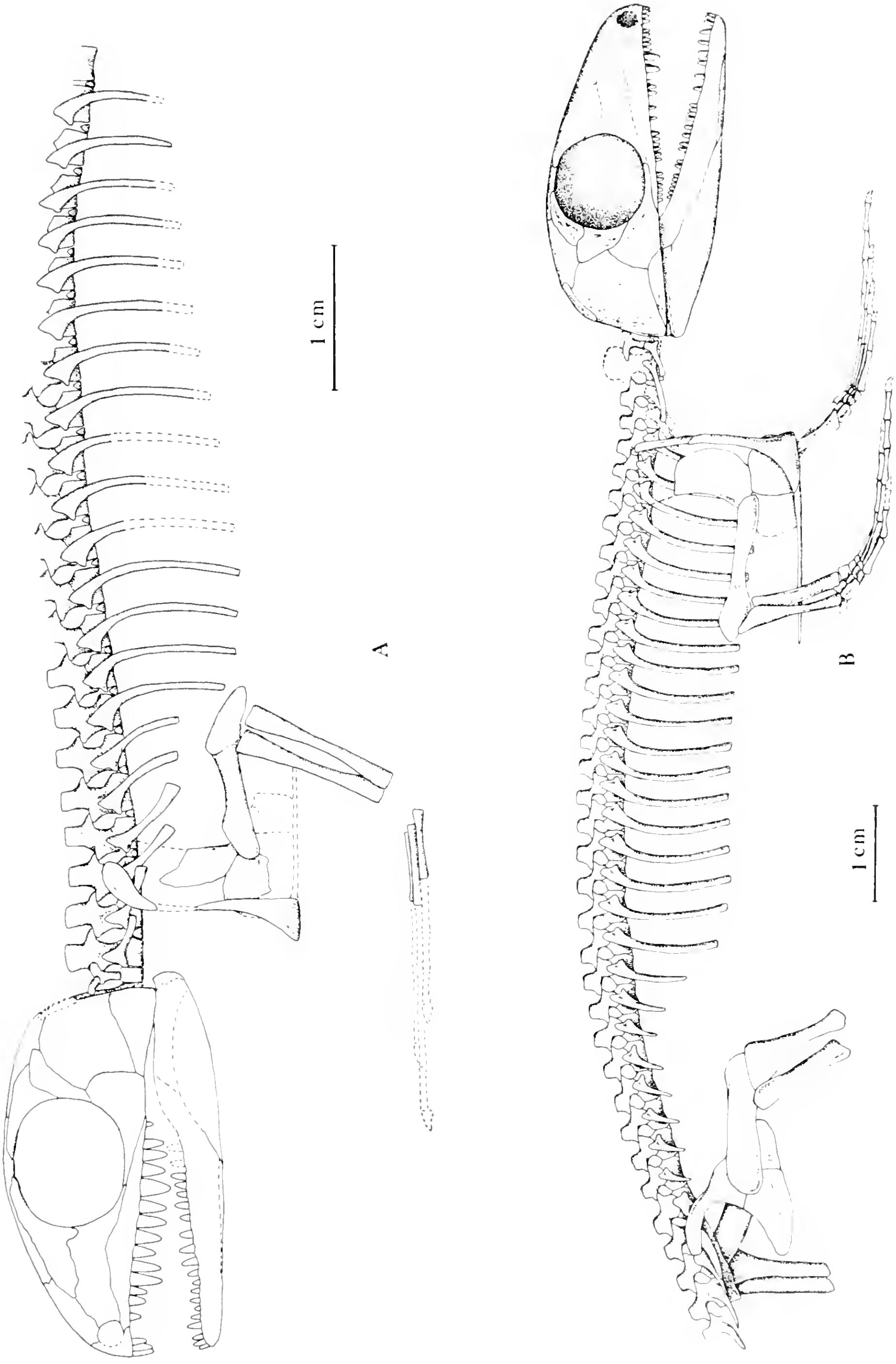


Figure 3. A. Restoration of the skeleton of *Cephalerpeton ventriarmatum*. × 2. B. Restoration of *Brouffia orientalis*. × 1.33.

ings, owing to the nature of preservation. The narrow rodlike structures that are visible are the posterior ridges of the scales, and the remainder of the surface is largely covered by matrix.

Small sections of the squamation have been illustrated in a slightly schematic manner in Figure 2D. The covering of scales is contiguous, in fact overlapping, rather than in the form of an open lattice. The medial ends of the scales overlap in an alternate fashion at the midline. The distal end of the medial scales overlaps the proximal end of the more lateral ones. Posteriorly, there are isolated scales that come from a third row.

Discussion. The absence of the posterior portion of the skull roof, the pelvic girdle, and the rear limb as well as the immaturity of the only known specimen make it difficult to compare *Cephalerpeton* with other romeriids. The most notable feature is the dentition, which immediately distinguishes this genus from all other members of the family (except *Anthracodromeus*, in which the dentition is not known). The reduction in the number of teeth and the increase in size of the postcanines indicate a significant change in diet from the primitive pattern. The cheek teeth in most romeriids were presumably employed primarily to hold and squash the prey. In *Cephalerpeton* they would be efficient for piercing the prey as well. A similar dentition is developed in the small and primitive eothyridid pelycosaurs. No later romeriids have such a pattern. This suggests that this particular feeding specialization may have been usurped by small pelycosaurs that had the advantage of a more sophisticated jaw musculature. The primitive distribution of the palatal denticles and the structure of the vertebrae suggest that the ancestors of *Cephalerpeton* diverged from the main romeriid lineage early in the Pennsylvanian. This genus might have evolved directly from *Hylonomus* or possibly from a slightly more primitive form. The dentition is too specialized for *Cephalerpeton* to have given rise to any of the known genera from the later Pennsylvanian or Permian.

Anthracodromeus n. gen.

Type species. Anthracodromeus longipes (Cope), new combination.

Known distribution. Middle Pennsylvanian of North America.

Etymology. Greek: *anthracos*, coal, plus *dromeus*, runner.

Diagnosis. Romeriid captorhinomorph. Thirty-one presacral vertebrae. One pair of sacral ribs. Neural arches anteroposteriorly elongate, lateral surfaces "sculptured." Pattern of bones of the posterior skull roof and nature of sculpturing very similar to those of *Paleothyris* and *Protorothyris*. Blade of ilium very long. Limbs long relative to body size; humerus and femur equal in length to eight trunk centra; radius and tibia equal in length to four trunk centra. Hands and feet very long.

Anthracodromeus longipes

Sauropleura longipes Cope, 1874: 270.
Tuditanus longipes Cope, 1875: 398–399, pl. XXVI, fig. 2; Moodie, 1916: 89–91, fig. 20.

Holotype. American Museum of Natural History (AMNH) 6940. Almost complete skeleton preserved in counterpart blocks. This is the only known specimen.

Horizon. Canneloid shale underlying Upper Freeport Coal, Allegheny Group, Middle Pennsylvanian, equivalent to the latest Westphalian D of Europe.

Locality. Diamond Mine, Linton, Saline Township, Jefferson County, Ohio; NE corner, sect. 13, T.9N., R.2W.

Diagnosis. Same as for genus.

Description. Although the Linton fauna has been studied for over a hundred years and scores of amphibian genera have been described, no true reptiles had been recognized. *Tuditanus punctulatus* has been referred to that class by several workers, but recent study has established that it is unquestionably a microsaur (Carroll and Baird, 1968). It is not surprising that reptiles are rare at this locality, considering the nature of the deposition and the aquatic and semi-aquatic adaptations of the amphibians. Judging from our knowledge of events leading up to the origin of reptiles (Carroll, 1967 and 1970b), the early members of that group were apparently primarily terrestrial in habit. Some aquatic lineages may have evolved later among primitive reptiles, but none are known in the Middle Pennsylvanian. As a result of a large-scale, systematic effort to prepare all material that has been found from the Linton locality, several specimens have been discovered that are definitely reptilian. Most of these are pelycosaurs and are being studied by Reisz; the single known romeriid consists of an almost entire skeleton preserved in counterpart blocks. The method used for preparing this material has been described by Baird (1955).

Like many of the specimens from Linton, this genus has a complex taxonomic history. It was initially described by Cope (1874) as one of numerous species of the genus *Sauropleura*, the type species of which is a nectridean. Cope was no doubt led to this initial identification by the configuration of the neural spines. He later placed it in the ill-defined genus *Tuditanus*. Moodie, in his 1916 monograph, accepted Cope's identification as a species of *Tuditanus* and noted the presence of ventral chevrons. In 1930, Romer identified the specimen as a coelacanth, largely on the basis of undoubted coelacanth scales that lie close to it on the block. Upon preparing the specimen, Baird (1958) diagnosed it as a romeriid reptile on the basis of skull characters, noting its close affinities to the Permian genus *Protorothyris*; he assigned the species tentatively to *Cephalerpeton* pending further study. Analysis of the specimen has been difficult, however, because extreme crushing has reduced the bones to paper-thinness. Mrs. Pamela Gaskill has contributed greatly to this work by her careful drawing of the specimen (Fig. 4). The skeleton is virtually complete, lacking only the skull anterior to the orbits, the ventral portion of the shoulder girdle, and the end of the tail.

Skull. The posterior portion of the skull is crushed so that the dorsal skull roof is exposed in one block and the right cheek region is seen in the other. None of the dentition can be seen and the posterior portion of the palate is completely covered by other bones. The bones at the posterior margin of the skull roof have a configuration similar to those seen in *Protorothyris*. The parietal extends a narrow lateral lappet over the top of the squamosal. Posteriorly the bone is deeply embayed for the supratemporal, tabular, and postparietal. These bones are spread out behind the skull roof. The supratemporal is in the shape of an elongate oval superficially sculptured, which must have extended ventrally over the posterior margin of the squamosal. The tabular was overlapped dorsomedially by the postparietal. Ventrally it is notched where it surrounds the posttemporal fenestra. The postparietals are simple oblong bones, smooth-surfaced like the tabulars. The supraoccipital is displaced slightly to the left of the midline behind the skull. It is incised laterally for the posttemporal fenestra. Dorsally the bone is marked by indentations where it was overlapped by the postparietals. Medially a narrow ridge extends dorsally between these bones. The dorsal margin of the foramen magnum is covered by the right exoccipital. The left exoccipital overlies the left margin of the supraoccipital, with the medial surface uppermost. The basioccipital is not visible. The right otic capsule may be represented by an ill-defined ossification visible behind the squamosal. The stapes may also be crushed into this area. The occipital surface may be restored according to the pattern of the other, better articulated romeriids.

The configuration of the bones of the cheek region and posterior parts of the jaw is essentially similar to that seen in other romeriids. The right quadrate has been forced out behind the quadratojugal. As in

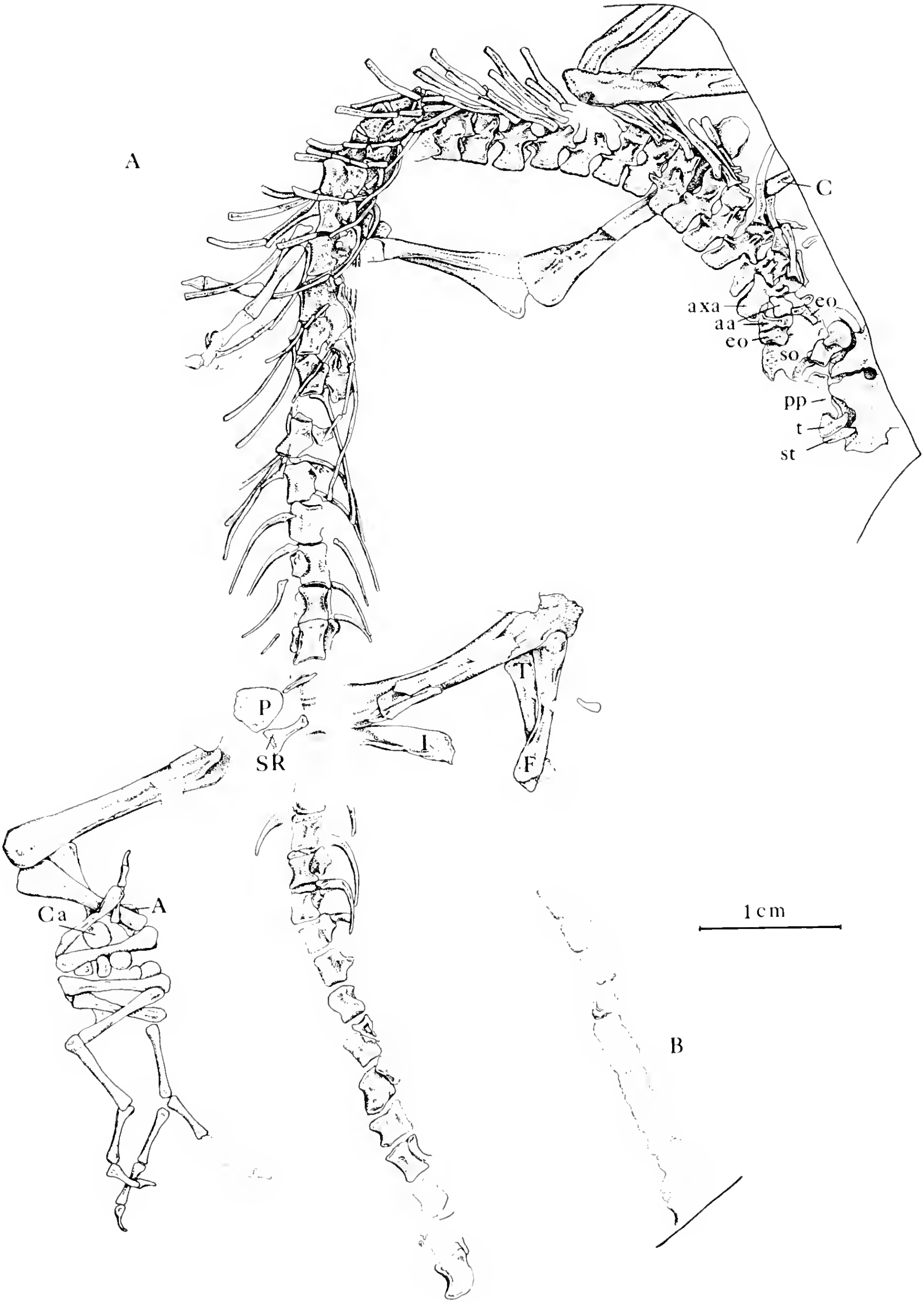


Figure 4. A–C. Counterparts of skeleton of *Anthracodromeus longipes*. Type AMNH 6940. × 2. B. Distal end of tail.

Protorothyris, the ventrolateral margin of the articulating surface was probably exposed laterally beneath this bone. The posterior margin of the squamosal was exposed on the occipital surface and is clearly demarked from the lateral surface. The sculpturing seen on the cheek region and dorsal surface of the posterior skull roof is very similar to that seen in *Protorothyris*, a series of relatively uniform, shallow pits. The outline of the skull may be restored on the basis of the known posterior portion and the general pattern of other romeriids. It may reasonably be reconstructed as having a length equivalent to that of nine or ten trunk vertebrae. There is no way of judging the nature of the dentition.

Postcranial skeleton. The vertebral column lies in more or less natural articulation behind the skull and extends to approximately the 24th caudal. There are 31 presacral vertebrae and one sacral. The tail probably had at least 12 more segments posterior to those that are present.

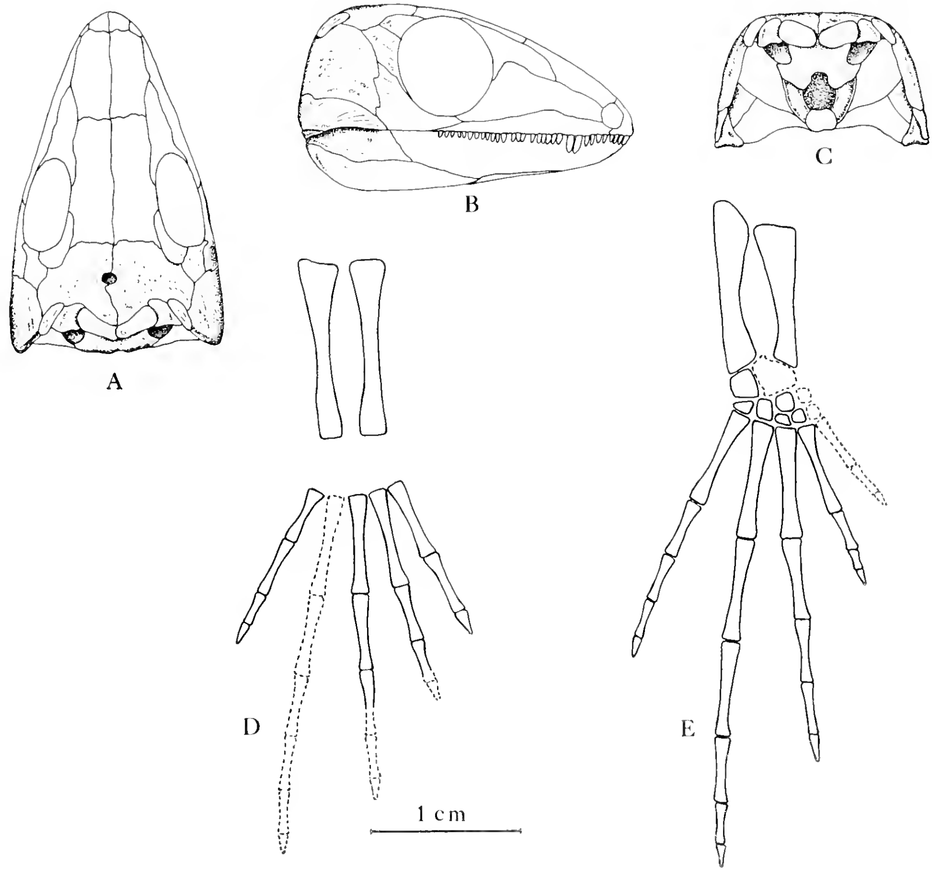


Figure 5. *Anthracodromeus longipes*. Restoration of skull in: A. dorsal; B. lateral; and C. occipital views. Unshaded areas are hypothetical. D. and E. Restoration of hand and foot. × 2.

The elements of the atlas-axis complex are somewhat disarticulated and partially obscured by the scattered bone of the occipital complex. The proatlas is not evident. The left atlas arch is preserved in essentially its normal position although its lateral surface is obscured by an unidentified bone fragment. Ventrally there is a well-developed lateral ridge that ends distally in an area for the articulation of the tuberculum of the first rib. The right atlas arch can be seen in medial view anterior to the dorsal margin of the axis neural spine. Ventrally there is a distinct surface for articulation with the centrum. Posteriorly there is an elongate portion that articulates with the anterior zygopophysis of the axis. As in other romeriids, the atlas lacks a spine. Neither the atlas intercentrum nor pleurocentrum can be identified. The axis, like that of other romeriids, has a large spine, fused to the centrum and overhanging the posterior margin of the atlas. The spine of this and all subsequent trunk vertebrae is narrow from side to side and marked by delicate pitting. All the spines have the appearance of metal, gently tapped by a ballpeen hammer. An identical pattern has been observed on an unnamed (but probably closely related) form from the Lower Permian of Texas (MCZ 1474). The large size of the neural spines probably contributed to the stability of the vertebral column by being deeply embedded in the axial musculature. Posterior to the twenty-third vertebra, the arches and spines are crushed down into the neural canal. The hatchet-shaped outline observed in the anterior segments probably continued at least to the sacral region, but there is no evidence for the more posterior elements. The arches are very narrow at the base with no evidence of the swelling noted in later captorhinomorphs. The transverse processes of the anterior vertebrae are narrow and extend a considerable distance ventrolaterally from the arch. More posteriorly the length diminishes and the configuration corresponds more closely to that seen in other Pennsylvanian romeriids. In none of the vertebrae is the area for articulation with the capitulum of the rib evident. The neural arches are strongly attached to the centra throughout the column. Only where there has been severe crushing have the elements been disarticulated. Where this has occurred, the typical line of sutural attachment in other primitive reptiles has been disclosed. Throughout the column, the pleurocentra are elongate cylinders, deeply indented at the ends for the notochord. The anteroventral margin is notched for the reception of the intercentrum, which appears as a narrow crescent. This element is rarely visible. It is unlikely that this bone continued dorsally in cartilage, as has been suggested for *Cephalerpeton.*

The sacral vertebra is specialized only in the larger size of its transverse process. A thin piece is broken from the dorsal block, so that posterior to the sixth caudal the tail is visible only ventrally. Well-developed intercentra are visible anterior to the first four caudals. No intercentral elements are evident in the succeeding three segments. Between the seventh and eighth is a typical haemal arch. No other haemal arches can be recognized. The first eleven caudal centra resemble those in the trunk region, except for their gradually diminishing size. More posteriorly, the preservation is too poor for even the number of segments to be determined with any assurance.

Ribs are present throughout the column. The first three pairs of cervical ribs have flattened blades and extend posteriorly as well as ventrolaterally. They are clearly double-headed. More posteriorly, the ribs extend primarily ventrolaterally and the shafts are essentially cylindrical, although they are crushed flat in the specimen. The length of the shaft increases rapidly to the eighth rib and then remains approximately the same back to the 24th segment, after which it decreases. The last three pairs of ribs are particularly short. The last several pairs of presacral ribs are short in all romeriids, but the specific number of short ribs varies from genus to genus.

There is only a single pair of sacral ribs. The tubercular head is much thicker than that of other ribs. The area of the capitular head is not visible. The blade is short and spatulate, like that of *Paleothyris.* Unlike that genus, the next succeeding rib does not contribute to the attachment of the pelvis. The first six caudal vertebrae have fused ribs which extend posteriorly to lie alongside the column. The length increases from the first to the third and then decreases rapidly. The sixth is only a short nubbin.

The endochondral shoulder girdle is not preserved. The general configuration is restored according to the pattern of other romeriids. There is no way of judging whether it developed as a single bone, or from two or more initially separate areas of ossification. The ventral portion of the dermal shoulder girdle is lost beyond the edge of the blocks. Nothing of the interclavicle is visible, and only the dorsal end of the stem of the clavicle. The right cleithrum is clearly exposed. It is in the shape of a long, narrow rod. The dorsal end is flattened but only slightly expanded, anteroposteriorly. The ventral end is pointed and notched posteriorly for attachment to the stem of the clavicle or the scapular blade. The anterior margin of the shoulder girdle, as preserved, is at the level of the fifth vertebra.

The humerus is a long, narrow bone, with the extremities well ossified. In general it resembles that of *Araeoscelis.* It is equivalent in length to eight trunk centra. The shaft is long and narrow. There is neither a supinator process nor an entepicondylar ridge. The distal articulating surfaces are obscured as a result of crushing. The outline of the entepicondylar foramen can be seen in dorsal view on the right humerus, although the posterior border is broken away.

The ulna and radius are long, lightly built bones. The olecranon is poorly ossified, but otherwise these bones are similar to their counterparts in other romeriids.

The carpals are lightly ossified. Their original configuration is impossible to determine. This area is crushed into the vertebral column on the right side and missing from the block on the left. Much of the proximal part of the right manus is in natural articulation. One of the digits and its metacarpal (apparently number four) is missing. The longer metacarpals are more than half the length of the radius. The proximal phalanges are only slightly shorter. The unguals of digits one and five are short and sharply pointed. They do not appear to bear a well-developed keel such as is reported in *Paleothyris.* If the manus is restored according to the pattern of other romeriids, it would be slightly longer than the humerus.

The pelvic girdle is poorly preserved. The most notable feature is the great length of the iliac blade. It is a narrow, flat structure oriented at approximately 15 degrees from the vertical. The ventral portion is poorly preserved, but appears to be quite small. The right pubis is visible medially; the margins are poorly defined, but it is roughly quadrangular in shape. The ischia are crushed against the ventral surface of the vertebrae so as to obscure their original shape. Only the general extent can be determined.

The femur has a long, narrow shaft. It is slightly shorter than the humerus—a very surprising feature among primitive tetrapods. Few structural details are evident. The tibia appears to be slightly shorter than the radius. Unfortunately the limits of the articulating surface are difficult to establish because of the extreme crushing. The tarsals are weakly ossified and scattered among the metatarsals of the right foot so that their specific configuration is impossible to determine, but they can be restored according to the general pattern observed in other romeriids. The astragalus and calcaneum are represented by roughly circular blobs. Most of the foot bones are present, but their manner of association is subject to various interpretations. The first digit appears to be missing. The remaining metatarsals are in essentially their original position relative to one another. The longest is approximately 80 percent as long as the tibia and at least 20 percent longer than the longest of the metacarpals. The posterior epipodials may be shorter than the anterior, but the rear foot as a whole is not shorter than the manus, although the first two digits of the pes are shorter than those of the manus. All the phalanges of the fourth digit are seen in contact with one another. Together with the metatarsal it is more than half again as long as the femur. A series of three short phalanges can reasonably be associated with the second metatarsal. Other phalanges can be attributed to the third and fourth digits. The series probably associated with the fifth is very poorly preserved and the number and configuration of the phalanges is difficult to establish. There may have been four.

Ventral scales are present in large numbers in the specimen. Crushing makes it impractical to illustrate them with the rest of the skeleton. They are considerably wider than those in the Joggins and Florence romeriids, but this may be accentuated by crushing. The lateral extent of the squamation of ventral scales appears to be greater than in these genera as well. No dermal dorsal scales are evident.

Age-Habits. It is difficult to judge the degree of maturity of the type of *Anthracodromeus* because of the nature of preservation. The poor definition of the articulating surfaces of the limb bones, carpals, and tarsals can be attributed either to incomplete ossification or extreme crushing. This specimen may be less mature than the material of *Paleothyris* or *Hylonomus*, but it is certainly more mature than the only known specimen of *Cephalerpeton* or the Czechoslovakian genera. The neural arch and centrum of the vertebra are firmly united and there is certainly some degree of ossification of the carpals and tarsals.

The great length of the limb bones and feet suggests a somewhat different habit than that of more conservative romeriids. Such long limbs and feet are seen in a number of modern lizards that are terrestrial or arboreal in habit. It would not be unreasonable to assign *Anthracodromeus* to such adaptive zones. To judge from the body and limb proportions, it was presumably an agile form. In the absence of any information on the dentition, there is little evidence of possible feeding habits.

Taxonomic position. The pattern of the bones of the skull roof and the structure of the postcranial elements indicate that *Anthracodromeus* is a member of the family Romeriidae. The configuration of the neural arches and the great relative length of the limb bones distinguish this form from all other described genera.

The presence of one pair of sacral ribs indicates that the ancestors of the genus evolved from the primary romeriid stock separately from *Paleothyris*, which has two.

It shows no close affinity with *Cephalerpeton* or the forms from Czechoslovakia. *Anthracodromeus* is probably directly ancestral to an, as yet, undescribed form from the Putnam Formation, Lower Permian of Texas, which has similarly shaped vertebrae and elongate limb elements. It shows no specific affinities with other, more advanced reptilian groups.

Brouffia n. gen.

Type species. *Brouffia orientalis* new species.

Known distribution. Middle Pennsylvanian of Central Europe.

Diagnosis (based on a single, immature specimen). Romeriid captorhinomorph, pattern of skull roof and dentition similar to *Paleothyris*, except for smaller number (26) of maxillary teeth. Four rows of denticles on pterygoid. Thirty-one presacral vertebrae, one sacral. Neural spines squarish in lateral view, not elongate. Scapulocoracoid is ossified from more than one unit. Limbs and feet not greatly elongate. Carpals ossified.

Brouffia orientalis n. sp.

Etymology. Generic name is in honour of Dr. Margaret Steen Brough, who initially recognized the specimen on which this genus is based. The species name emphasizes the presence of the family Romeriidae in Europe.

Holotype. Counterpart blocks including the natural cast of an almost complete skeleton. Dorsal surface from the Czechoslovakian National Museum in Prague ČGH III B.21.C.587 and the ventral surface from the Natural History Museum in Pilzen MP 451. This is the only recognized specimen.

Horizon and locality. Middle Pennsylvanian, Westphalian D, of Nýřany, Czechoslovakia.

Diagnosis. Same as for genus.

Description. Although the type specimen of *Anthracodromeus* is the only reptile currently recognized from the coal swamp deposit of Linton, Ohio, a number of forms are known from Nýřany, Czechoslovakia, a locality of roughly equivalent age and generally similar ecology.

The exact taxonomic position of *Solenodonsaurus* (Carroll, 1970a) remains subject to controversy, but it has attained an essentially reptilian level of development. Three additional specimens will be discussed here that are apparently members

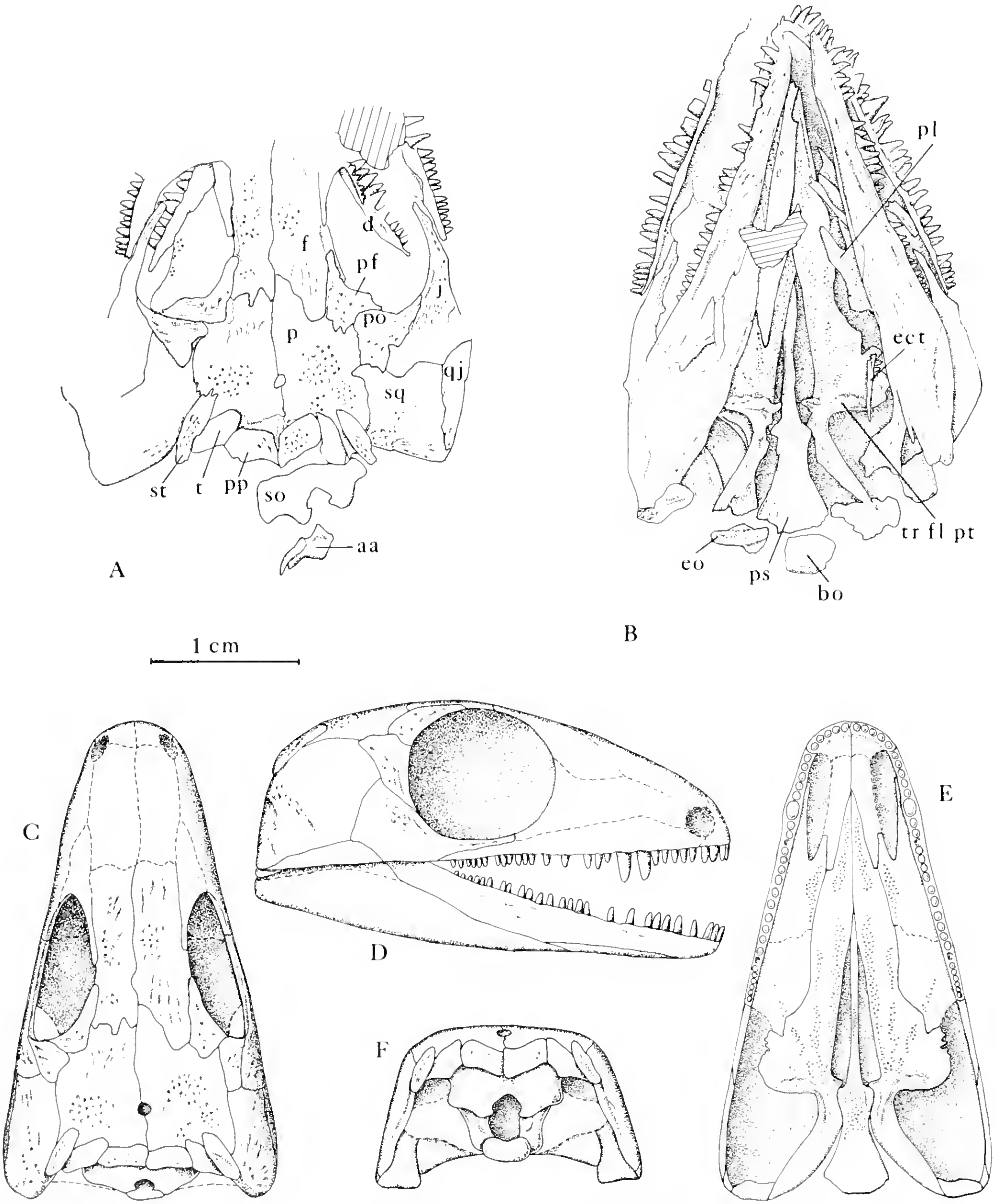


Figure 6. Type of *Brouffia orientalis*. A. Dorsal surface of skull ČGH 111B.21.C.587. B. Ventral surface of skull MP. 451. Restoration of skull in: C. dorsal; D. lateral; E. palatal; and F. occipital views. × 2.

of the family Romeriidae. The most completely known specimen is a skeleton preserved in counterpart blocks from the museums in Prague and Pilzen, described by Brough and Brough (1967) as *Gephyrostegus bohemicus* specimen I. It is an almost complete skeleton of an immature animal. Considerable attention has already been paid to the fact that this specimen does not belong to the genus *Gephyrostegus* (a taxon now much better known than it was at the time of the publication of the Broughs' work). The pattern of the bones of the skull roof and the morphology of the palate are comparable to the North American genera of the family Romeriidae. This is especially noteworthy, since this is the first recognized member of this family in Europe.

The specimen is preserved as a natural mold in coal shale. The cavities have been cast in latex. The restoration of the postcranial skeleton (Fig. 3B) is based primarily on drawings (their figs. 10A and B) made by the Broughs. The skull (Fig. 6) has been redrawn from the original latex casts.

Skull. The pattern of the bones of the skull roof and the nature of the sculpturing in *Brouffia* is very similar to that of the contemporary genus *Paleothyris.* The skulls would be very difficult to differentiate in dorsal or lateral views. The parietal is broadly in contact with the squamosal and postorbital. The postfrontal does not extend as far posteriorly as that of *Protorothyris*, nor is the posterior margin of the parietal as deeply embayed for the tabular and postparietal as in *Anthracodromeus.* Several features that distinguish this skull from that of *Paleothyris* (Fig. 10) can be noted in palatal view. There are significantly fewer marginal teeth: *Brouffia* has room for 26 teeth in the maxilla, in contrast with 35 in *Paleothyris.* The presence of a single pair of "canines" in the type of *Brouffia*, rather than two pairs, is probably not significant since the number is variable in *Paleothyris. Brouffia* has room for approximately five teeth in the premaxilla. *Paleothyris* and members of the most primitive reptilian groups have two rows of denticles on the pterygoid, radiating out from the area of the basicranial articulation, anterior to the transverse flange; *Brouffia* has three rows. The ectopterygoid may also be seen to bear large denticles. The pterygoids extend anteriorly to the level of the "canines," separating the vomers for most of their length. A further, minor difference is the presence of a carpet of fine denticles on the ventral surface of the parasphenoid, rather than a single or double row of larger teeth.

Most of the occipital elements are spread out behind the skull. A large, platelike supraoccipital is visible dorsally. It lacks the well-developed recesses to accomodate the postparietals, characteristic of *Anthracodromeus*, nor does it bear a prominent medial keel. The basioccipital is displaced, so that the entire ventral surface is exposed behind the parasphenoid. The more anterior position of the exoccipitals indicates that such a posterior position did not occur in life. The exoccipitals (termed stapes by Brough and Brough) are badly crushed and extend primarily laterally as the skull is preserved. The opisthotics have not been recognized. The occipital surface can be restored according to the general pattern seen in other romeriids.

Postcranial skeleton. There are 31 presacral vertebrae, one sacral and four caudals preserved. The elements of the atlas-axis complex are disarticulated and not all can be recognized. The proatlas has not been identified. The atlas arch is paired and had a long posterior process for articulation with the axis arch. Neither the atlas pleurocentrum nor intercentrum can be distinguished. The axis centrum is only slightly longer than the more posterior elements. The arch was suturally attached rather than fused and has become separated. The extent of the spine cannot be determined. The more posterior trunk vertebrae also have a distinct suture between the arch and centrum and most of the elements are at least slightly displaced. The left and right halves of the neural arches are also displaced at the midline. The neural spines are squarish in outline, but without the elongation noted in *Cephalerpeton.* No intercentra are observed in the column, but the ventral margins of the pleurocentra are bevelled for their reception.

Only a single vertebra, the 32nd, bears a sacral rib. The vertebra itself is little modified, except for the large size of the transverse process. No haemal arches are present among the four anterior caudal vertebrae preserved.

Double-headed ribs are present throughout the column. The first two pairs are specialized cervicals with flattened shafts that extend posteriorly, as well as ventrolaterally. The configuration of the next two pairs cannot be established. Those in the remainder of the column have cylindrical shafts that extend primarily ventrolaterally. Their length increases rapidly to the 8th rib, remains essentially constant to the 22nd, and then diminishes rapidly. The last six pairs of presacral ribs are very short. The sacral rib has a simple, spatulate blade, which apparently was not in contact with either of the adjacent ribs. The anterior caudal ribs are fused to the vertebrae, and extend posteriorly to lie alongside the tail.

The dermal elements of the shoulder girdle are all clearly exposed. The cleithrum is a flattened rod of bone, with little elaboration of the dorsal blade. The clavicle resembles that of other romeriids in having a small, neatly sculptured blade. The interclavicle has a long stem and a smoothly rounded anterior margin. The endochondral shoulder girdle is ossified in three separate units, as is the case in *Cephalerpeton.* The scapula is illustrated by the Broughs. Its margins must have been considerably extended by cartilage in the living animal. One of the anterior coracoids is visible just dorsal to the left scapula. It is vaguely oval in outline. The posterior element has not been recognized. It may have been slow to ossify.

The forelimb is not well ossified; only the general configuration and proportions of the bones can be established. The size of the humerus, ulna, and radius relative to the length of the trunk vertebrae is similar to the condition in *Paleothyris.* The limbs are relatively shorter than those of *Cephalerpeton* and *Anthracodromeus.* Considering the small degree of ossification in the shoulder girdle and limbs, the carpals are surprisingly well ossified. Because they are somewhat jumbled, their exact configuration is obscured, but their pattern closely resembles that seen in *Paleothyris.*

The manus is not complete and the elements are somewhat disarticulated. Nevertheless, the number of digits and the phalangeal formula is almost certainly similar to that noted in other romeriids. Brough and Brough restored the hand in this specimen on the basis of Watson's specimen of *Gephyrostegus bohemicus* (which they designated the type of a new species *G. watsoni*). As has been demonstrated by the senior author (1970a), Watson's specimen is an anthracosaur, not at all closely related to the specimen under consideration here.

The three elements of the pelvic girdle are only weakly attached to one another. The configuration of the ilium resembles that of *Hylonomus* and *Paleothyris.* It certainly lacks the peculiarities of *Anthracodromeus.* The outline of the pubis is roughly oval. The ischium is quite small.

The rear limb is poorly ossified. The tibia is primitive in having a broad distal articulating area like that of *Hylonomus* but in contrast to *Paleothyris.* Nothing remains of the tarsus or rear feet.

Many ventral scales are present in the blocks. They are quite broad, rather than being narrowly wheat-shaped, as has been considered typical in early reptiles. A faint impression of dorsal scales is evident also, but these are too insubstantial to illustrate.

Discussion. One of the most notable features of *Brouffia* is the incomplete nature of the ossification. Although the presacral length of the type is approximately 123 millimeters, the limbs and endochondral shoulder girdle are much less well ossified than are these elements in *Paleothyris acadiana.* The type specimen of that species has a presacral length of 118 millimeters, and other specimens are considerably smaller. Presumably *Brouffia* grew to a considerably greater adult size before ossification was completed. Alternatively, this genus may have retained a low degree of ossification as an adult. The larger size of the skull, relative to the trunk region (Table 1), suggests that the adult was larger than the typical North American Pennsylvanian romeriids.

Owing to obvious immaturity of the only known specimen, the generic distinction of *Brouffia* from more mature romeriids, particularly *Paleothyris*, is subject to some doubt. Until we have more knowledge of changes that occur ontogenetically, as well as more information on variability within species and genera, it is not possible to state positively what differences are required to define genera. The presence of only a single pair of sacral ribs, the broad distal articulating surface of the tibia, and possibly the extra row of palatine denticles are primitive features that might be expressed also in an immature member of a more advanced species. The smaller number of maxillary teeth and other minor differences might indicate differentiation from *Paleothyris acadiana* only at the level of the species. Even if all members of the Family Romeriidae are considered, however, there is relatively little variability within the group. If the features that can be observed in this immature specimen also characterize the adult, this animal would be as different from *Paleothyris* as are other forms recognized as distinct genera. On this basis, a new genus is named to include this specimen.

The presence of the romeriids in Europe immediately suggests comparison with primitive eosuchians, which are (on present knowledge) restricted to the Old World. There is little to preclude the evolution of a genus such as *Millerosaurus* (Watson, 1957) from *Brouffia*. There are no specialized features, however, that favour this genus over other generalized romeriids for such an ancestral position. There is no evidence for the development of an otic notch formed from the quadrate. The posterior margin of the squamosal may be more nearly erect than in other early romeriids, but the jaw suspension definitely lies posterior to the rear margin of the skull roof. One feature that might be considered of significance in deriving millerosaurs directly from such romeriids is the smaller size of the skull relative to vertebral length in the known eosuchian genera.

Coelostegus prothales

Brough and Brough described as belonging to the same species as the preceding animal, a second specimen that they termed *Gephyrostegus bohemicus* specimen II. It consists of the axial skeleton, girdles, and proximal portions of the humeri and right femur of an animal in which the trunk region was approximately 17 percent longer. It is almost as poorly ossified, however. The skull (Fig. 7) shows only superficial similarities to the type of *Brouffia*. The pineal opening is larger and the postfrontal extends posteriorly so that a distinct lateral lappet of the parietal is formed. The posterior margin of the parietal is much more deeply embayed for the tabular and postparietal. These differences cannot be attributed to growth. Although the remains are incomplete, this animal certainly belongs to a genus other than *Brouffia*.

Coelostegus n. gen.

Type species. Coelostegus prothales new species.

Known distribution. Middle Pennsylvanian of Central Europe.

Diagnosis. Large romeriid captorhinomorph. Parietals deeply embayed for postparietals and tabulars. Distinct lateral lappet of parietal. Frontals and postfrontals marked with deep grooves. Frontals shorter than nasals. Numerous, small posterior maxillary teeth; enlarged canines. Twenty-nine presacral vertebrae. Two sacral vertebrae. Vertebral centra relatively short. In the only known specimen (which is immature) the scapulocoracoid is ossified from

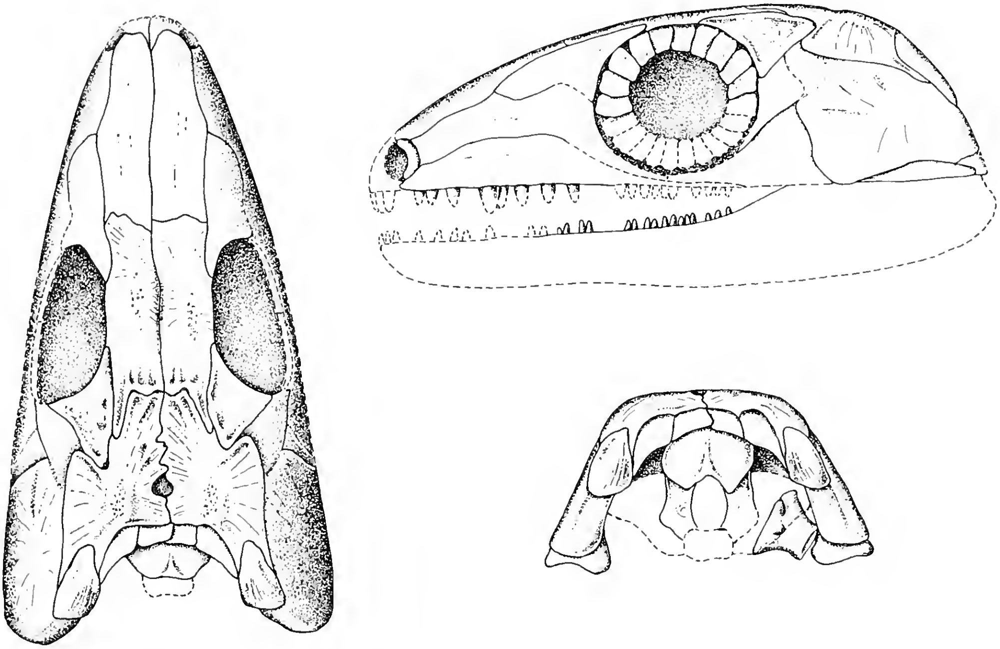


Figure 7. Reconstruction of skull of *Caelostegus prothales* in dorsal, lateral, and accipital views. × 2.

more than one unit, and neural arches are suturally attached to the centra.

Coelostegus prothales n. sp.

Etymology. Greek *coelo*, embayed; plus *stegos*, roof; in reference to the deep embayment of the parietals. *Prothales*, from the Greek, meaning precocious, in reference to the early attainment of embayed parietals and large size.

Holotype. National Museum of Prague, Czechoslovakia, ČGH 3027. Axial skeleton and girdles of an immature individual. This is the only specimen that can definitely be assigned to this taxon.

Horizon and locality. Middle Pennsylvanian, Westphalian D of Nýřany, Czechoslovakia.

Diagnosis. Same as for genus.

Description. Much of the dorsal surface of the skull roof and the left cheek region are preserved. The area anterior to the left orbit is folded under, so that the bone is visible in medial rather than lateral view. The skull can be restored in dorsal and lateral views, but the exact angle between the skull roof and the cheek region cannot be established without more knowledge of the palate. The bones of the skull roof are conspicuously sculptured. There are fine pits near the centre of ossification of the parietal, and radiating grooves extending to the periphery. There are deep grooves at the posterior margin of the frontal and on the lateral portion of the postfrontal. The squamosal and quadratojugal, in contrast, are almost smooth.

The most conspicuous feature of the skull roof is the deep posterior embayment of the parietals. In this character *Coelostegus* resembles the Lower Permian romeriid *Protorothyris* more than it does any of the other Pennsylvanian genera. The postfrontal extends posteriorly, demarcating a conspicuous lateral lappet. The marginal bones of the skull roof, supratemporal, tabular, and postparietal have slipped from the parietal and are mixed with displaced elements of the palate, occiput, and cervical vertebrae. There is a large sheet of bone behind the right parietal that is probably the displaced right squamosal. The supratemporal fitted into a deep groove in the posterolateral corner of the parietal, which extends superficially beyond the deeper medial recess for the tabular. The supratemporal is much wider than in other romeriids, and sculptured by linear grooves. There is a wide triangular shelf of the parietal that extended underneath the tabular and postparietal. A bone that is probably the left tabular is visible just medial to the supratemporal. Its extent is difficult to determine since the margins are overlapped by surrounding bones. The postparietal is also only questionably identified. Near the midline, just behind the posterior margin of the superficial portion of the parietal is an oblong bone that may be so designated.

The frontal has a broad margin above the orbit and extends narrow processes posteriorly between the parietals and postfrontals. The nasal is apparently longer than the body of the frontal. The left maxilla, lacrimal, and prefrontal are exposed in medial view. The maxillary teeth are almost entirely covered by the nasal. The ridge bearing the teeth is swollen anteriorly, as is the case in other romeriids at the level of the canines. There are four teeth anterior to this area. The tooth count cannot be accurately established. The lacrimal comes to a point anteriorly, indicating that the posterior margin of the external nares was formed by a superficial expression of the septomaxilla. That bone lies just anterior to its normal position relative to the maxilla and lacrimal. Its posterior margin is rounded. Approximately a dozen roughly rectangular sclerotic plates can be seen in the area of the left orbit.

The squamosal is displaced laterally and posteriorly from its normal position. Dorsally, the margin of the bone curves medially to pass beneath the parietal. The skull roof simply overlaps the cheek region, apparently without any firm attachment. The rear margin of the squamosal slopes ventrally at an angle of approximately 40 degrees from the vertical. The supratemporal would have extended approximately halfway down this slope. The quadratojugal is a narrow bone, pointed at both ends. The postorbital is not preserved, but its posterior extent may be judged by an area for its reception on the anterior portion of the squamosal. The dorsal portion of the jugal is visible in medial view, having been folded beneath the skull roof. Although the anterior portion of the bone is not preserved, restoration of the skull indicates that the suborbital extension must have been narrow, in contrast with the condition in Lower Permian romeriids.

The quadrate is exposed where it was forced dorsally from beneath the squamosal. The articulating surface is not visible. The dorsal portion is a fairly thin plate of bone extending nearly to the top of the squamosal.

The occipital elements are scattered and obscured by other bones. The central portion of the supraoccipital is visible above the atlas pleurocentrum. It has a median ridge, extending dorsally from the rim of the foramen magnum. The lateral margins of the bone cannot be accurately established. The dorsal portion of the left exoccipital can be seen just medial to the left tabular. The lateral and ventral portions are covered by other bones. A fragment of bone lying just below the right side of the supraoccipital may be part of the right exoccipital. Neither the basioccipital nor otic bones are visible. The otic bones are probably incompletely ossified, since they are not clearly shown in any of the Pennsylvanian romeriids. Because of the poor preservation of this area, the restoration of the occiput (Fig. 7) is only tentative.

The stapes is visible between the atlas intercentrum and the quadrate. It has a very short stem, ending in a broad surface of unfinished bone. The dorsal process (extending posteriorly, as preserved) is proportionately large, as is the footplate. Except for the incomplete ossification of the stem, the stapes resembles closely that of other romeriids.

The quadrate rami of both pterygoids are exposed dorsally, lying among the bones of the occiput. As in other romeriids, they are wide but very thin plates of bone that would have been oriented vertically. They helped support the quadrates and formed an almost complete medial wall to the area of temporal musculature. The anterior portion of the left pterygoid is visible through the orbit. The area of the basicranial articulation is crushed flat. This bone is too incompletely known to attempt a restoration of the palate.

The left lower jaw is folded medially beneath the skull. A portion of the tooth row is visible through the orbit and much of the margin is indicated by deformation of the bones of the overlying skull roof and cheek region. The thickened rim of the adductor fossa can be seen through the very thin squamosal, with part of the surangular and the most posterior portion of the dentary visible between that bone and the postfrontal. Sixteen small teeth can be seen lateral to the frontal. More anteriorly, the tooth row interdigitates with that of the maxilla. Unfortunately, this area is almost completely obscured by the left nasal bone. The articulating surface of the articular bone is visible behind the quadrate, retaining its normal orientation relative to the skull roof.

The vertebral column is fairly well articulated from the skull back to the 13th caudal. There are 29 presacrals and two sacral vertebrae. The centra and neural arches are separately ossified throughout the column, but the general configuration is typical of other romeriid captorhinomorphs.

The atlas-axis elements are somewhat disarticulated, but obviously follow the pattern seen in other romeriids. A very thin, oval bone, flattened onto the posterior notochordal pit of the atlas pleurocentrum, is apparently the proatlas. It lies just anterior to the appropriate articulating surface of the atlas arch. The atlas intercentrum is a broad, openly crescentic bone. It probably bears processes for the attachment of the capitula of the first ribs, but these are not exposed. The atlas pleurocentrum is partially obscured by the left atlas arch and the supraoccipital. It appears to be basically cylindrical, but deeply recessed dorsally. There is a large notochordal canal that was probably much more restricted in the adult. The posteroventral margin appears somewhat recessed, as if to accommodate an axis intercentrum. Such an element is typically absent in advanced romeriids, and is not visible in this specimen.

The left atlas arch is displaced slightly ventrally from its normal relationship with the axis. It closely resembles its counterpart in *Ophiacodon* in having a sharp spine projecting behind the posterior articulating surface.

The centrum of the axis and the next three vertebrae are missing. In view of the generally low degree of ossification in this specimen, it is probable that the atlas arch and centrum were not fused, although they are in the adults of other romeriid species. The neural spines of all the vertebrae are poorly ossified, and have very irregular outlines. This is particularly evident in the axis. The arch and spine are obviously large, as in most primitive reptiles, but the outline cannot be accurately established. The transverse processes of all the anterior vertebrae are quite long, so that the two heads of the ribs are separated by a wide gap.

The arches and centra are loosely attached and variably disarticulated throughout the column. The neural spines are poorly defined, but have a generally rounded outline. This is almost certainly not their normal adult configuration. The length of the neural spines and the transverse processes gradually decrease posteriorly. The centra are crushed flat, making it difficult to estimate their original proportions. As preserved, the height is equal to, or even greater than, the length. Although no accurate measure can be given, the centra appear unusually short for a primitive reptile. Unless the nature of preservation is significantly different, these vertebrae seem to be proportionately much shorter than those of *Brouffia*.

Numerous intercentra are visible in the trunk region. All are very thin, narrow crescents. The bases of the centra are slightly notched for their reception. Unlike the condition in *Cephalerpeton* and MB 1901.1379 (described below), there is no evidence that the intercentra formed a structurally significant part of the column, or had extensive dorsal cartilaginous components. Neither the intercentra nor the anterior or posterior rims of the centra exhibit specialized areas for the articulation of the capitular rib heads.

It is difficult to establish the number of sacral vertebrae. The column is slightly bent in this area, and the elements are disarticulated. In restoring the column, it appears that all of the neural arches are present, but that at least three pleurocentra are missing. Trunk ribs can be associated with the first 28 presacral vertebrae. The next arch has a small transverse process that almost certainly bore a small presacral rib. As the Broughs pointed out, the transverse processes of arches 30 and 31 are considerably larger. They are in a position, relative to the iliac blade, expected for sacral vertebrae. The arch of the 32nd vertebra is so crushed that the transverse processes cannot be seen. Immediately adjacent lies a well-developed sacral rib. It is of smaller size than would be expected for the principal sacral rib and has a slightly more posterior position. Dorsal to the arch of the 31st vertebra is a poorly preserved bone of somewhat larger size. It might be interpreted as the principal sacral. In restoring the skeleton, the size and orientation of the iliac blade makes it extremely unlikely that there were more than two pairs of sacral ribs. Both must have been displaced posteriorly, and the most anterior caudal rib lost or obscured by other bones.

The 13 caudal vertebrae are badly crushed. The neural arches are similar in configuration to those in the trunk region. The ventral region of the centra is not visible.

Ribs are present throughout the column. The heads of the cervical ribs are conspicuously double-headed. The shaft of the first is narrow, fairly short, and flattened. The second through fifth are increasingly long and spatulate. They evidently all extended posteriorly, more than ventrally. They rather resemble the anterior ribs of *Seymouria*. The third and fourth ribs in the type specimen of *Brouffia* are not preserved. The fifth is apparently similar to those more posterior. In *Coelostegus*, the sixth through 19th are of more or less uniform length. The next six are progressively shorter and the last four are very short. The only well-preserved sacral rib has conspicuously separated heads and a narrowly expanded blade. The most anterior caudal rib is apparently missing. The next six curve sharply posteriorly to lie alongside the tail.

Elements of the shoulder girdle lie alongside vertebrae two through seven. The cleithrum is a long, narrow rod, slightly expanded along the anterodorsal margin. The blade and lower portion of the stem of the clavicle are considerably expanded, although not beyond the range that might be expected of romeriids. The interclavicle underlies the anterior portion of the column. The anterior margin is fimbriated. The remainder of the outline is difficult to establish, but apparently conforms to the typical romeriid pattern. The scapula is considerably better ossified than its counterpart in the type of *Brouffia*. There is a well-defined supraglenoid buttress, within which, apparently, opened a supraglenoid foramen. The ventral margin of the bone extends anteriorly from the centre of the glenoid area. One or more coracoid elements must have ossified separately. Very limited portions of the proximal articulating surface of both humeri are present. No diagnostic features are evident. None of the distal elements of the fore limb are present.

The three elements of the pelvic girdle are disarticulated. The margins are partially obscured by other bones, but they resemble in general their counterparts in other early reptiles. The medial surface of the iliac blade shows a series of linear grooves for the attachment of epaxial musculature. The size and configuration of the ilium corresponds almost exactly with that of an isolated pelvic girdle from Florence, Nova Scotia (Fig. 14D). This is definitely distinct from the ilium of *Paleothyris* in the width of the blade. This suggests the presence of a second, rare, romeriid genus within the tree stump fauna. Only the proximal portion of the femur is preserved. The texture of the surface indicates an immature stage of development. Enough of the shaft is present to indicate that the total length did not exceed 20 cm, roughly equivalent to the length of five trunk centra.

The numerous ventral scales are similar to those observed in the type of *Brouffia* and *Cephalerpeton*. They form a continuous, wide, but thin covering from the pectoral to the pelvic girdle. There are at least five rows of scales on each side. There is no trace of dorsal scales.

Discussion. The configuration of the posterior bones of the skull roof and the proportions of the vertebral centra suggest that this specimen is taxonomically distinct from all other Pennsylvanian romeriids. It resembles the Lower Permian genus *Protorothyris* in some features of the skull, but the vertebrae appear quite different. The specific phylogenetic position of *Coelostegus* is difficult to establish on the basis of this specimen, since it is immature and lacking most of the limb elements.

Although immature, the trunk region alone is 120 millimeters in length. If the low degree of ossification is indicative of immaturity, the adult size would probably be in excess of that in all other Pennsylvanian romeriids but comparable to that of the Lower Permian members of the family.

Humboldt Museum 1901.1379

A further specimen which came from the Nýřany locality may be discussed here. It consists of 16 posterior trunk vertebrae, the sacral and associated ribs and limb material (Fig. 8). This specimen (No. 1901.1379) from the Humboldt Museum in Berlin, is from a much larger animal than any of the previously described Pennsylvanian romeriids and even exceeds the size of the Lower Permian members of the family. The bones are well ossified, suggesting an adult condition. As restored, this section of the presacral column would be 120 mm in length. Given a typical romeriid length of 31 or 32 presacrals, the entire trunk region would be approximately 240 mm long.

Despite being well ossified, the vertebrae display a distinct suture between arch and centrum. The neural arch is squarish in outline, as might be expected in adult specimens of the preceding two species, but the two sides are solidly fused at the midline. The arches are not swollen. The transverse processes extend a short distance laterally from the base of the pedicel. The articulating surfaces face obliquely ventrolaterally. The centra are well-developed, deeply amphicoelous cylinders. Laterally, they are deeply concave. Ventrally they are notched to provide space for large, crescentic intercentra. The dorsal area of the posterior rim of the more posterior centra is recessed to receive the anterior margin of the next succeeding vertebra. As restored there is a considerable gap between the intercentrum and this dorsal articulating area. It is probable that the sides of the intercentra extended a considerable distance dorsally in cartilage. This form illustrates an advanced stage in the reduction of the intercentra from the condition in anthracosaurs to the definitive reptilian configuration.

Numerous ribs are present in the block. At least as far back as the fourth vertebra anterior to the sacrum, they are similar to those in the trunk region of most early

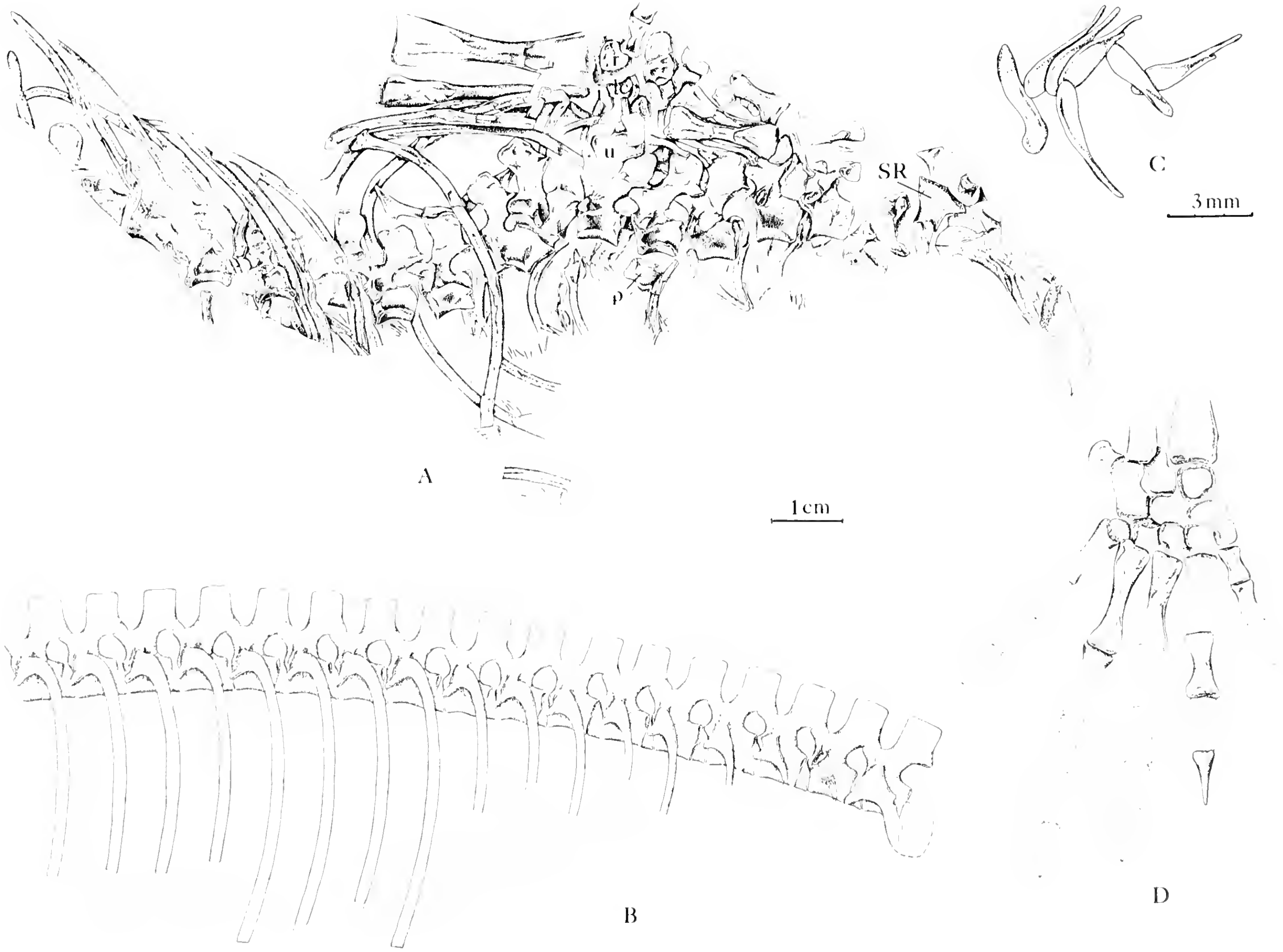


Figure 8. MB 1901.1378: A. Partial skeleton. × 1. B. Restoration of posterior portion of axial skeleton. × 1. C. Detail of scales. × 4. D. Restoration of hand. × 1. Abbreviations: i, intermedium; lc, lateral centrale; p, pisiform; r, radiale; u, ulnare; SR, sacral rib.

tetrapods. In their great length relative to the size of the vertebrae, they resemble those of pelycosaurs more than those of typical romeriids. The length of the posterior ribs shortens gradually. The last presacral rib is apparently only slightly longer than a single centrum. Where present the rib heads are typically double-headed. The capitulum must have articulated with the dorsal, cartilaginous portion of the intercentrum. A single massive sacral rib is preserved. The head has two articulating surfaces set at a slight angle to each other and separated by only a short gap. The shaft narrows only slightly before expanding again as a simple blade. Its natural orientation and distal extent is obscured by crushing. The first presacral vertebra is visible only in anterior view, so it is not possible to determine the nature of the articulation of the capitular head of the sacral rib.

Neither any part of the shoulder girdle nor the humerus is preserved. The radius and ulna resemble those of *Cephalerpeton* and *Anthracodromeus* in being long, lightly built, and with the articulating surfaces ill defined. The radius is the length of four trunk centra. The ends are flattened and expanded to about an equal extent. The ulna is only slightly longer and the olecranon little ossified and poorly preserved.

The carpal bones are preserved in essentially their natural position. They are well ossified, but crushing has made determination of their original outlines difficult to establish. Eleven bones can be recognized. The specific identity of some is in doubt owing to partial disarticulation and the fact that the margins are somewhat obscured by other bones. A bone that is probably the pisiform is the furthest from its natural position, lying more than a centimeter to the left of the other bones.

The elements can be reassembled with little likelihood of serious error to a pattern similar to that of the romeriid *Paleothyris* and most pelycosaurs (Romer and Price, 1940, fig. 40). The configuration of the individual bones is distinct from that of *Paleothyris*, but without more knowledge of the range of variability in the configuration of the carpus in romeriids, it is not possible to establish whether the pattern seen in this specimen is sufficiently different to suggest assignment to a different family.

The radiale is oval in outline, the dorsal surface somewhat flattened. The distal articulating surface of the radius is slightly concave and considerably wider than the radiale, with the lateral portion apparently resting on the intermedium. As in other primitive reptiles, the intermedium has distinct articulating surfaces for the radius and ulna, which are set at approximately a 45-degree angle to one another and separated by a notch. The ulnare is by far the largest carpal. The proximal articulating facet is obscured, but was probably essentially horizontal. The medial surface is incised to form the margin of the perforating foramen. In contrast with the condition in *Paleothyris*, this opening is bordered medially by the intermedium, rather than by the lateral centrale. The ulna articulates with the lateral centrale by a well-developed, medially facing facet. Little of the lateral centrale is visible, but this bone appears to be relatively smaller than its counterpart in *Paleothyris*. The medial centrale is only tentatively distinguished from a number of distal bones.

At least the proximal portions of all the metacarpals can be seen in their normal sequence. The fourth is complete and slightly more than half the length of the radius. The first is very short. A tentative restoration of the hand is shown in Figure 8D, although fragments of only four phalanges are visible. A single ungual is seen in ventral view. It is sharply pointed and has a pronounced keel ending in a large knob for the attachment of ligaments for retraction.

Except for a fragment of bone lying beneath the end of the femur, none of the pelvic girdle is preserved. The femur itself

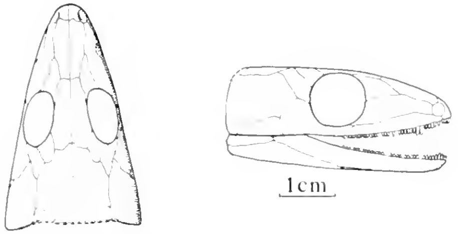


Figure 9. Skull of *Hylonomus lyelli*, in dorsal and lateral views. × 0.75.

is very incomplete. It was clearly heavily built, but no structural details can be ascertained.

Scales are scattered throughout the block. They appear quite large, but not surprisingly so for such a large animal.

Discussion. The taxonomic position of this specimen is difficult to establish. Since there are still comparatively few reptiles known from the Carboniferous, it seems worthwhile to publish this account even though the remains are very incomplete and the affinities of the animal uncertain. There is little question but that this specimen is a reptile, at least as that term is broadly used. The relatively large size of the animal suggests comparison with *Solenodonsaurus.* Although the general vertebral proportions are similar, the intercentrum was apparently not greatly extended in cartilage in *Solenodonsaurus*, nor are there special articulating surfaces on the dorsal margins of the pleurocentra. The proportions of the ulna and radius are entirely different in the two forms.

The proportions of the radius and ulna also distinguish it from *Brouffia.* It is more difficult to compare it with *Coelostegus prothales* because of the paucity of corresponding elements. The low degree of ossification of the vertebrae in that specimen makes it difficult to compare their configuration with the more mature animal from the Berlin Museum. The extent of the intercentra and the proportions of the pleurocentra are quite different, but these might change with increasing maturity. The position of the articulating facet for the capitulum is apparently similar in the two forms. Since there are few corresponding elements in the appendicular skeleton, there is not sufficient evidence to establish whether or not they might be included in the same genus.

Outside the Nýřany fauna, perhaps the closest comparison can be made with *Cephalerpeton*, which also had extensive intercentra, squarish neural spines, and long epipodials. The vertebral features are typical of a wide range of primitive tetrapods, and long epipodials have evolved in many

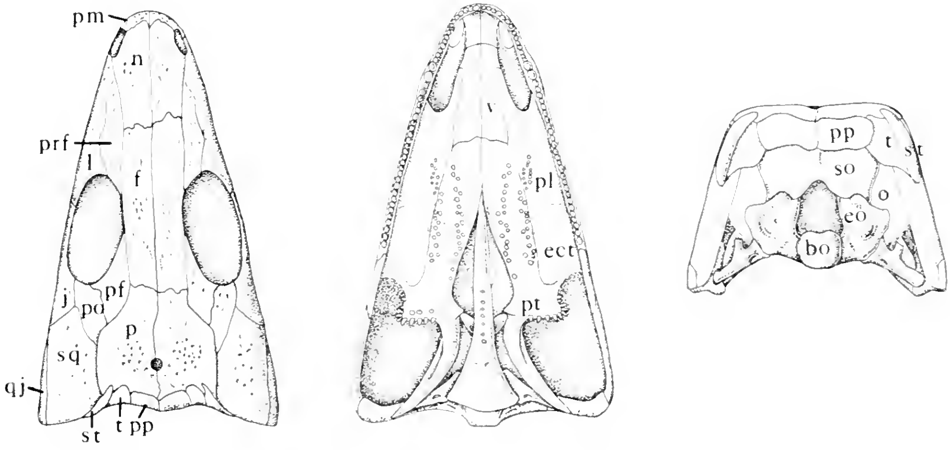


Figure 10. Skull of *Paleothyris acadiana* in dorsal, palatal, and occipital views. × 2.

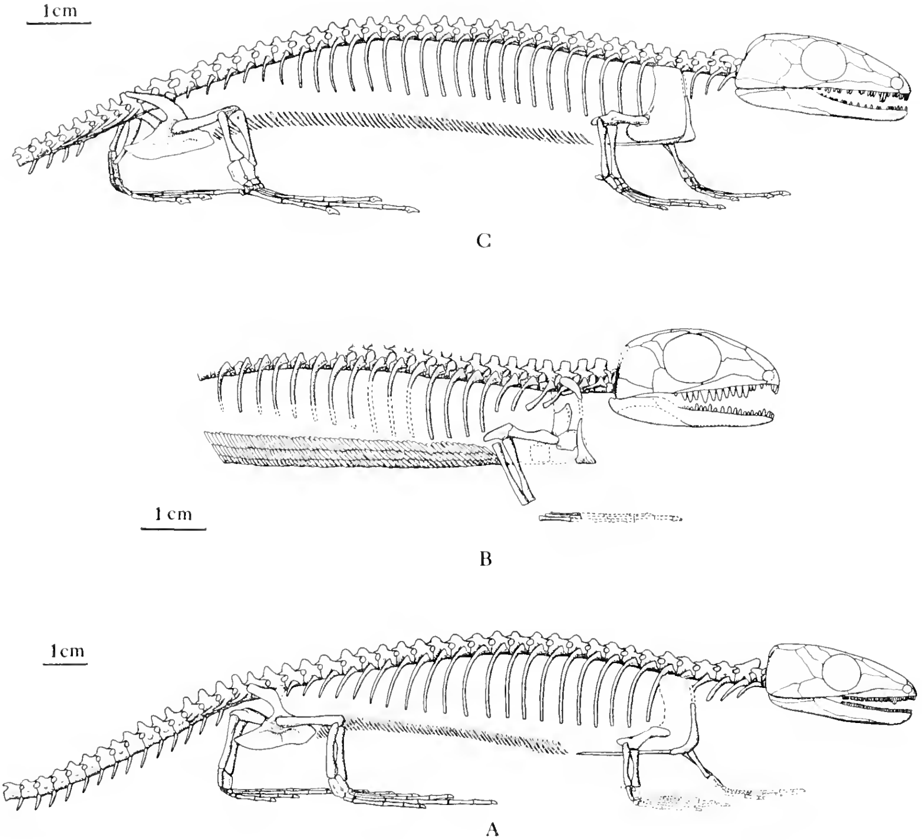


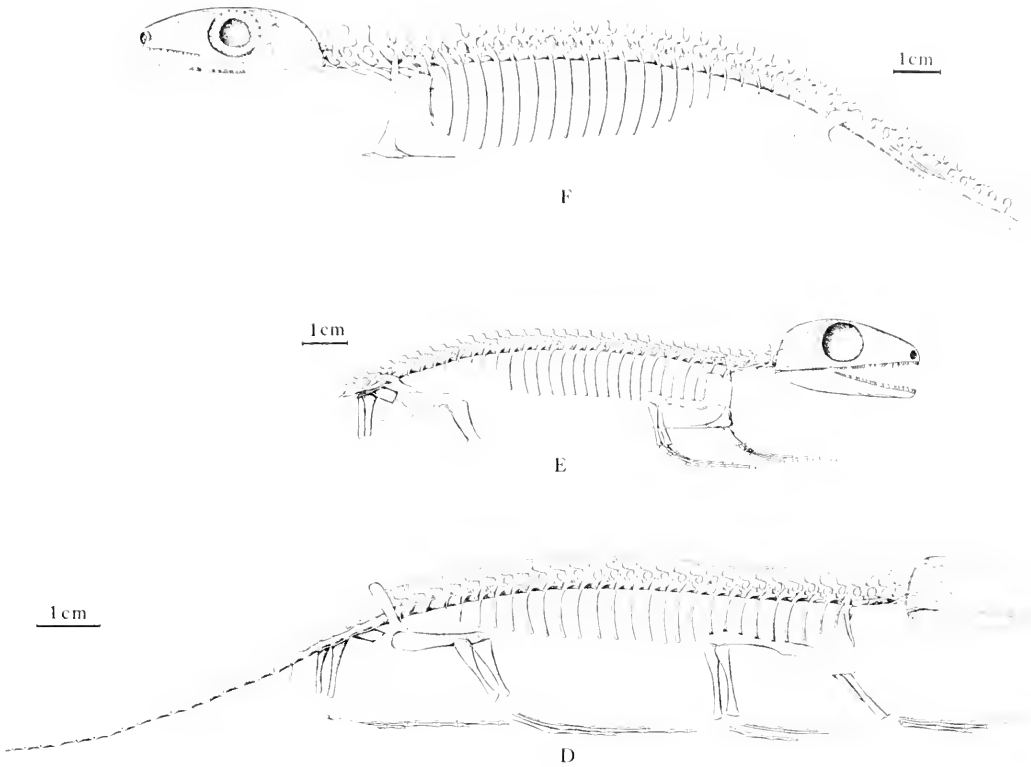
Figure 11. Skeletal reconstruction of Pennsylvanian romeriids. A. *Hylonomus lyelli*—Westphalian B. B. *Cephalerpeton ventriarmatum*—Westphalian D. C. *Paleothyris acadiana*—Westphalian D. D. *Anthracodromeus longipes*—Westphalian D. E. *Brouffia orientalis*—Westphalian D. F. *Coelostegus prothales*—Westphalian D. Scale indicated on figures.

groups. The relatively great size suggests comparison with pelycosaurs, but no significant similarities with any member of that group have been recognized. Without cranial material, not even the order to which this specimen belongs can be established with certainty.

RECONSTRUCTIONS

Reconstructions of the skeleton and flesh have been made of the six, more or less completely known, Pennsylvanian romeriids (Figs. 11 and 12). In terms of body size and general proportions, all fall within the range exhibited by small, iguanid lizards (excepting *Phrynosoma*). This is reflected in the restorations. Feeding patterns and general ecology were probably broadly comparable as well. The only feature that is shown as distinguishing these genera from lizards is the nondivergence of the fifth digit of the foot. Since the footprints of some Paleozoic forms (*e.g., Dromopus*) show a divergence of the fifth digit, romeriids may have resembled modern lizards in this feature as well.

The known body proportions of romeriids appear to follow a sufficiently restricted range of variation that missing elements (*e.g.*, the rear limbs of *Cephalerpeton* and the distal extremities of *Coelostegus*) can be restored with a fairly high degree of confidence. The extent of the tail is not known in any romeriids. In analogy with



typical pelycosaurs and modern lizards, it is shown approximately as long as the trunk region. All are shown lacking epidermal scales, since they are known to be missing in *Cephalerpeton.*

The particular poses are copied from a variety of iguanids illustrated in Smith's *Handbook of Lizards* (1946). The nature of preservation and generally low degree of definition of the extremities of the limbs and articulating surfaces of the girdles make it impossible to define the range of limb positions in the romeriids, but the postures exhibited here could be assumed without doing violence to the known anatomy.

DISCUSSION

Variation among Pennsylvanian Romeriids

Six romeriid genera from the Pennsylvanian are known from almost complete skeletons. The remains of *Archerpeton* (which are substantially smaller than those of other Pennsylvanian romeriids) and MB 1901.1379 (which are significantly larger) are much less complete, and will not be included in this discussion. The position of *Brouffia orientalis* is considered on the basis of the characters shown in the single, immature specimen, although it is conceivable that they are altered somewhat in the adult.

With the possible exception of the relative skull size, in which the Czechoslovakian genera differ from the North American forms, there is no consistent pattern evident in terms of either geographic or temporal distribution, at least among the characters listed (Table 1). The presence of a single pair of sacral ribs is certainly more primitive than two pairs, and a large number of maxillary teeth is more primitive than a reduced number. On the basis of the known specimens, there are no consistent

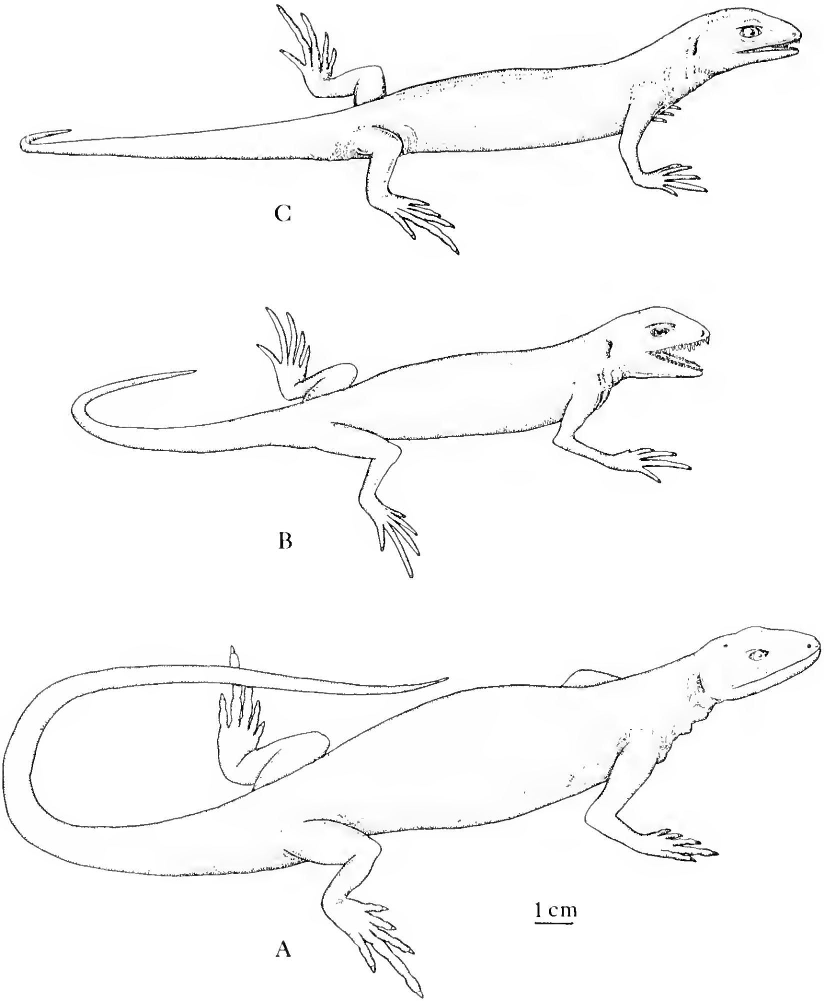
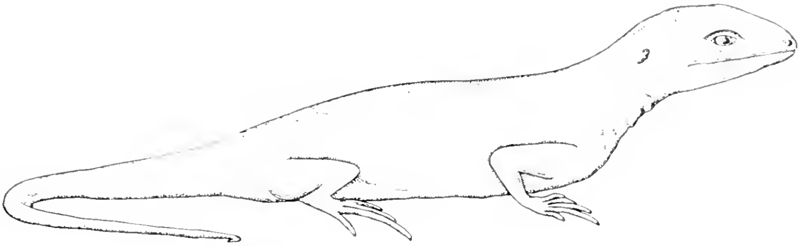


Figure 12. Flesh reconstruction of Pennsylvanian romeriids. A. *Hylonomus lyelli;* B. *Cephalerpeton ventriarmatum;* C. *Paleothyris acadiana;* D. *Anthracodromeus longipes;* E. *Brouffia orientalis;* F. *Coelostegus prothales.* × 0.5.

trends evident in either overall body size or in the specific number of presacral vertebrae. If a low degree of ossification can safely be correlated with immaturity and body size significantly less than that of adults, mature specimens of *Cephalerpeton*, *Brouffia*, and *Coelostegus* may be considerably larger than the ones known. The proportionately larger skull size in the latter two genera may also be correlated with the larger absolute body size. The pelycosaurs, for instance, typically have proportionately larger skulls than romeriids. If early Permian romeriids are considered as well, the family does show a general increase in size through time. Mature skulls from the Redbeds of Texas range from 50 to 60 mm in length. Very roughly, there is a doubling in size throughout the history of the family.

In comparison with size increase observed among pelycosaurs during a comparable time interval, romeriids appear quite conservative. It is probable that the definable features of the family are closely related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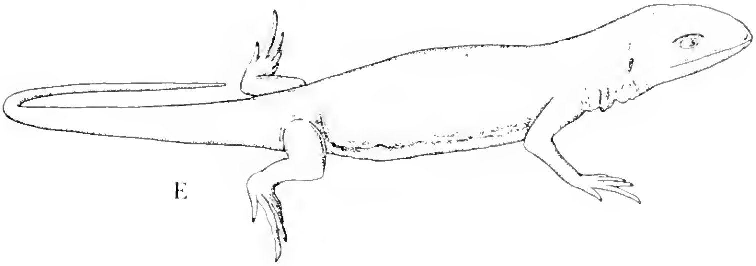
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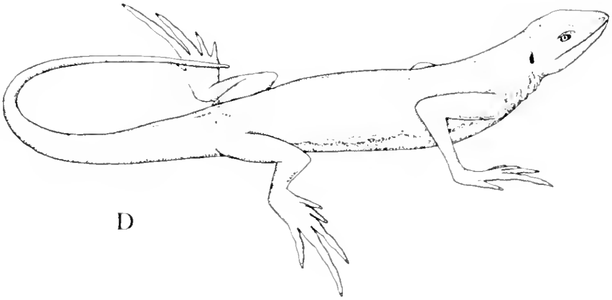
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to absolute body size. Adjustments for great increase in bulk would probably lead to sufficiently extensive reorganization of the skeleton for support and of the skull in relationship to feeding that the resultant form would have to be recognized as a member of a distinct family.

Early pelycosaurs (see Reisz, 1972) may be considered romeriids grown large. It is probable that once pelycosaurs had differentiated in the early Pennsylvanian, specialization by simple increase in size was strictly limited in later romeriids.

Within the limits of small, insectivorous primitive reptiles, the most significant specialization among romeriids occurred in the dentition and limb proportions. Both may be associated with pursuit and capture of particular prey. There is no consistent correlation between particular specializations of any of the romeriid genera and their specific mode of preservation.

The pattern of the skull roof is very conservative. The most significant change is seen in *Coelostegus*, in which the posterior margin is deeply embayed. This may be correlated with an anterior extension of the axial musculature to give more efficient control to movement of the head. An analogous, but not exactly equivalent, specialization is seen in the Lower Permian genus *Protorothyris*.

TABLE 1. MEASUREMENTS OF PENNSYLVANIAN ROMERIIDS (BASED IN ALL CASES ON THE TYPE SPECIMENS). *Archerpeton* and MB 1901.1379 not included.

	Number of maxillary teeth	Number of presacral vertebrae	Pairs of sacral ribs	Length of presacral column (mm)	Length of skull (mm)	Skull/trunk	Humerus (mm)	Humerus[2]	Radius (mm)	Ulna (mm)	Femur (mm)	Tibia (mm)	Fibula (mm)
Hylonomus lyelli BM(NH) R.4168	35	26?	1	108	33	31%	20	5	–	–	22	11	12
Cephalerpeton[1] *ventriarmatum* YPM 796	16	–	–	–	25.5	–	15	6	10	10	–	–	–
Paleothyris *acadiana* MCZ 3481	35	32	2	89	27.2	31%	13	5	8	8.5	14	9	9+
Anthracodromeus *longipes* AMNH 6940	–	31	1	80	–	–	20.5	8	10.2	11.3	18.5	10	12
Brouffia *orientalis*[1] ČGH IIIB. 21.C.587 MP 451	26	31	1	89	32.4	36%	14.6	5	10	11.2	15.8	11.6	13.1
Coelostegus *prothales*[1] CGH 3027	26+	29	2	104	40	38%	–	–	–	–	–	–	–

[1] Poorly ossified, presumably immature specimen.

[2] Length of humerus measured in terms of number of trunk vertebrae.

Stratigraphic Distribution and Depositional Environment of Romeriid Fossils

Romeriids are known from at least three basic depositional environments: *Hylonomus* and *Paleothyris* from upright trees; *Cephalerpeton, Anthracodromeus, Brouffia,* and *Coelostegus* from coal swamp deposits; and the Lower Permian genera from the redbeds of a huge delta complex. The relative abundance of the specimens in each type of deposit is significant. The tree stump genera are relatively common elements in their respective faunas. All of the genera from the coal swamps are represented by single specimens. Tetrapods of any sort are rare at Mazon Creek, so the presence of a single reptile is no measure of its original frequency. The deposits at Linton, Ohio, and Nýřany, Czechoslovakia, are extremely rich in aquatic and semiaquatic forms, suggesting that the few romeriids are exotics, preserved by chance. Five romeriid genera may be recognized in the Lower Permian of Texas (see Watson, 1954). Three are known from unique specimens. *Romeria* is known from two individuals, and *Protorothyris* from five, all from a single locality. In comparison with the rich fauna of both reptiles and amphibians in the Texas beds, romeriids are very rare elements.

Numerous specimens of *Melanothyris* are known from a single locality in the Dunkard Group of Pennsylvania, roughly equivalent in age to the Wichita beds in Texas. All the individuals are small, presumably immature, and come from a single block of freshwater limestone. Except for the smaller size of the specimens, *Melanothyris* is very similar to *Protorothyris* and may not be generically distinct. The presence of a large number of individuals in a definitely aquatic deposit is difficult to explain, in light of the apparent terrestrial habits of all the other members of the group.

The frequency of early romeriids in tree stump faunas certainly reflects their terrestrial habits. The relative diversity in terms of genera, but rarity of individuals in later, essentially aquatic deposits suggests that the family remained a dominant element of the Middle Pennsylvanian fauna, but probably remained more common in a more terrestrial environment. The complete absence of romeriids in the Stephanian deposits of aquatic and deltaic nature is surprising. Reptiles and even amphibians of that age are comparatively rare, but most faunal elements are represented, at least by fragments.

The subsequent rarity of romeriids in the Wichita Group and their absence in the later Clear Fork Group of the Texas Lower Permian apparently indicate a marked reduction from their original frequency in the early and middle Pennsylvanian. The generalized reptilian habitus originally defined by the romeriids was apparently usurped by a host of derivative groups, each more successful in some portion of the environment. Romeriids may, however, have remained relatively common in more upland environments than are represented in either the typical Stephanian or Lower Permian deposits. Certainly some lineages must have survived into at least the Middle Permian to give rise to eosuchians and possibly to ancestral archosaurs.

The absence of romeriid fossils prior to the early Pennsylvanian Joggins horizon may be attributed to the absence of any deposits reflecting a sufficiently terrestrial environment in the latest Mississippian or earliest Pennsylvanian. The slightly more primitive features of *Hylonomus*, particularly in the structure of the atlas-axis complex and in the absence of well-defined tooth rows on the palatal elements, suggest that the group had only recently evolved from some distinguishably more primitive family of reptiles. The subsequent evolution of the family is consistent with differentiation of all major lineages no earlier than the early Pennsylvanian.

Geographical Distribution

The discovery of romeriids from Czechoslovakia very much extends the range of a group that was originally known only from North America. Although *Brouffia* and *Coelostegus* are clearly distinct from all described New World genera, they are not particularly closely related to each other, nor give any evidence that their evolution had proceeded in isolation from that undergone by the North American forms. There is, in fact, no consistent correlation between the geographic distribution of the known specimens and their taxonomic relationship. Genera from Texas, Illinois, Ohio, Pennsylvania, Nova Scotia, and Czechoslovakia appear to represent a single evolving complex that was essentially worldwide in range. No romeriids are known from anywhere in the southern hemisphere. In view of the rarity of other tetrapods during the appropriate period of time, this is hardly surprising. Indirect evidence of the family in the land masses now recognized as South America and Africa is provided by the presence of mesosaurs, which certainly evolved from primitive romeriids, as well as primitive eosuchians.

Interrelationships of Pennsylvanian Romeriids

Several lineages may be recognized among the Pennsylvanian romeriids (Fig. 13). A central stock consists of the genera *Hylonomus* (Figs. 9 and 11A) from the Westphalian B and *Paleothyris* (Figs. 10 and 11C) from the Westphalian D, which gave rise to the early Permian forms *Melanothyris* and *Protorothyris*. The denti-

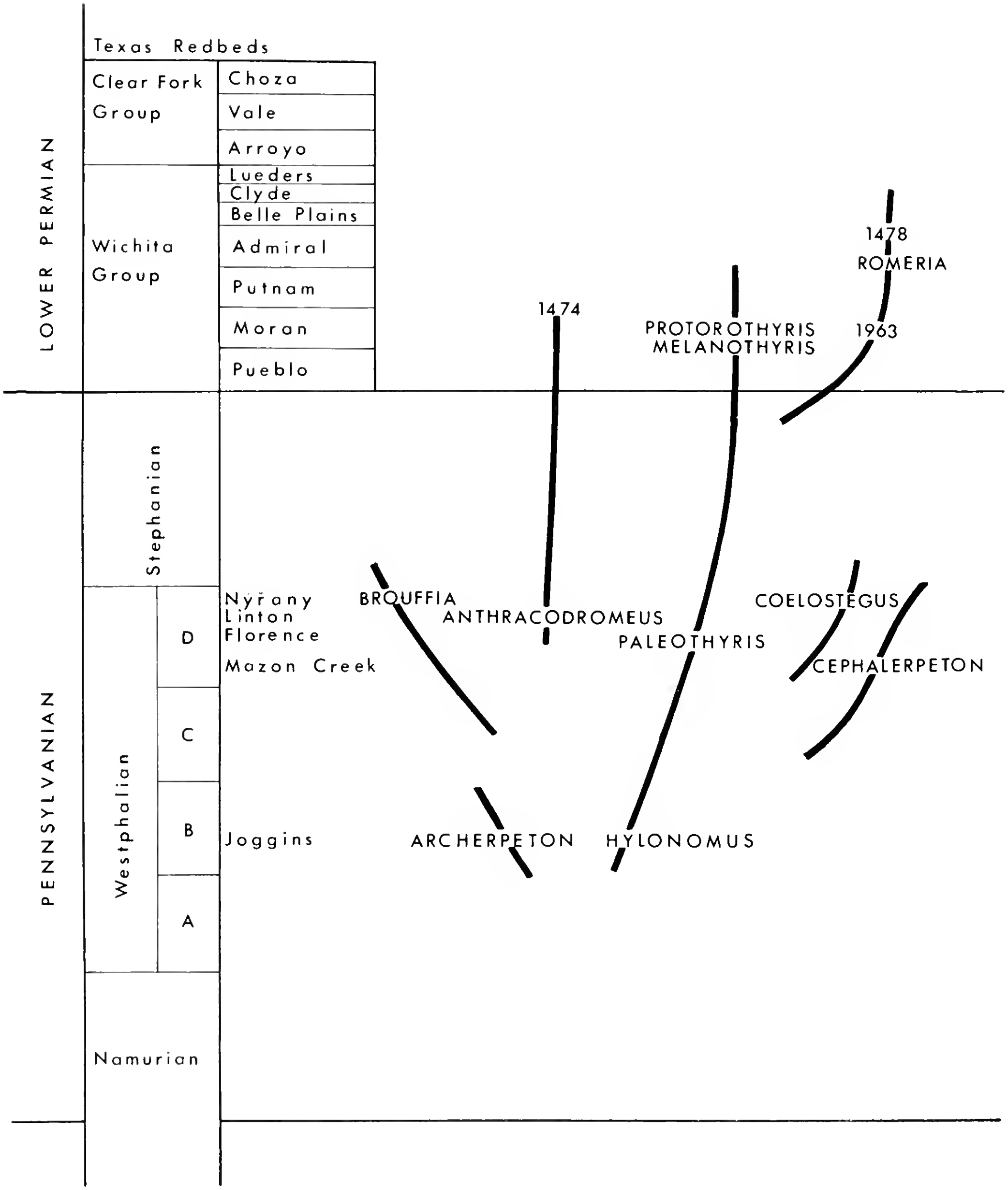

Figure 13. Phylogeny and stratigraphic distribution of romeriids. Numbers indicate unnamed MCZ specimens.

tion remains similar throughout this group. The overall body size increases and the neural spines become elongate. The relative length of the limb elements increases somewhat. The presence of only a single sacral rib and a primitively large distal articulating surface of the tibia suggest that *Brouffia* diverged from this lineage in the early Pennsylvanian. *Coelostegus*, in contrast, appears as advanced as the Permian members of the family. The apparent shortness of the vertebral centra and the large size of the supratemporal and small postparietal indicate that it is not directly ancestral to these forms, however.

The dentition of *Cephalerpeton* clearly distinguishes this genus from all other members of the family. It presumably evolved from *Hylonomus* or other early Pennsylvanian members of the central lineage. The dentition is too specialized to suggest the ancestry of any later forms. It is comparable with that seen in some of the small carnivorous pelycosaurs.

Anthracodromeus represents another divergent group. The peculiar nature of the neural spines and the great elongation of the limbs is matched in an undescribed specimen from the Lower Permian of Texas. There is no evidence that this particular lineage gave rise to any later reptilian groups. The relationships of romeriids with other primitive reptiles was discussed with the descriptions of *Paleothyris* (Carroll, 1969a) and *Batropetes* (Carroll and Gaskill, 1971). The knowledge of additional Pennsylvanian romeriids does not substantially alter the conclusions reached in those papers.

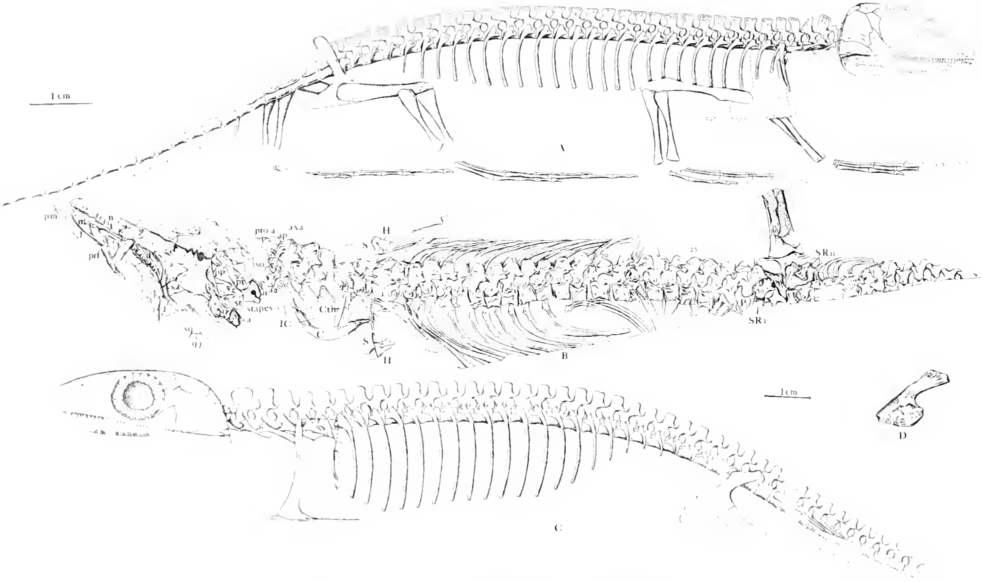

Figure 14. (Fold-out). A. Restoration of the skeleton of Anthracodromeus longipes × 2. B. Coelostegus prothales type CGH 3027 × 1.5. C. Restoration of axial skeleton and girdles of Coelostegus prothales × 1.5. D. Ilium of romeriid from Florence, Nova Scotia, MCZ 4109 × 1.5.

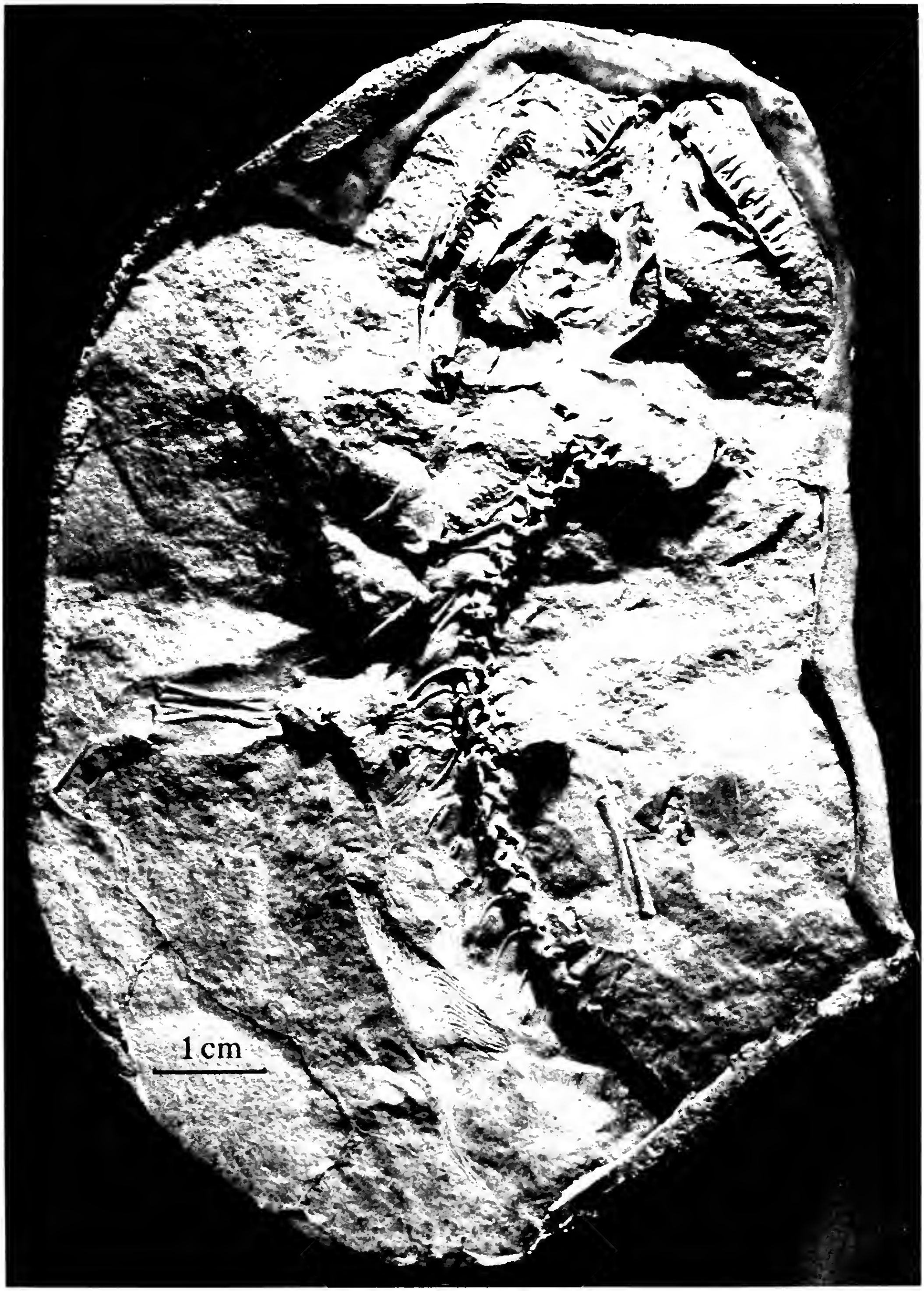

Plate 1. Latex cast of *Cephalerpeton ventriarmatum*. Scale indicated on figure.

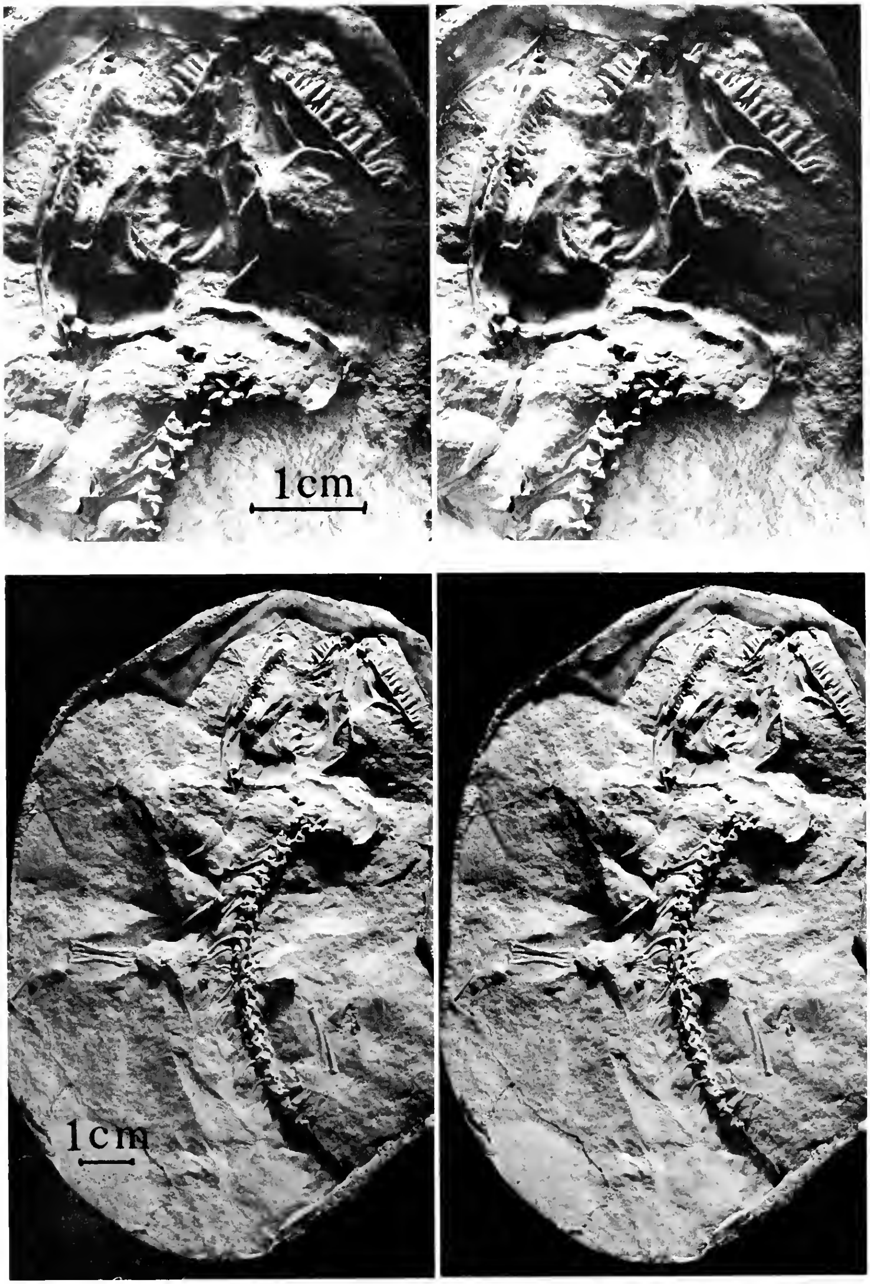

Plate 2. Stereo pairs of *Cephalerpeton*. Upper, Skull; Lower, Skeleton. Scale indicated on figure.

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Bulletin OF THE
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HARVARD UNIVERSITY VOLUME [illegible]
CAMBRIDGE, MASSACHUSETTS, U.S.A. [illegible]

PUBLICATIONS ISSUED
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MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
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THE LOWER TRIASSIC (SCYTHIAN) AMMONOID *OTOCERAS*

BERNHARD KUMMEL

ABSTRACT. The ammonoid genus *Otoceras* has long been recognized as identifying the lowest Triassic (Scythian) zone. The genus was first described from the Himalayas and is now known from Siberia and from Arctic North America. Diener (1897) recognized seven species of *Otoceras* in his collections from the Himalayas; data are presented to demonstrate that only one species—*O. woodwardi* Griesbach—is present. In addition the circum-Arctic *Otoceras boreale* Spath and *O. indigirense* Popov are considered to be subspecies of *O. woodwardi* Griesbach. Associated with *Otoceras* in the Himalayas is the genus *Ophiceras*, which is by far the predominant element in the fauna. Wherever it occurs *Otoceras* tends to be quite rare. A number of other genera have been reported from the *Otoceras-Ophiceras* Zone, and each of these is reviewed in detail. Analysis of the worldwide extent of this zone suggests that *Otoceras* did not survive as long in the Arctic as it did in Tethys.

Otoceras is a direct descendant of the late Permian genus *Pseudotoceras* of the family Araxoceratidae Ruzhentsev and is the last surviving element of that evolutionary lineage. The family Otoceratidae Hyatt (1900) should take precedence over the name Araxoceratidae Ruzhentsev (1959).

INTRODUCTION

The first proposed sequence of zones for the marine Triassic of "pelagic facies," by Mojsisovics, Waagen, and Diener (1895), listed as the basal Triassic zone that of *Otoceras woodwardi*, a species first described by Griesbach (1880) from the Himalayas and thoroughly monographed by Diener (1897). Ever since that time *Otoceras* has been recognized as a primary index fossil of the lowest Triassic zone. At the same time it was recognized that the associated genus *Ophiceras* also was a marker of the lowest Triassic. It has been a matter of complete orthodoxy that *Otoceras* identifies the lowest zone of the Triassic. It has also been taken as a matter of course that *Otoceras* was a descendent of so-called primitive "otocerids" first recorded by Abich (1878) from the Upper Permian of Soviet Dzhulfa. One of the most interesting discoveries of the last decade has been the recognition of a large-scale and significant radiation of the so-called "otocerids" in the late Permian (Ruzhentsev, 1959, 1962, 1963). This radiation is expressed by nine genera and 30 species from the Dzhulfian strata of Soviet Dzhulfa representing an extremely complex array of forms, brought together in the family Araxoceratidae by Ruzhentsev (1959). Among the genera of this family is one genus, *Pseudotoceras*, that appears to be the direct ancestor of *Otoceras*. The data available lead to the conclusion that *Otoceras* is the final evolutionary descendant of the late Permian radiation of the "otocerids."

The primary purpose of this contribution is to review the evolutionary and biostratigraphic status of the genus *Otoceras*. Soon after the introduction of the genus and its type species by Griesbach (1880), a number of new species were introduced by Diener (1897). The thesis presented here is that only one species of the genus is present in the lowest Triassic beds of the

Himalayas. In addition it is proposed that *Otoceras boreale* Spath of northern Alaska, Arctic Islands of Canada, Spitsbergen, and northwestern Siberia is a subspecies of the Tethyan *Otoceras woodwardi.* Another conclusion of this review is that the family Araxoceratidae Ruzhentsev is, from an evolutionary viewpoint, best placed in synonymy of the older family Otoceratidae Hyatt (1900).

Finally it is suggested that *Otoceras woodwardi* survived in the earliest Triassic in the circum-Arctic region for a shorter period of time than in Tethys.

ACKNOWLEDGMENTS

In June of 1970 I had the opportunity of visiting the Paleontological Institute in Moscow and the Geological Institute in Leningrad to discuss with Soviet specialists the Permian-Triassic boundary beds of Soviet Dzhulfa. One result of these discussions was a need for a thorough review of the genus *Otoceras* and the lowest Triassic (Scythian) zone, and this paper is an attempt to serve that goal. I have been most fortunate in the reading and comments on the manuscript by W. M. Furnish, B. F. Glenister, N. D. Newell, Norman F. Sohl, and Curt Teichert. Miss Victoria Kohler ably assisted throughout preparation of the manuscript, especially in preparation of the plates and text-figures. Mrs. Agnes Pilot cheerfully typed the various drafts of the manuscript. Study of the type collections of ammonoids from the *Otoceras-Ophiceras* Zone of the Himalayas deposited in the Geological Survey of India in Calcutta was made possible by N.S.F. grant G-19066. Further work on these faunas was supported by N.S.F. grant GB-12909. My visit to the Soviet Union was supported by a grant from the Shaler Fund of Harvard University.

Otoceras—Morphology and Intraspecific Variation

All workers on the Himalayan ammonite genus *Otoceras* (Griesbach, 1880; Diener, 1897; v. Krafft and Diener, 1909; and Spath, 1930, 1934, 1935) are agreed as to the great variability in most if not all of its shell characters. Disagreement exists, though, in the taxonomic treatment of the genus. Griesbach concluded that "though it seems that there are several varieties, if not species, amongst the numerous specimens obtained, I prefer to include them for the present under one collective name" (Griesbach, 1880: 106). Diener (1897: 154) concurred with Griesbach's suspicion that "several varieties if not species" were represented, but at the same time added that "the distinction of the different species, or rather, the selection from among the numerous forms, which are all alike and all again different from each other, of those which ought to be considered as proper species, is no easy matter. For in no genus of Triassic ammonites known to

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Figure 1. Diagrammatic representation of the suture of specimens of *Octoceras woodwardi woodwardi* Griesbach from Otoceras beds in the Himalayas. A, topotype *O. woodwardi* (Diener, 1897, pl. 2, fig. 1; Pl. 2, figs. 3, 4 of this report) at a whorl height of approximately 45 mm, GSI 5924; B, topotype *O. woodwardi* (Diener, 1897, pl. 5, fig. 3; Pl. 1, figs. 5, 6 of this report) at a whorl height of 35 mm, GSI 5937; C, topotype *O. woodwardi* (Diener, 1897, pl. 5, fig. 5; Pl. 1, figs. 9, 10 of this report) at a whorl height of 27 mm, GSI 5939; D, paralectotype *O. woodwardi* (Diener, 1897, pl. 4, fig. 4; Pl. 1, figs. 3, 4 of this report) at a whorl height of 27 mm, GSI 5932; E, topotype *O. woodwardi* (Frech, 1902: 575, fig. 4d) at a whorl height of 21 mm; F, topotype *O. woodwardi* (Diener, 1897, pl. 4, fig. 5; Pl. 1, figs. 11, 12 of this report) at a whorl height of 13 mm, GSI 5933; G, topotype *O. woodwardi* (Frech, 1902: 575, fig. 4e) at a whorl height of 11 mm; H, topotype *O. woodwardi*, at a whorl height of 3.2 mm, BM(NH) C28513; I, holotype *O. undatum* (Diener, 1897, pl. 4, fig. 6; Pl. 3, figs. 9, 10 of this report) at a whorl height of approximately 20 mm, GSI 5934; J, holotype *O. parbati* (Diener, 1897, pl. 4, fig. 1; Pl. 4, figs. 9, 10 of this report) at a whorl height of 30 mm, GSI 5929; K, syntype *O. clivei* (Diener, 1897, pl. 5, fig. 4; Pl. 3, figs. 5, 6 of this report) at a whorl height of approximately 32 mm, GSI 5938; L, syntype *O. clivei* (Diener, 1897, pl. 3, fig. 4; Pl. 3, figs. 1, 2 of this report) at a whorl height of 35 mm, GSI 5928; M, suture specimens *O. clivei* (Diener, 1897, pl. 7, fig. 17; Pl. 3,

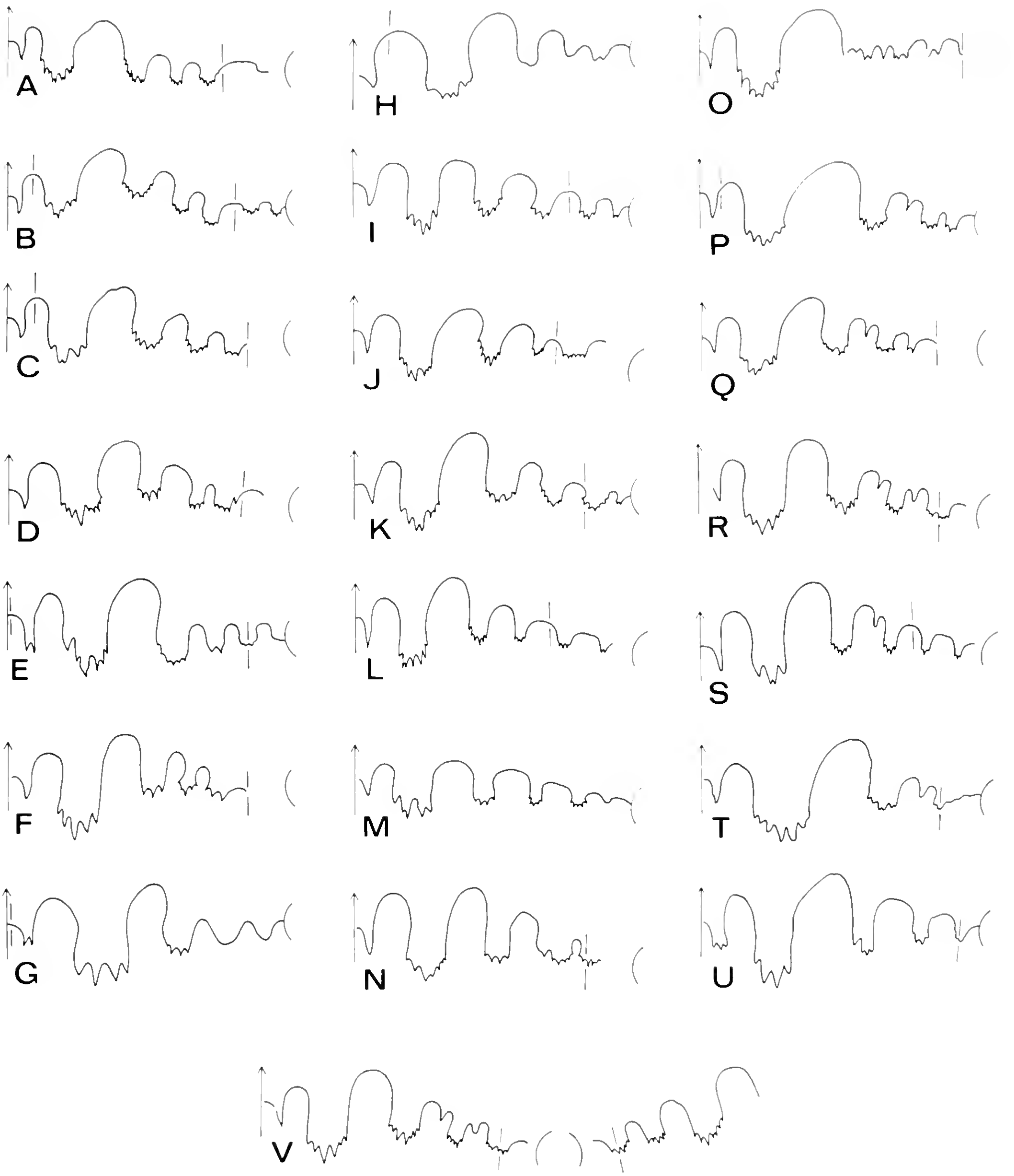

fig. 11 of this report) at a whorl height of approximately 20 mm, GSI 5964; N, syntype O. *clivei* (Diener, 1897, pl. 3, fig. 2; Pl. 3, figs. 7, 8 of this report) at a whorl height of 20 mm, GSI 5926; O, O. sp. ind. aff. *clivei* (Krafft and Diener, 1909, pl. 29, fig. 3) at a whorl height of approximately 35 mm, GSI 5936; P, suture specimens of O. *draupadi* (Diener, 1897, pl. 7, fig. 15; Pl. 4, figs. 5, 6 of this report) at a whorl height of approximately 35 mm, GSI 5962; Q, suture specimens O. *draupadi* (Diener, 1897, pl. 5, fig. 6; Pl. 4, figs. 3, 4 of this report) at whorl height of 25 mm, GSI 5940; R, syntype O. *draupadi* (Diener, 1897, pl. 4, fig. 3; Pl. 4, figs. 1, 2 of this report) at a whorl height of 30 mm, GSI 5931; S, lectotype O. *fissisellatum* (Diener, 1897, pl. 3, fig. 3c) at a whorl height of 25 mm, GSI 5927; T, paralectotype O. *fissisellatum* (Diener, 1897, pl. 5, fig. 2; Pl. 4, figs. 7, 8 of this report) at a whorl height of 25 mm, GSI 5936; U, O. (*Metatoceras*) *dieneri* Spath = *Hungarites* sp. indet. (Diener, 1897, pl. 23, fig. 5: Pl. 3, figs. 3, 4 of this report) at a whorl height of 27 mm, GSI 6058; V, left and right suture of syntype of O. *draupadi* (Diener, 1897, pl. 4, fig. 3; Pl. 4, figs. 1, 2 of this report) at a whorl height of approximately 25 mm, GSI 5931.

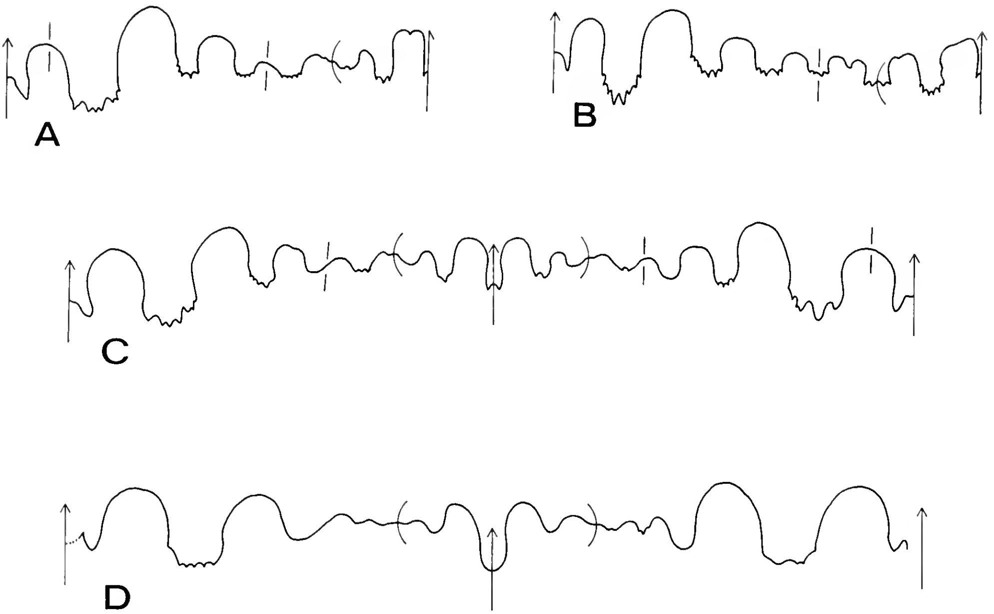

Figure 2. Diagrammatic representation of the sutures of specimens of *Otoceras woodwardi woodwardi* Griesbach from Otoceras beds, Shalshal Cliff near Rimkin Paiar encamping ground, Niti region, Himalayas. A, complete suture of specimen figured on Plate 2, figures 5–7 at a whorl height of 11.8 mm, BM(NH) 28512; B, complete suture of specimen of *Otoceras clivei* (Diener, 1897, pl. 7, fig. 16; illustrated here on Plate 3, figure 12) at a whorl height of 25 mm, GSI 5963; C, complete left and right suture of specimen figured on Plate 2, figures 8–10, at a whorl height of 5.7 mm, BM(NH) C28514; D, complete left and right suture of specimen figured on Plate 2, figures 13–15, at a whorl height of 1.5 mm, BM(NH) C28513b.

me, not even in the group of *Dinarites spiniplicati,* are the variations so great as in this." Diener concluded that the sutures showed criteria by which species could be recognized, and proposed the following classification:

- Group of *Otoceras woodwardi* Griesbach
  - *O. woodwardi* Griesbach
  - *O. parbati* Diener
  - *O. clivei* Diener
  - *O. undatum* Griesbach
- Group of *Otoceras fissisellatum* Diener
  - *O. fissisellatum* Diener
  - *O. draupadi* Diener

The basis for separating the two species groups was the presence or absence of small secondary lobes in one or more of the lateral saddles. The group of *Otoceras fissisellatum* has such secondary lobes, whereas the species of the group of *O. woodwardi* do not have them. The place of intersection of the umbilical shoulder and the suture was used to further subdivide the group of *Otoceras woodwardi.* In one of these subdivisions, which includes *O. clivei* and *O. parbati,* the first auxiliary saddle is divided by the umbilical shoulder. In the second subdivision, which includes only *O. woodwardi,* the first auxiliary saddle lies outside the umbilical shoulder. *Otoceras undatum* was distinguished on the basis of presence of wavy, lateral folds. Within the group of *Otoceras fissisellatum* the name-giving species has generally only one saddle with a small secondary lobe, but in *O. draupadi* generally two saddles have small secondary lobes.

That the suture of the Himalayan *Otoceras* was highly variable was freely admitted by Diener (1897). Griesbach (1880: 107) was the first to note that in some of his specimens the sutures varied in details

TABLE 1. TABULATION OF SPECIMENS PER LOCALITY FROM *OTOCERAS*-*OPHICERAS* BEDS IN THE HIMALAYAS AVAILABLE TO DIENER (1897).

Locality of specimens studied by von Krafft and Diener (1909) indicated by an X. These authors generally did not indicate the precise number of specimens in their collections but it appears to have been very few for each species.

	Muth	Ensa	Kuling	Kaga	Tengdi	Khar	Gaichund	Kiunglung	Shalshal
Episageceras dalailamae	X			X					2
Ophiceras sakuntala	X	X		X				6	140
medium								5	5
tibeticum	X	X	X	X		3		16	13
gibbosum									10
demissum					5	X		11	12
ptychodes									3
chamunda			2			2	X	3	30
platyspira								1	6
serpentinum						2		37	1
Glyptophiceras himalayanus									1
Proptychites scheibleri									1
Vishnuites pralambha									2
Otoceras woodwardi	X	X	X			X		1	31
undatum		X							2
clivei	X	X	1				X		7
draupadi									5
parbati								1	
fissisellatum									4
Prionolobus hodgsoni									2
Anotoceras nala								5	1

of the elements on the left and right sides of the specimens. Diener (1897: 155) described and illustrated a suture in which "the specimen is a perfect *Otoceras woodwardi* on one, and a perfect *O. draupadi* on the other side." The sutures of the various species of *Otoceras* from the Himalayas reproduced by Diener (1897) are illustrated here in Figure 1. The sutures of three small specimens in the British Museum (Natural History) are shown in Figure 2. In two of these specimens the complete suture could be observed, and showed obvious minor differences on the two sides of the conch (Fig. 2C, D).

As I have shown (Kummel, 1969), sutures of many Scythian ammonoids exhibit the same high degree of variability as any other morphological feature.

Diener (1897) recorded that he had 56 specimens of *Otoceras* from the Shalshal Cliff locality, opposite the Rimkin Paiar encamping ground, most of which came from the so-called main layer of *Otoceras woodwardi*, a unit only one foot thick. Of these specimens only the 17 figured by him are preserved in the Geological Survey of India at Calcutta. Diener (1897: 154) observed that "the relative proportions of height and thickness and the size of the umbilicus are so variable, even in specimens which agree in all other characters, that they cannot serve for specific distinction." Considering the fact that all 56 specimens from Shalshal Cliff, which provided the main material for Diener's study, came from a one-foot thick bed at one locality it appears more logical to consider

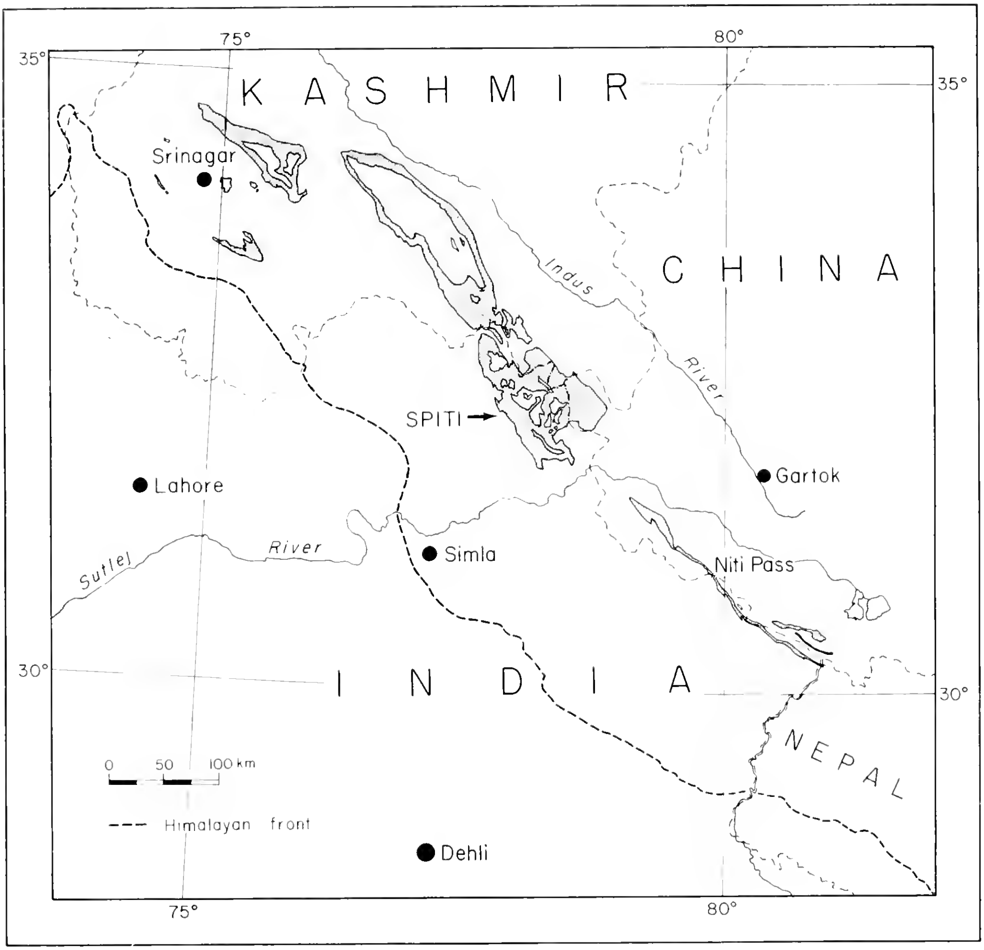

Figure 3. Outcrop map of Triassic formations in the Himalayas (from Geological Map of India, Geological Survey of India, 1957).

this assemblage as a natural population, in which variations in sutures are no more than what one would expect. On Table 1 are listed the numbers of specimens of each species of *Otoceras* Diener recognized in the Shalshal fauna. Of the 56 specimens of *Otoceras,* 31 were assigned to *O. woodwardi* and only four specimens to *O. fissisellatum,* which has a small lobe in the first auxiliary saddle; *O. draupadi,* which has a small lobe in each of the first and second auxiliary saddles, is represented by five specimens, and *O. clivei* by only seven specimens. The sutures of the specimens assigned to species other than *O. woodwardi* are no more than intraspecific variants. Although presence or absence of a minor lobe in an auxiliary saddle is conspicuous, it does not necessarily represent a specific difference. This suggestion could, of course, only be tested by examination of large population samples. The specimens of *Otoceras* recorded by von Krafft and Diener (1909) from Spiti are few in number and poorly preserved. All the localities that have yielded the *Otoceras-Ophiceras* fauna studied by Diener (1897) and von Krafft and Diener (1909)

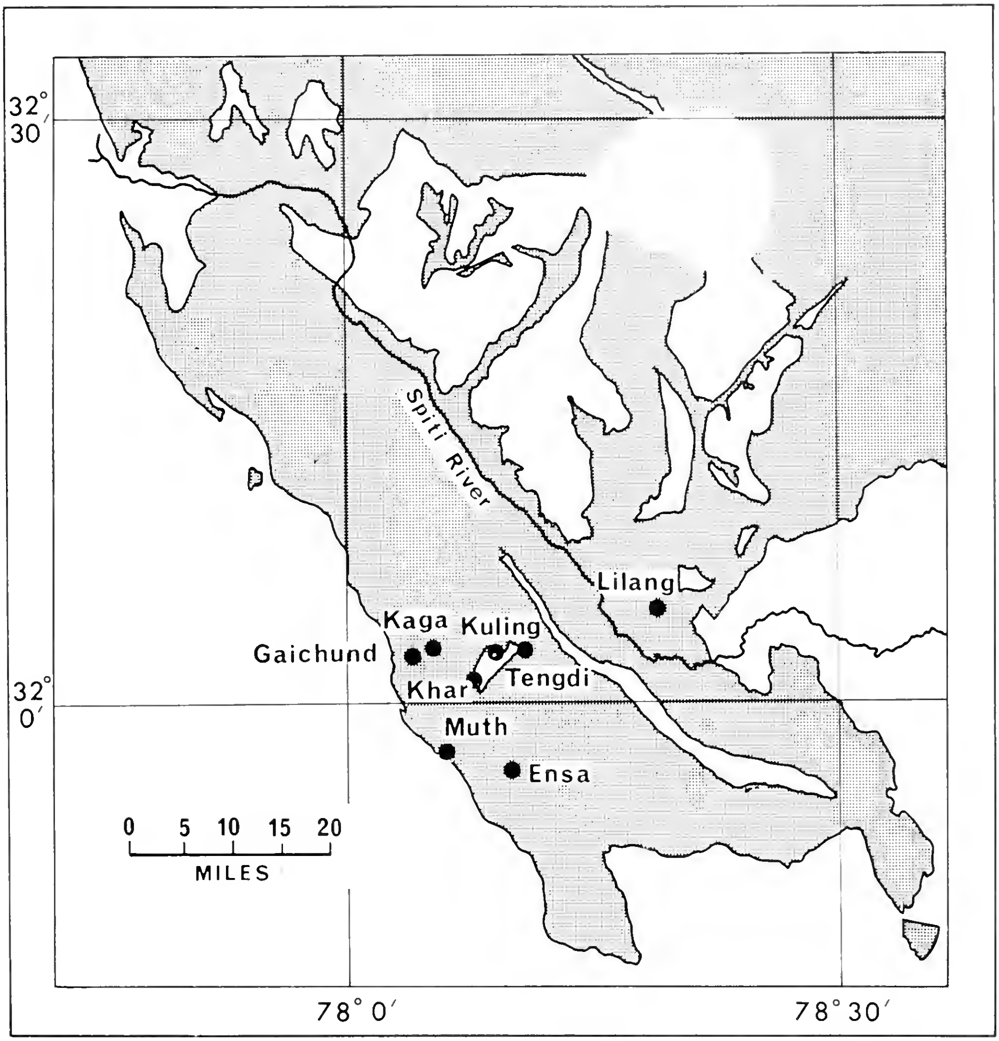

Figure 4. Outcrop map of Triassic formations in the Spiti region showing principal localities that have yielded faunas from the *Otoceras-Ophiceras* Zone (adapted from H. H. Hayden, 1904, pl. 18).

are shown on Figures 3 to 5. The Eigil Nielsen collection in Copenhagen from Muth in the Spiti region contains 14 specimens of *Otoceras*, all poorly preserved.

The descriptions of the Himalayan otocerids by Diener (1897) are quite thorough, and examination of his figured specimens leaves little to be added. As all of Diener's illustrations were line-drawings, unretouched photographs of the types are published here (Plates 1–4). It can readily be seen that Diener's drawings tended to be idealized and do not indicate the general state of preservation. The smallest specimen described by Diener is approximately 28 mm in diameter (Pl. 1, figs. 11, 12) and was assigned by him to *O. woodwardi.* The tray in the collections of the Geological Survey of India that contains Griesbach's lectotype (Pl. 1, figs. 1, 2) also

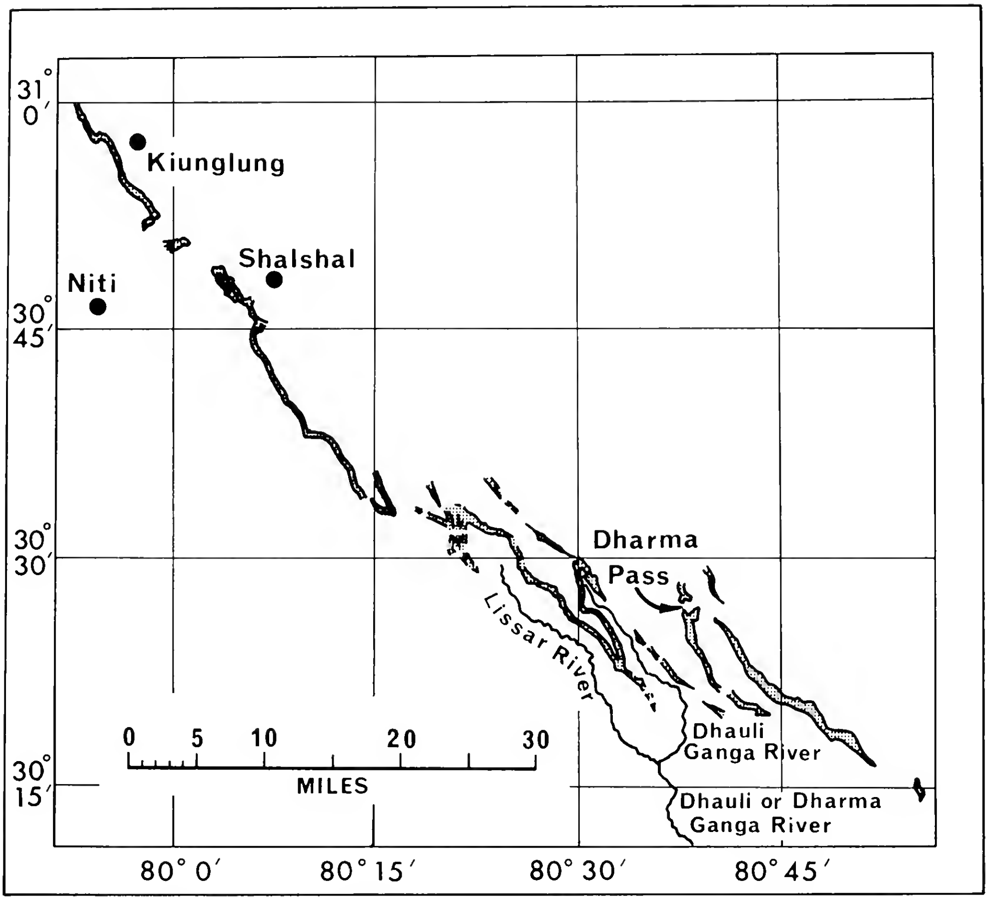

Figure 5. Outcrop map of Triassic formations in the Niti Pass region showing the principal localities that have yielded faunas from the *Otoceras-Ophiceras* Zone (adapted from C. L. Griesbach, 1891, Map No. 1).

contains an unnumbered specimen, not figured by Diener, which has a diameter of 9 mm (Pl. 1, figs. 7, 8). The collections of the British Museum (Natural History) contain some fragmentary specimens from the Shalshal Cliffs, including fragments of inner whorls. The smallest specimen is a third whorl section with a height of 1.8 mm (Pl. 2, figs. 13–15). At that whorl height the median keel is well marked, but the dorsal area shows no impression of a keel. The lateral keels adjoining the ventral keel are just faintly visible. The lateral areas bear two broad, low folds. The complete suture of this specimen is illustrated in Figure 2D. Another specimen, having a diameter of approximately 8.5 mm, shows the three ventral keels very well (Pl. 2, figs. 11, 12). A third specimen (Pl. 2, figs. 8–10) has a diameter of 13.5 mm. Its complete suture at a whorl height of 5.7 mm is reproduced in Figure 2C.

I include in *Otoceras woodwardi* of the Himalayas the specimen Diener (1897: 150) described as *Hungarites* sp. ind., here illustrated on Plate 3, figures 3, 4. Diener recognized the close similarity of this fragmentary specimen of a third volution to *Otoceras woodwardi*. He, however, considered it distinct because the "remarkable difference from *Otoceras* is in the denticulate development of the siphonal lobe,

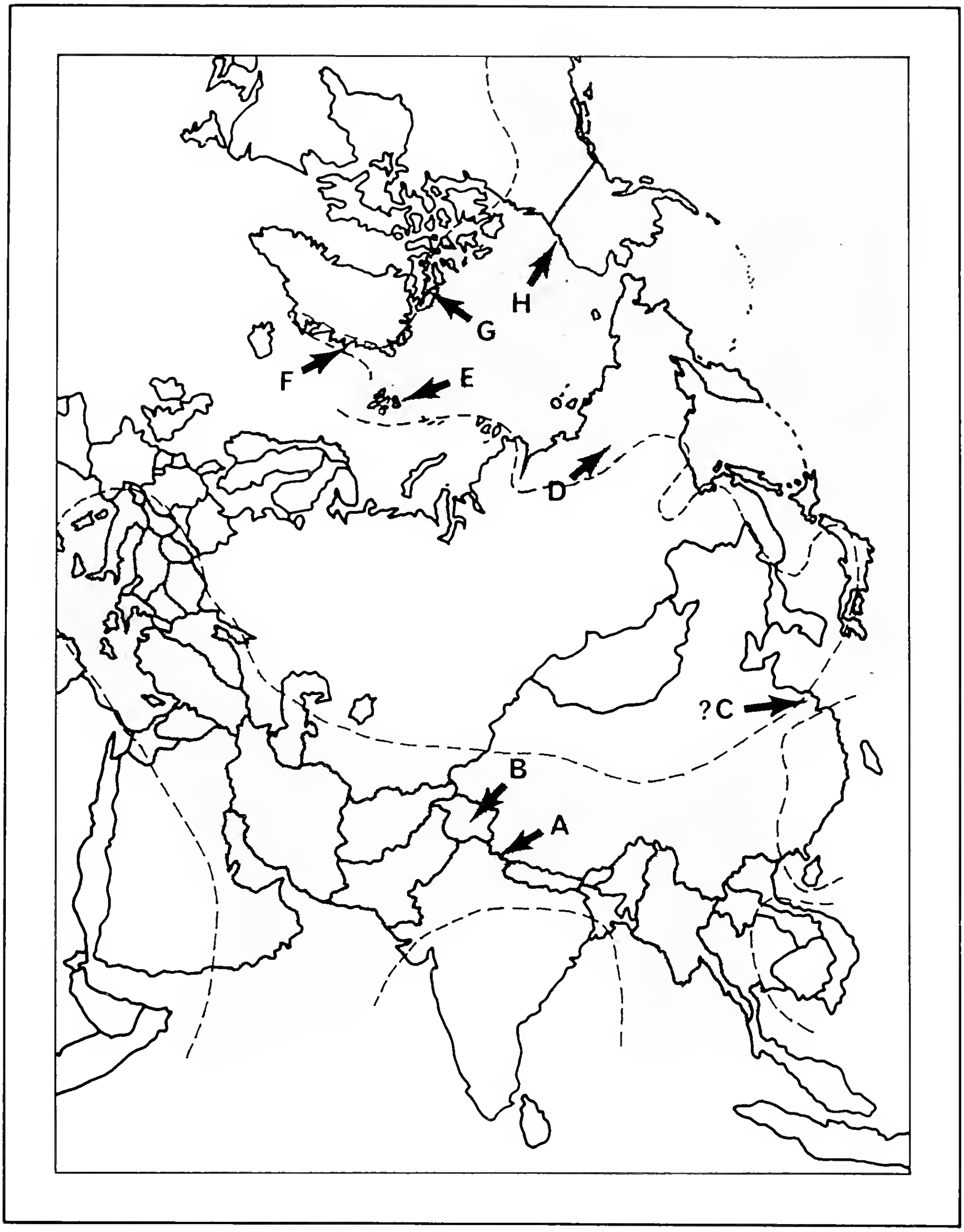

Figure 6. Geographic distribution of the genus Otoceras. A, central Himalayas; B, Kashmir; C, Nanking region; D, eastern Verkhayansk, Siberia; E, Spitsbergen; F, East Greenland; G, Arctic Canada; H, northern Alaska.

which is bifid in *Otoceras*, whereas each of its lateral branches is denticulate in *Hungarites*" (Diener, 1897: 150). The ventral lobe, in fact, is trifid on one side and bifid on the other (Diener, 1897, pl. 23, fig. 5c; Fig. 1V of this report). The auxiliary series is not as fully developed as in the specimens assigned to *Otoceras* but, here again, the differences are not considered to be significant. All characters of this specimen fall well within the range of variability of *Otoceras woodwardi.* Spath (1930: 8) proposed the subgenus *Metotoceras* for Diener's specimen of *Hungarites* sp. ind., making special note of the absence of an umbilical rim; however, such a rim is present on the adoral portion of the specimen (Pl. 3, fig. 3).

Within Tethys *Otoceras* of earliest Scythian age is known only from the Himalayas, the Niti and Spiti regions of Kumaon, and in Kashmir near Srinagar. Recently Nakazawa et al. (1970) have illustrated several well-preserved specimens that they assign to *O. clivei* Diener and *O. draupadi* Diener from the Guryul Ravine, Kashmir. The other localities where the genus has been recorded are in the circum-arctic region (Fig. 6). The genus was first recorded from East Greenland by Spath (1930), who assigned a few fragmentary specimens to *Otoceras fissisellatum.* A larger collection was available to Spath (1935) in a later report where he introduced the name *Otoceras boreale* for the East Greenland forms. The genus *Otoceras* was next reported from the eastern Verkhoyansk region by Popov (1958), who recognized two species—*O. boreale* Spath and *O. indigirense* Popov. The latter species, which was based on four specimens, was separated on the basis of the presence of a vertical umbilical wall and slight differences in the sutures. In North America *Otoceras boreale* has been reported from the Canning River region of northern Alaska (Kummel *in* Reeside et al., 1957: 1501) and described and illustrated from Ellesmere and Axel Heiberg Islands (Tozer, 1961, 1967). The lowest Triassic fauna on Axel Heiberg Island has yielded a small number of specimens of a single species that Tozer (1967) described as *Otoceras concavum*, considering concave flanks on the inner whorls as distinguishing characters. Considering the range of variability seen in the larger Himalayan fauna, I find it difficult, on the basis of such a small sample, to recognize *O. concavum* as a distinct species.

The only author who attempted a general assessment of the relationships between the Arctic *O. boreale* and the species of *Otoceras* known from the Himalayas was Spath (1930, 1934, 1935). It was in his second report on the East Greenland Lower Triassic fauna that Spath, on the basis of much larger faunas, recognized *O. boreale* as being distinct from the Himalayan species of the genus, justifying his separation of these forms on the basis of slight differences in the suture, especially in the dorsal suture (Spath, 1935: 11). Information on the dorsal suture of *Otoceras woodwardi* is limited. Griesbach (1880, pl. 2, fig. 6) reproduced a complete suture of *O. woodwardi* and so did Diener (1897, pl. 7, fig. 16; Fig. 2B of this report). The specimen which yielded the suture reproduced by Diener is figured here on Plate 3, figure 12. Though there are differences in detail between the sutures illustrated by Griesbach and Diener, there is a suspicion that they were both taken from the same specimen. Frech (1901: 575) illustrated a series of sutures taken at whorl heights of 2.5 mm, 6 mm, 11 mm, and 21 mm. The complete sutures of three small specimens of *Otoceras woodwardi* at whorl heights of 1.5 mm, 5.7 mm, and 11.8 mm are illustrated in Figures 2A, C, D. There are only three published sutures of *Otoceras boreale* that include the dorsal suture, but two of these are incomplete (Fig. 7). In *Otoceras boreale* the dorsal lateral saddles contain adventitious lobes that are larger than in those of *O. woodwardi.* However, the three dorsal sutures of *O. boreale* were taken at

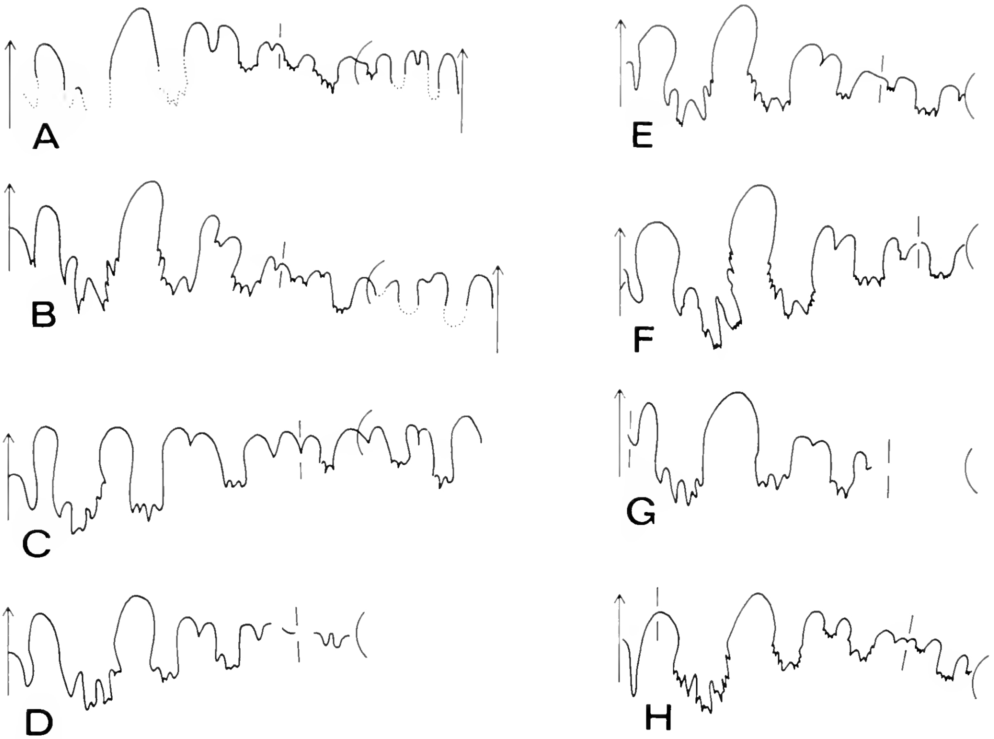

Figure 7. Diagrammatic representation of the suture of specimens of *Otoceras woodwardi boreale*. A, complete suture of specimen from *Ophiceras (Metophiceras)* Zone from Clavering Island, East Greenland (Spath, 1935, pl. 2, fig. 3b) at whorl height of approximately 75 mm; B, complete suture of specimen from Blind Fiord Formation, Axel Heiberg Island (Tozer, 1961, fig. 7) at a diameter of approximately 90 mm; C, complete suture of *Otoceras indigirense* Popov (1958, fig. 1, 1) from eastern Verkhoyansk region, Kerekhtyokh brook, Siberia, scale uncertain; D, specimen from eastern Verkhoyansk region, Kerekhtyokh brook, Siberia (Popov, 1958, figs. 1, 2), scale uncertain; E, specimen from upper Indigirka River, Verkhoyansk Mountains, Siberia, MCZ 6103, at a diameter of 35 mm; F, specimen identified as *O. indigirense* by Yu. N. Popov from East Khandiga River, Verkhoyansk region, Siberia, MCZ 8685, at a whorl height of 25 mm; G, specimen from upper member of Sadlerochit Formation, Canning River, northern Alaska, at a whorl height of 100 mm; H, paratype of *O. concavum* Tozer (1967, fig. 20) from Blind Fiord Formation, Axel Heiberg Island, northern Canada, at a whorl height of approximately 45 mm.

whorl heights of 50 or more millimeters, while those known in *O. woodwardi* are from much smaller specimens. Adventitious elements in the dorsal saddles of *O. woodwardi* are present at a whorl height of 11.8 mm (Fig. 2A) and are more marked in Diener's specimens (Fig. 2B), which I believe to be taken at a whorl height of 25 mm. It is quite apparent that much more data on the development of dorsal suture in *O. boreale* are needed.

In addition, Spath (1935: 11) noted the larger size of the Arctic forms over those from the Himalayas. Both Spath (1935) and Tozer (1961) stated that they had seen specimens of *O. boreale* probably having a diameter of 300 mm or more. The largest of the Himalayan specimens (Pl. 2, figs. 3, 4) has a diameter of 152 mm.

Finally, Spath (1935: 11) noted that in the lower *Glyptophiceras* beds *Otoceras* was represented by a number of fragmentary and mostly crushed specimens. He had, however, one specimen (Spath, 1935, pl. 3, fig. 4) representing only a part of a whorl which was very inflated in cross section. On this basis he suggested that it was probably not conspecific with *O. boreale*.

Considering the great variability in all

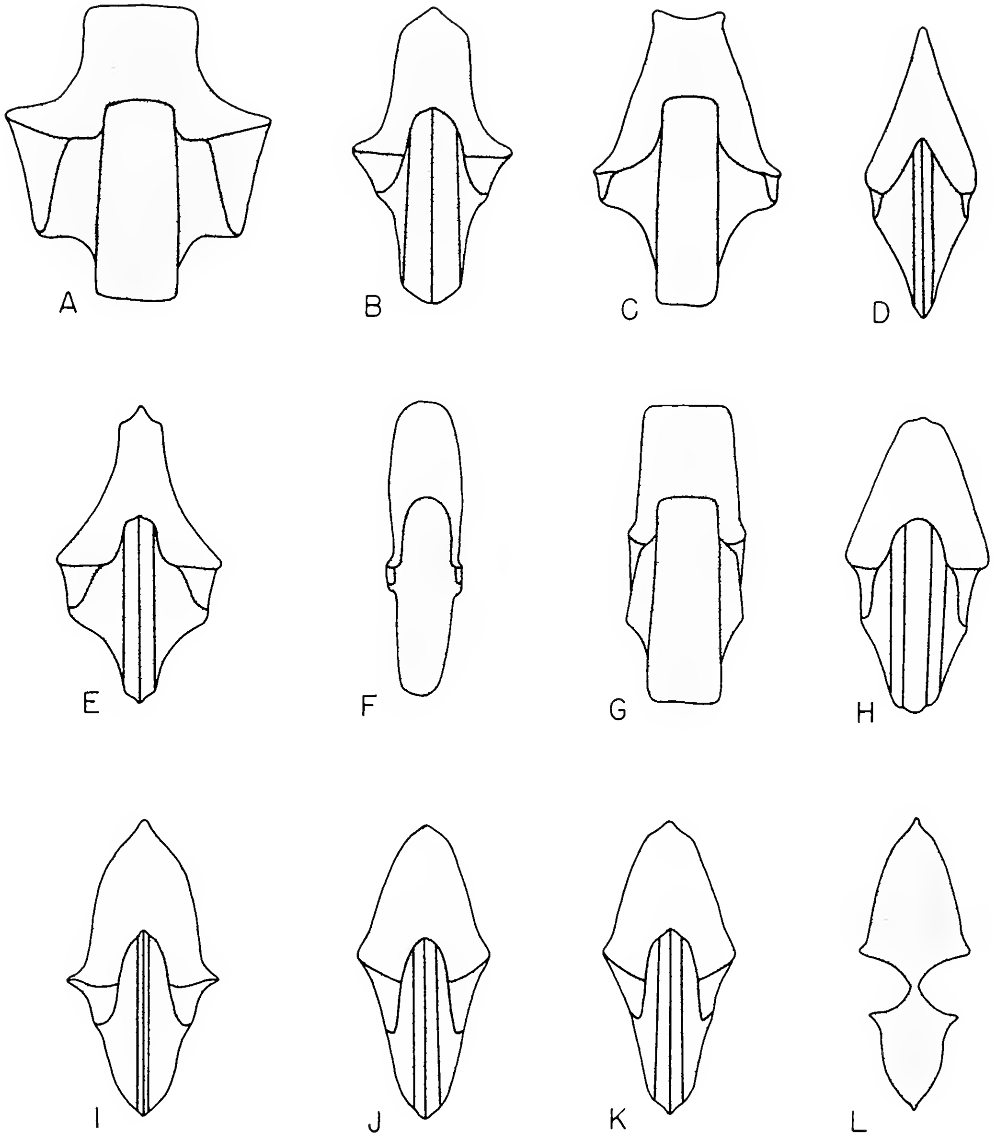

Figure 8. Cross sections of the conch of A, *Araxoceras latissimum* Ruzhentsev, 1959, fig. 1a, diameter 58 mm; B, *Prototoceras tropitum* (Abich), Ruzhentsev, 1959, fig. 1c, diameter 23 mm; C, *Rotaraxoceras caucasium* Ruzhentsev, 1959, fig. 1b, diameter 33 mm; D, *Pseudotoceras djoulfense* (Abich), Ruzhentsev, 1963, pl. 6, fig. 2b, diameter 110 mm; E, *Urartoceras abichanum* Ruzhentsev, 1959 fig. 1g, diameter 75 mm; F, *Dzhulfoceras furnishi* Ruzhentsev, 1962, pl. 5, fig. 1b, diameter 36 mm; G, *Vedioceras ventroplanum* Ruzhentsev, 1962, pl. 5, fig. 3a, diameter 75 mm; H, *Avushoceras jakowlewi* Ruzhentsev, 1962, pl. 5, fig. 5a, diameter 72 mm; I, *Otoceras woodwardi woodwardi*, Diener, 1897, pl. 2, fig. 1b, diameter 140 mm; J, *Otoceras undatum* Griesbach, Diener, 1897, pl. 4, fig. 6b, diameter 40 mm; K, *Otoceras clivei* Diener, 1897, pl. 3, fig. 2b, diameter 40 mm; L, *Otoceras woodwardi borealis* Spath, 1935, pl. 1, fig. 1b, diameter 115 mm.

morphologic features of the Himalayan *Otoceras woodwardi*, the criteria used by Spath (1935) in separating the Arctic forms as a distinct species do not appear to be convincing. It is granted that more data are needed, especially on the Arctic representatives of *Otoceras*, that is, data on variation in shell form, ontogeny, and suture. As known at present, however, it is only in the dorsal suture that consistent differences between the Himalayan and Arctic forms can be observed. This being the case, and considering the fact that the two forms are geographically distinct, I choose to consider the Arctic *O. boreale* as a subspecies of the Himalayan *Otoceras woodwardi*.

The Ancestry of Otoceras

It has long been recognized that the Dzhulfian otocerids are closely related to the earliest Triassic *Otoceras woodwardi* (Diener, 1897; Spath, 1930, 1934). However, until recently the relationship has been obscure, as only the few Dzhulfian species described by Abich (1878) were known. One of the most interesting results of the renewed field studies in Soviet Dzhulfa was the discovery of a large and diversified fauna of "otocerids" that have been described by Ruzhentsev (1959, 1962, 1963; Ruzhentsev and Shevyrev *in* Ruzhentsev and Sarycheva, 1965). This fauna now includes nine genera and thirty species brought together in the family Araxoceratidae Ruzhentsev. The family was diagnosed as follows (Ruzhentsev, 1959: Translation by Mrs. Mary L. Davis, University of Iowa): "The shell is from pulley-shaped to disc-shaped. The ventral side is flat, concave, or tectiform, of various widths. All have 14–16 lobes, not counting supplementary ones. The ventral lobe is narrow, poorly dissected, with wedge-shaped branches; by length it is shorter or equal to the primary umbilical lobe. There are not more than two well-developed external umbilical lobes, they have ceratitic crenulations at their base. Out from them to the umbilical suture goes a small wedge-shaped lobe, the quantity, form, and situation of which are highly changeable. The dorsal lobe is narrow, long, bifid. The inner lateral lobe is narrow and wedge-shaped. The inner umbilical lobes are one or more; they are also wedge-shaped." Ruzhentsev placed the following genera in this family: *Araxoceras* Ruzhentsev, 1959; *Rotaraxoceras* Ruzhentsev, 1959; *Urartoceras* Ruzhentsev, 1959; *Prototoceras* Spath, 1930; *Pseudotoceras* Ruzhentsev, 1962; *Vescotoceras* Ruzhentsev, 1962; *Dzhulfoceras* Ruzhentsev, 1962; *Vedioceras* Ruzhentsev, 1962; and *Avushoceras* Ruzhentsev, 1962. This family includes ammonoids with a bewildering array of shell shapes (Fig. 8). The whorl sections vary from forms with flat venters (*Araxoceras*, *Vedioceras*), to forms with fastigate venters, some broad, some narrow (*Prototoceras*, *Urartoceras*, *Pseudotoceras*), to forms with rounded venters (*Dzhulfoceras*, *Avushoceras*). All genera are involute and some have prominent flared umbilical rims (*Araxoceras*, *Urartoceras*, *Prototoceras*). The sutures, though varying in detail from one genus to the other, have the same basic pattern (Fig. 9).

The apparent sudden appearance of this large diversified fauna of "otocerids" in the late Permian Dzhulfian strata is a puzzle. Ruzhentsev (*in* Ruzhentsev and Sarycheva, 1965) suggested that the radiation of the Araxoceratidae was made possible by the great decline among the agoniatites and goniatites. While he believed that the Araxoceratidae were endemic to the general Dzhulfian region, it is now known that the family is quite widely distributed. Stepanov, Golshani, and Stöcklin (1969) recorded the presence of *Araxoceras*, *Vescotoceras*, *Vedioceras*, *Pseudotoceras*, and *Avushoceras* from the Julfa beds at Kuh-e-Ali Bashi, northwestern Iran. Recently Taraz (1969) listed *Prototoceras*, *Vescotoceras*, and *Pseudotoceras* from upper Permian strata near Abadeh in central Iran. In the overlying unit from which Taraz

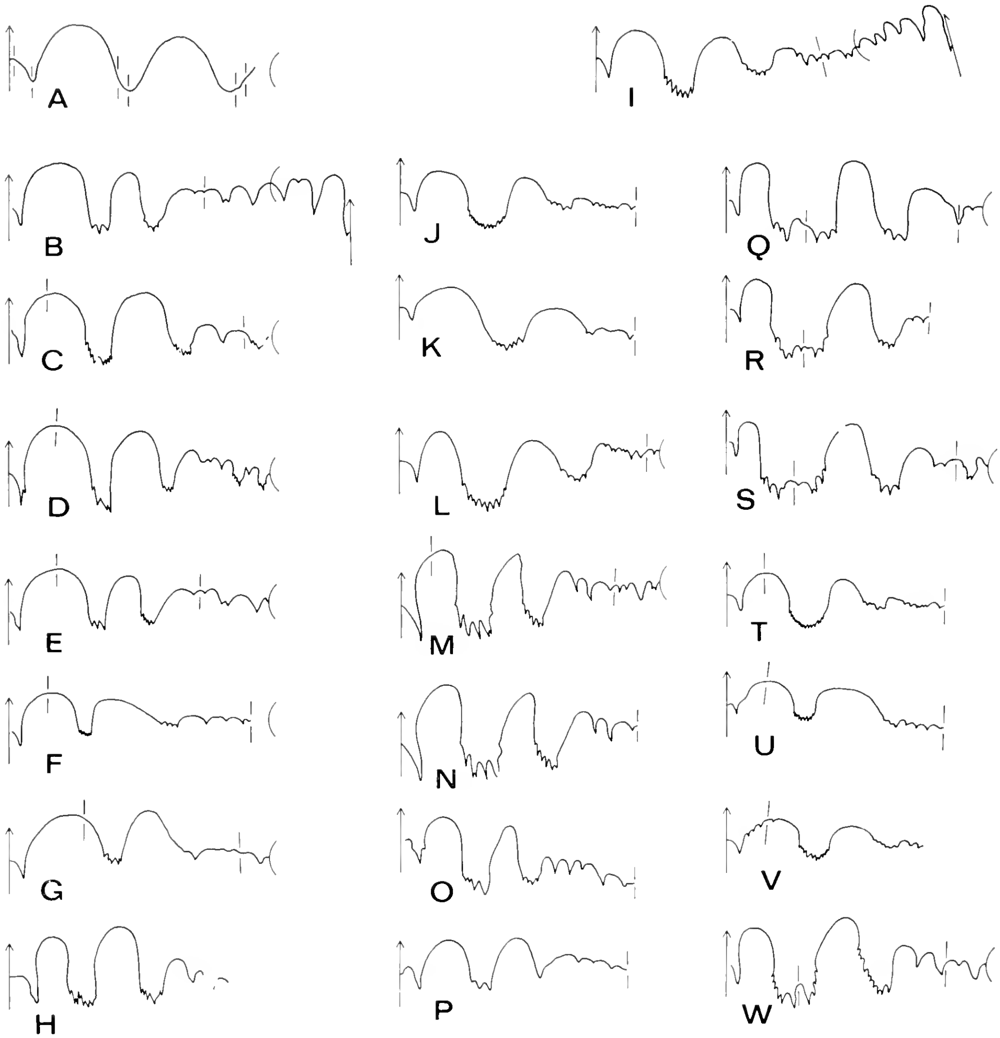

Figure 9. Diagrammatic representation of the suture of A, *Glyphioceras* (*Anderssonoceras*) *anfuense* Grabau (1924, fig. 301), holotype, at diameter of approximately 20 mm; B, *Araxoceras latissimum* Ruzhentsev, 1959, fig. 2a; C, *Araxoceras glenisteri* Ruzhentsev, 1962, fig. 2d; D, *Araxoceras latum* Ruzhentsev, 1962, fig. 2b; E, *Araxoceras latissimum* Ruzhentsev, 1962, fig. 2a; F, *Rotaraxoceras caucasium* Ruzhentsev, 1962, fig. 4a; G, *Rotaraxoceras deruptum* Ruzhentsev, 1962, fig. 4b; H, *Pseudotoceras armenorum* Ruzhentsev, 1962, fig. 6; I, *Prototoceras tropitum* (Abich), Ruzhentsev, 1959, fig. 2c; J, *Prototoceras acutum* Ruzhentsev, 1959, fig. 2d; K, *Prototoceras parallelum* Ruzhentsev, 1959, fig. 2e; L, *Discotoceras raddei* (Arthaber), Ruzhentsev, 1959, fig. 2f; M, *Urartoceras abichianum* Ruzhentsev, 1962, fig. 5; N, *Urartoceras abichianum* Ruzhentsev, 1959, fig. 2g; O, *Dzhulfoceras furnishi* Ruzhentsev, 1962, fig. 8a; P, *Dzhulfoceras paulum* Ruzhentsev, 1962, fig. 8b; Q, *Vedioceras ogbinense* Ruzhentsev, 1962, fig. 10c; R, *Vedioceras ventroplanum* Ruzhentsev, 1962, fig. 10b; S, *Vedioceras ventroplanum* Ruzhentsev, 1962, fig. 10a; T, *Vescotoceras acutum* Ruzhentsev, 1962, fig. 7a; U, *Vescotoceras evanidum* Ruzhentsev, 1962, fig. 7c; V, *Vescotoceras serratum* Ruzhentsev, 1962, fig. 7b; W, *Avushoceras jakowlewi* Ruzhentsev, 1962, fig. 10d.

(1969: 691) records *Pseudogastrioceras*, *Dzhulfites*, *Bernhardites*, *Abichites*, and *Paratirolites*, Curt Teichert was able to collect a small fauna including not only several of these genera but also a specimen of *Vedioceras*. Chao (1965) recorded *Prototoceras*, *Araxoceras*, and *Vescotoceras* from the Laoshan shale member of the Loping coal series of Kwangsi, South China. The family is now also known from the western hemisphere. Spinosa, Furnish, and Glenister (1970) have described a new genus, *Eoaraxoceras*, from strata of uppermost Guadalupian age from the La Colorado beds of Valle de las Delicias, Coahuila, Mexico, an occurrence that is presumably older than that of Soviet Dzhulfa, Abadeh, and South China.

The phylogenetic relations of the various genera of the Araxoceratidae are by no means understood. The data on the South China fauna are still of a preliminary nature and are of no help to the present problem. Another difficulty is that the preservation of many Dzhulfa and Kuh-e-Ali Bashi specimens leaves much to be desired. The specimens are internal casts, and many are fragmentary and crushed, at least on one side. The inner whorls are filled with coarse crystalline calcite and are commonly deformed. The significance of the stratigraphic distribution of the genera at Soviet Dzhulfa is uncertain at this stage. *Araxoceras* and *Vescotoceras* appear to be confined to the *Araxoceras* beds; *Urartoceras, Dzhulfoceras, Vedioceras*, and *Avushoceras* are confined to the overlying *Vedioceras* beds; but *Rotaraxoceras, Prototoceras*, and *Pseudotoceras* are present in both the *Araxoceras* and *Vedioceras* beds (Ruzhentsev and Sarycheva, 1965: 48).

Ruzhentsev's (1959) conclusion that the ancestral form of the Araxoceratidae is *Glyphioceras* (*Anderssonoceras*) *anfuense* Grabau (1924) appears to be well founded. Ruzhentsev (1959) established the family Anderssonoceratidae for the single genus *Anderssonoceras*. The pattern of radiation within the Araxoceratidae is not at all understood. In his first paper on this family Ruzhentsev (1959) considered the then known araxoceratids to be divisible into three groups: (1) *Araxoceras* and *Rotaraxoceras*, (2) *Prototoceras* and *Discotoceras*, and (3) *Urartoceras*. He considered each of these groups to be an independent development from an unknown genus with ceratitic lobes close in form to *Anderssonoceras*. The genus *Eoaraxoceras* Spinosa et al. (1970) appears to be such a form. Ruzhentsev (1959) suggested that the Triassic *Otoceras* was derived from the *Prototoceras-Discotoceras* group. Continued study of additional collections from Soviet Dzhulfa led to the recognition of a number of new genera and species (Ruzhentsev, 1962, 1963). With this great increase in data on the araxoceratids, Ruzhentsev (1962, and Ruzhentsev *in* Ruzhentsev and Sarycheva, 1965) came to the conclusion that the immediate ancestor of *Otoceras* was *Pseudotoceras*. With this conclusion I completely agree. *Pseudotoceras* has a simpler suture with fewer lobe elements and lacks the flaring of the umbilical rim (Figs. 8D, I).

There is one other genus of the Otoceratidae that needs comment and this is *Anotoceras* Hyatt (1900: 553; type species *Prosphingites nala* Diener, 1897: 54, pl. 1, fig. 4). This is a relatively rare form from the *Otoceras-Ophiceras* beds of the Himalayas. Diener (1897) had only seven specimens available for study and of these only four are still preserved in the Geological Survey of India collections in Calcutta. I have seen the Eigil Nielsen collection from the *Otoceras-Ophiceras* beds at Muth which contains only one fragmentary phragmocone of *Anotoceras*. In addition to the species selected as type for this genus Diener (1897) described another species, *Anotoceras kama*, that was differentiated on the basis of a fastigate venter (Pl. 12, figs. 13, 14). My own examination of this specimen showed that it is slightly crushed, mainly along the venter. In all other aspects it resembles specimens of *Anoto-*

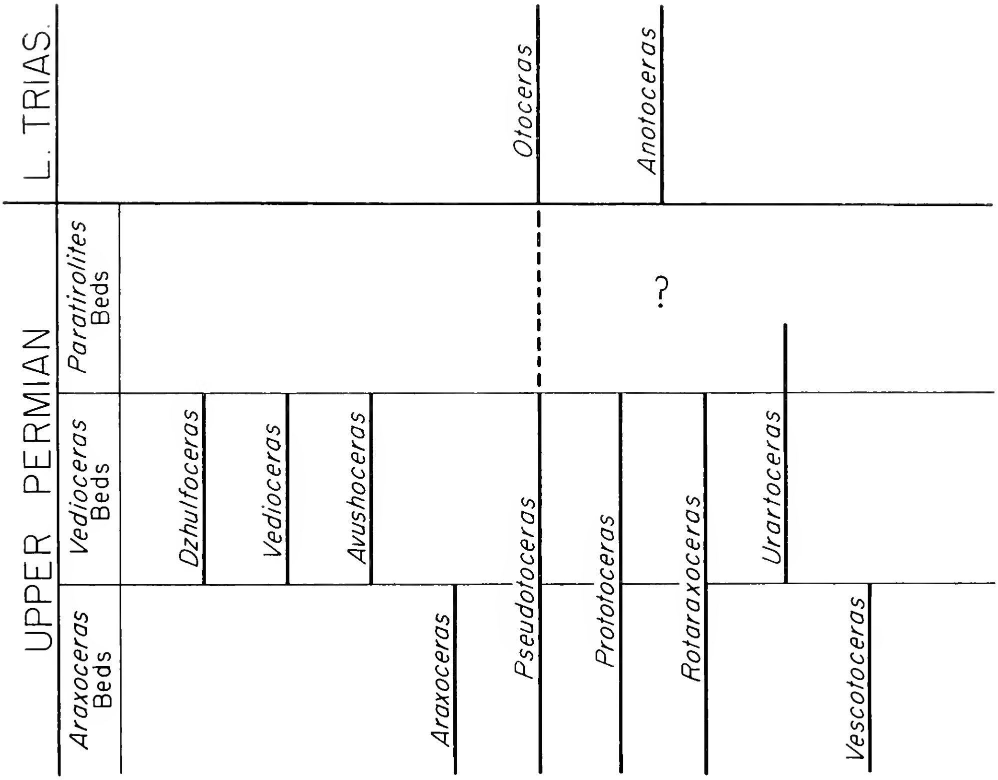

Figure 10. Suggested phylogenetic relations of late Permian and early Triassic genera of family Otoceratidae.

ceras nala, as already noted by Diener (1897: 56). Spath (1930: 7) established the species *Anotoceras intermedium* for one of the figured paratypes of *Anotoceras nala* (Diener, 1897, pl. 7, fig. 13; Pl. 12, figs. 9, 10 of this report). This specimen is slightly broader but does not differ in whorl section nor in the umbilical rim as suggested by Spath. I believe neither of these criteria to be of specific significance. As now understood, *Anotoceras* is a monotypic genus, known only from the *Otoceras-Ophiceras* beds of the Himalayas, on which data are extremely incomplete. For the time being I am inclined to follow Spath (1934: 70), who concluded that the genus "may, however, be retained in the present family [Otoceratidae] for reduced otoceratids with open umbilicus and rounded venter." There is, however, no clue as to where one could identify the ancestral form within the araxoceratids.

In spite of the uncertainty of the position of *Anotoceras* the relationships of *Pseudotoceras* and *Otoceras* (ancestor-descendant) are very impressive, especially when one considers that the differences between these genera are only the result of evolutionary changes along certain adaptive lines—conch form and suture. Another important feature to point out here is that *Otoceras* survived only during the lowest Scythian (Lower Triassic) zone. Considering its fairly close relationship to *Pseudotoceras* it does not seem reasonable to separate *Otoceras* in a family distinct from that of its late Permian ancestor. All the araxoceratids and *Otoceras,* plus *Anotoceras,* comprise a single unified family group (Fig. 10). The great radiation of this group is a characteristic feature of late Permian time. The genus *Otoceras* is the only member of the group that survived into early Triassic time. This genus, aside from its presence in the Himalayas, became widely distributed in the circum-Arctic region. *Otoceras* is the terminal member of a diverse and unique ammonoid family. The family Araxoceratidae Ruzhentsev (1959) should be included in the Otoceratidae Hyatt (1900).

Otoceras as a Zone Fossil

The *Otoceras-Ophiceras* beds of the Himalayas have long been recognized as representing the basal Triassic biostratigraphic zone. Diener (1912) thoroughly reviewed the data and the evolution of thought on its stratigraphy and fauna. His concluding remarks summarize quite well the accepted view (Diener, 1912: 32): "Thus the fauna of the *Otoceras* stage represents one single palaeontological zone only, which, from its most conspicuous types, should be called zone of *Otoceras Woodwardi* and *Ophiceras Sakuntala*."

The *Otoceras-Ophiceras* beds of the Spiti and Painkhanda regions in the Himalayas are approximately one meter thick (Diener, 1912). The lower and upper thirds of this unit are abundantly fossiliferous. At Spiti, *Otoceras* is confined to the lower third of this unit; but in Painkhanda, 130 miles to the southeast, *Otoceras* is present in both the lower and upper thirds of the unit. Species of *Ophiceras* are the predominant elements in the lower and upper thirds of this unit. This difference in representation of *Otoceras* and *Ophiceras* in the lowest Scythian unit of the Himalayas is well documented in the numbers of specimens of each species from nine collections studied by Diener (1897) (Table 1). It is clear from these data that *Ophiceras* is by far the predominant element, and *Otoceras* the second-ranking element in the ammonoid fauna.

Discussion of this biostratigraphic zone for the Himalayas has centered primarily on *Otoceras* and *Ophiceras*. Strangely there has been little discussion of the six other genera described from this fauna by Diener (1897), namely: *Episageceras, Glyptophiceras, Proptychites, Vishnuites, Prionolobus,* and *Anotoceras*, which was discussed previously. Noetling (1901) questioned the accuracy of the horizon from which some of the specimens assigned to these genera were claimed to have come. It should be recalled that in the first monograph on the fauna of the Himalayan Lower Triassic (Diener, 1897), the *Otoceras-Ophiceras* and *Meekoceras* faunas were not differentiated. In the second monograph (v. Krafft and Diener, 1909) the *Otoceras-Ophiceras* faunas and the *Meekoceras* faunas were clearly differentiated. In that monograph Diener (*in* v. Krafft and Diener, 1909: 164) discussed this point and presented a list of those species which he considered "with full certainty" as belonging to the *Otoceras-Ophiceras* Zone. The list of these species is given in Table 1. He reaffirmed his conclusion at a later date (Diener, 1912: 23).

It is appropriate to review the data on each of these genera. The only genus that appears to have passed through the Permo-Triassic threshold is *Episageceras*, type species: *Sageceras* (*Medlicottia*) *wynnei* Waagen (1880) from the Upper Permian of the Salt Range. Species of this genus have also been recorded from the Ambilobe beds of northern Madagascar associated with *Cyclolobus* (Treat, 1933) and from Timor (Haniel, 1915; Wanner, 1932). In the Spiti region of the Himalayas, *Episageceras dalailamae* Diener occurs in the lowest five-inch bed (Fig. 11), along with *Otoceras*, *Anotoceras*, and *Ophiceras* (Diener, 1912: 17). In Painkhanda this same species is known from a fragment in the main layer of *Otoceras* (Fig. 11, bed 1) and by a well-preserved, nearly complete specimen from bed 2 associated with *Proptychites scheibleri* Diener. These two specimens were collected personally by

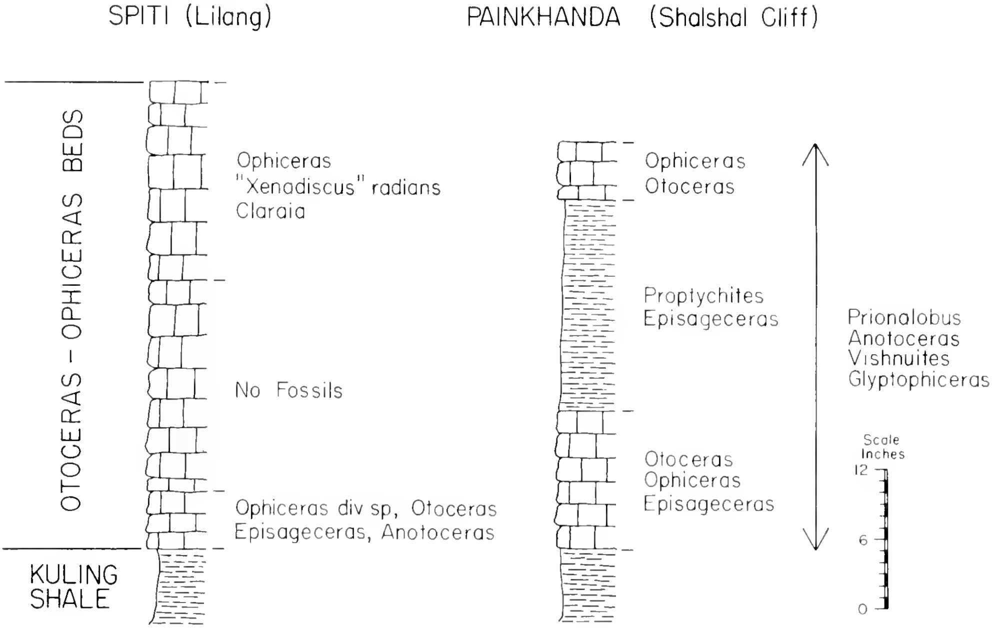

Figure 11. Stratigraphic section of *Otoceras-Ophiceras* beds at Spiti (Lilang) and Painkhanda (Shalshal Cliff), Himalayas. (Data from Diener, 1912.)

Diener (Diener, 1897: 59) and are illustrated here on Plate 11, figures 1–4.

The single specimen assigned to *Ophiceras himalayanum* Griesbach (1880: 111, pl. 3, fig. 8) and discussed in more detail by Diener (1897: 41, pl. 14, fig. 14) is a species of *Glyptophiceras*. This species is based on a single specimen embedded in a slab of rock adjacent to a specimen of *Otoceras woodwardi* (Pl. 11, fig. 7). A single specimen from the Dolomite unit of the Kathwai Member of the Mianwali Formation in the Salt Range of west Pakistan is believed to be conspecific with Griesbach's type specimen (Kummel *in* Kummel and Teichert, 1970).

Proptychites scheibleri Diener (1897: 79, pl. 6, fig. 3; Pl. 11, figs. 5, 6 of this report) was established on a single specimen collected by Diener in 1892 from bed 2 of the *Otoceras-Ophiceras* beds (Fig. 11) at Shalshal Cliff. Diener (1912: 23) made particular stress of the fact that he personally collected this specimen. The same bed at Shalshal Cliff yielded only one other specimen of ammonoid, *Episageceras dalailamae* Diener. This is the oldest species of the genus *Proptychites*, but the genus is extensively distributed in the remaining lower half of the Scythian.

Another rare ammonoid in the *Otoceras-Ophiceras* beds at Shalshal is *Vishnuites pralambha* Diener. This is a compressed form with an acute venter. Diener (1897) had available two specimens that are illustrated here on Plate 12, figures 1–4. Unfortunately, there are no data as to the precise level within the *Otoceras-Ophiceras* beds from which these specimens were collected.

The stratigraphic position of *Meekoceras hodgsoni* Diener had been a source of intense debate between Noetling (1901) and Diener (1901). Noetling maintained that the type specimen must have come from the overlying *Meekoceras* beds and Diener held to his original position that it came from the *Otoceras-Ophiceras* beds. Von

Krafft (*in* v. Krafft and Diener, 1909: 26) redescribed Diener's type specimen and was able to demonstrate that the venter was truncate to the earliest diameter of the specimen. In that same monograph, Diener described and illustrated a specimen in von Krafft's collection from the *Otoceras* beds at Shalshal that he believed to be a new example of *Meekoceras hodgsoni.* In his comments on that specimen Diener (*in* v. Krafft and Diener, 1909: 28) again discussed the stratigraphic position of this species as follows: "A. v. Krafft was, however, mistaken, when he spoke of the absence of any new examples of *Meekoceras hodgsoni* in Noetling's and his own collections. Among his collection from the *Otoceras* beds of the Shalshal Cliff I found a well-preserved specimen of *Meekoceras*, marked on the label as *Meekoceras* sp. ind., Shalshal Cliff near Rimkin Paiar E. G., *Otoceras* beds, found along with *Ophiceras.* That both specimen and label actually belong together is indisputable both being marked with figures K 10, 859.

"This specimen, which has been figured on Pl. XXX, Fig. 1 (Pl. 12, figs. 7, 8 of this report) cannot be separated specifically from *Meekoceras Hodgsoni*, with which it agrees in all its characters of specific importance. I wish to draw the special attention of the reader to the remarkable narrowness of the external area and to the compressed shape of the whorls in general, two leading features in *Meekoceras Hodgsoni.*

"The discovery of a specimen of *Meekoceras Hodgsoni* in the *Otoceras* beds (*sensu stricto*) is of great stratigraphical interest. It fully confirms my statement (Centralblatt f. Miner, etc., 1901, p. 656) that my type specimen had been collected in the *Otoceras* beds of the Shalshal cliff and not in the horizon of *Meekoceras Markhami*, as had been suggested by Noetling. But even if the identification of the present specimen with *Meekoceras Hodgsoni* should be questioned, the presence of a true *Meekoceras* in the *Otoceras* beds of Painkhanda would remain an indisputable fact, in contradiction to what has been suggested by Noetling as to the first appearance of this genus in the Himalayas."

I have had the opportunity of examining the collection of Permian and Triassic fossils from the Spiti area assembled by Eigil Nielsen, formerly of the Universitetets Mineralogiske og Geologiske Museum, Copenhagen. The largest collection came from Muth in Spiti and this contains five specimens of *Meekoceras hodgsoni* bearing labels as coming from the *Otoceras-Ophiceras* beds.

Before discussing the genus *Ophiceras*, which is by far the predominant form in the *Otoceras-Ophiceras* beds, we need to consider *Xenodiscus radians*, von Krafft, *non* Waagen (*in* v. Krafft and Diener, 1909, p. 95, pl. 25, fig. 2; Pl. 12, fig. 15 of this report). In discussing the horizon of the specimens he assigned to *Xenodiscus radians*, von Krafft stated that most of the specimens came from the *Meekoceras* beds at various localities in the Spiti region and a few were listed with question as from the *Otoceras* beds. Diener, however, added a footnote to those statements (*in* v. Krafft and Diener, 1909: 95) as follows: "One specimen from A. v. Krafft's own collection —illustrated on Pl. XXV, fig. 2 (Pl. 12, fig. 15 of this report)—is marked on the accompanying label in A. v. Krafft's handwriting: 'Lilang, Spiti, horizon of *Ophiceras Sakuntala*.' This would prove the specimen to have been found in the *Otoceras* beds S. S." *Xenodiscus radians* von Krafft (*non* Waagen) appears to be a species of *Xenodiscoides.*

Finally, there is the genus *Ophiceras*, which has been somewhat overshadowed by the attention investigators have paid to the genus *Otoceras.* Diener, throughout his writings on the Lower Triassic ammonoids of the Himalayas, has emphasized the predominance of *Ophiceras* in the lowest Triassic beds. In his first monograph on this fauna, Diener (1897) had approximately 400 specimens from these beds of which roughly 330 were species of *Ophiceras* (Table 1). Diener (1897: 100) began his discussion of the genus *Ophiceras* in the following fashion: "The forms which will be described in the following pages under the generic designation proposed by C. L. Griesbach, surpass enormously, in number of individuals, all the other members of the Cephalopoda, which are contained in the geologically oldest strata of the Himalayas, *viz.*, the *Otoceras* beds. All these forms appear at first sight to be linked together most intimately by similarity of shape and sutural lines. Groups of forms, it is true, may be distinguished among them, without great difficulty, which owing to remarkable characters seem to constitute excellent species, but a closer examination most conclusively shows that even groups, the typical form of which seems to be widely different, are connected by transitional forms with such different characters, that it is scarcely possible to identify them with either the one or the other species." This statement expresses well the great plasticity of this stock. Diener (1897: 104) stated his taxonomic philosophy on the genus as follows: "The genus *Ophiceras* is represented in the Himalayas by ten species, which may most conveniently be arranged in groups according to the differences in sculpture. One group of forms, which is closely allied to *O. tibeticum* Griesbach is distinguished by a sculpture, which consists of strong falciform folds and knob-like elevations, but which are not as distinctly demarcated as the tubercles in the *Trachyostraca*. In the other group the surface of the shell is either perfectly smooth or covered with low and broad falciform folds. This group is named from the most common species of the genus *O. Sakuntala*. It must be borne in mind, however, that a distinct boundary does not exist between the two groups, and that, even in species with a strongly developed sculpture, transitional forms occur, which point to the most intimate connection of the different varieties, among which the most prominent ones have been singled out as prototypes of my species." Diener (1897: 104) then classified the species of *Ophiceras* as follows:

- Group of *Ophiceras tibeticum* Griesbach
  - *Ophiceras tibeticum* Griesbach
  - " *gibbosum* Griesbach
  - " *serpentinum* Diener
  - " *platyspira* Diener
- Group of *Ophiceras Sakuntala* Diener
  - *Ophiceras sakuntala* Diener
  - " *medium* Griesbach
  - " *ptychodes* Diener
  - " *demissum* Oppel
  - " *chamunda* Diener
  - " *dharma* Diener

At a later date, Diener (*in* v. Krafft and Diener, 1909: 164) revised the list by excluding *Ophiceras dharma*, as the geological horizon of this sample was uncertain. At the same time he added *Ophiceras stricturatum* Frech and Noetling.

The only specimens studied by Diener that are still available are those figured in his monograph (Diener, 1897). As these figures are all line drawings, photographs of these specimens are reproduced here on Plates 5 to 10. There are only 42 figured specimens, which is a small sample of the more than 300 specimens that were available to Diener. In the discussion of each of these species Diener (1897) devoted much attention to variation within his species and forms transitional to others of his species. Considering the stratigraphic placement of the specimens, the fact that a large part of the samples came from one locality, Shalshal, and the nature of the variation discussed by Diener and also shown to some extent in the figured specimens, I cannot believe the genus is represented by ten species. It seems more reasonable that the fauna includes no more than two or three species. A suggested regrouping of these species is represented in the legends of Plates 5 to 10.

Regardless of whether one considers

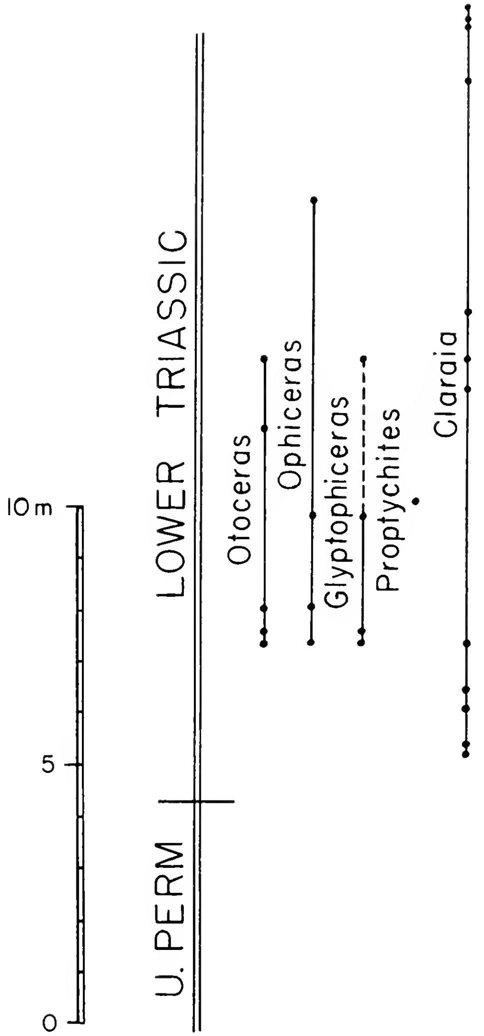

Figure 12. Stratigraphic range of ammonoid genera and the bivalve *Claraia* at Guryul Ravine, Kashmir. (Data from Nakazawa et al., 1970.)

Ophiceras in the Himalayas to include a few or many species, it is clear that the genus was undergoing a very extensive evolutionary radiation. None of the other genera of the *Otoceras-Ophiceras* beds show any comparable speciation. This fact has been almost completely overlooked in the numerous discussions on the Permo-Triassic boundary in the Himalayas. Diener, in his summary paper on the Triassic of the Himalayas (Diener, 1912), centers his discussion of this problem predominantly on *Otoceras*. It has been shown in the previous chapters that *Otoceras* is the last surviving element of a family that underwent a broad-scale radiation in the late Permian. In addition, the genus *Otoceras* is believed to be represented by a single species and two subspecies. This is in great contrast to what we can see for *Ophiceras*.

Nakazawa et al. (1970) have contributed significant new data on the *Otoceras-Ophiceras* Zone in the Himalayas. Very detailed stratigraphic measurements and collecting of lowest Triassic formations exposed in Guryul Ravine, near Srinagar, Kashmir, show that in the beds containing *Otoceras* there also occur *Ophiceras*, *Glyptophiceras*, and *Proptychites*. A summary of their ammonoid distribution data is shown in Figure 12.

It was pointed out above that *Otoceras boreale* of the circum-Arctic region is considered to be a subspecies of the Himalayan *Otoceras woodwardi* and is known from Siberia, Spitsbergen, East Greenland, Arctic Canada, and northern Alaska.

There is one other reported occurrence of *Otoceras*. Hsu (1937) has described and illustrated two poorly preserved, crushed specimens, one of which preserved much of the suture, from Chinglung Limestone at Chinglungshan near Nanking. The stratigraphy of this area and field data on this specimen were described by Chi, Hsu, and Sheng (1937). The specimen illustrated by Hsu (1937, pl. 2, fig. 2) shows a tri-carinate venter and indication that the umbilical area was flared. The second specimen was illustrated only by its suture, which appears simplified. Though the specimen is completely crushed, the character of the venter, umbilical region, and the suture strongly suggests that the generic assignment is not unreasonable. In addition Chi, Hsu, and Sheng (1937) show these two specimens as coming from a one-meter bed of yellowish gray, micaceous

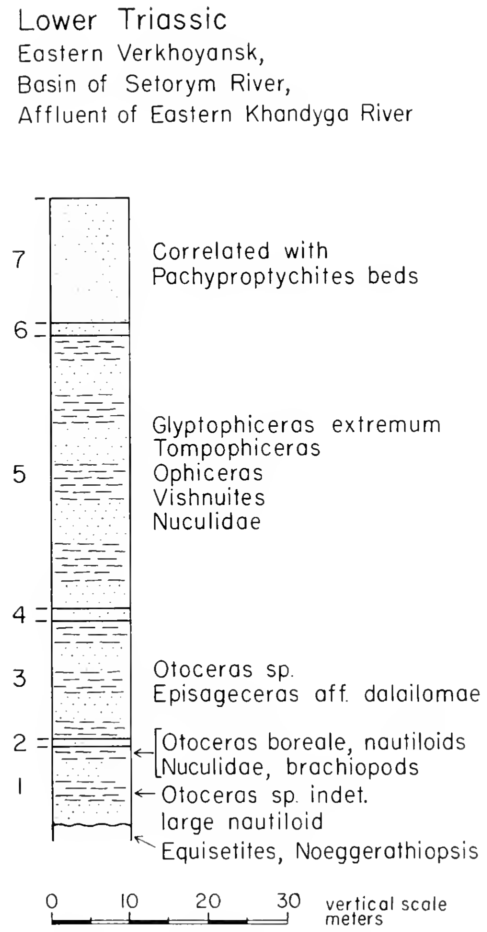

Figure 13. Detailed stratigraphic sections with fossil horizons of lowest Triassic strata in a part of Siberia. (Data kindly furnished by A. N. Oleynikov, VSEGEI, Leningrad.)

shale that is separated from the Lungtan coal series containing a *Gigantopteris* flora by a covered zone of eight meters. This record of *Otoceras* will remain questionable until additional data become available.

The presence of *Otoceras* in Siberia was first reported by Popov (1958) from the eastern Verkhoyansk region. No data are given in that paper as to the thickness and nature of the sediments. However, Popov (personal communication to the author) writes that the beds with *Otoceras* that he described also contain *Ophiceras, Glyptophiceras, Tompophiceras*, and *Episageceras.* In the summer of 1970 Dr. L. V. Kiparisova led a team of geologists to examine the Permian-Triassic boundary beds in the basin of the Setorym River in the eastern Verkhoyansk region. Dr. A. N. Oleynikov has kindly furnished me with data on the stratigraphic succession and faunal associations for that region, summarized here on Figure 13. In that section *Otoceras* is found within the lower 20 meters of the section. In an overlying bed approximately 35 m in thickness the ammonoid fauna includes *Glyptophiceras, Tompophiceras, Ophiceras,* and *Vishnuites.* Above this are strata correlated with the *Pachyproptychites* beds of that region. For Spitsbergen all we know is the presence of *Otoceras.*

The lowest Triassic is well represented in East Greenland by richly fossiliferous strata well documented by Spath (1930, 1935) and Trümpy (1969). Spath recognized a sequence of beds which are from bottom to top as follows: *Glyptophiceras* beds, *Ophiceras* beds, and the *Vishnuites* beds. The species recognized from these beds by Spath (1935) are as follows:

Glyptophiceras Beds:
  Otoceras sp. ind.
  Ophiceras? sp. ind.
  Glyptophiceras triviale
  Glyptophiceras polare

Ophiceras Beds:
  Otoceras boreale
  Ophiceras greenlandicum
    " (*Lytophiceras*) *commune*
    " " *subsakuntala*
    " " aff. *ptychodes*
    " " *ligatum*
    " " *chamunda*
    " " *kilenense*
    " (*Discophiceras*) *kochi*
    " " *compressum*
    " " *wordiei*
    " " *subkyokticum*
    " (*Metophiceras*) *subdemissum*

" " *noe-nygaardi*
" " *praecursor*
" (*Acanthophiceras*) *poulseni*
Vishnuites (*Paravishnuites*) *oxynotus*
" " *striatus*
Glyptophiceras pseudellipticum
" *gracile*
" *serpentinum*
" *nielseni*
" *pascoei*
" *subextremum*
" *extremum*
Vishnuites Beds:
Ophiceras transitorium
" *kilenense*
" *ultimum*
" *dubium*
" *vishnuoides*
" *leptodiscus*
" (*Acanthophiceras*) *subgibbosum*
Vishnuites wordiei
" *decipiens*
Proptychites grandis
" *subdiscoides*
" (*Koninckites*?) sp. ind.

Spath tended to conceive ammonoid species in very narrow terms and this is especially true of his study of these East Greenland faunas. For the immediate purpose this is of no concern, as it is the sequence and association of genera which is of primary concern. Trümpy (1969: 86) recommended raising *Paravishnuites* to full generic rank primarily on the basis that *Vishnuites* and *Paravishnuites* are derived from different stocks within *Ophiceras* and that the Himalayan *Vishnuites* are not directly related to those from East Greenland, but rather are homeomorphs. The point was also made that *Vishnuites* of the *decipiens* and *wordiei* type were younger than *Paravishnuites*. However, Spath (1935, pl. 12, fig. 3) illustrated a specimen he assigned to *Vishnuites* sp. nov. aff. *wordiei* that came from the same horizon as his two species of *Paravishnuites*, that is, the Upper *Ophiceras* beds. I readily recognize that compressed forms with fastigate venters are often (generally) polyphyletic, but, in this particular instance, I do not think sufficient data are as yet available to make a convincing case. I believe it best for the moment to place all these compressed forms with fastigate venters in a single genus *Vishnuites*.

Schindewolf (1954), Tozer (1967, 1969), and Trümpy (1969) interpret *Metophiceras* as being generically distinct from *Ophiceras*. In fact the first two of these authors believe *Metophiceras* to be a member of the *Xenodiscidae*, primarily on slight differences in the suture. It appears equally plausible that *Metophiceras* is part of the general ophiceratid radiation tending toward a more evolute conch and slightly simpler suture. I am following Spath (1935) in considering *Metophiceras* to be a subgenus of *Ophiceras*.

The lowest Scythian strata of East Greenland thus contain five genera of ammonoids, namely *Otoceras*, *Ophiceras*, *Vishnuites*, *Glyptophiceras*, and *Proptychites*. The genus *Otoceras* is present only in the *Glyptophiceras* beds and the *Ophiceras* beds. Tozer (1967: 16) has made the following comment on the range of *Otoceras* in the *Ophiceras* beds of East Greenland: "Spath (1935, p. 11) records *Otoceras boreale* from the Upper *Ophiceras* beds, but no specimens from this level were illustrated, and according to Dr. Trümpy (written communication, 1966) it is probable that *Otoceras boreale* is restricted to the Lower *Ophiceras* beds . . ." These authors apparently overlooked the specimen Spath (1935) figured on his plate 1, figure 6 that is stated to have come from the *Ophiceras commune* Zone (= Upper *Ophiceras* beds). It was stated above that Curt Teichert and I have two good specimens of *Otoceras woodwardi boreale* from the *Glyptophiceras* beds at Kap Stosch.

In East Greenland *Otoceras* is likewise a minor element of the fauna in contrast to *Ophiceras* (Tove Birkelund, personal communication). My own observations during a stay of approximately one month at Kap Stosch have confirmed this. Data are not available on the relative abundance of *Otoceras* and *Ophiceras* from northern Alaska, the Arctic Islands of Canada, Spitsbergen, and Siberia.

The Blind Fiord Formation of Ellesmere and Axel Heiberg Islands of Arctic Canada has yielded a fine sequence of faunas of lowermost Triassic age (Tozer, 1961, 1965, 1967). Four distinct zones have been recognized and brought together in a newly proposed stage, the Griesbachian. These zones and their included species are as follows (from bottom to top):

- Concavum Zone
  - *Otoceras concavum*
- Boreale Zone
  - *Otoceras boreale*
  - *Metophiceras* cf. *M. subdemissum*
  - *Ophiceras* sp. indet.
- Commune Zone
  - *Ophiceras commune*
  - *Ophiceras decipiens*
  - *Discophiceras wordiei*
  - "*Glyptophiceras*" *extremum*
- Strigatus Zone
  - *Pachyproptychites strigatus*
  - *Ophiceras decipiens*

A few comments are needed regarding the taxonomic usage adopted by Tozer (1967). It was mentioned above (p. 374) in the discussion of *Otoceras* that I consider *Otoceras concavum* nothing more than an intraspecific variant of *Otoceras woodwardi boreale*. Likewise, that *Metophiceras* is part of the ophiceratid radiation, and it is more consistent to consider it a subgenus of *Ophiceras,* as I also consider *Discophiceras* to be. The *Ophiceras decipiens* is equivalent to the *Vishnuites decipiens* Spath of East Greenland. Even though Tozer interpreted his species of *Ophiceras* very broadly, for which he is to be commended, the whole fauna is not as diverse as that of East Greenland and much less than that of the Himalayas.

It is the associations within each of these local zones that are of particular interest. *Otoceras* is restricted to the Concavum and Boreale Zones. It is the only genus of ammonoid known from the Concavum Zone. In the Boreale Zone, *Otoceras* is associated with *Ophiceras* of the *subdemissum* type and an indeterminant species. In addition, Tozer (1967: 53) records a "species of *Ophiceras* that has an acute venter" in a loose block containing specimens of *Otoceras boreale*. This I would interpret as a species of *Vishnuites*. Tozer (1967: 15) came to the conclusion that "exact correlatives of the Concavum Zone are not known," and that for the Boreale Zone "The presence of *Otoceras boreale* indicates a correlation with the Lower *Ophiceras* beds of East Greenland." It was pointed out above, however, that (a) *Otoceras concavum* is nothing more than an intraspecific variant of *Otoceras woodwardi boreale*, (b) that this species of *Otoceras* is present in the *Glyptophiceras* beds of East Greenland, and (c) it is also present in the Upper *Ophiceras* beds of East Greenland.

The Commune Zone contains *Ophiceras*, *Vishnuites*, and *Glyptophiceras*. The reason Tozer places quotes around *Glyptophiceras* is explained in a later paper (Tozer, 1969) and is of no particular concern here. This author then suggested that the Commune Zone of Arctic Canada, at least in its lower part, was correlative with the Upper *Ophiceras* beds of East Greenland. Tozer (1967: 16) commented further that: "the presence of *Ophiceras decipiens* [= *Vishnuites*] in the Commune Zone suggests that equivalents of the "*Vishnuites*" beds of East Greenland may also be present. A case might be made for recognizing a zone of *Ophiceras decipiens* between the Commune and Strigatus Zones in some sections, e. g. on Griesbach Creek. However, ophiceratids with acute venters that closely resemble *Ophiceras decipiens* occur as low as the Boreale Zone and this indicates that species of the *decipiens* group range through much of the Griesbachian."

In East Greenland *Ophiceras commune* is present in both the Lower and Upper *Ophiceras* beds, as is *Otoceras woodwardi boreale*. Also, as mentioned above, species of *Vishnuites* are present in the Upper *Ophiceras* beds.

In summary it can be seen that in most places *Otoceras* and *Ophiceras* occur together and that *Ophiceras* is by far the predominant form, *Otoceras* tending to be relatively rare. In the Himalayas the ranges of *Otoceras* and *Ophiceras* are the same at Painkhanda but not at Spiti. In the circum-Arctic region, for those regions where stratigraphic data are available, *Ophiceras* ranges stratigraphically higher than *Otoceras*. It would appear that for the circum-Arctic region the survival into the Lower Triassic (Scythian) was by no means the same from one locality to another. The Commune Zone of Arctic Canada does not contain *Otoceras*, but in East Greenland it does. In the eastern Verkhoyansk region *Ophiceras* ranges beyond *Otoceras*, but more data are needed on this section.

Thus, on the basis of available data, the lowest Scythian ammonoid zone is characterized by the predominance of *Ophiceras* and the much smaller presence of *Otoceras*. In most places the two genera occur together and thus cannot be used to mark two distinct biostratigraphic zones for purposes of intercontinental correlation. Separating the genera into two distinct zones for purposes of provincial correlation, as has been done in East Greenland and Arctic Canada, is quite acceptable, but this scheme breaks down when extended beyond these particular regions. The fact that even in the two principal areas of Triassic outcrops in the Himalayas (Spiti and Painkhanda) *Otoceras* is present throughout the range of *Ophiceras* in one locality but is confined to the lowermost bed in the other clearly demonstrates that the absence of *Otoceras* needs to be evaluated very carefully. More data are needed, but it appears that the present distributional pattern of *Otoceras* suggests that this genus became extinct in the Arctic region shortly after the beginning of the Triassic but persisted slightly longer in Tethys.

SYSTEMATIC SUMMARY OF OTOCERATIDAE

The Permian genera and species are listed from the writings of Ruzhentsev (1959, 1962, 1963) and Spinosa, Furnish, and Glenister (1970), with no attempt to evaluate either generic or specific taxa. The Triassic genera and species have been personally and carefully analyzed and represent my own personal assessment.

Genus *Araxoceras* Ruzhentsev, 1959

Type species, *A. latissimum* Ruzhentsev, 1959

A. latissimum Ruzhentsev, 1959: 58, figs. 1a, 2a; Ruzhentsev and Sarycheva, 1965, pl. 17, fig. 4.

A. trochoides (Abich), Ruzhentsev, 1959: 59.

A. latum Ruzhentsev, 1962: 90, pl. 1, fig. 1; Ruzhentsev and Sarycheva, 1965, pl. 17, fig. 5.

A. varicatum Ruzhentsev, 1962, pl. 4, fig. 2; Ruzhentsev and Sarycheva, 1965, pl. 17, fig. 6.

A. glenisteri Ruzhentsev, 1962, pl. 4, fig. 3; Ruzhentsev and Sarycheva, 1965, pl. 17, fig. 7.

A. rotoides Ruzhentsev, 1963: 57, pl. 5, fig. 1; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 2; Stepanov et al., 1969: 33, pl. 9, fig. 3.

A. tectum Ruzhentsev, 1963: 58, pl. 5, fig. 2; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 1.

Genus *Rotaraxoceras* Ruzhentsev, 1959

Type species, *R. caucasium* Ruzhentsev, 1959

R. caucasium Ruzhentsev, 1959: 61, figs. 1b, 2b; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 3.

R. deruptum Ruzhentsev, 1962: 93, pl. 4, fig. 4; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 4.

Genus *Prototoceras* Spath, 1930

Type species, *Ceratites tropitus* Abich, 1878 (= *Otoceras trochoides* Arthaber, non *Ceratites trochoides* Abich, 1878; = *Discotoceras* Spath, 1930).

P. tropitum (Abich) Abich, 1878: 13, pl. 2, fig. 3; pl. 11, fig. 21; Arthaber *in* Frech and Arthaber, 1900: 240; *Otoceras trochoides* Arthaber *in* Frech and Arthaber, 1900: 241, pl. 19, figs. 1–3; Ruzhentsev, 1959: 62, figs. 1c, 2c; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 6.

P. djoulfense (Abich), Abich, 1878: 11, pl. 2, fig. 1; pl. 11, fig. 20; Arthaber *in* Frech and Arthaber, 1900: 238; Ruzhentsev, 1959: 62.

P. intermedium (Abich), Abich, 1878: 12, pl. 2, fig. 4; Ruzhentsev, 1959: 62.

P. fedoroffi (Arthaber), Arthaber *in* Frech and Arthaber, 1900: 241, pl. 18, fig. 11; Ruzhentsev, 1959: 62.

P. discoidale Ruzhentsev, 1963: 58, pl. 5, fig. 3; pl. 6, fig. 1; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 7.

Genus *Urartoceras* Ruzhentsev, 1959

Type species, *U. abichanum* Ruzhentsev, 1959.

U. abichanum Ruzhentsev, 1959: 65, figs. 1g, 2g; Ruzhentsev, 1962: 94, fig. 5; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 5.

Genus *Pseudotoceras* Ruzhentsev, 1962

Type species, *P. armenorum* Ruzhentsev, 1962

P. armenorum Ruzhentsev, 1962, pl. 4, fig. 5; Ruzhentsev and Sarycheva, 1965, pl. 18, fig. 8.

P. djoulfense (Abich), Abich, 1878: 11, pl. 2, fig. 1; pl. 11, fig. 20; Ruzhentsev, 1963: 60, pl. 6, fig. 2; Ruzhentsev and Sarycheva, 1965, pl. 19, fig. 1; Stepanov et al., 1969, pl. 10, figs. 6, 7.

Genus *Vescotoceras* Ruzhentsev, 1962

Type species, *Prototoceras acutum* Ruzhentsev, 1959

V. acutum (Ruzhentsev), Ruzhentsev, 1959: 63, figs. 1d, 2d; Ruzhentsev, 1962: 96; Ruzhentsev and Sarycheva, 1965, pl. 19, fig. 2; Stepanov et al., 1969: 33, pl. 9, fig. 7.

V. parallelum (Ruzhentsev), Ruzhentsev, 1959: 63, figs. 1e, 2e; Ruzhentsev, 1962: 97; Ruzhentsev and Sarycheva, 1965, pl. 19, figs. 3, 4; Stepanov et al., 1969: 33, pl. 9, fig. 5.

V. pessoides (Abich), Abich, 1878: 15, pl. 1, fig. 5; Arthaber *in* Frech and Arthaber, 1900: 235, pl. 18, fig. 9; Ruzhentsev, 1959: 63; Ruzhentsev, 1962: 97.

V. serratum Ruzhentsev, 1962: 97, pl. 4, fig. 6.

V. evanidum Ruzhentsev, 1962: 97, pl. 4, fig. 7; Ruzhentsev and Sarycheva, 1965, pl. 19, fig. 5.

Genus *Dzhulfoceras* Ruzhentsev, 1962

Type species, *D. furnishi* Ruzhentsev, 1962

D. furnishi Ruzhentsev, 1962: 99, pl. 5, fig. 1; Ruzhentsev and Sarycheva, 1965, pl. 19, fig. 6.

D. paulum Ruzhentsev, 1962: 99, pl. 5, fig. 2.

D. inflatum Ruzhentsev, 1963: 61, pl. 5, fig. 4; Ruzhentsev and Sarycheva, 1965, pl. 19, fig. 7.

Genus *Vedioceras* Ruzhentsev, 1962

Type species, *V. ventroplanum* Ruzhentsev, 1962

V. ventroplanum Ruzhentsev, 1962: 100, pl. 5, fig. 3; Ruzhentsev and Sarycheva, 1965, pl. 20, fig. 1: Stepanov et al., 1969: 33, pl. 9, fig. 6.

V. oghinense Ruzhentsev, 1962: 102, pl. 5, fig. 4.

V. umbonovarum Ruzhentsev, 1963: 62, pl. 5, fig. 5; Ruzhentsev and Sarycheva, 1965, pl. 20, fig. 2; Stepanov et al., 1969: 33.

V. ventrosulcatum Ruzhentsev, 1963: 63, pl. 5, fig. 6; Ruzhentsev and Sarycheva, 1965, pl. 20, fig. 3.

Genus *Avushoceras* Ruzhentsev, 1962

Type species, *A. jakowlewi* Ruzhentsev, 1962

A. jakowlewi Ruzhentsev, 1962: 103, pl. 5, fig. 5; Ruzhentsev and Sarycheva, 1965, pl. 20, fig. 4; Stepanov et al., 1969: 33.

Genus *Eoaraxoceras* Spinosa, Furnish, and Glenister, 1970

Type species, *E. ruzhencevi* Spinosa, Furnish, and Glenister, 1970.

E. ruzhencevi Spinosa, Furnish, and Glenister, 1970: 732, pl. 109, figs. 1–9.

Genus *Anotoceras* Hyatt, 1900

Type species, *Prosphingites nala* Diener, 1897.

A. nala (Diener), Diener, 1897: 54, pl. 1, fig. 4; pl. 7, fig. 13; Hyatt, 1900: 553; von Krafft and Diener, 1909: 159; Diener, 1915: 233; Spath, 1930: 7, 8; Spath, 1934: 70, figs. 12a, b; Kummel *in* Arkell et al., 1957: L132, figs. 162, 7a, b; Ruzhentsev, 1959: 66.

Prosphingites kama Diener, 1897: 56, pl. 1, fig. 5; Diener, 1915: 233; Spath, 1934: 70, fig. 12c.

Anotoceras intermedium Spath, 1930: 8; Spath, 1934: 70.

Genus *Otoceras* Griesbach, 1880

Type species, *Otoceras woodwardi* Griesbach, 1880

Subspecies *Otoceras woodwardi woodwardi* Griesbach

Otoceras woodwardi Griesbach, 1880: 106, pl. 1, figs. 4, 5; pl. 2, figs. 1–6; Frech, 1901: 575, figs. 4a–d; Frech, 1902: 628, 629; von Krafft and Diener, 1909: 116; Diener, 1915: 213; Diener, 1925: 34, pl. 22, fig. 1; Spath, 1930: 9–11; Spath, 1934: 66, fig. 10; Spath, 1935: 11; Kummel *in* Arkell et al., 1957: L132, fig. 162, 10.

Hungarites (*Otoceras*) *woodwardi*, –Diener, 1897: 156–160, pl. 2, fig. 1; pl. 3, fig. 1; pl. 4, figs. 2, 4, 5; pl. 5, figs. 1, 3, 5; pl. 6, fig. 16.

Otoceras woodwardi var. *undatum* Griesbach, 1880: 107, pl. 1, fig. 5.

Hungarites (*Otoceras*) *undatum*, –Diener, 1897: 162, pl. 4, fig. 6.

Otoceras undatum, –Diener, 1915: 213; Spath, 1934: 69.

Otoceras cf. *undatum*, –von Krafft and Diener, 1909: 116.

Hungarites (*Otoceras*) *parbati* Diener, 1897: 160, pl. 4, fig. 1.

Otoceras parbati Diener, 1915: 213.

Otoceras clivei Diener, 1897: 161, pl. 3, figs. 2, 4; pl. 5, fig. 4; pl. 7, fig. 17; von Krafft and Diener, 1909: 116; Diener, 1915: 213; Nakazawa et al., 1970, pl. 28, figs. 1a–c.

Otoceras nov. sp. ind. aff. *clivei* Diener *in* von Krafft and Diener, 1909: 116, pl. 29, fig. 3; Diener, 1915: 213.

Hungarites (*Otoceras*) *fissisellatum* Diener, 1897: 163, pl. 3, fig. 3; pl. 5, fig. 2.

Otoceras fissisellatum Diener, 1915: 213; Spath, 1930: 10.

Hungarites (*Otoceras*) *draupadi* Diener, 1897: 164, pl. 4, fig. 3; pl. 5, fig. 6; pl. 7, fig. 15.

Otoceras draupadi Diener, 1915: 213; Nakazawa et al., 1970, pl. 28, figs. 3a, b.

Hungarites sp. indet. Diener, 1897: 150, pl. 23, fig. 5; Diener, 1915: 154.

Otoceras (*Metotoceras*) *dieneri* Spath, 1930: 8; Spath, 1934: 69; Kummel *in* Arkell et al., 1957: L132.

Subspecies *Otoceras woodwardi boreale* Spath, 1935

Type species, *Otoceras boreale* Spath, 1935

Otoceras aff. *fissisellatum*, Spath, 1930: 10–12, pl. 1, figs. 1a–d; Koch, 1931: 79; Spath, 1934: 68.

Otoceras boreale Spath, 1935: 9–11, pl. 1, figs. 1a, b, 6; pl. 2, figs. 2, 3; pl. 3, figs. 1–3; pl. 4, fig. 1; pl. 5, fig. 1; pl. 6, fig. 8; Kummel *in* Reeside et al., 1957: 1501; Popov, 1958: 107, text-figs. 1, 2 (A.G.I. translation, 1960); Popov, 1961: 20–22, pl. 3, figs. 4, 5; Tozer, 1961: 45–47, pl. 6, figs. 1a–3; pl. 7, figs. 1–3b; pl. 8, figs. 1–4b; Keller et al., 1961: 187; Trümpy, 1961: 249; Vozin and Tikhomirova, 1964: 17, pl. 25, figs. 1a, b; Trümpy, 1969: 83.

Otoceras indigirense Popov, 1958: 109, text-figs. 1a, 2a, b; Popov, 1961: 22, pl. 1, fig. 3.

Otoceras sp. indet. Petrenko, 1963: 51, pl. 1, fig. 1.

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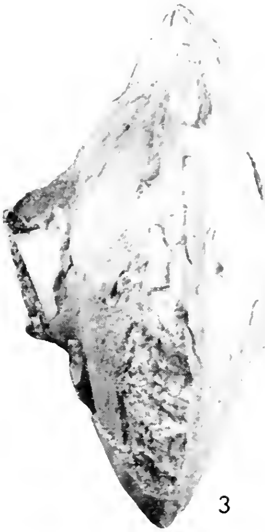
Plate 1. *Otoceras woodwardi woodwardi*

Figures 1–12. *Otoceras woodwardi woodwardi* Griesbach 391

1, 2. Lectotype (Griesbach, 1880, pl. 1, fig. 4; Diener, 1897, pl. 4, fig. 2) GSI 5930. × 1.
3, 4. Paralectotype (Griesbach, 1880, pl. 2, fig. 2; Diener, 1897, pl. 4, fig. 4) GSI 5932. × 1.
5, 6. Topotype (Diener, 1897, pl. 5, fig. 3) GSI 5937. × 1.
7, 8. Small, juvenile specimen, in same tray as Griesbach's lectotype (GSI 5930). × 3.
9, 10. Topotype (Diener, 1897, pl. 5, fig. 5) GSI 5939. × 1.
11, 12. Topotype (Diener, 1897, pl. 4, fig. 5) GSI 5933. × 1.

All specimens from *Otoceras* beds, Shalshal Cliff, near Rimkin Paiar encamping ground, Painkhanda, Niti region, Himalayas, India.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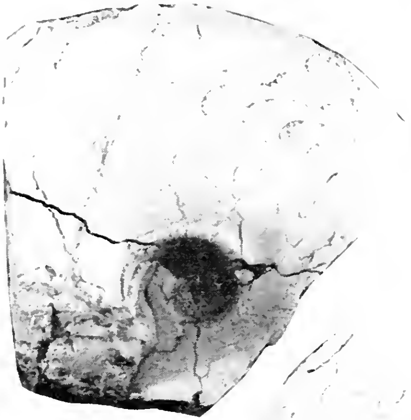
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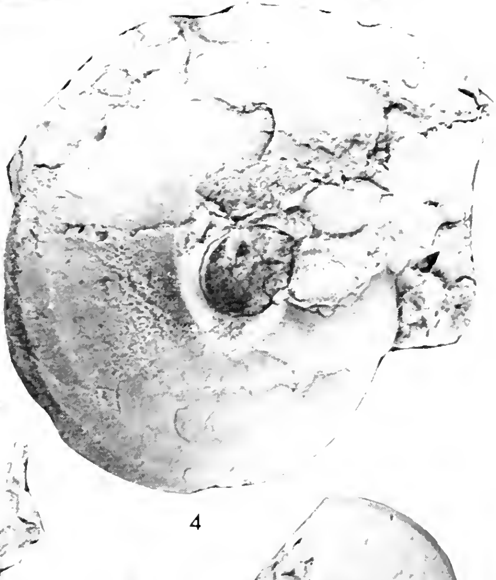
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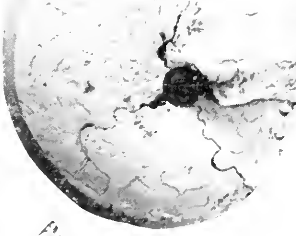
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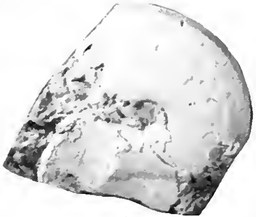
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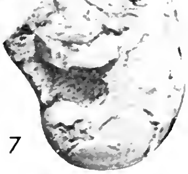
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Plate 2. *Otoceras woodwardi woodwardi*

Figures 1–15. *Otoceras woodwardi woodwardi* Griesbach 391

1, 2. Topotype (Diener, 1897, pl. 3, fig. 1) GSI 5925. × $\frac{2}{3}$.

3, 4. Topotype (Diener, 1897, pl. 2, fig. 1) GSI 5924. × $\frac{1}{2}$.

5–7. Topotype, BM(NH) 28512. × $1\frac{1}{2}$.

8–10. Topotype, BM(NH) 28514. × 3.

11, 12. Topotype, BM(NH) 28513a. × 4.

13–15. Topotype, BM(NH) 28513b. × 8.

All specimens from *Otoceras* beds, Shalshal Cliff, near Rimkin Paiar encamping ground, Painkhonda, Niti region, Himalayas, India.


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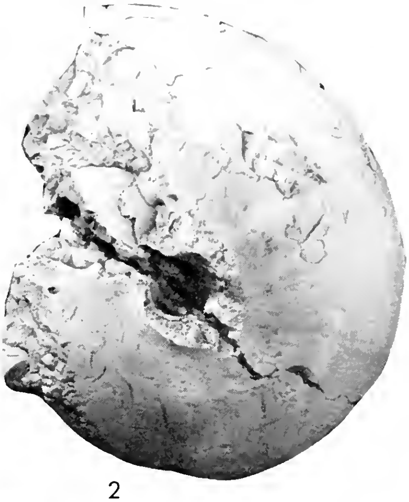
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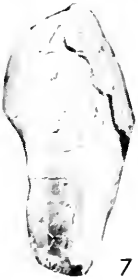
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Plate 3. *Otoceras woodwardi woodwardi*

Figures 1–12. *Otoceras woodwardi woodwardi* Griesbach

391

- 1, 2. Syntype, *Otoceras clivei* Diener (1897, pl. 3, fig. 4) GSI 5928. × 1.
- 3, 4. Holotype, *Otoceras* (*Metotoceras*) *dieneri* Spath (1950: 8) = *Hungarites* sp. ind. Diener (1897: 150, pl. 23, fig. 5) GSI 6058. × 1.
- 5, 6. Syntype, *Otoceras clivei* Diener (1897, pl. 5, fig. 4) GSI 5938. × 1.
- 7, 8. Syntype, *Otoceras clivei* Diener (1897, pl. 3, fig. 2) GSI 5926. × 1.
- 9, 10. Holotype, *Otoceras woodwardi* var. *undatum* Griesbach (1880, pl. 1, fig. 5) GSI 5934. × 1.
- 11. Suture specimen of *Otoceras clivei* (Diener, 1897, pl. 7, fig. 17) GSI 5964. × 1.
- 12. Suture specimen of *Otoceras woodwardi* (Diener, 1897, pl. 7, fig. 16) GSI 5963. × 1.

All specimens from *Otoceras* beds, Shalshal Cliff, near Rimkin Paiar encamping ground, Painkhanda, Niti region, Himalayas, India.

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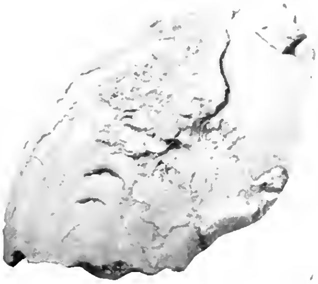

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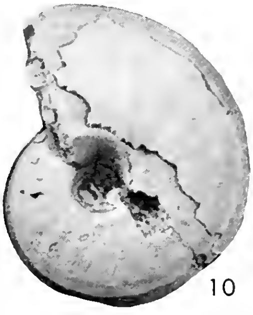

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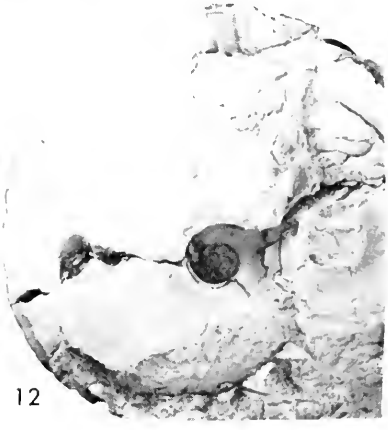

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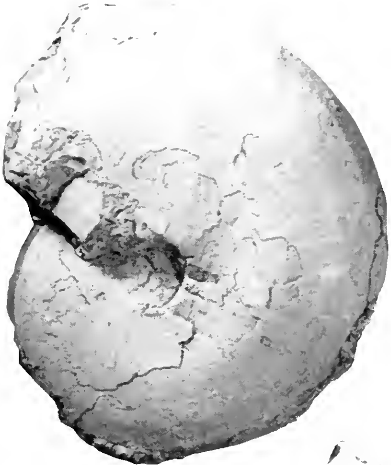
Plate 4. *Otoceras woodwardi woodwardi*

Figures 1–10. *Otoceras woodwardi woodwardi* Griesbach

1, 2. Syntype, *Otoceras draupadi* Diener (1897, pl. 4, fig. 3) GSI 5931. × 1.
3, 4. Suture specimen of *Otoceras draupadi* Diener (1897, pl. 5, fig. 6) GSI 5940. × 1.
5, 6. Suture specimen of *Otoceras draupadi* Diener (1897, pl. 7, fig. 15) GSI 5962. × 1.
7, 8. Paralectotype, *Otoceras fissisellatum* Diener (1897, pl. 5, fig. 2) GSI 5936. × 1.
9, 10. Holotype, *Otoceras parbati* Diener (1897, pl. 4, fig. 1) GSI 5929. × 1.

Specimens of figures 1–8 from *Otoceras* beds, Shalshal Cliff, near Rimkin Paiar encamping ground, Painkhanda, Niti region, Himalayas, India. Specimen of figures 9, 10 from *Otoceras* beds, Kiunglung encamping ground, Painkhanda, Niti region, Himalayas, India.



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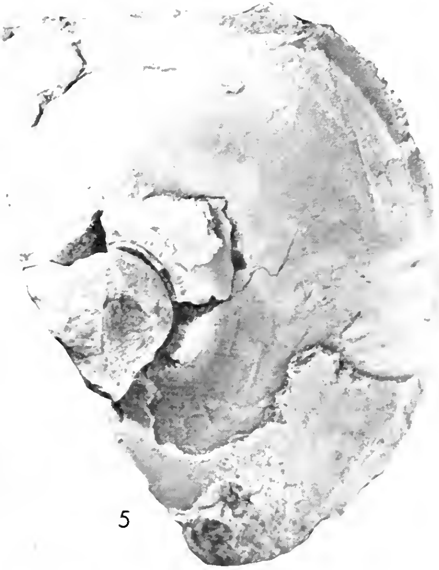

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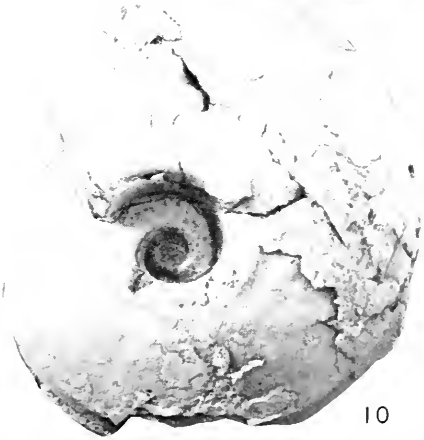

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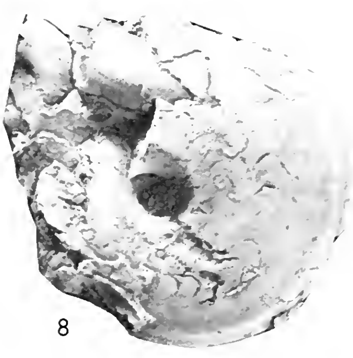

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Plate 5. *Ophiceras tibeticum*

Figures 1–10. *Ophiceras tibeticum* Griesbach 384

1, 2. Lectotype (Griesbach, 1880, pl. 3, fig. 4; Diener, 1897, pl. 8, fig. 1) GSI 5965. × 1.
3, 4. Plesiatype (Diener, 1897, pl. 8, fig. 2) GSI 5966. × 1.
5, 6. Plesiatype (Diener, 1897, pl. 8, fig. 5) GSI 5969. × 1.
7, 8. Plesiatype (Diener, 1897, pl. 8, fig. 6) GSI 5970. × 1.
9, 10. Plesiatype (Diener, 1897, pl. 8, fig. 3) GSI 5967. × 1.

Specimen of figures 1, 2 from *Otoceras* beds at Shalshal Cliff near Rimkin Paiar encamping ground, those of figures 3–10 from Kiunglung encamping ground, Painkhanda, Niti region, Himalayas, India.

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Plate 6. *Ophiceras serpentinum*

Figures 1–12. *Ophiceras serpentium* Griesbach

1, 2. Paralectotype (Diener, 1897, pl. 13, fig. 4) GSI 6002. × 1.
3, 4. Paralectotype (Diener, 1897, pl. 13, fig. 5) GSI 6003. × 1.
5, 6. Paralectotype (Diener, 1897, pl. 13, fig. 6) GSI 6004. × 1.
7, 8. Paralectotype (Diener, 1897, pl. 13, fig. 1) GSI 5999. × 1.
9, 10. Paralectotype (Diener, 1897, pl. 13, fig. 7) GSI 6005. × 1.
11, 12. Paralectotype (Diener, 1897, pl. 13, fig. 3) GSI 6001. × 1.

All specimens from *Otoceras* beds of Kiunglung encamping ground, Painkhanda, Niti region, Himalayas, India.


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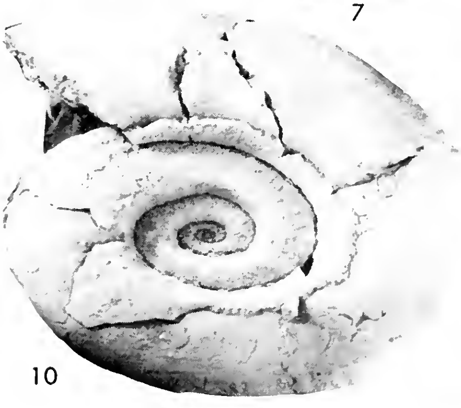
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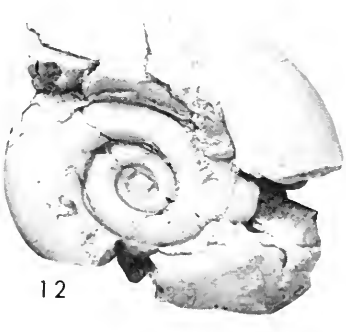
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Plate 7. *Ophiceras medium*

Figures 1–13. *Ophiceras medium* Griesbach	384

1, 2. Syntype, *Ophiceras platyspira* (Diener, 1897, pl. 12. fig. 6) GSI 5998. × 1.
3, 4. Syntype, *Ophiceras platyspira* (Diener, 1897, pl. 12, fig. 5) GSI 5997. × 1.
5, 6. Paralectotype, *Ophiceras chamunda* (Diener, 1897, pl. 12, fig. 1) GSI 5993. × 1.
7, 8. Paratype (Diener, 1897, pl. 9, fig. 1) GSI 5972. × 1.
9. Plesiotype, *Ophiceras demissum* (Diener, 1897, pl. 14, fig. 1) GSI 6006. × 1.
10, 11. Lectotype, *Ophiceras chamunda* (Diener, 1897, pl. 12, fig. 3) GSI 5995. × 1.
12, 13. Plesiotype, *Ophiceras demissum* (Diener, 1897, pl. 14, fig. 2) GSI 6007. × 1.

Specimens of figures 1–6, 10, 11 from *Otoceras* beds at Rimkin Paiar encamping ground, Shalshal Cliff, and those of figures 7–9, 12, 13 from Kiunglung encamping ground, Painkhanda, Niti region, Himalayas, India.


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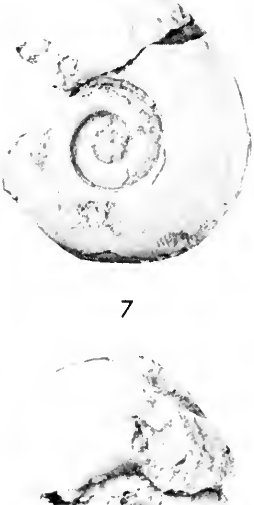
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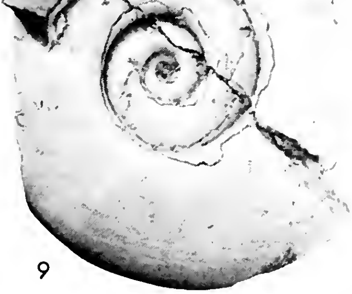
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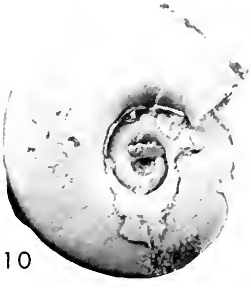
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Plate 8. *Ophiceras medium*

Figures 1–16. *Ophiceras medium* Griesbach 384

1, 2. Topotype, *Ophiceras gibbosum* (Diener, 1897, pl. 9, fig. 7) GSI 5978. × 1.
3, 4. Topotype, *Ophiceras gibbosum* (Diener, 1897, pl. 9, fig. 6) GSI 5977. × 1.
5, 6, 7. Topotype, *Ophiceras gibbosum* (Diener, 1897, pl. 9, fig. 3) GSI 5974. × 1.
8, 9. Topotype, *Ophiceras gibbosum* (Diener, 1897, pl. 9, fig. 5) GSI 5976. × 1.
10–12. Holotype, *Ophiceras gibbosum* (Griesbach, 1880, pl. 3, fig. 10; Diener, 1897, pl. 9, fig. 4) GSI 5975. × 1.
13, 14. Paralectotype, *Ophiceras chamunda* (Diener, 1897, pl. 12, fig. 2) GSI 5994. × 1.
15, 16. Holotype (Griesbach, 1880, pl. 3, fig. 9; Diener, 1897, pl. 9, fig. 2) GSI 5973. × 1.

Specimens of figures 1–16 from *Otoceras* beds at Rimkin Paiar encamping ground, Shalshal Cliff, Painkhanda, Niti region, Himalayas, India.

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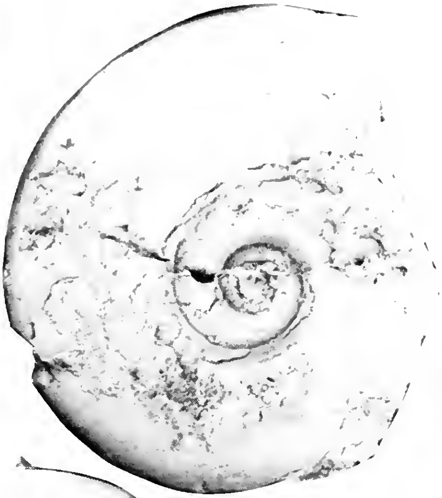

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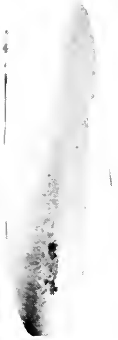

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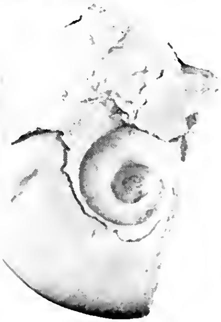

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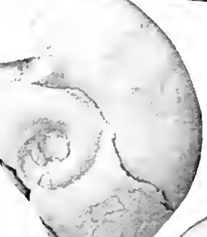

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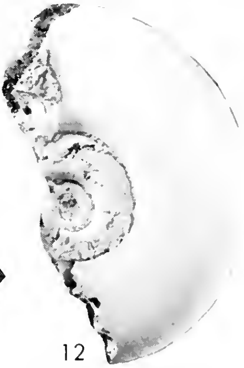

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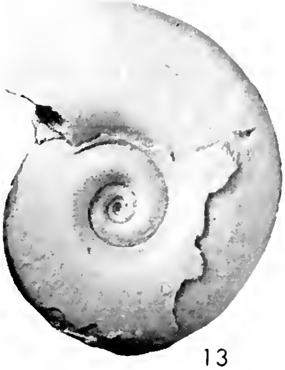

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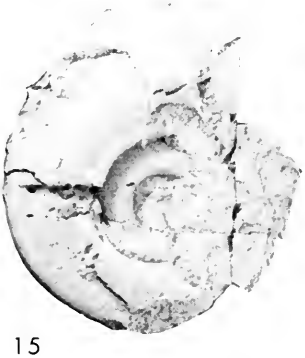

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Plate 9. *Ophiceras medium*

Figures 1–14. *Ophiceras medium* Griesbach 384

1, 2. Lectotype, *Ophiceras ptychodes* (Diener, 1897, pl. 11, fig. 5) GSI 5991. × 1.
3, 4. Paralectotype, *Ophiceras ptychodes* (Diener, 1897, pl. 11, fig. 6) GSI 5992. × 1.
5, 6. Paralectotype, *Ophiceras ptychodes* (Diener, 1897, pl. 11, fig. 3) GSI 5989. × 1.
7, 8. Lectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 1) GSI 5979. × $^2/_3$.
9, 10. Plesiotype, *Ophiceras demissum* (Diener, 1897, pl. 14, fig. 3) GSI 6008. × 1.
11, 12. Plesiotype, *Ophiceras demissum* (Diener, 1897, pl. 14, fig. 6) GSI 6011. × 2.
13, 14. Plesiotype, *Ophiceras demissum* (Diener, 1897, pl. 14, fig. 7) GSI 6010. × 2.

Figure 15. *Ophiceras tibeticum* Griesbach 384

Lectotype, *Ophiceras serpentinum* Diener (1897, pl. 13, fig. 2) GSI 6000. × 1.

Specimens of figures 1–8, 11, 12 from *Otoceras* beds, Rimkin Paiar encamping ground, Shalshal Cliff, those of figures 9, 10, 15 from Kiunglung encamping ground, Painkhanda, Niti region, Himalayas, India; specimens of figures 13, 14 from Tengdi, Spiti, Himalayas, India.


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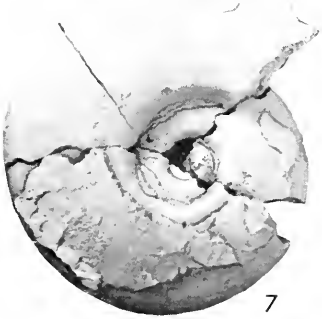
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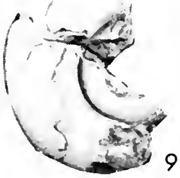
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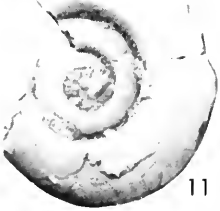
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Plate 10. *Ophiceras medium*

Figures 1–18. *Ophiceras medium* Griesbach 384

1, 2. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 11, fig. 4) GSI 5990. × 1.
3, 4. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 11, fig. 2) GSI 5988. × 1.
5, 6. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 11, fig. 1) GSI 5987. × 1.
7, 8. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 7) GSI 5985. × 2.
9, 10. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 6) GSI 5984. × 1.
11, 12. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 8) GSI 5986. × 1.
13, 14. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 5) GSI 5983. × 1.
15, 16. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 3) GSI 5981. × 1.
17, 18. Paralectotype, *Ophiceras sakuntala* (Diener, 1897, pl. 10, fig. 2) GSI 5980. × 1.

Specimen of figures 7, 8 from *Otoceras* beds southeast of Muth, Spiti, all the remaining specimens from same horizon at Rimkin Paiar encamping ground, Shalshal Cliff, Painkhanda, Niti region, Himalayas, India.


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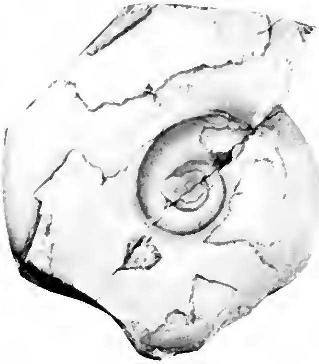
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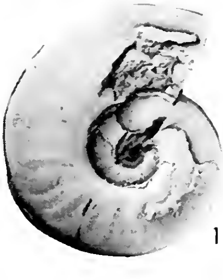
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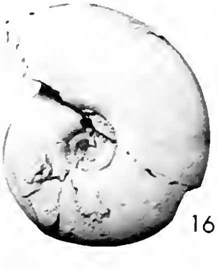
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Plate 11. *Episageceras, Proptychites, Glyptophiceras*

Figures 1–4. *Episageceras dalailamae* (Diener) 381

1, 2. Holotype (Diener, 1897, pl. 1, fig. 6) GSI 5922. × 1.
3, 4. Paratype (Diener, 1897, pl. 7, fig. 7) GSI 5953. × 1.

Figures 5, 6. *Proptychites scheibleri* Diener 382

Holotype (Diener, 1897, pl. 6, fig. 3) GSI 5943. × 1.

Figure 7. *Glyptophiceras himalayanum* (Griesbach) 382

Holotype (Griesbach, 1880, pl. 3, fig. 8; Diener, 1897, pl. 14, fig. 14) GSI 6019. × 1.
Upper specimen is *Otoceras woodwardi*.

All specimens from *Otoceras* beds at Rimkin Paiar encamping ground, Sholshal Cliff, Painkhanda, Niti region, Himalayas, India.


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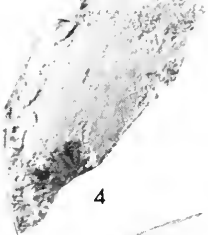
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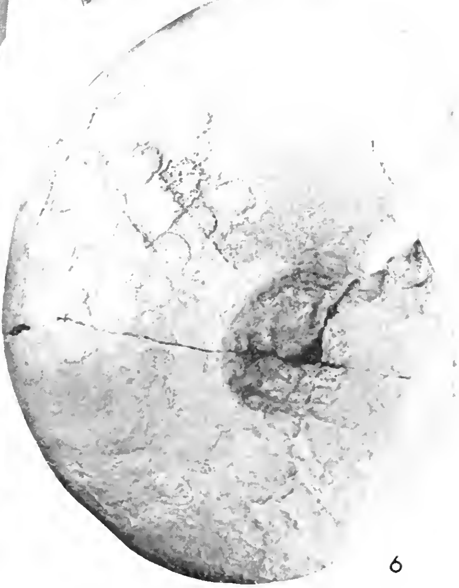
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Plate 12. *Vishnuites, Prionolobus, Anotoceras,* and "*Xenodiscus*"

Figures 1–4. *Vishnuites pralambha* Diener	382
1–3. Holotype (Diener, 1897, pl. 7, fig. 4) GSI 5950. × 1.	
4. Paratype (Diener, 1897, pl. 7, fig. 5) GSI 5951. × 1.	
Figures 5–8. *Prionolobus hodgsoni* (Diener)	382
5, 6. Holotype (Diener, 1897, pl. 6, fig. 1) GSI 5941. × 1.	
7, 8. Topotype (v. Krafft and Diener, 1909, pl. 30, fig. 1) GSI 9537. × 1	
Figures 9–14. *Anotoceras nala* (Diener)	379
9, 10. Paralectotype (Diener, 1897, pl. 7, fig. 13) GSI 5959. × 1.	
11, 12. Lectotype (Diener, 1897, pl. 1, fig. 4) GSI 5920. × 1.	
13, 14. Holotype, *Prasphingites kama* Diener (1897, pl. 1, fig. 5) GSI 5921. × 1.	
Figure 15. "*Xenodiscus*" *radians* von Krafft (non Waagen)	383
Illustrated in von Krafft and Diener (1909, pl. 25, fig. 2) GSI 9504. × 1.	

Specimens of figures 1–8 from *Otoceras* beds, Rimkin Paiar encamping ground, Shalshal Cliff, those of figures 9–14 from Kiunglung encamping ground, Painkhanda, Niti region; that of figure 15 from *Otoceras* beds, Lilang, Spiti region, Himalayas, India.

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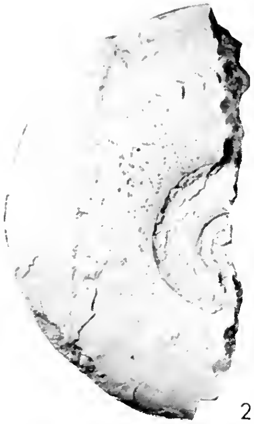

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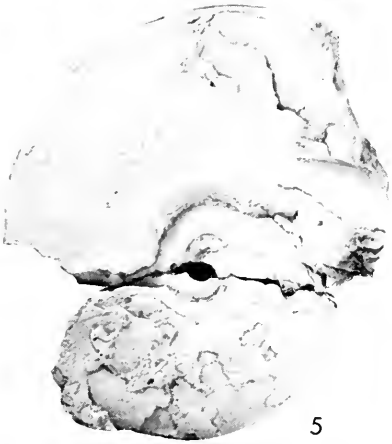

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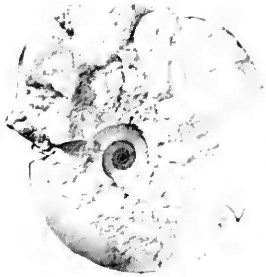

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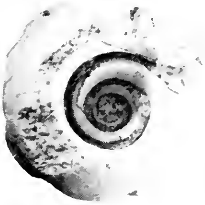

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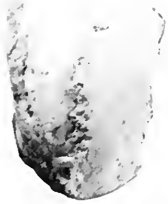

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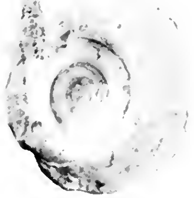

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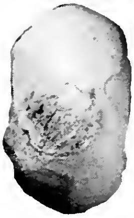

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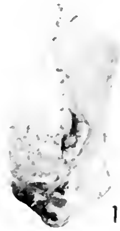

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