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A STUDY OF THE SPECIES OF THE GENUS *BASILISCUS*

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No. 1 — *A Study of the Species of the Genus Basiliscus*

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Santiago, Chile

INTRODUCTION

Five species have been described in the genus *Basiliscus:* ***B. vittatus*** Wiegmann 1834, *B. plumifrons* Cope 1876, *B. basiliscus* Linnaeus 1758 (= *americanus* Bocourt 1874), *B. barbouri* Ruthven 1914, and *B. galeritus* A. Duméril 1851. Of these five species only *B. vittatus* and *B. plumifrons* have overlapping ("sympatric") geographic distributions, both occurring in the same localities in various parts of Costa Rica and northwest of Panama. *B. vittatus,* however, has a range extending up to Tamaulipas and Michoacan in Mexico, while *B. plumifrons* is restricted to the northwest of Panama, Costa Rica, Nicaragua, and part of Honduras. The remaining three species, on the other hand, are at present known with certainty only from non-overlapping ("allopatric") territories: *B. basiliscus* from Panama and Atrato Region in Colombia, *B. barbouri* from the north of Colombia and (new records not previously published) from Venezuela, and finally, *B. galeritus* from Gorgona Island and the Choco in Colombia, and from Ecuador.

All of these species were distinguished originally on the morphological examination of relatively few specimens (Boulenger, 1885; Ruthven, 1914). Furthermore, no analysis of this genus has been carried out in modern terms — considering the species "as actually or potentially interbreeding populations" (Mayr, 1942) rather than mere morphological types. In these circumstances, it appeared to me that a restudy of the genus was desirable, examining from a modern point of view the morphological variability of the various forms in preserved specimens. The present work represents an attempt to do such a study. The evidence that I present here may not be conclusive, but to the degree that it is based on the analysis of a larger sample than the original discussions, it may be expected to provide a better basis for the assessment of the biological status of the various forms and for future more formal revisions. (Material and ecological data in the critical area of southern Costa Rica has been gathered by a party from the University of Southern California and will be reported by them.) I have also tried to indicate some of the questions and problems which should be considered in future field studies of the genus.

MORPHOLOGICAL ANALYSIS

In 1885 Boulenger recognized four species in the genus *Basiliscus: B. vittatus, B. plumifrons, B. americanus* and *B. galeritus*, synonymizing with these several forms previously considered distinct species. No change in the systematics of the genus has occurred since, except for the description of a new species, *B. barbouri*, by Ruthven in 1914, and the change of name from *B. americanus* to *B. basiliscus* by Barbour in 1905.

The characters used by Boulenger in his discussion of the species of this genus were the following:

1. Head crest: shape of the crest and size of the scales.
2. Dorsal crest: relative height with respect to the body height, and size of the scales.
3. Caudal crest: relative height with respect to the body height, and size of scales.
4. Number of labials to below the center of the eye.
5. Number of chin-shields in contact with the infralabials.
6. Lateral fringe of the toes (toe flap): relative width (large or small).
7. Abdominal scales: keeled or not keeled.
8. Coloration.

Of these characters, 1, 2 and 3 are adult male features which vary with the size of the animal. Character 8 shows differences in color and pattern between the several forms but also ontogenetic changes within each form and it is as a rule difficult to evaluate in preserved specimens. The other characters, however, may be studied in individuals of both sexes and all ages. No additional features were used by Ruthven in his description of the species *B. barbouri* and, indeed, I have found only a few new characters present in both sexes and all ages useful in the present study. It has been possible, however, to assess on a much broader basis the systematic value of those previously used.

In this study I have examined 440 specimens, most of these from the collection of the Museum of Comparative Zoology. A few come from the collection of the Museo de Biologia, Caracas, Venezuela, and some from the collection of the American Museum of Natural History. The species are very unequally represented: 283 *B. vittatus;* 38 *B. plumifrons;* 71 *B. basiliscus;*

17 *B. barbouri,* and 38 *B. galeritus.* This reflects in part the wide geographic range of *B. vittatus* but also the fact that the area it inhabits is better collected than the areas where the other forms occur. Table 2 shows the geographic distribution, sex, and size of all individuals studied.

CHARACTER ANALYSIS

In what follows I describe the characters used in this paper and analyze their variability in the several forms. (For the moment and for the purpose of the discussion I shall treat all the named populations as if of equivalent taxonomic value.)

1). *Head crest:* The head crest originates in the middorsal line of the head, behind the pineal eye. It extends backwards, laterally compressed, to end in the middle of the neck. The head crest finds its fullest expression in the adult males of all populations and seems to be one of the earliest secondary male characters to appear.

The head crests of the different forms have rather different profiles, as is shown in Figures 1 and 2, but there is a good degree of variability around these modal shapes. In *plumifrons* the division of the crest into two lobes is characteristic, the anterior lobe being always small and narrow; in *galeritus* the general profile is rounded and in *vittatus* is triangular. The Colombian form, *barbouri,* was separated from *basiliscus* by Ruthven (1914) mainly, if not exclusively, by the shape of the head crest. Thus, he described *barbouri* as having "the head crest single, not erect but pendent on the side of the neck, ribbonlike, narrowing rapidly from its base . . . to form a narrow lobe." This description could also apply to the head crest of *basiliscus* in Panama, although these populations may be more variable in the length of the narrow lobe and in its degree of bending over the neck (Fig. 2). The variability of the head crest of *basiliscus* and of *barbouri* appears to center around a single morphological pattern; the divergence found between the 'typical' Colombian and Panamanian forms could be the result either of sampling or of intraspecific geographic variation. Unfortunately, no information appears to exist about the genus *Basiliscus* in the area between Golfo de Uraba and Santa Marta in Colombia, the region where the two forms, *basiliscus* and *barbouri,* might come into contact.

The females of all groups do not have a true head crest, but instead a hoodlike lobe on the posterior part of the neck.

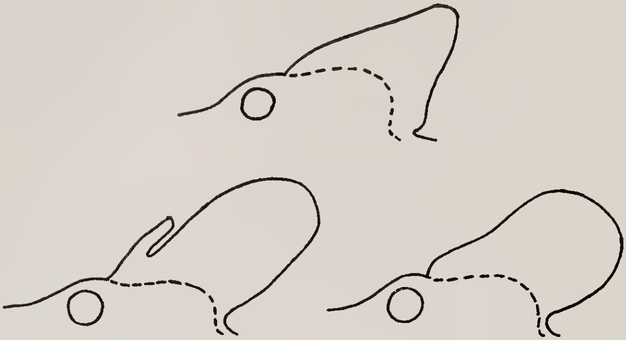


Figure 1. Head crests of adult male *Basiliscus. Top: B. vittatus. Bottom left: B. plumifrons. Bottom right: B. galeritus.*

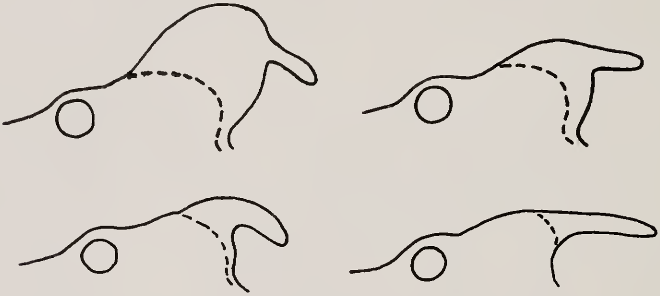


Figure 2. Head crests of adult male *Basiliscus. Top left:* typical *B. basiliscus. Bottom right:* typical *B. barbouri. Top right and bottom left:* intermediate variants occurring in both Panama and Colombia.

2). *Dorsal crest.* This is also an adult male character, present in four of the five forms: *vittatus, plumifrons, basiliscus* and *barbouri.* It is not present in *galeritus,* where it is replaced by a *periodic* pattern in a row of large triangular scales separated at regular intervals by two to four small intervening scales (Fig. 3). This replacement of the dorsal crest by a distinctive pattern of scalation appearing in both sexes and in juveniles as well is a constant character in *galeritus.* In the other groups, females and young individuals do not have a dorsal crest nor does their middorsal row of scales resemble that of *galeritus* since there is not the same striking variation in size of the scales nor the same well-defined periodicity (Fig. 3).

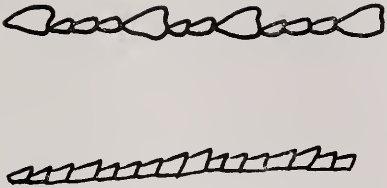


Figure 3. Dorsal crest pattern in adult and juvenile *Basiliscus galeritus* (*top*), in juveniles of other species of the southern group (*bottom*).

The dorsal crest, when present, is supported by bony rays which are longer at the middle of the body and diminish in size towards both girdles where they disappear. In *plumifrons, basiliscus* and *barbouri* the dorsal crest is large and conspicuous, with its maximal height of 4 to 5 cms in adult males. The border is serrated, because the tissue between the rays forms a concave border. In these three groups the dorsal crests are very similar. In *vittatus,* on the other hand, the dorsal crest is low, the bony rays are not conspicuous and the border is not serrated; its maximal height appears to be not more than 1½ to 2½ cms. The dorsal crest develops after the head crest is well advanced, especially in *vittatus.*

3). *Caudal crest.* In *plumifrons, basiliscus* and *barbouri,* there is a well developed caudal crest, which is similar in appearance to the dorsal crest, but less high. This crest is poorly developed in *vittatus* where it has no serrated border and appears simply as a compression of the upper border of the tail. In *galeritus* the caudal crest is absent and, like the dorsal crest, it is replaced by a single row of alternating large and small scales, at least at the beginning of the tail.

4). *Number of chin-shields in contact with the infralabials.* This is a well defined character, represented in Figure 4. Two conditions are identifiable, although there is some variability in each of them. These two conditions split the genus into two groups:

Condition 1. Three to four large chin-shields in contact with the infralabials, no small scales between them.

Condition 2. One or two large chin-shields in contact with the infralabials; this contact is incomplete and small scales cause a partial or total separation between them. Only occasionally two or three large chin-shields appear in complete contact with the infralabials at one side, but the very small scales are found farther back and on the other side (Fig. 4).

Condition 1 is found in *plumifrons, basiliscus, barbouri* and *galeritus.* Condition 2 is found only in *vittatus.* The number of chin-shields is not necessarily the same on the two sides. The character can be easily recognized in adults and in juveniles.

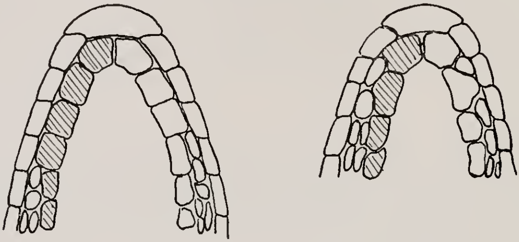


Figure 4. Pattern of chin-shields. *Basiliscus vittatus* (*right*); species of southern group (*left*). The two sides of each figure show the extremes of variation.

5). *Lateral fringe of the toes.* All members of the genus have on the external border of the toes a fringe in the form of a scaly flap extending over the whole length. This feature has been taxonomically used in a very imprecise way by simply stating that the fringe is larger in one group than in the other; it is difficult to measure it adequately. However, its relative width can be estimated by observing whether it covers, when folded, more or less than half of the ventral width of the toe. Furthermore, the number of scales in the flap can be used as a measure of the length of the toe or size of the foot. As these animals have bipedal habits and are even able to run on the surface of water, the size of the fringe, reflecting the size of the functional surface of the foot, probably correlates with their habitat preferences and aquatic behavior.

The number of scales in the flap of the fourth toe varies within certain definite limits in each population. Thus, both *basiliscus* and *barbouri* have a range of between 33 and 41 scales; specimens which have less than 35 scales in the flap are rare. In *galeritus* we find a range of 37 to 46 scales, and in *plumifrons.* which is sympatric with *vittatus,* we find a range of variation of 36 to 46 with a rather uniform distribution. In *vittatus* the situation deserves special comment since this form has a very wide geographic distribution extending from Panama to central Mexico (see map). In Panama and Costa Rica where it is sympatric with *plumifrons* the number of scales in the flap ranges between 28 and 36, but 95 per cent of the population has between 30 and 34, and the most frequent numbers are 32 and 33. Towards the north the number of scales in the flap increases to a range between 32 and 44 in Mexico, but here more than 90 per cent of the specimens have over 35 scales.

With respect to the relative width of the flap, this is more than half the width of the ventral surface of the toe in *plumifrons, basiliscus, barbouri,* and *galeritus.* In *vittatus* the width of the flap is generally smaller, although it varies with the size of the animal. The adults have exceedingly small scales in the flap, to such a degree that it loses its characteristic aspect of an expansion of the border of the toe. In young individuals the situation is different and the flap is proportionately almost as wide as in *plumifrons;* the shape of scales, however, is slightly different (Fig. 6) with a clear tendency to have the smaller ones at the level of the articulations. The flap in young *vittatus* (up to between 52 and 62 mm) looks as efficient in increasing the foot surface as in any of the other forms. From that size onwards, however, the flap becomes relatively smaller in *vittatus* while it remains wide in *plumifrons* and the other forms, covering most of the undersurface of the toe, even at 100 to 120 mm of body length. This difference in relative width of the toe flap in *vittatus* of different sizes probably reflects differences in habitat preferences.

6). *Abdominal scales.* The presence or absence of a keel on the abdominal scales is a clear cut feature. Only *vittatus* has abdominal scales keeled; all the others have them smooth. Usually the keeling can be recognized easily in every individual and is present over the whole abdominal surface.

7). *Coloration.* Coloration offers two variables, color and pattern. Pattern seems to be in general uniform and is specially obvious in *vittatus*, although there are variations whose constancy and significance are difficult to assess. In general, young individuals have two bright longitudinal bands along each side of the body, the more dorsal one going from the base of the hind leg to the orbit; the lower band, less conspicuous, extends from the groin to the axilla and thence to the angle of the mouth. This band merges with the clear coloration of the abdomen. There are also transverse dark bands, five on the dorsum and one or two on the neck. These bands maintain their width as far as the dorsal midline in *vittatus,* but taper dorsally in *basiliscus* and *barbouri.* This pattern is more or less clearly retained in adult *vittatus, basiliscus* and *barbouri,* the last two being practically indistinguishable in color and pattern. In *plumifrons* the longitudinal lines break into two rows of bright spots in the adult although the juvenile shows the usual pattern of longitudinal and transverse bands in a very dark ground color. In *galeritus* the pattern is never very clear and while small individuals show a very uniform brownish coloration, the adults have brown spots on the sides and brown transverse bands on the dorsum. The ground color itself varies from clear brown to olive brownish in *vittatus, basiliscus,* and *barbouri,* but is dark green in *plumifrons* and olive green in adult *galeritus.*

8). *Number of scales between the supraorbital semicircles.* This character has not commonly been used in the genus. The number of rows of scales between the supraorbital semicircles (minimal number) varies from 1 to 5 in the whole genus, but the individual groups have a more restricted variability. In *vittatus* the variation is from 1 to 3, but 75 per cent have 2 and 13 per cent have 1 in the specimens examined. In *plumifrons* 1 to 5 rows of interorbital scales may be found, but 75 per cent of the specimens have 3 or more. In *basiliscus* most (86 per cent) individuals have only one row of interorbital scales, the rest have 2. Of the 17 specimens of *barbouri,* 9 have 2, 5 have 3, and 3 have 1. In *galeritus,* most specimens have 2 (74 per cent) (Fig. 5).

9). *Number of scales between the interparietal (pineal) scale and the supraorbital semicircles.* In the genus as a whole this number ranges from 0 to 3 and is not strictly symmetrical. There is wide overlapping in the variability of the different forms, but there are some regularities which suggest that these may have different types of variability. Thus, in Panama and Costa Rica *vittatus* almost always (more than 95 per cent) has one scale on one side; if the other side has a different number this is two. The majority of *basiliscus* also have one or none, while in the other groups, specially *plumifrons,* the majority of the individuals have two or more (Fig. 5).

10). *Number of scales in the dorsal and ventral midline in the breaking segment of the tail.* This character is also variable, but one difference is observable which splits the genus into two groups: *vittatus* has almost constantly the combination of 5 scales in the dorsal and 4 scales in the ventral midline of the breaking rings, counted at the beginning of the middle third of the tail. When this count varies, it is usually in the direction of smaller numbers, i.e. 5 dorsal, 3 ventral or 4 dorsal, 4 ventral. The *vittatus* populations from Panama and Costa Rica have a high proportion of individuals with the combination 4/4 — about 45 per cent. This proportion diminishes towards the north where less than 10 per cent have 4/4, while most have 5 dorsal, 4 ventral, and a few 5/5 or 6/4. The other forms have a larger

	Minimal number of scales between supra-orbital semi-circles:	percent:	Minimal number of scales between pineal scale and supra-orbital semi-circles:	percent:	Ratio of mid-dorsal to mid-ventral scales in tail rings:
vittatus	1	13%	0		5/4 or less
	2	79	1	98%	
	3	8	2	2	
	4		3		
	5				
plumifrons	1	3%	0		6/4 or more
	2	13	1	4%	
	3	58	2	74	
	4	23	3	1	
	5	3			
basiliscus	0	1%	0	25%	6/4 or more
	1	90	1	69	
	2	9	2	6	
	3		3		
	4				
barbouri	1	18%	0		6/4 and 5/4
		53	1	35%	
	3	29	2	65	
	4		3		
	5				
galeritus	1	16%	0	3%	6/4 and 5/4
	2	74	1	21	
	3	10	2	76	
	4		3		
	5				

Figure 5. Scale count differences between *Basiliscus* species.

number of dorsal scales in the breaking ring of the tail, 6 or 7, and 4 ventrals. Only *galeritus* and *barbouri* have occasionally 5 dorsals, 4 ventrals. This difference in the number of scales on the breaking rings of the tail seems to be related to a more general but less readily measurable feature, namely, that *vittatus* seem to have larger and fewer scales in the tail and dorsum than any of the other populations (Fig. 5).

11). *Pattern of scale arrangement in the toes.* (The third phalanx of the fourth toe has been selected as an arbitrary point of reference for the study of the scale pattern.) The pattern of scale arrangement of the dorsal and ventral surfaces of the toe is not uniform within the genus and there is variation within each population and even within each individual. Nevertheless, a few patterns can be described around which variation affecting the shape, number, and arrangement of the scales occurs. Two principal patterns of dorsal scale arrangement are clearly distinguishable.

Pattern A: Present in *vittatus,* characterized by three longitudinal rows of scales which have a pointed and serrated anterior border (Fig. 6, *top*). The lateral scale row, nearest to the flap, may be wanting in some places and the middle scales then become less pointed and wider. The pattern, however, remains distinct and recognizable.

Pattern B: Present in all other groups, characterized by a row of large broad and rectangular scales which reach the internal border of the toe, replacing the middle and internal rows of pattern A. The anterior border of these scales is serrated and of the same length as their bases. Sometimes an extra row of scales is present on the external side, near to the flap, a condition prevalent in *galeritus,* but not uncommon in the other forms which have this pattern (Fig. 6, *bottom*). In their variability these two patterns sometimes seem to approach each other, but a close examination always shows that they are clearly distinguishable.

In the ventral surfaces of the toes also, two patterns can be identified: pattern C, present in *vittatus*, and pattern D, present in all other forms (Fig. 7). The significant features in the ventral scale pattern are the number of scales which cover the ventral surface of the toe and the structure and color of the contact pad present in the medial border along it. This pad is nothing but the angular border of the scale that covers the internal side of the toe at the level where it bends sharply to

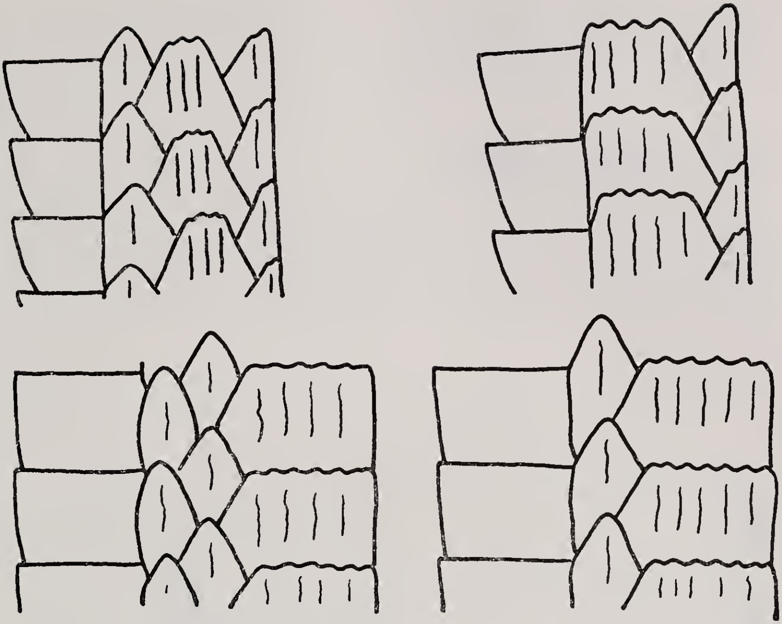


Figure 6. Scale pattern on dorsal surface of 3rd phalanx of fourth toe. *Top: Basiliscus vittatus,* pattern A, usual condition (*left*), variation (*right*). *Bottom:* species of southern group, pattern B, usual condition (*left*), variation (*right*). Lateral margin with toe flap to the left in each figure.

cover the ventral surface. In *vittatus*, however, it appears as if it were a distinct structure on the surface of the scale, with clear limits and outline; this is an appearance produced by its strong dark brown or black color (Figs. 7 and 8). With respect to the scales themselves, in pattern C the scale that covers the internal side of the toe, after bending to the ventral surface at the level of the pad, covers its whole width and comes into contact with the fringe of the toe. Small scales may be present, producing partial separation of this scale and the flap scale. In pattern D the large scale that covers the internal side of the toe covers only half of the undersurface; between this and the flap is another large scale, with or without additional small scales, or several rows of small scales. This last condition is frequent in *galeritus*, but the whole range of conditions can be found in the other populations which present this pattern: *plumifrons, basiliscus* and *barbouri* (Fig. 7, *right*).

Figure 7. Medial aspect of 3rd phalanx of fourth toe to show the appearance of the contact pad and of the dorsal scales in a side view. *Left, Basiliscus vittatus* with dark contact pad. *Right,* any member of the southern group. In these the contact pad is not marked off by dark coloration.

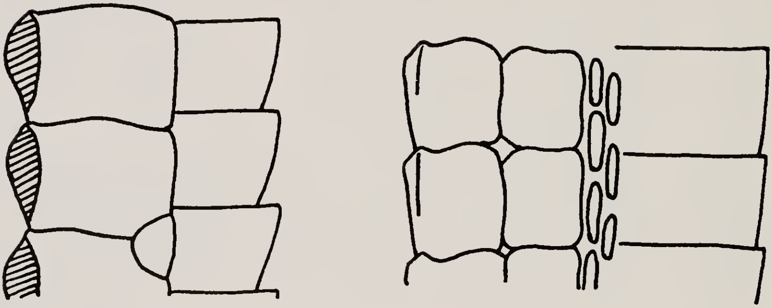


Figure 8. Scale pattern on ventral surface of 3rd phalanx of fourth toe. *Left: Basiliscus vittatus,* pattern C with dark contact pad. *Right:* species of southern group, pattern D. Medial margin to the left in each figure.

Figures 5, 9, and 10 afford a general summary of the characters studied in the various populations. It will be noticed that *vittatus* can be distinguished in more ways from all the remaining forms than any of these among themselves. Table 1 presents the data of Figures 5 and 10 arranged in a different way. Here it will be evident that there are indications of what is called "character displacement" (Brown and Wilson 1956) between *vittatus* and the other forms which I shall call "the southern group." These points will be amplified and discussed below.

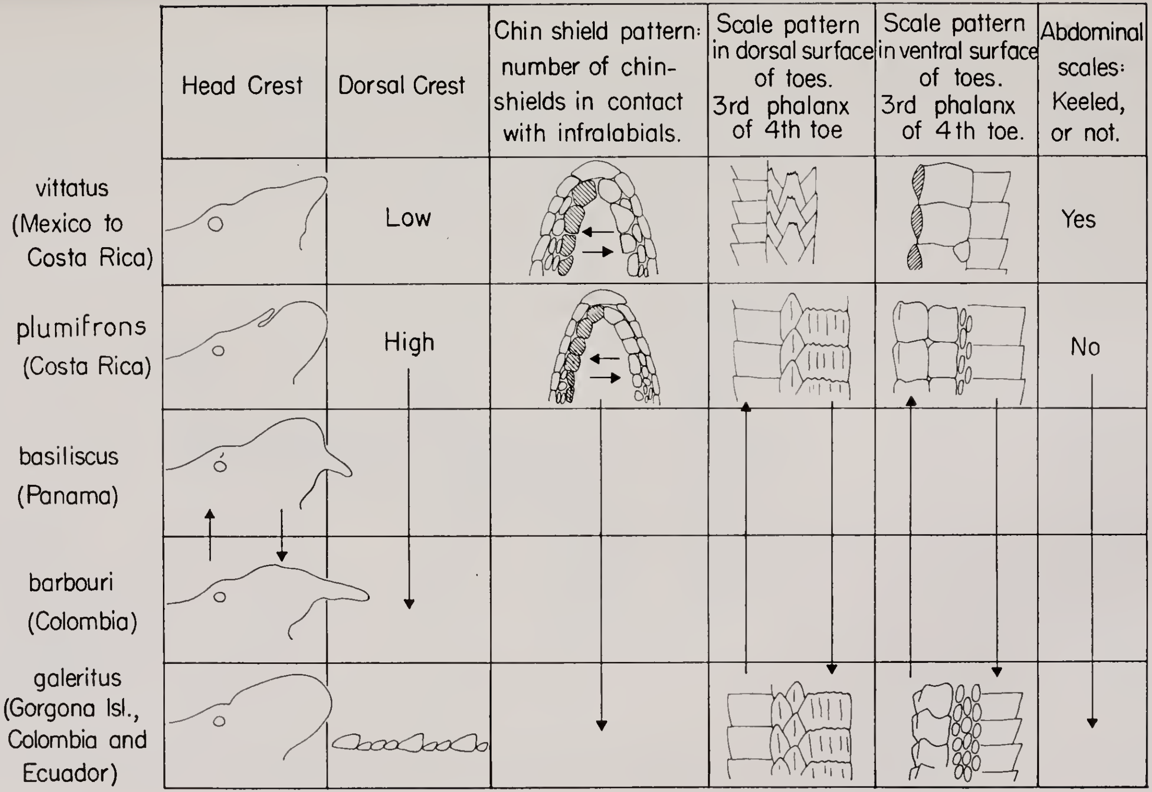


Figure 9. Crest and scale pattern differences between *Basiliscus* species.

ADDITIONAL DATA: ECOLOGY AND DISTRIBUTION

The populations currently distinguished appear on the whole to have similar ecological preferences. They are consistently found near the streams or on the seashore, and feed on terrestrial as well as on aquatic insects. Small aquatic vertebrates may also be eaten (Barden, 1943a).

In Panama and Costa Rica where *vittatus* and *plumifrons* are found sometimes in the same general localities, *vittatus* is found on the seashore, where the forest ends, while *plumifrons* is found along the streams and rivers which open into the sea (C. Gans, personal communication). In inland streams far from the coast, *plumifrons* is also reported, but not *vittatus*.

In the northern part of its range, Guatemala and Mexico, information about the habitat of *vittatus* is incomplete but, according to Conant (1951) it is found near the coast and in inland rivers and ponds. In general, it seems in the north to occupy niches similar to those that *plumifrons* occupies in Costa Rica and appears to replace it ecologically, although *vittatus* may also occupy drier regions than *plumifrons*.

In Panama *basiliscus* has been found in inland and in seashore areas, at the side of streams or where the forest comes to the border of the sea (Barden, 1943b). In Santa Marta, Colombia, *barbouri* is also found along the streams. *Galeritus* also lives near the streams at the border of the forest (Fowler, 1913).

All populations have been reported to have bipedal habits and *basiliscus*, *plumifrons* and *galeritus* have been observed running on the water surface (Snyder, 1949, 1954; Evans, 1947). The absence of any habit of running on the surface of water in *vittatus*, on the other hand, may be correlated with the foot structure. The functional surface of the foot in *vittatus, especially in adults,* is smaller than in the other forms. This is due both to the smaller number of scales in the toe flap (which reflects shorter toes) and to the narrower toes and toe fringes. Whether this situation changes towards the north, where *vittatus* seems to replace *plumifrons* in inland streams, is not known. Nevertheless, juveniles up to 60 mm in body length have feet and toes which appear as well adapted to aquatic behavior as the other groups do, and probably they exploit the aquatic (i.e. the water surface) habitat while the adults behave otherwise. A change like this in habitat preferences when passing from juvenile to adult would not be surprising in itself, and it is probable that it also occurs in the other forms in which young are known to be able to run on the water surface. In these, however, since the adult size is larger than in *vittatus,* above 160 mm and below 120 mm respectively, the change would seem to occur when these animals have attained a greater body length.

Further information about the ecology may also be provided by the fact that *basiliscus* and *barbouri* are the only groups in

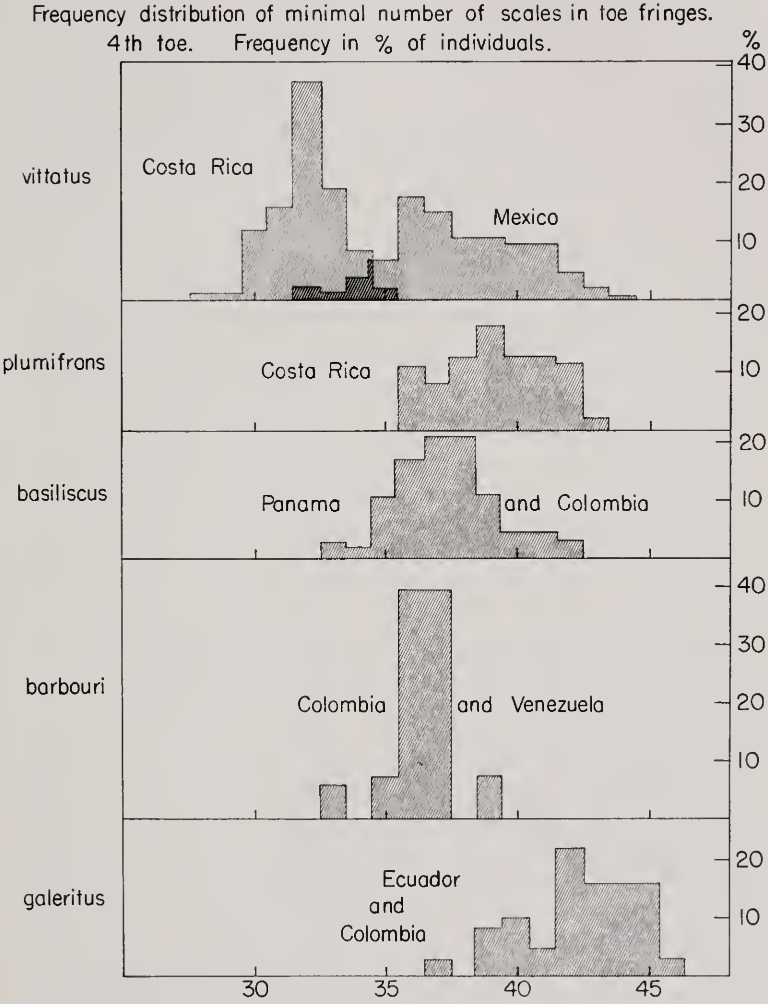


Figure 10. Histograms of scale count frequencies in *Basiliscus* species.

which ectoparasites were found. These were ticks which attached themselves strongly to the head crest and toe flap in adults as well as in young individuals. The significance of this situation is not clear, but it would appear to represent either a similarity in habits which exposes the two forms to similar infestations, or that they have a comparable susceptibility to the ectoparasites.

With respect to distribution, the various groups, as has been mentioned, appear on the evidence available to me to be allopatric, with the exception of *vittatus* and *plumifrons* (Maps 1-3). In reality, I do not have accurate information about the actual range of all forms or about the regions of contact, if they exist. Thus, as far as the available data go, *galeritus* and *barbouri* have been found in areas separated by a few hundred miles, with *basiliscus* in between. *Basiliscus* and *galeritus* meet along the Pacific coast of Colombia in Choco. *Barbouri* and *basiliscus* appear to be less widely separated, but there is a stretch of about 150 miles of coast between Golfo de Uraba and Santa Marta in Colombia from which I have no records. There is no obvious reason to suppose that the genus is not represented in the intermediate regions and it seems more probable that the lack of data from these areas is a sampling problem.

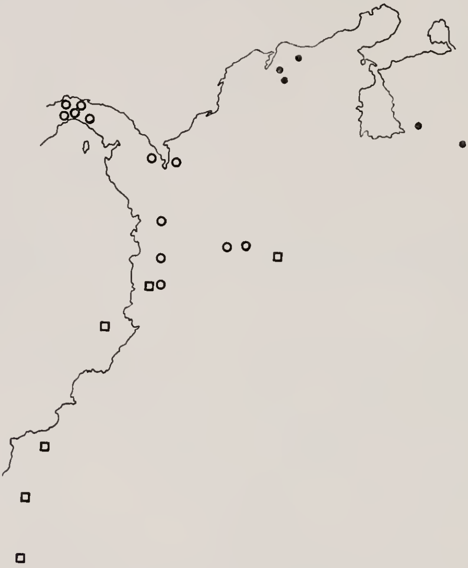
Although *basiliscus* has been reported from many places in Panama, both on the coast and inland, it has not been reported from Almirante where *vittatus* and *plumifrons* are found. The absence of *basiliscus* in the region of Almirante may be significant and related to an actual territorial competition, rather than only to sampling in collections. Along a line uniting Almirante to Puerto Armuelles there is a zone of potential contact between *basiliscus* and *plumifrons* and/or *vittatus*, but, although the information is scant, there is no evidence of sympatry or hybridization. The coloration of *vittatus* and *basiliscus* (and *barbouri*) is extremely similar, although there are differences in the intensity and clarity of the stripe pattern. It seems that this coloration may be related to the preference that *vittatus* (Gans, personal communication) and *basiliscus* (Evans, 1947) show for sandy and exposed areas near the coast and inland, in contradistinction to the marked preference for shady areas in the woods at the border of streams shown by *plumifrons* (Gans, personal communication). *B. basiliscus,* however, seems also to share the arboreal habits of *plumifrons,* as well as the aquatic preferences (Evans, 1947; Barden, 1943b). In these circumstances, it may well be that *basiliscus* is able to replace ecologically both *vittatus* and *plumifrons* in Panama, a condition which

Map. 1. Distribution of the species of *Basiliscus* (based on the specimens examined only). Southern Mexico to Guatemala. Crosses = *B. vittatus.*

Map 2. Distribution of the species of *Basiliscus* (based on the specimens examined only). Guatemala to northern Colombia. Crosses = *B. vittatus;* squares = *B. plumifrons;* circles = *B. basiliscus basiliscus.*

may account for the absence of sympatry between *basiliscus* and the other forms.

In Costa Rica, *plumifrons* probably occupies the whole country. It has been observed on both coasts and in the inland, while *vittatus* has been found only on the Atlantic side in several localities where *plumifrons* is also found. From northern Nicaragua to Mexico *vittatus* is found on both coasts and inland; the extreme north of its range seems to be Tamaulipas and Michoacan.



Map 3. Distribution of the species of *Basiliscus* (based on the specimens examined only). Southern Panama, Colombia, Ecuador and Venezuela. Circles = *B. basiliscus basiliscus;* solid circles = *B. basiliscus barbouri;* squares = *B. galeritus.*

DISCUSSION

From the morphological analysis it seems evident that the five species studied form two main groups: (1) *vittatus* with a northern distribution, and (2) all the other forms which together constitute a rather sharply set off southern group (see Fig. 8 and Table 1). These two groups, of course, have many characters in common and differ in many others, but in four of the features studied they differ sharply and clearly enough to permit the distinction of every individual. These features are: the two scale patterns of the toes, the keeling of the abdominal scales and the pattern of chin-shields. It is also evident from this study that *vittatus* can be clearly distinguished from each of the other forms by almost the same degree of morphological difference. This suggests that there is the same order of genetic gap between it and all members of the southern group. To assess the magnitude of this genetic gap, however, one can only consider *vittatus* and *plumifrons* which are sympatric in part of their range.

As has been said, *vittatus* and *plumifrons* are found in the same general localities in parts of Panama and Cost Rica. They are, however, ecologically separated in such a fashion that they have opportunity for contact only where their habitats come together at the opening of rivers and streams into the sea. Furthermore, these seem to be the only places where both forms can be found simultaneously (Gans, personal communication), and even here they remain clearly distinct and separate. It is to be inferred in these circumstances that these two forms retain their individuality by maintaining reproductive isolation. It is not known what other isolating mechanisms in addition to the ecological preferences maintain this separation, but it appears from the overall difference between *vittatus* and *plumifrons* (and all the other southern forms) that there can be little or no genetic exchange.

Although *vittatus*, as the northern group, seems to be a unit, it is not strictly uniform and shows some noticeable geographic variation. This is mainly in the frequency distribution of some scale patterns. Thus, the frequency of 3 rows of scales between the orbital semicircles increases from 8 per cent in Panama-Costa Rica to 44 per cent in Honduras and 54 per cent in Guatemala-Mexico. Similarly, the frequency of two scales (minimal number) between the pineal scale and orbital semicircles increases from 2 per cent in Panama-Costa Rica to 35 per cent in Honduras and to 40 per cent in Guatemala-Mexico. A comparable shift occurs in the formula of the breaking rings of the tail, see Table 1. Changes also occur with respect to the number of scales in the flaps of the toes, which from a range of 28 to 35 (minimal numbers) shifts to 31-38 in Honduras and to 32-44 in Guatemala-Mexico. The lower numbers become increasingly rarer and there is a progressive flattening of the curve of distribution. The two first-mentioned characters may be a function of the shape of the head, and as characters correlated with the appearance of the animals they may, in a certain sense be associated, like body coloration and shape of crests, with intraspecific recognition. The number of scales in the toe fringes, on the other hand, seems to be related to aquatic habits and its variability may be of some significance in relation to the ecological preferences of *vittatus* along its range. As the number of these scales increases towards Mexico there are also some indications that the flap may remain for a longer time wide enough to be useful in water dwelling in the northern populations. This is inferred from the body size at which the flap becomes clearly smaller than half of the width of the ventral surface of the toe. In Panama-Costa Rica this size is about 52 mm body length while in Mexico it is about 62 mm. Whether or not this is related to a more aquatic habit of the young individuals is not clear. If success in water dwelling is to be judged by *plumifrons* or *basiliscus* in which the flap of the toes produces a great increase in the foot surface, *vittatus* is far behind in the more mature stages of development if not so much so in the very juvenile stages. Towards the north the maximal size attained by adult *vittatus* increases from 135 mm to 175 mm (which is about the same length that *plumifrons* attains in Costa Rica) but the wide flap is retained only to about 62 mm of body length.

It is not clear whether *vittatus* replaces *plumifrons* ecologically in the part of its territory where *plumifrons* is not found, but it seems that this may be the case. In this allopatric part of its range *vittatus* is found near the inland streams as well as at the coasts, always near water, and can be caught during the night underneath bridges or nearby stones in the river margin (Conant, 1951). It seems likely also that the juveniles of *vittatus* are more aquatic than the adults, and that the higher variability of the northern populations of this group is the result of a wider ecological distribution. Examining Table 1 and Figure 10 it will be noticed that northern *vittatus* tends to differ less in some characters from *plumifrons* than does Costa Rican *vittatus*. This phenomenon which has been called "character displacement" (Brown and Wilson, 1956) is obviously related to the ecological separation which occurs in closely related species in the regions of sympatry. This ecological separation produces a different emphasis in the selective pressure which can be expected to result in the divergence of a whole complex of characters which otherwise could have remained similar. In these circumstances, beyond the regions of sympatry, if there is ecological replacement, a certain convergence towards the replaced type could be expected to occur. This may possibly happen to some degree in *vittatus* which appears to replace *plumifrons* in the inland in Guatemala and Mexico. It should be said that this convergence to the replaced type will only be of a very general nature, unless there are features which represent unique solutions to certain ecological problems. The degree of convergence will also be dependent on the amount of genetic difference accumulated in the two species. Thus, for example, the possible tendency of *vittatus* to be more aquatic appears in the increased number and width of scales in the toe flaps, but this is not accompanied by a change in the scale pattern of the toes, or in the shape of the scales of the flap.

In the case of the southern group, examination of the summary of morphological characters in Table 1 and in Figures 5, 9 and 10 clearly shows that none of the species which compose it differs from the others in the same degree as *vittatus* differs from *plumifrons.* Thus, inference from morphology alone that these forms are reproductively isolated is not on nearly so secure a footing as our decision that reproductive isolation exists between this group and *vittatus.* Nevertheless, several facts are significant and deserve close consideration.

That the southern group represents a phylogenetic unit as opposed to *vittatus* seems evident, but it is also evident that there are important discontinuities. Thus, *galeritus* in the extreme south of the genus range looks to some extent like an isolate. (Taylor's description of young "*galeritus*" from Cost Rica [Taylor, 1956] is, I believe, based on young *plumifrons.*) *Galeritus* stands clearly apart from the rest of the southern group in the absence of a dorsal crest (which is replaced by a sharply distinctive pattern of dorsal scales) as well as in typical body coloration. These features are also diagnostic in the juveniles which show the peculiar dorsal scale pattern and a characteristic coloration which, however, is different from the adult one. The head crest of the adult males is also typical. Judging by these notable differences from the rest of the southern group and their possible significance in sexual recognition, *galeritus* appears to me to have attained specific status.

Among the remaining forms, *plumifrons* can be recognized by its coloration and shape of the head crest, when this is present. The number of interorbital scales and the number of scales between the pineal eye and the orbital semicircles vary in a rather characteristic way for this form and are consistently larger than in *basiliscus.* The shape of the head and dorsal crests, as well as color, are of special significance, being secondary sexual characters which are probably used in display for intraspecific recognition. This may also apply to the shape of the head, the width of which is reflected in the number of interorbital scales. As these lizards (*Basiliscus*) are in general diurnal animals and some of them exhibit arboreal habits, visual clues may be important for the sexual behavior. For these reasons I believe that the constant difference in color and shape of the head crest between *basiliscus* and *plumifrons* is a sign of reproductive isolation and a strong argument in favor of their specific status.

The fact — if it is a fact — that these species of the southern group are non-sympatric deserves a special comment. There is a significant difference between separation produced by a geographic barrier and separation in which such a physical barrier does not exist, and geographic as well as ecological contiguity seem to be present. The first is usually described by the term allopatry. This kind of separation may not be accompanied by a biologically significant discontinuity expressed by the presence of reproductive isolating mechanisms (although it may eventually lead to this), and is maintained primarily by the geographic barrier itself. The second kind of separation with no geographic barrier or gross ecological discontinuity (which amounts to the same thing) is maintained by a biological process and requires the presence of isolating mechanisms. This type of separation may be called parapatry. The situation found in *basiliscus* and *plumifrons*, which occupy neighboring regions but are not found together (and which show no obvious territorial interpenetration), may correspond to the latter type. The territorial separation of *vittatus* and *basiliscus* may be a similar case. If one considers what situation is most likely to be the origin of this kind of separation one finds that ecological competition appears as the best candidate. As is well known, for ecological competition to occur there must be close similarities in the ecological preferences of the forms in contact; if this is not the case and the habitats intermingle the result will be sympatry. It is also necessary that the forms be reproductively isolated at least by one efficient isolating mechanism; otherwise, hybridization will occur with the resulting fusion into a single form. If, however, reproductive isolation exists, the populations can be expected to compete when they first meet and become separated at the level of an ecological boundary. On its own side of this boundary each population will have some sort of advantage which does not need to involve the factor in regard to which there is competition. The nonsympatric condition of *basiliscus* and *plumifrons,* if it is real, seems to depend on this kind of phenomenon since no obvious geographic or ecological barrier appears responsible for their separation. In any event this situation can be used as an argument in favor of the specific status of *plumifrons* and *basiliscus: basiliscus* and *plumifrons* may be separated by ecological preferences not yet detected, but such separation would appear to imply reproductive isolation. Since *basiliscus* appears to replace *vittatus* ecologically on the coast, in the same manner that it seems to replace *plumifrons* in the interior, the presence of *vittatus* in this critical region is of similar significance for the assessment of the reproductive isolation between these forms. However, as I have said above, the nature of the boundary between these species is not at all clear and requires further study. Collecting in a line uniting Puerto Armuelles and Almirante, and on the Pacific and Caribbean coasts in both directions from these points, together with a more detailed study of the ecological preferences and behavioral habits of these animals will certainly contribute to the solution of the problem.

In the case of *basiliscus* and *barbouri,* the situation is different. The gap which separates these two forms, making them allopatric, may be entirely due to sampling since there is a region of about 150 miles between Golfo de Uraba and Santa Marta in regard to which there seems to be no information. It is in this region that intergradation of the two forms may occur, and the great resemblances between them indicate this as a strong probability. The shape of the head crest, for example, suggests a single pattern of variation in the whole range of the two forms, and even in the absence of knowledge from the intermediate region this situation suggests gene flow between *basiliscus* and *barbouri.* The two forms are furthermore indistinguishable in body coloration. There are indeed differences in the number of interorbital scales and in the number of scales between the pineal eye and the orbital semicircles, but these differences may well correspond to extremes of variability in a single form. On the whole, there seems to be insufficient ground to infer reproductive isolation between *basiliscus* and *barbouri.*

Thus, in conclusion, it is possible to say that the genus *Basiliscus* is composed of two groups: a northern group formed by *vittatus,* and a southern group formed by all the other species.

B. vittatus appears to be a strongly marked species and stands out clearly as a phylogenetic unit as compared to the southern group. The latter also appears to be a phylogenetic unit, but it is composed of three species: *B. plumifrons, B. basiliscus* and *B. galeritus.* In *B. basiliscus* should be included the form from Santa Marta, Colombia, and Venezuela (*barbouri*) since all the available data suggest that it is conspecific.

There are considerable gaps in the knowledge of the distribution of these four species. Further information is necessary to demonstrate or clarify the apparent allopatry of the species of the southern group; in particular, a more detailed study of the region of contact between *plumifrons* and *basiliscus* is needed. Also, more needs to be known about the distribution of *galeritus,* especially in the area where it seems to meet *basiliscus* in Choco, Colombia. In general, a more complete study of the ecological preferences and behavioral habits of all populations is required, and in particular investigation of the aquatic habits of *vittatus* in various parts of its range. If my interpretations of the morphological observations are correct, this further evidence should not alter the specific distinctions here supported. Nevertheless, proof of these interpretations can only be obtained by direct observation and the conclusions here presented should be considered as a probable working hypothesis for further research.

Key to the species of *Basiliscus*

1. Keeled abdominal scales; pattern A for the scale arrangement on the dorsal surface of the toes, and pattern C for the ventral surface . . . . *vittatus*
   No keeled abdominal scales; pattern B for the scale arrangement of the dorsal surface of the toes, and pattern D for the ventral surface; southern group 2
2. In the dorsal midline a clear alternation of large and small scales, 1 large for each 2 to 4 small ones; no dorsal crest in the adult male *galeritus*
   Middorsal line with scales of nearly uniform size with some semiperiodicity; adult males with dorsal crest 3
3. Minimum number of scales between the orbital semicircles 1 to 2 and brownish coloration . . . . *basiliscus*
   Minimum number of scales between the orbital semicircles 3 to 5, rarely 2, and blue-green coloration; bifurcated head crest in the adult males . . *plumifrons*

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TABLE 1

Morphological characters of the specimens examined

		galeritus		*barbouri*		*basiliscus*		*plumifrons*		*vittatus*					
										Costa Rica		Nicaragua Honduras		Guatemala Mexico	
		%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.
Minimal no. of scales between supra-orbital semicircles.	0					1	1								
	1	16	6	18	3	90	62	3	1	13	12	2	2	5	4
	2	74	28	53	9	9	6	13	5	79	75	54	52	42	36
	3	10	4	29	5			58	22	8	8	44	44	53	43
	4							23	9						
	5							3	1						
Minimal no. of scales between pineal scale and supra-orbital semicircles.	0	3	1			25	17								
	1	21	8	35	6	69	47	10	4	98	96	65	61	64	57
	2	76	29	65	11	6	4	74	28	2	2	35	33	36	32
	3							16	6						
Ratio of mid-dorsal to mid-ventral scales in tail rings.	4/4	12	4							45	41	10	9	7	6
	4/5	3	1												
	5/4	15	5	35	6	3	1			55	50	88	82	84	75
	5/5	9	3											3	3
	6/4	38	13	35	6	46	26	37	14			2	2	6	5
	6/5	17	6	12	2	3	1								
	7/4	3	1	18	3	39	33	45	17						
	7/5	3	1			3	2	13	5						
	8/4					3	1	3	1						
	8/5					3	1	2	1						

TABLE 1 (Cont.)

		galeritus		*barbouri*		*basiliscus*		*plumifrons*		*vittatus*					
										Costa Rica		Nicaragua Honduras		Guatemala Mexico	
		%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.
Minimal no. of scales in toe fringe of the 4th toe.	28									1	1				
	29									1	1				
	30									13	13				
	31									16	15	1	1		
	32									39	36			2	2
	33			6	1	3	2			19	18	4	4	1	1
	34					2	1			9	9	13	13	4	4
	35			7	1	11	7			2	2	15	14	7	6
	36			40	6	17	11	11	4			24	23	18	16
	37	3	1	40	6	21	14	8	3			23	22	16	14
	38					21	14	13	5			14	14	12	11
	39	8	3	7	1	12	8	18	7			6	6	12	11
	40	10	4			5	3	13	5					10	9
	41	5	2			5	3	13	5					10	9
	42	23	9			3	2	11	4					5	4
	43	16	6					11	4					2	2
	44	16	6					2	1					1	1
	45	16	6												
	46	3	1												

TABLE 2

Distribution, sex, number and size of the specimens examined

Form	Country	Locality	Sex	No.	Size ranges in cm
B. galeritus					
	Ecuador	"Ecuador"	M	1	15.0
	”	Bucay, Guayas	F	1	11.0
			M	1	16.0
			J	7	4.0- 8.8
	”	Ventura, Río Chanchan	M	1	17.0
	”	Esmeraldas	F	1	14.0
			M	1	14.0
			J	4	4.3- 4.9
	Colombia	Gorgona Island	F	6	11.0-16.5
			M	3	15.0-19.0
			J	6	4.4- 5.5
	”	Gorgonilla Island	J	1	4.5
	”	Boyacá	J	2	4.1- 4.6
	”	Río Puné, Atrato Region, Chocó	M	1	9.0
			J	1	5.9
B. barbouri					
	Venezuela	Trujillo, Trujillo	F	1	10.0
	”	Valencia, Esperanza	J	1	4.1
	Colombia	Santa Marta:			
		Palomino	M	1	18.0
		Fundación	M	1	17.2
		Río Frío	M	3	13.0-17.0
		” ”	F	1	10.1
		” ”	J	5	4.4- 7.2
	”	Concepcion	J	4	4.4- 5.1
B. basiliscus					
	Colombia	Mendellin, Antioquía	F	2	11.5-13.0
			M	1	11.0
			J	5	4.5- 7.3
	”	Envigado, Antioquía	J	1	4.2
	”	Ensenada Coredó	F	1	10.0
	”	Atrato Region, Chocó	J	4	4.7- 8.7
	”	Río Puné, Atrato Region, Chocó	J	2	8.0- 8.7
	”	Boca de la Raspadura, upper Quibdo, Chocó	F	2	12.2-13.5
			M	4	13.5-18.5
	”	Río Sn. Juan, Meta, Andagoya (Pacific)	F	2	11.7-14.5

Form	Country	Locality	Sex	No.	Size ranges in cm
B. basiliscus					
	Colombia	Boca de la Raspadura, Río Sn. Pablo, Chocó	F	1	14.3
	”	Golfo de Urabá	F	2	14.1-14.4
	Panamá	Río Esnape	M	1	18.7
			J	3	3.9- 7.0
	”	Pintupó	J	1	6.7
	”	Darien:			
		Rio Tapia	M	1	18.3
			F	1	14.5
			M	2	4.3- 7.5
		Camp Townsend	M	1	17.0
		Rio Sucubti	F	1	16.5
		Rio Chico	F	1	12.6
		Camp Creek	J	1	5.9
	”	La Chorrera	J	1	4.5
	”	Los Santo, Punta Mala	J	1	4.3
	”	El Valle de Anton, Cocle	J	1	2.9
	”	Pedro Gonzales, Archipielago de las Perlas	F	1	15.5
	Panamá	San Jose Island, Chiriqui, Gulf of Panamá	M	2	19.5-20.0
			F	2	11.5-13.5
	”	Canal Zone:			
		Rio Chagres	M	1	16.8
			F	3	14.5-16.0
		Albrook Field	M	1	16.5
		Frijoles	M	2	17.0-17.5
		Barro Colorado	F	1	16.0
			M	1	14.0
			J	1	8.2
	”	Panamá	M	1	17.5
	”	Panamá City	F	2	12.5-14.5
			M	3	16.7-17.0
	”	Río Sn. Pablo	F	1	14.6
			M	1	14.6
	”	Puerto Armuelles	J	4	6.5- 9.7
B. plumifrons					
	Panamá	Almirante	M	2	15.0-16.0
	”	United Fruit Co. Farm No. 6	F	1	14.0
	Costa Rica	Rio Zent	F	1	15.2
			M	2	9.1-16.0
			J	3	4.5- 9.0

TABLE 2 (Cont.)

Form	Country	Locality	Sex	No.	Size ranges in cm
B. plumifrons					
	Costa Rica	Turrialba	M	1	
			J	3	4.5- 9.0
	’’	Tortuguero	F	1	12.0
			J	1	6.6
	’’	Salamanca, Cordillera	F	2	12.9-15.5
			M	3	10.4-17.0
			J	3	4.6- 6.7
	Costa Rica	Guapiles	F	1	14.2
			J	1	3.9
	’’	Navarro	J	1	5.1
	’’	Río Baru	J	8	4.0- 8.7
	Nicaragua	Sn. Juan del Norte	M	1	20.5
	’’	Matagalpa	M	1	13.2
			F	1	14.5
	Honduras		F	1	12.0
B. vittatus					
	Panamá	Almirante	M	6	8.5-13.5
			F	2	10.6-10.7
			J	1	6.0
	’’	Río Torres	M	1	11.7
	Costa Rica	Río Zent	M	3	10.5-12.5
			F	1	10.4
			J	5	3.3- 6.3
	’’	Tortuguero	M	11	8.2-13.5
			F	3	8.9- 9.1
			J	64	4.1- 7.5
	Nicaragua	Camoapa	M	1	
	Honduras	Tegucigalpa	J	5	4.1- 7.4
	’’	Río Yequare	J	3	3.6- 6.7
	’’	Caparrosa	F	1	13.2
	’’	Lago Yojoa	F	2	11.2-11.5
	’’	Río Ardilla	M	1	
	’’	El Negrito	M	1	8.2
	Honduras	Valle Subirana	J	2	5.1- 6.6
	’’	Siguantepeque	J	1	4.7
	’’	Sn. Pedro Sula	M	1	7.9
	’’	Río Ulua	J	6	5.2- 6.1
	’’	Sula	M	9	8.2-14.5
			F	13	7.5-11.9
			J	50	4.2- 7.4
	British Honduras		J	1	7.7

Form	Country	Locality	Sex	No.	Size ranges in cm
B. vittatus					
	Guatemala	Chimoxan	J	1	7.0
	’’	El Paso, Río Sn. Pedro	M	1	12.2
			F	1	11.8
	’’	Scapulas	J	2	6.1- 6.2
	’’	Finca Ciprés	M	1	11.0
			J	1	4.7
	’’	Chamá	M	1	16.0
			F	1	12.9
	’’	La Primavera	M	1	12.2
	Mexico	Yucatan, Merida	M	2	14.5-15.5
			F	4	10.6-13.2
			J	9	6.1- 8.2
	’’	’’ Chichen Itza	M	1	12.1
			J	4	6.3- 7.3
	’’	’’ Tehuantepec	M	1	17.0
	’’	Chiapas, Monte Libano	J	3	4.1- 5.1
	’’	’’ Ocosingo	M	1	10.1
			J	2	3.6- 4.0
	’’	’’ Laguna Ocotal	M	1	8.5
			F	1	11.4
			J	4	3.3- 3.9
	Mexico	Oaxaca, Ispan Alepec	M	9	10.7-15.7
			F	14	8.6-14.7
			J	13	4.2- 7.2
	’’	Guerrero,			
		Chilpancingo	M	1	14.0
		Montzorongo	M	2	12.1-13.6
			J	1	9.1
		Potrero	M	1	14.0
	’’	Vera Cruz,			
		Miramar	F	2	12.4-13.4
		Córdoba	F	1	13.0
		Cerro del Gallo	J	1	4.6
			M	1	11.0
		Jalapa	M	1	16.5
			F	1	14.5

Maximal measured body length:

B. galeritus	19.5 cm
B. barbouri	18.0 cm
B. basiliscus	20.0 cm
B. plumifrons	20.5 cm
B. vittatus:	
a—in Panama-Costa Rica	13.5 cm
b—in Nicaragua-Honduras	14.5 cm
c—in Guatemala-Mexico	17.0 cm

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 128, No. 2

EIGHT NEW SPECIES OF *XARIFIA* (COPEPODA, CYCLOPOIDA), PARASITES OF CORALS IN MADAGASCAR.

By

Arthur G. Humes

Boston University, Boston, Massachusetts
and
Associate in Marine Invertebrates, Museum of Comparative Zoology

PRINTED FOR THE MUSEUM
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November 15, 1962

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY AT HARVARD COLLEGE

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BREVIORA (octavo) 1952 — No. 169 is current.

MEMOIRS (quarto) 1864–1938 — Publication was terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1 and 2, 4 and 6 are out of print; volumes 3, 5, 7, 9, and 15 are sold by the Museum, and future volumes will be published under Museum auspices.

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No. 2—*Eight new species of* Xarifia (*Copepoda, Cyclopoida*), *parasites of corals in Madagascar.*

By

Arthur G. Humes

Boston University, Boston, Massachusetts
and
Associate in Marine Invertebrates, Museum of Comparative Zoology

INTRODUCTION

The copepods to be described here were collected in the vicinity of the island of Nossi Bé, Madagascar (Malagasy Republic), during August through mid-November, 1960, while the author was the leader of a collecting expedition to Madagascar sponsored by the Academy of Natural Sciences of Philadelphia. I wish to thank Dr. R. Tucker Abbott for arranging my return to Madagascar and to acknowledge with appreciation the financial help received from the Academy. I wish also to express my thanks to Dr. Renaud Paulian, then Directeur-adjoint of the Institut de Recherche Scientifique de Madagascar, for placing at my disposal certain facilities of the Station Océanographique at Nossi Bé.

I am indebted to Dr. Donald F. Squires of the American Museum of Natural History for the identification of the coral hosts.

The laboratory study of the copepods has been supported by a grant from the National Science Foundation of the United States.

SYSTEMATIC DESCRIPTION

The genus *Xarifia* (family Xarifiidae) was described by Humes (1960) on the basis of two new species from the Maldive Islands, *X. maldivensis* and *X. fimbriata*, both from madreporarian corals, *Pocillopora* sp. Eight new species of this genus are now described from Madagascar. All specimens are from the shores of Nossi Bé or nearby islands. The collecting localities are indicated on the accompanying map.

XARIFIA GERLACHI, n. sp.

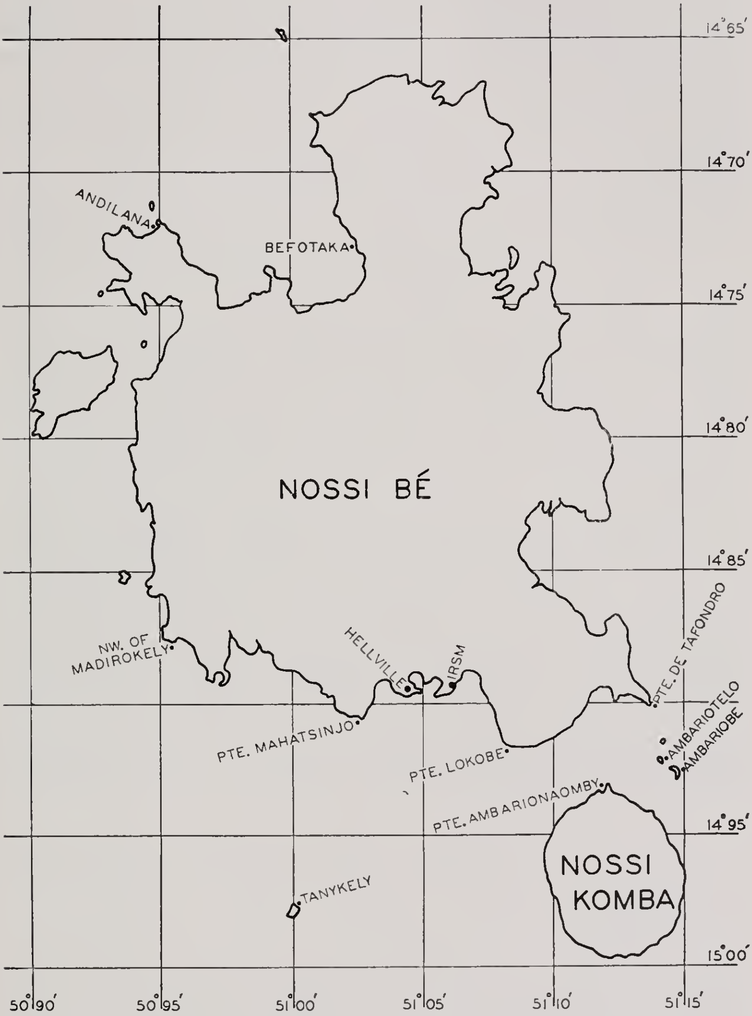
Pls. I; II; III, figs. 26-33

Type material. — 619 specimens (427 females and 192 males) from washings of a single colony of *Acropora corymbosa* (Lamarck) about 45 cm in diameter, at a depth of 1 meter at low tide at Pointe Lokobe, Nossi Bé, Madagascar, November 1, 1960. Holotype, allotype, and 119 paratypes (83 females and 36 males) deposited in the Muséum National d'Histoire Naturelle at Paris, the same number of paratypes in the Institut de Recherche Scientifique de Madagascar at Tananarive, the Academy of Natural Sciences at Philadelphia, the United States National Museum at Washington, and the remaining paratypes in the author's collection.

Other specimens. — 5 males from *Acropora* cf. *A. teres* (Verrill) in 0.5 meter at Ambariotelo, NE of Nossi Komba, September 23, 1960. One female and 2 males from *Acropora cytherea* Dana in 3 meters at Pointe Lokobe, Nossi Bé, October 16, 1960. 21 females, 1 male, and 3 immature specimens from *Acropora cytherea* Dana in 1 meter at Andilana, Nossi Bé, September 4, 1960. 7 females from *Acropora cytherea* Dana in 2 meters at Pointe Lokobe, Nossi Bé, September 2, 1960.

Female. — Body moderately stout (Figs. 1, 2), about 5 times longer than wide, 2.044 mm (1.856-2.400 mm) × 0.407 mm (0.384-0.445 mm), based on 10 individuals. Body of living specimens flexible and contractile, especially so in the abdominal region. Alcoholic specimens in various states of flexure and contraction and therefore measurements approximate. Ventral body wall tumid behind each of legs 1-4. Segmentation obscure and indicated externally only by slight swellings of the body. (In contracted specimens segmentation more evident.) Region dorsal to the fifth legs bearing 3 short, posteriorly-directed processes (Fig. 1), the median one shorter than the two lateral ones which are about 145µ in length. A broad protuberance (Fig. 3) below the median process. The two oviducal openings dorsal in position. Genital segment and abdomen (Fig. 1) slenderer than the thorax, with a short transverse flap over the anal region. Rows of minute setules on the anal area as indicated in Figure 4. Caudal ramus (Figs. 4, 5) consisting of a rounded lobe not sharply delimited from the abdomen and bearing a terminal row of 4 (sometimes 3) setules and a subterminal outer setule. A few minute hairs on the dorsal surface of the ramus. Egg sacs (Figs. 6, 7) flattened and held dorsolaterally to the abdomen. Each egg sac usually containing from 8-13 eggs (one female had sacs with only 2 eggs), arranged in one or (in the central region of the sac) 2 layers. Each egg about 105µ in diameter.

Rostral area broadly rounded (Fig. 8). First antenna (Fig. 9) short (35µ in length without the setae), probably with 5



COLLECTING LOCALITIES IN THE NOSSI BÉ REGION, MADAGASCAR segments, but the last 4 incompletely separated from each other. With 3 long aesthetes and naked hyaline setae as indicated in the figure. Second antenna (Fig. 10) having 4 segments (the last 2 rather indistinctly separated, the basal one showing an incomplete transverse line). First and second segments with an inner marginal seta. Third segment with 2 inner marginal setae. Last segment terminally with a long outer seta and a short inner digitiform process. Mandible (Fig. 11) an attenuated blade bearing a distal row of spinules. Paragnath absent. First maxilla (Fig. 11) a small rounded lobe bearing 2 setae. Second maxilla (Fig. 11) having a broad base extended distally to form a slender, hyaline, somewhat expanded process. Maxilliped (Fig. 11) having 2 segments, the first with an anterior expansion, the second smaller with a series of very fine striae on its posterior margin, a ventral and subterminal hyaline lobe (in some specimens slightly incised) with 2 very small setae near its base, and 2 unequal terminal processes. Arrangement of the head appendages as in Figures 12 and 13. Labrum bell-shaped in ventral view (Fig. 12) and showing a posterior ventral expansion in lateral view (Fig. 13). A median raised area posterior to the labrum. Posterior part of labrum concealing the mandibles in ventral view, and its posterior margin formed as in Figure 14.

Legs 1-4 similar in general form and size. Exopods having the 3 segments mostly fused (the tripartite nature indicated by occasional very weak incomplete joints on the inner margin and by 3 sclerotized areas seen on the anterior surface of each exopod as shown in Figure 15). Endopods composed of a single segment, with the 2 sclerotized areas on the posterior surface (Fig. 16) suggesting a bipartite origin. The basipod of all 4 legs with an outer seta, but without an inner seta. Intercoxal plates similar in all 4 pairs of legs. Spine and setal formula as follows (Roman numerals referring to spines, Arabic numerals to setae):

	leg 1		leg 2		leg 3		leg 4	
	exp	end	exp	end	exp	end	exp	end
1st segment	I:0	2	I:0	2	I:0	1	I:0	1
2nd segment	I:0		I:0		I:0		I:0	
3rd segment	I(+3)		I(+3)		I(+2)		I(+2)	

Leg 1 (Fig. 16) with the exopod (54 × 22μ) having 3 stout claw-like spines along the outer margin of its distal half, each claw being swollen basally and attenuated distally to form a

recurved hook directed posteriorly (Fig. 17); 3 small subterminal inner setae near the distalmost claw. Inner margin of the exopod with an angular indentation near its base. Endopod (40 × 27μ) broadened basally and rounded distally, with 2 inner subterminal setae and a band of hairs along the outer edge of the ramus. Leg 2 (Fig. 18) similar to leg 1. Leg 3 (Fig. 19) similiar to leg 1, but the exopod with only 2 inner subterminal setae instead of 3. Exopod claws (Fig. 20) more swollen basally than in the first leg (much like the claws of legs 2 and 4). Endopod with only 1 seta instead of 2. Leg 4 (Fig. 21) similar to leg 3.

Leg 5 (Fig. 22) composed of a single elongated segment 55 × 30μ, arising on the side of the body ventral to the lateral, posteriorly-directed process (see Fig. 3), and bearing 2 long terminal setae. A slender seta arising from the body wall dorsal to the base of the segment. Leg 6 absent.

Body colorless in living specimens, eye red, egg sacs opaque gray.

Male. — Body (Figs. 23, 24) not stout in the thoracic region as in the female, but, instead, of about the same width throughout. Much shorter than the female, 0.894 mm (0.818-0.963 mm) × 0.129 mm (0.112-0.140 mm), based on 10 specimens. Region dorsal to the fifth legs smooth, without the 3 short processes as in the female. Thoracic segmentation not evident externally except for slight swellings. Genital area and abdomen (Figs. 25, 26) without external segmentation. Caudal ramus (Fig. 27) similar to the female, but a little less pronounced.

Rostral area as in the female. First antenna (Fig. 28) similar to the female but smaller (only 23μ long, not including the setae) and with 4 aesthetes instead of 3. Second antenna, labrum, mandible, first maxilla, and second maxilla like those of the female. Paragnath absent. Maxilliped (Fig. 29) large, with 4 segments, the first unarmed and short, with a small group of very fine striae or hairs (?), thè second large with its inner, somewhat concave edge bearing 2 setae and a little expanded distally, the third very short and unarmed, and the last segment in the form of a recurved claw 33μ in length, with 2 very unequal setae on its basal inner half and with its tip bifurcated. Arrangement of the head appendages as in the female, with the enlarged maxillipeds projecting conspicuously (Figs. 24, 30).

Legs 1-4 as in the female, with the same spine and setal formula, but with the rami smaller (exopod of leg 1, 31 × 13μ, endopod 20 × 17μ) and with the claw-like spines on the exopods not conspicuously swollen basally and more elongate (Fig. 31). Leg 5 (Fig. 32) located on the side of the body, without a distinct segment, composed of 2 setae measuring 6 and 9μ, respectively, arising from a small protuberance, and an adjacent more dorsal seta. Leg 6 (Figs. 24, 26, 33) apparently represented by a slightly crescentic, well-sclerotized ridge with 2 small setae.

Color as in the female.

(The species is named in recognition of Dr. Sebastian A. Gerlach who first discovered the existence in madreporarian corals of copepods belonging to the genus *Xarifia.*)

Remarks. — The female of *X. gerlachi* may be readily distinguished from the two previously described species, *X. maldivensis* Humes and *X. fimbriata* Humes, by its larger size, by the nature of the processes on the posterior part of the thorax, by the structure of the caudal ramus, and by many details of the armature of the appendages. The male of *X. gerlachi* may be recognized by the structure of the caudal ramus, by the nature of the maxilliped, and by the armature of legs 1-4.

XARIFIA LONGIPES, n. sp.

Pls. III, figs. 34-39; IV;V, figs. 55-57.

Type material. — 141 specimens (72 females and 69 males) from *Pavona angulata* Klunzinger at a depth of 0.5 meter at low tide at Befotaka, on the northern shore of Nossi Bé, September 24, 1960. Holotype, allotype, and 31 paratypes (16 females and 15 males) deposited in the Muséum National d'Histoire Naturelle at Paris, the same number of paratypes in the Institut de Recherche Scientifique de Madagascar at Tananarive, the United States National Museum at Washington, and the remaining paratypes in the author's collection.

Female. — Body (Figs. 34, 35) about 7 times longer than wide, 1.483 mm (1.434-1.557 mm) × 0.213 mm (0.202-0.220 mm), based on 10 individuals. Abdominal region contractile. Segmentation obscure and indicated externally only by slight swellings. Region dorsal to the fifth legs bearing 3 very long, slender, posteriorly directed processes (Figs. 36, 37), the middle one only slightly shorter than the other two. Openings of the oviducts dorsal. Abdomen (Fig. 36) slenderer than the thorax. Caudal ramus (Fig. 38) elongated and slender, 110 × 30μ, bearing 3 terminal setae and one subterminal outer seta. A few minute hairs on the surface of the ramus. Egg sac unknown.

Rostral area broadly rounded (Figs. 34, 39). First antenna (Fig. 40) about 66μ in length (not including the setae), the segmentation obscure but apparently only 3-segmented. With 3 broad aesthetes and numerous naked setae as shown in the figures. Second antenna (Fig. 41) with 4 segments. First and second segments with an inner marginal seta, the third with 2 such setae, and the last with a subterminal outer seta and a falciform terminal claw. Mandible (Fig. 42) a slender blade with a slightly recurved tip and apparently not having minute spinules as in the previous species. First and second maxillae similar to those of *X. gerlachi.* Maxilliped (Fig. 43) with 2 segments, the first with an inner anterior expansion, the second with a large inner lobe with 2 small setae near its base, a small round subventral lobe, and 2 digitiform terminal processes. Labrum and the arrangement of the head appendages as in the previous species.

Legs 1-4 similar, with the exopods 3-segmented and the endopods composed of a single segment (though a bipartite origin is suggested by an inner marginal notch). All 4 legs with an outer basipod seta and with a tuft of long hairs on the inner basipod area. Intercoxal plates similar in all 4 pairs of legs. Spine and setal formula as follows:

	leg 1		leg 2		leg 3		leg 4	
	exp	end	exp	end	exp	end	exp	end
1st segment	I:0	2	I:0	1	I:0	1	I:0	1
2nd segment	I:0		I:0		I:0		I:0	
3rd segment	I(+3)		I(+3)		I(+3)		I(+3)	

Leg 1 (Fig. 44) with the first segment of the exopod subtriangular and bearing a short broad spine on its outer distal corner; the second segment subrectangular with a similar outer distal spine, a rounded expansion of the outer margin below the spine, and a few long hairs on the inner margin; the third segment slender with a crescent-shaped ridge on the posterior surface of its basal half, a large terminal spine, and 3 subterminal spinules. The 3 outer spines slightly recurved posteriorly, their tips surrounded by hyaline expansions (Fig. 45). Endopod elongated, with a row of long hairs along its outer margin, a small notch in the middle of its inner margin, and 2 slender terminal setae. Leg 2 (Fig. 46) similar to leg 1, but with only one terminal seta on the endopod. Leg 3 (Fig. 47) and leg 4 (Fig. 48) very similar to leg 2.

Leg 5 (Fig. 49) a single, greatly elongated, slender segment 170µ long, arising on the side of the body ventral to the lateral, posteriorly-directed process (see Fig. 37) and bearing 2 unequal terminal setae, 36 and 16µ, respectively. A slender seta arising from the body wall dorsal to the base of the leg. Leg 6 absent.

Body colorless in living specimens, eye red.

Male. — Body (Figs. 50, 51) with the thoracic and abdominal regions not conspicuously different in width. Only slightly shorter than the female, 1.426 mm (1.344-1.504 mm) × 0.163 mm (0.157-0.175 mm), based on 10 specimens. Segmentation indicated only by slight swellings. Genital segment (Fig. 52) with 2 ventrolateral ridges (bearing the sixth legs). Caudal ramus (Fig. 53) short, 39 × 21µ, somewhat tapered posteriorly, and bearing setae as in the female, though relatively longer.

Rostral area as in the female. First antenna (Fig. 54) similar to that of the female, but apparently with only 3 aesthetes which are relatively longer than in the female. Second antenna, labrum, mandible, first maxilla, and second maxilla like those of the female. Paragnath absent. Maxilliped (Fig. 55) composed of 4 segments, the first broad, unarmed, and rather poorly defined, the second large with 2 inner setae, the third short and unarmed, and the fourth in the form of a recurved claw 50µ long, with 2 very unequal setae and an inner projection near its base, and with 3 terminal teeth (in one specimen only 2). Arrangement of the head appendages as in the female, but the enlarged maxillipeds projecting conspicuously (Fig. 51).

Legs 1-4 as in the female, with the same spine and setal formula. Leg 5 (Fig. 56), arising on the side of the body, consisting of a small protuberance bearing 2 setae and an adjacent dorsal seta. Leg 6 (Fig. 57) represented by 2 setae arising from a ventrolateral ridge.

Color as in the female.

(The specific name *longipes*, long-footed, alludes to the very elongated fifth legs.)

Remarks. — The female of *X. longipes* may be readily separated from *X. maldivenesis, X. fimbriata,* and *X. gerlachi* by the 3 very long, posteriorly-directed processes above the fifth legs and by the elongated fifth legs themselves, by the structure of the caudal ramus, and by the nature of the claws on the exopods of legs 1-4. The male of *X. longipes* may be distinguished by the structure of the caudal ramus, the form of the maxilliped, and the armature of legs 1-4.

XARIFIA DISPAR, n. sp.

Pls. V, figs. 58-69; VI, figs. 70-80

Type material. — 255 specimens (111 females and 144 males) from *Echinopora carduus* Klunzinger at a depth of 2 meters at low tide at Pointe Ambarionaomby, Nossi Komba, near Nossi Bé, August 27, 1960. Holotype, allotype, and 60 paratypes (26 females and 34 males) deposited in the Muséum National d'Histoire Naturelle at Paris, the same number of paratypes in the Institut de Recherche Scientifique de Madagascar at Tananarive, the United States National Museum at Washington, and the remaining paratypes in the author's collection.

Female. — Body (Figs. 58, 59) about 6 times longer than wide, in alcoholic specimens arched ventrally in the thoracic region and again in the abdominal area, with the caudal rami directed dorsally and somewhat anteriorly. Length (from tip of rostral area to posterior edge of curved abdomen, plus estimated correction of 50μ for curvature) 1.407 mm (1.266-1.456 mm), width 0.234 mm (0.224-0.246 mm), based on 10 specimens. Segmentation indicated only faintly. Region dorsal to the fifth legs bearing 3 moderately long, slender, posteriorly-directed processes (Figs. 60, 61), the middle one slightly shorter than the other two. Oviducal openings dorsal. Genital segment and abdomen (Fig. 60) slenderer than the thorax. Abdomen probably 3-segmented (though the joint between the genital segment and the first abdominal segment is obscure). Caudal ramus (Fig. 62) about twice as long as wide, 51 × 25μ, bearing 3 terminal setae and one seta on the outer margin. With the arching of the abdomen the rami come to be directed dorsally, as in Figure 61.

Egg sac (Fig. 63) with 2 eggs (in each of 6 ovigerous females), each egg about 100μ in diameter.

Rostral area broadly rounded (Fig. 59). First antenna (Fig. 64) about 73μ long (not including the setae), and 5-segmented, with a suggestion of a sixth terminal segment. With an aesthete on the penultimate segment and 2 aesthetes on the terminal segment. Second antenna (Fig. 65) 4-segmented, the second segment long and slender, the terminal claw distinctly falciform and the adjacent seta short. Mandible (Fig. 66) a slender unarmed blade with a recurved tip. Paragnath absent. First maxilla (Fig. 67) with the 2 setae unequal in size. Second maxilla (Fig. 68) with a broad terminal lamelliform process with hyaline edges (possibly representing a modified seta). Maxilliped

(Fig. 69) with 2 segments, the first with a small rounded distal lobe, the second with a large inner lobe having 2 hyaline setae near its base, a smaller outer lobe, and 2 slender digitiform processes. Labrum with its contour in lateral view (Fig. 70) slightly different from that of *X. gerlachi,* but otherwise generally similar.

Legs 1-4 similar, with the exopods 3-segmented and the endopods 2-segmented. All 4 legs with a slender outer basipod seta and with a group of short hairs on the inner basipod area. Intercoxal plates similar in all 4 pairs of legs. Spine and setal formula as follows:

	leg 1		leg 2		leg 3		leg 4	
	exp	end	exp	end	exp	end	exp	end
1st segment	I:0	0:0	I:0	0:0	I:0	0:0	I:0	0:0
2nd segment	I:0	2	I:0	2	I:0	1	I:0	1
3rd segment	I(+3)		I(+3)		I(+2)		I(+2)	

Leg 1 (Fig. 71) with first and second exopod segments bearing a short slender spine very slightly hooked at its tip; the last segment bearing terminally a large, nearly straight claw and 3 slender, inner subterminal setae. Endopod with the first segment with its outer margin expanded and bearing a few hairs distally; second segment slenderer with 2 delicate terminal setae and a row of hairs along its outer margin. Leg 2 (Fig. 72) similar to leg 1 in general form and armature. Legs 3 and 4 similar to leg 2, but with only one terminal seta on the endopod and only 2 subterminal, inner, small setae on the exopod.

Leg 5 (Fig. 73) elongated and slender, 156µ long, arising laterally ventral to the lateral, posteriorly-directed process (see Fig. 61) and bearing 2 small terminal setae unequal in length. A slender seta arising from the body wall dorsal to the base of the leg. Leg 6 absent.

Body colorless in living specimens, intestine red, eye bright red.

Male. — Body (Figs. 74, 75) with the segmentation weakly indicated. Of about the same length as the female but slenderer, 1.423 mm (1.355-1.456 mm) × 0.205 mm (0.196-0.213 mm), based on 10 specimens. Abdomen (Fig. 76) weakly segmented. Genital segment bearing the two ventrolateral ridges of the sixth legs. Caudal ramus (Fig. 77) very small, 20 × 15µ, and directed inwardly, bearing setae as in the female, though relatively longer.

Rostral area as in the female. Antennae, mouth parts (except maxilliped) and labrum similar to those in the female. Paragnath absent. Maxilliped (Fig. 78) generally like that of *X. longipes,* but with the claw about 58μ long and having a bifurcated tip.

Legs 1-4 as in the female, with the same spine and setal formula. Leg 5 (Fig. 79) consisting of a minute process 9 × 8μ bearing 2 setae and an adjacent dorsal seta. Leg 6 (Fig. 80) represented by 2 small setae arising from a ventrolateral ridge.

Color as in the female.

(The specific name *dispar*, dissimilar, is given in reference to the difference in size of the exopod claws on legs 1-4.)

Remarks. — Both sexes may be distinguished from known species by the nature of the three claws on the exopods of legs 1-4 and by the elongated, clearly 2-segmented endopods of these legs.

XARIFIA REDUCTA, n. sp.

Pls. VI, figs. 81-84; VII; VIII, figs. 102-104

Type material. — 654 specimens (370 females and 284 males) from *Seriatopora octoptera* Ehrenberg at a depth of 2 meters at low tide at Pointe Ambarionaomby, Nossi Komba, near Nossi Bé, August 18, 1960. Holotype, allotype, and 136 paratypes (78 females and 58 males) deposited in the Muséum National d'Histoire Naturelle at Paris, the same number of paratypes in the Institut de Recherche Scientifique de Madagascar at Tananarive, the United States National Museum at Washington, and the remaining paratypes in the author's collection.

Other specimens. — 47 specimens (35 females and 12 males) from *Seriatopora caliendrum* Ehrenberg in 1 meter at Ambariotelo, NE of Nossi Komba, September 9, 1960.

Female. — Body (Figs. 81, 82) about 7 times longer than wide. Length (including the caudal rami) 1.056 mm (0.997-1.120 mm), width 0.147 mm (0.134-0.159 mm), based on 10 specimens. External segmentation scarcely discernible. Region dorsal to the fifth legs lacking processes, but with 2 minute internal sclerotized bars (Fig. 83). Oviducal openings dorsolateral, more widely separated than in the previous species. Abdomen showing very slight evidence of segmentation. Caudal ramus (Fig. 84) about twice as long as wide, 23 × 11μ, bearing 3 terminal setae (the innermost shorter than the other two) and an outer marginal seta.

Egg sac (Figs. 83, 85) with 1, 2 or 3 eggs, each egg about 127 × 81μ. Most commonly with 1 egg in each sac, but 3 females seen with 2 eggs in each sac, and 2 females with 3.

Rostral area (Fig. 86) broad, with 3 lobes ventrally. First antenna (Fig. 87) about 44µ long (not including the setae) and apparently 4-segmented (though the second segment may actually represent 2 segments). Two long aesthetes on the terminal segment and one on the penultimate. Second antenna (Fig. 88) 4-segmented, the terminal claw rather weak, and the seta adjacent to the claw greatly elongated. Mandible (Fig. 89) a slender blade. Paragnath absent. First maxilla (Fig. 90) with the 2 setae very unequal in size. Second maxilla (Fig. 91) with the terminal hyaline process rather attenuated. Maxilliped (Fig. 92) with 2 segments, the first unarmed, the second with an inner lobe with 2 setae near its base and with a distal lobe bearing 2 rather hyaline setae. Labrum in lateral view with its contour indented (Fig. 93).

Legs 1-4 similar, with the exopods 3-segmented and the endopods of a single segment. All 4 legs with a slender outer basipod seta and without ornamentation on the inner basipod area. Intercoxal plates V-shaped and similar in all 4 pairs of legs. Spine and setal formula as follows:

	leg 1		leg 2		leg 3		leg 4	
	exp	end	exp	end	exp	end	exp	end
1st segment	I:0	2	I:0	2	I:0	1	I:0	1
2nd segment	0:0		0:0		0:0		0:0	
3rd segment	I(+3)		I(+2)		I(+1)		I(+1)	

Leg 1 (Fig. 94) with the first exopod segment bearing a short claw-like spine, the second bearing only a small knob, and the third bearing a large terminal claw and 3 small subterminal inner setae. Tips of the claws with a hyaline fringe. Endopod composed of a single segment somewhat tapered distally, bearing 2 long terminal setae, a minute hair on its outer middle area, and a few hairs along the outer margin. Leg 2 like leg 1, but usually with only 2 small subterminal inner setae on the last exopod segment. Leg 3 (Fig. 95) similar to the preceding legs but with only one small subterminal inner seta on the last exopod segment and with only one long terminal seta on the endopod. Leg 4 like leg 3.

Leg 5 (Fig. 96) about 34µ long, tapering toward the tip, bearing 2 unequal terminal setae. A slender seta arising dorsal to the base of the leg. Leg 6 absent.

Body colorless in living specimens, intestine yellow-red, eye red, egg sacs brown to gray.

Male. — Body (Figs. 97, 98) with the external segmentation very obscure. Length of body 0.914 mm (0.843-0.974 mm), width 0.101 mm (0.090-0.112 mm), based on 10 specimens. Genital segment and abdomen (Fig. 99) with very slight swellings probably indicating segmentation. Caudal ramus (Fig. 100) minute, 12 × 7.5μ, bearing setae as in the female.

Rostral area as in the female. First antenna similar to that of the female but with 4 long aesthetes, the longest seta on the antepenultimate segment in the female here forming an aesthete. Second antenna, mandible, first maxilla, second maxilla, and labrum as in the female. Paragnath absent. Maxilliped (Fig. 101) elongated and slender, the claw 39μ long and in addition to the usual 2 setae bearing a row of slender dentiform spinules along its concave surface.

Legs 1-4 as in the female, with the same spine and setal formula. Leg 5 (Fig. 102) consisting of 2 unequal setae arising from a slight ridge and an adjacent dorsal seta. Leg 6 (Fig. 103) composed of 2 setae.

Spermatophore (Fig. 104) 224 × 45μ, not including the neck.

Color as in the female.

(The specific name *reducta*, reduced, refers to the rudimentary condition of the middle exopod claw on legs 1-4.)

Remarks. — The 2-clawed condition of the exopods of legs 1-4, with only a remnant of the middle claw, serves to separate both sexes of this species from other known species. The male may further be distinguished by the slender, elongated maxilliped.

XARIFIA SERRATA, n. sp.

Pls. VIII, figs. 105-119; IX; X, figs. 134-136

Type material. — 45 specimens (22 females and 23 males) from *Pocillopora damicornis* Dana in 15 cm of water at low tide on sand flat with *Cymodocea ciliata* west of Pointe Mahatsinjo, Nossi Bé, September 22, 1960. Holotype, allotype, and 11 paratypes (5 females and 6 males) deposited in the Muséum National d'Histoire Naturelle at Paris, the same number in the United States National Museum at Washington, and the remaining paratypes in the author's collection.

Other specimens. — 9 specimens (7 females and 2 males) from *Seriatopora subseriata* Ehrenberg in 1 meter on sand flat with *Cymodocea ciliata* at Pointe Mahatsinjo, Nossi Bé, September 5, 1960. 5 specimens (3 females and 2 males) from the same mass of *Pocillopora verrucosa* (Ellis and Solander) from which the type specimens of *X. comata* (to be described below) were obtained, in 2 meters, west of Pointe Mahatsinjo, Nossi Bé, November 2, 1960. 1 male from *Pocillopora* cf. *P. verrucosa* (Ellis and Solander) (along with *X. comata*) in 2 meters, west of Pointe Mahatsinjo, Nossi Bé, October 18, 1960. 32 specimens (16 females and 16 males) from *Pocillopora damicornis* Dana in 30 cm on sand at Ambariobe, NE of Nossi Komba, September 23, 1960.

Female. — Body (Figs. 105, 106) about 6 times longer than wide. Length (including the caudal rami) 1.302 mm (1.176-1.400 mm), width 0.205 mm (0.190-0.220 mm), based on 10 specimens. External segmentation not visible except in abdomen. Region dorsal to the fifth legs lacking separate processes (Fig. 107), but may be produced as a transverse ridge (Fig. 110). Oviducal openings dorsolateral and rather widely separated (Fig. 108). Abdomen sometimes showing slight evidence of segmentation (Fig. 109) and much slenderer than the thoracic region. Caudal ramus (Fig. 111) 55μ long and somewhat tapered distally, with the usual outer marginal seta, 3 terminal setae (the innermost of these shorter than the other two), and a very small seta at the bases of the terminal setae.

Egg sac (Fig. 112) with as many as 7 eggs, each 117μ in diameter, arranged in an arcuate row.

Rostral area broad and rounded. First antenna (Fig. 113) about 50μ long (not including the setae) and 3-segmented, though the middle segment shows evidence of a subdivision into 3 segments. Three long aesthetes as in *X. reducta*. Second antenna (Fig. 114) 4-segmented, the terminal claw recurved and the seta adjacent to the claw greatly elongated. Mandible (Fig. 115) with the slender blade bearing minute lateral spinules. Paragnath absent. First maxilla (Fig. 116) with 2 unequal setae. Second maxilla (Fig. 117) bearing a rather hyaline slender setiform process; near the base of this process a minute, pointed projection and a very small knob. Maxilliped (Fig. 118) 2-segmented, the first segment unarmed, the second bearing an inner lobe with 2 small hyaline setae near its base and a distal lobe with terminally a seta and an elongated blunt process and with subterminally a minute, inner, digitiform process. Labrum with its contour in lateral view (Fig. 119) not deeply indented and with its posterolateral angles bearing a small spiniform projection (Fig. 120).

Legs 1-4 similar, with the exopods 3-segmented and the endopods of a single segment. All 4 pairs of legs with an outer basipod seta and with a tuft of long hairs on the inner basipod area. Intercoxal plates broadly U-shaped and alike in all 4 pairs of legs. Spine and setal formula as follows:

	leg 1		leg 2		leg 3		leg 4	
	exp	end	exp	end	exp	end	exp	end
1st segment	I:0	3	I:0	2	I:0	1	I:0	1
2nd segment	0:0		0:0		0:0		0:0	
3rd segment	I(+3)		I(+2)		I(+2)		I(+2)	

Leg 1 (Fig. 121) with the first exopod segment bearing a small outer claw-like spine, the second without a spine, and the third with a large claw-like spine (Fig. 122) and 3 small inner subterminal setae. Endopod composed of a single segment constricted so as to suggest subdivision into 2 segments. In addition to the hairs on the outer and inner margins, a single hair on the posterior surface of the segment and 3 long setae on the distal end. Leg 2 (Fig. 123) similar to leg 1, but with only 2 small subterminal inner setae on the last exopod segment and with only 2 long terminal setae on the endopod. Leg 3 (Fig. 124) like leg 2 but with only one long terminal seta on the endopod. Leg 4 like leg 3.

Leg 5 (Fig. 125) elongated and slender, 122μ in length (measured along the shorter edge), tapered distally, and bearing 2 small unequal terminal setae. Seta arising dorsal to the base of the leg very small. Leg 6 absent.

Body colorless in living specimens, intestine often greenish, eye red, egg sacs green.

Male. — Body (Figs. 126, 127) about 8 times longer than wide, with external segmentation suggested only in the abdominal region. Length 1.345 mm (1.243-1.546 mm), width 0.169 mm (0.157-0.210 mm), based on 10 specimens. Genital segment and abdomen as in Figure 128. Caudal ramus (Fig. 129) much shorter than in the female, about 39μ in length, and with the 3 terminal setae nearly equal.

Rostral area as in the female. First antenna similar to that of the female, but with 4 long aesthetes as in *X. reducta*. Second antenna, mandible, first maxilla, and second maxilla as in the female. Paragnath absent. Labrum as in the female but with 6 minute setules on its posterior border (Fig. 130). Maxilliped (Fig. 131) rather robust, the claw moderately short, about 60μ in length, and bearing in addition to the usual 2 setae a row of irregular blunt serrations along its concave margin (Figs. 132, 133).

Legs 1-4 as in the female, with the same spine and setal formula. Leg 5 (Fig. 134) composed of 2 unequal setae arising from a small ridge and an adjacent slender dorsal seta. Leg 6 (Fig. 135) consisting of 2 subequal setae.

Spermatophore (Fig. 136) 314 × 101μ, not including the neck.

Body colorless in living specimens, eye red.

(The specific name *serrata*, toothed like a saw, alludes to the serrations on the claw of the male maxilliped.)

Remarks. — The absence of the middle exopod claw of legs 1-4 in both sexes distinguishes this species from other described species. The serrations on the claw of the male maxilliped serve to distinguish this from other known males. In several ways (terminal claw and seta of the second antenna, armature of legs 1-4, absence of processes dorsal to the fifth legs, armature of the claw of the male maxilliped) this species seems to be closely related to *X. reducta.*

The five specimens from *Pocillopora verrucosa* (Ellis and Solander), collected November 2, 1960, differ slightly from those in the type material. The body is slightly larger, the length of the female being 1.471 mm, width 0.221 mm; the male, 1.557 mm and 0.185 mm. The row of hairs on the inner edge of the second exopod segment of legs 1 and 2 appears to be absent. Otherwise the specimens are clearly referable to *X. serrata.*

XARIFIA TENUIS, n. sp.

Pls. X, figs. 137-151; XI, figs. 152-158

Type material. — 15 specimens (10 females and 5 males) from *Acropora cytherea* Dana in 1 meter at low tide west of Pointe de Tafondro, Nossi Bé, October 19, 1960. Holotype, allotype, and 5 paratypes (4 females and 1 male) deposited in the United States National Museum at Washington, and the remaining paratypes in the author's collection.

Female. — Body (Figs. 137, 138) slender, about 11 times longer than wide. Length (including the caudal rami) 1.382 mm (1.288-1.478 mm), width 0.126 mm (0.123-0.134 mm), based on 5 specimens. External segmentation not apparent. Region dorsal to the fifth legs with 3 slender processes (Fig. 139), the median one about twice as long (130μ) as the other two (60μ). Abdomen (Figs. 139, 140) only slightly narrower than the thorax and with only slight traces of segmentation. Caudal ramus (Fig. 141) greatly elongated and slender, 115 × 13μ, with 4 short terminal setae, the outermost corresponding to the outer marginal seta in other species. With surficial hairs as in the figure.

Egg sac (Fig. 142), observed in 2 females, with 2 elongated eggs, each 160 × 78μ.

Rostral area rounded. First antenna (Fig. 143) about 42μ in length (not including the setae) and probably 3-segmented, although the joints are difficult to observe. Apparently only 2 long aesthetes instead of 3 as in other species. Second antenna (Fig. 144) with probably 4 segments, though the last two are incompletely separated; the terminal claw weak and the adjacent seta elongated. Mandible, first maxilla, and second maxilla as in Figure 145. Paragnath absent. Maxilliped (Fig. 146) 2-segmented, the first segment with a pronounced inner distal lobe, the second with 2 setiform processes terminally and 2 small setae near its base. Labrum with its contour in lateral view as in Figure 147.

Legs 1-4 similar, with the exopods 3-segmented and the endopods of a single segment. All 4 pairs of legs with an outer basipod seta and lacking ornamentation on the inner basipod area. Intercoxal plates V-shaped. Behind each pair of legs a median rounded projection (Figs. 148, 149), about 22μ high. Spine and setal formula as follows:

	leg 1		leg 2		leg 3		leg 4	
	exp	end	exp	end	exp	end	exp	end
1st segment	0:0	0	0:0	0	0:0	0	0:0	0
2nd segment	0:0		0:0		0:0		0:0	
3rd segment	1		1		1		1	

Leg 1 (Fig. 150) with the exopod segments unarmed except for a very minute process on the distal outer angle of the first segment and a large terminal claw on the last segment. Endopod oval, 16 × 12μ, with only a slight suggestion of subdivision along the inner edge. A row of hairs along the outer margin. Four of these hairs slightly stronger than the others. Legs 2, 3, and 4 similar to leg 1.

Leg 5 (Fig. 151) 33μ long, tapering distally, with 2 unequal terminal setae. Small seta arising dorsal to the base of the leg. Leg 6 absent.

Body colorless in living specimens, eye red.

Male. — Body (Figs. 152, 153) very slender, about 12 times longer than wide, with segmentation not visible except for traces in the abdominal region. Length 1.271 mm (1.220-1.299 mm), width 0.104 mm (0.100-0.112 mm), based on 4 specimens. Genital segment and abdomen as in Figure 154. Caudal ramus (Fig. 155) 28 × 11µ, much shorter than in the female, and with 4 terminal setae.

Rostral area as in the female. First antenna like that of the female, but with 3 long aesthetes, the large seta arising in the female near the middle of the antenna here transformed to an aesthete. Second antenna, mandible, first maxilla, and second maxilla as in the female. Paragnath absent. Maxilliped (Fig. 156) 4-segmented, the claw short, 22µ long, and bearing in addition to the usual 2 setae a prominent bidentate process near the middle of its concave edge. Tip of the claw tridentate and having a short row of minute subterminal spinules.

Legs 1-4 as in the female, with the same spine and setal formula. Leg 5 (Fig. 157) composed apparently of 2 setae about 13µ long. Leg 6 (Fig. 158) also consisting of 2 minute setae.

Body colorless in living specimens, eye red.

(The specific name *tenuis*, slender, refers to the very slender body in this species.)

Remarks. — The extremely minute spiniform process on the first exopod segment and the absence of armature on the second exopod segment of legs 1-4 in both sexes separate this species from other known forms. The nature of the processes on the region dorsal to the fifth legs in the female and the conformation of the claw of the maxilliped in the male also serve as useful distinguishing features.

Xarifia infrequens, n. sp.

Pls. XI, figs. 159-167; XII, figs. 168-171

Type material. — 8 specimens (5 females and 3 males) from *Acropora corymbosa* (Lamarck) in 1 meter at low tide at Pointe Lokobe, Nossi Bé, November 1, 1960 (type specimens of *X. gerlachi* collected from this coral also). Holotype, allotype, and 2 paratype females deposited in the United States National Museum at Washington, and the remaining paratypes in the author's collection.

Other specimens. — One female and 1 male from *Acropora cytherea* Dana in 3 meters at Pointe Lokobe, Nossi Bé, October 16, 1960 (3 specimens of *X. gerlachi* also in this coral).

Female. — Body (Figs. 159, 160) slender, about 10 times longer than wide. Length (including caudal rami) 1.540 mm, width 0.140 mm, based on 2 specimens. External segmentation not apparent. Region dorsal to the fifth legs with 3 slender processes (Fig. 161), the median one about twice as long (109μ) as the other two (49μ), but all shorter than in *X. tenuis*. Abdomen (Figs. 161, 162) with almost no evidence of segmentation. Caudal ramus (Fig. 163) elongated and moderately slender, 88 × 21μ, with the usual 3 terminal setae and the outer marginal seta inserted at some distance from the tip of the ramus. Small hairs scattered over the surface of the ramus.

Egg sac unknown.

Rostral area rounded. First antenna resembling that of *X. tenuis*, but with 3 aesthetes, one terminal, one subterminal, and the third still more proximal. Second antenna (Fig. 164) with probably 4 segments, but the last 2 indistinctly separated; the terminal claw a little stronger than in *X. tenuis*, the seta adjacent to the claw elongated. Mouthparts resembling those of *X. tenuis*. Paragnath absent. Labrum with its contour in lateral view as in Figure 165.

Legs 1-4 similar, with the exopods 3-segmented (the joint between the 3rd segment and the claw being obscure on the anterior surface of the leg). Endopods of a single segment. All 4 pairs of legs with an outer basipod seta and a small group of minute hairs on the inner basipod area. Intercoxal plates broadly U-shaped. Behind each pair of legs a median rounded projection (Fig. 166) as in *X. tenuis*. Spine and setal formula as follows:

	leg 1		leg 2		leg 3		leg 4	
	exp	end	exp	end	exp	end	exp	end
1st segment	I:0	0	I:0	0	I:0	0	I:0	0
2nd segment	0:0		0:0		0:0		0:0	
3rd segment	I		I		I		I	

Leg 1 (Fig. 166) with a small spine on the first exopod segment, a minute projection on the outer distal angle of the second, and with a stout terminal claw on the third segment. Endopod oval with a very slight suggestion of subdivision on the inner margin. A row of hairs on the outer margin and 4 pairs of hairs on the surface of the ramus as indicated in the figure. Legs 2, 3, and 4 like the first leg, but lacking the minute outer projection on the second exopod segments.

Leg 5 (Fig. 167) 47μ long, tapering distally, with 2 very unequal distal setae. Small seta arising dorsal to the base of the leg. Leg 6 absent.

Body colorless in living specimens, eye red.

Male. — Body (Figs. 168, 169) very slender, about 11 times longer than wide, with external segmentation not visible. Length 1.266 mm, width 0.117 mm, based on 2 specimens. Abdomen similar to that of *X. tenuis.* Caudal ramus (Fig. 170) 48 × 19μ with the setae as in the female.

Rostral area as in the female. First antenna like that of *X. tenuis,* but with 4 long aesthetes, the longest seta in the middle region of the female antenna here forming an aesthete. Second antenna, mandible, first maxilla, and second maxilla as in the female. Paragnath absent. Maxilliped (Fig. 171) 4-segmented, the claw 33μ long and somewhat angular, bearing the usual 2 setae and a row of 4 or 5 minute teeth near the distal end of the concave surface. Tip of claw trifid.

Legs 1-4 as in the female, with the same spine and setal formula. Legs 5 and 6 as in *X. tenuis.*

Color as in the female.

(The specific name *infrequens,* infrequent, rare, alludes to the small numbers of specimens found in the type collection, even though over 600 *X. gerlachi* were found in the same mass of coral.)

Remarks. — This species seems to be close to *X. tenuis,* but clearly differs from it in several significant details, among which in the female are the armature of legs 1-4, the relative length of the processes dorsal to the fifth legs, and the size and shape of the caudal rami and the arrangement of their setae, and in the male the armature of legs 1-4, the caudal ramus, and even more significantly the nature of the claw on the maxilliped.

Xarifia comata, n. sp.

Pls. XII, figs. 172-179; XIII

Type material. — 43 specimens (14 females and 29 males) from *Pocillopora verrucosa* (Ellis and Solander) in 2 meters at low tide west of Pointe Mahatsinjo, Nossi Bé, November 2, 1960. Holotype, allotype, and 13 paratypes (4 females and 9 males) deposited in the Muséum National d'Histoire Naturelle at Paris, the same number of paratypes in the United States National Museum at Washington, and the remaining paratypes in the author's collection. (A few specimens of *X. serrata* occurred in this collection also.)

Other specimens. — One female and 1 male from *Pocillopora verrucosa* (Ellis and Solander) in 2 meters at Pointe Mahatsinjo, Nossi Bé, October 26, 1960. 3 females and 3 males from *Pocillopora* cf. *P. verrucosa* (Ellis and Solander) in 2 meters west of Pointe Mahatsinjo, October 18, 1960 (1 specimen of *X. serrata* occurred in this collection also).

Female. — Body (Figs. 172, 173) about 6 times longer than wide. Length (including the caudal rami) 1.158 mm (1.086-1.221 mm), width 0.195 mm (0.190-0.220 mm), based on 10 specimens. External segmentation not visible. Region dorsal to the fifth legs with 3 long, slender, nearly equal processes (Fig. 174) each about 180µ in length. Oviducal openings dorsal and closely approximated. Abdomen without external segmentation and much slenderer than the thoracic region (Fig. 175). Caudal ramus (Fig. 176) 53 × 16µ, with the marginal seta rather far from the tip and about 30µ in length. Distal end of the ramus with the usual 3 setae elongated and with 2 additional short slender setae. A few long hairs on the surface of the ramus.

Egg sac (Fig. 177) with usually 2 eggs, each about 104µ in diameter. Two females with only one egg on one side but 2 eggs on the other, one female with 3 eggs on both sides, and one female (not a type specimen) with 4 eggs on both sides (Fig. 178).

Rostral area rounded. First antenna about 45µ long, similar to that of *X. serrata*, with 3 similarly placed aesthetes, but with the setae rather long. Second antenna (Fig. 179) 4-segmented, slender, the terminal claw about 13µ long and the adjacent seta of about the same length. Mandible and first maxilla similar to those of *X. longipes*. Paragnath absent. Second maxilla (Fig. 180) with the setiform process terminating in a conspicuous hyaline expansion bearing distally a minute spiniform scale. Maxilliped (Fig. 181) 2-segmented, with the usual lobes and 2 pairs of setae, one pair terminal, the other near the inner base of the second segment. Labrum with its contour in lateral view as in Figure 182.

Legs 1-4 similar, with the exopods 3-segmented and the endopods probably 2-segmented, though the separation is not clear. All legs with an outer basipod seta and a row of long hairs on the inner basipod area. Intercoxal plates V-shaped. Region immediately posterior to each pair of legs covered with long hairs. Spine and setal formula as follows:

	leg 1		leg 2		leg 3		leg 4	
	exp	end	exp	end	exp	end	exp	end
1st segment	I:0	0	I:0	0	I:0	0	I:0	0
2nd segment	0:0	2	0:0	2	0:0	2	0:0	1
3rd segment	I(+1)		I(+1)		I(+1)		I(+1)	

Leg 1 (Fig. 183) with the first exopod segment bearing a minute outer spine and an inner row of long hairs, the second unarmed, the third with a large terminal spine and a minute subapical inner spinule. Endopod distinctly constricted into 2 regions, probably representing 2 segments. Outer margin with a row of long hairs. Two long terminal hyaline setae, difficult to distinguish from the adjacent hairs. Inner margin of the basal half of the endopod with a row of long hairs. Legs 2 and 3 similar to leg 1. Leg 4 also like leg 1, but with only one terminal seta on the endopod.

Leg 5 (Fig. 184) elongated and slender, 135μ in length, bearing 2 terminal nearly equal setae from 35-40μ in length. Seta adjacent to the base of the leg about 40μ long. Leg 6 absent.

Body colorless in living specimens, sometimes with a dark brown intestine, eye red.

Male. — Body (Figs. 185, 186) about 8 times longer than wide, without external segmentation. Length 1.128 mm (1.086-1.176 mm), width 0.159 mm (0.146-0.168 mm), based on 10 specimens. Genital segment and abdomen as in Figure 187. Caudal ramus (Fig. 188) much shorter and relatively stouter than in the female, about 31μ in length, the setae relatively much longer. Rostral area as in the female. First antenna as in the female but with 4 aesthetes, the long seta on the distal part of the middle segment (possibly to be interpreted as the 3rd segment) of the female antenna here forming an aesthete. Second antenna, mandible, first maxilla, second maxilla, and labrum as in the female. Paragnath absent. Maxilliped (Fig. 189) with the second segment outwardly expanded. Claw short, about 33μ in length, with a small process on the concave edge near the base of the inner seta, and terminating in 2 unequal teeth.

Legs 1-4 as in the female, with the same spine and setal formula, and with similar long hairs behind each pair of legs. Leg 5 (Fig. 190) composed of 2 long setae arising from a common base and an adjacent dorsal seta. Leg 6 (Fig. 191) consisting of 2 subequal setae; with 2 long hairs nearby.

Color as in the female.

(The specific name *comata*, long-haired, refers to the long hairs seen on legs 1-4.)

Remarks. — This species may be distinguished from the 3 other species which have 3 long, nearly equal processes on the region above the fifth legs (*X. maldivensis*, *X. dispar*, and *X. longipes*) by the absence here of a spine or seta on the distal outer region of the second exopod segment of legs 1-4. The arrangement of the long hairs on these legs is also distinctive. The male may be further separated from other known species by the nature of the claw of the maxilliped.

Revised Diagnosis of the Genus *Xarifia*

The discovery of the eight new species of *Xarifia* has so broadened our understanding of the limits of specific variation in this genus that a revision of the original generic diagnosis seems desirable.

Female. — Body elongated, rather slender, the thorax a little broader than the abdomen. Segmentation rather weakly defined. Region dorsal to the fifth legs usually bearing posteriorly-directed processes. Rostral area broadly rounded. Caudal ramus usually with 3 terminal setae and 1 lateral seta.

First antenna with several segments (3-5, but often difficult to determine) bearing numerous naked setae and a few long aesthetes. Second antenna consisting of 4 segments (the last 2 sometimes incompletely separated) and a terminal claw or process. Labrum bell-shaped in ventral view. Mandible a small lobe bearing a slender blade. Paragnath absent. First maxilla a small lobe bearing 2 setae. Second maxilla somewhat variable, usually a basal lobe bearing a hyaline distal process. Maxilliped 2-segmented, the second segment lying parallel to the long axis of the body and bearing 2 inner basal setae and 2 distal processes.

Legs 1-4 similar in segmentation, the exopod with 3 usually clearly defined segments, the last always with a terminal spine. Endopod either 2-segmented or consisting of a single segment showing evidence of a bipartite origin. Leg 5 with 2 setae arising from a separate segment or from the body directly, and an adjacent dorsal seta. Leg 6 absent.

Two egg sacs attached dorsally, with the small number of eggs either in a cluster or in a row.

Male. — Body more slender than in the female and of nearly the same width throughout, lacking the processes on the region dorsal to the fifth legs. Maxilliped large, 4-segmented, terminating in a prominent claw. Head appendages, legs 1-4, rostral area, and the caudal ramus generally as in the female. Leg 5 with usually 3 setae as in the female, but without a distinct segment. Leg 6 consisting of 2 small setae.

Living on or in various madreporarian corals.

Type species. — *Xarifia maldivensis* Humes, 1960.

Keys to the described species of the genus *Xarifia*

Females

1. With 2 or 3 posteriorly-directed processes on the region dorsal to the fifth legs 2
   Without such processes 9
2. With 2 processes, the median one being absent .... *fimbriata*
   With 3 processes 3
3. Median process a rounded knob, shorter than the 2 lateral processes; caudal ramus a small rounded lobe not clearly delimited from the abdomen .... *gerlachi*
   Median process elongate; caudal ramus of more usual form 4
4. Median process approximately as long as the 2 lateral processes 5
   Median process distinctly longer than the 2 lateral processes 8
5. Leg 5 very small, only about 1/10 the length of the processes .... *maldivensis*
   Leg 5 at least ½ as long as the processes 6
6. Second exopod segment of legs 1-4 unarmed .... *comata*
   Second exopod segment of legs 1-4 with a distal outer spine 7
7. Caudal ramus about 2× longer than wide; second exopod segment of legs 1-4 with a slender spine .... *dispar*
   Caudal ramus about 3½× longer than wide; second exopod segment of legs 1-4 with a stout spine .... *longipes*
8. Caudal ramus about 9× longer than wide; first exopod segment of legs 1-4 without a distal outer spine but only a minute spiniform projection at that point .... *tenuis*
   Caudal ramus about 4× longer than wide; first exopod segment of legs 1-4 with a distinct outer spine .... *infrequens*
9. Second exopod segment of legs 1-4 with a small distal outer knob but no spine; caudal ramus about 23μ long .... *reducta*
   Second exopod segment of legs unarmed; caudal ramus 55μ long *serrata*

Males

1. Caudal ramus a small rounded lobe not clearly delimited from the abdomen .... *gerlachi*
   Caudal ramus of more usual form and more or less delimited from the abdomen 2
2. A distinct spine or seta on both first and second exopod segments of legs 1-4 3
   Second exopod segment of legs 1-4 without a distinct spine or seta (although a minute knob may be present, as in *reducta*), or both first and second segments lacking a spine or seta 5
3. The two spines or setae on the first and second exopod segments of legs 1-4 subequal; inner margin of claw of maxilliped smooth 4
   A stout spine on the first exopod segment, a slender seta on the second exopod segment of legs 1-4; inner margin of the claw of maxilliped with a row of spinules .... *maldivensis*

4. Spines on first and second exopod segments of legs 1-4 stout; caudal ramus 3½× longer than wide . . . . *longipes*
   Spines on first and second exopod segments of legs 1-4 slender; caudal ramus 2× longer than wide . . . . *dispar*
5. A spine on first exopod segments only of legs 1-4, second segment at most with only a knob or minute spiniform protuberance; caudal ramus not more than 5× longer than wide 6
   A distinct spine lacking on both first and second exopod segments of legs 1-4; caudal ramus 11× longer than wide . . . . *tenuis*
6. Second exopod segment of legs 1-4 with a small digitiform knob; inner margin of claw of maxilliped with a row of about 12 long spinules . . . . *reducta*
   Second exopod segment of legs 1-4 without a digitiform knob; inner margin of claw of maxilliped with at most only a few minute spinules near the tip, smooth, or serrated 7
7. Inner margin of claw of maxilliped with irregular rounded serrations . . . . *serrata*
   Inner margin of claw of maxilliped not with such serrations 8
8. Claw of maxilliped about 51μ long . . . . *fimbriata*
   Claw of maxilliped about 33μ long 9
9. Claw of maxilliped slender, slightly angular; a few minute teeth on the inner margin near the tip . . . . *infrequens*
   Claw of maxilliped fairly stout, its outer margin with a slight concavity; inner margin without teeth but with a small protuberance near the base of the seta . . . . *comata*

INCIDENCE AND HOSTS OF *XARIFIA*

The number of *Xarifia* recovered from a coral mass appears to vary with the method used. When a fresh coral is rinsed gently in alcoholized sea water (about 5% alcohol), a few *Xarifia* may be washed out, but more of these copepods will be recovered from the sediment obtained after crushing the coral with a hammer under the water. For example, a mass of *Echinopora carduus* yielded 7 *Xarifia dispar* after being rinsed whole, but 35 of these copepods after the coral had been crushed. In several cases, however, large numbers of *Xarifia* were found in the sediment after leaving the uncrushed coral in a pail of alcoholized sea water for 7-10 hours. Using this method 624 *X. gerlachi* and 8 *X. infrequens* were recovered from a mass of *Acropora corymbosa.* The copepods apparently are stimulated by the dilute alcohol to leave the polyps, when they fall to the bottom of the container. Since they are incapable of swimming, they are unable to regain their positions in the polyps even though the effect of the alcohol gradually diminishes over the hours. This last method is very useful, since the very small amount of debris and mucus in the sediment greatly facilitates collection of the copepods.

No specimens of *Xarifia* were found in the following species of corals from the region of Nossi Bé:

Acropora hemprichi (Ehrenberg) from Pointe Lokobe, Nossi Bé
Acropora scherzeriana Brueggemann from Pointe Lokobe, Nossi Bé
Pavona cactus (Forskål) from Pointe de Tafondro, Nossi Bé
Porites cf. *P. andrewsi* Vaughan from Pointe Lokobe, Pointe de Tafondro, and NW of Madirokely, Nossi Bé; Ambariotelo; Tany Kely.
Psammocora sp. from Pointe de Tafondro, Nossi Bé, and Pointe Ambarionaomby, Nossi Komba.

The following list gives the known hosts and distribution of the ten species of the genus *Xarifia:*

species	*coral host*	*locality*
X. maldivensis Humes	*Pocillopora* sp.	Maldive Islands
X. fimbriata Humes	*Pocillopora* sp.	Maldive Islands
X. gerlachi, n. sp.	*Acropora corymbosa*	All from the Nossi Bé region in northwestern Madagascar (see preceding text for precise localities)
	Acropora cf. *A. teres*	
	Acropora cytherea	
X. longipes, n. sp.	*Pavona angulata*	
X. dispar, n. sp.	*Echinopora carduus*	
X. reducta, n. sp.	*Seriatopora octoptera*	
	Seriatopora caliendrum	
X. serrata, n. sp.	*Pocillopora damicornis*	
	Pocillopora verrucosa	
	Pocillopora cf. *P. verrucosa*	
	Seriatopora subseriata	
X. tenuis, n. sp.	*Acropora cytherea*	
X. infrequens, n. sp.	*Acropora corymbosa*	
	Acropora cytherea	
X. comata, n. sp.	*Pocillopora verrucosa*	
	Pocillopora cf. *P. verrucosa*	

In addition to these described species, Humes (1960) has listed an undescribed *Xarifia* from *Stylophora* sp. in the Red Sea. Reexamination of this single female shows that it possesses three very long slender processes above the equally long fifth legs (not four processess as previously mentioned). It seems impossible to assign it to any of the species already described. The fragment of the second undetermined species listed by Humes remains also unassignable at the present.

REFERENCE CITED

HUMES, ARTHUR G.

1960. New copepods from madreporarian corals. Kieler Meeresforschungen **16**: 229-235.

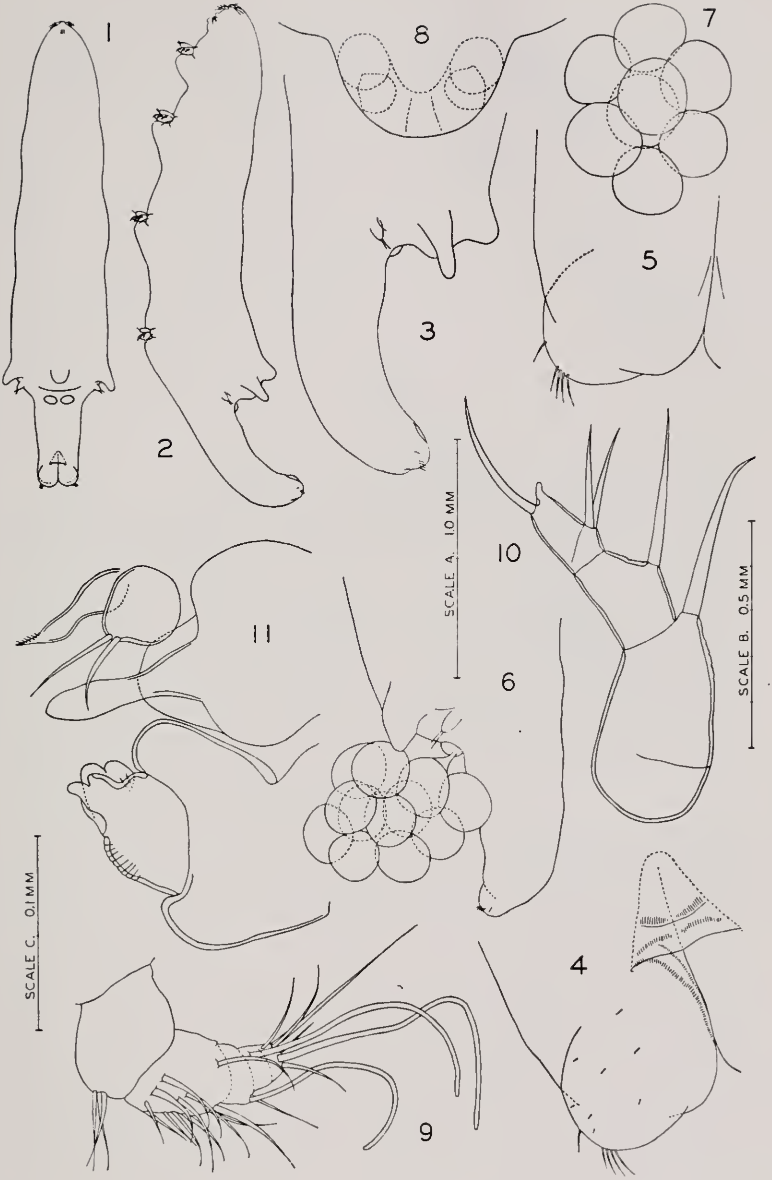
EXPLANATION OF FIGURES

All figures were drawn with the aid of a camera lucida. The letter after each figure refers to the scale at which it was drawn.

PLATE I

Xarifia gerlachi, n. sp., female

FIG. 1. Dorsal (A).
FIG. 2. Lateral (A).
FIG. 3. Posterior part of body, lateral (B).
FIG. 4. Caudal ramus, dorsal (C).
FIG. 5. Caudal ramus, ventral (C).
FIG. 6. Egg sac attached to posterior part of body, lateral (B).
FIG. 7. Egg sac (D).
FIG. 8. Rostral area, dorsal (E).
FIG. 9. First antenna, dorsal (F).
FIG. 10. Second antenna (F).
FIG. 11. Mouthparts, lateral (F).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SCALE A. 1.0 MM
SCALE B. 0.5 MM
SCALE C. 0.1 MM

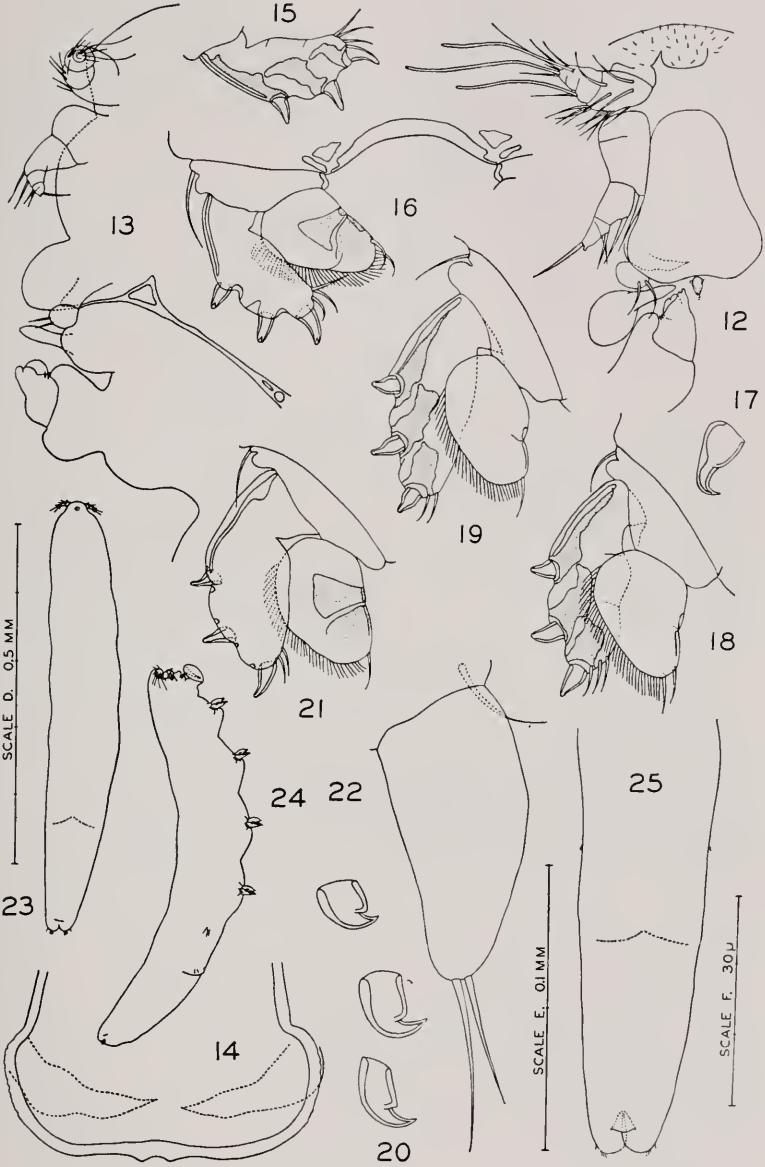
PLATE II

Xarifia gerlachi, n. sp., female, continued

FIG. 12. Oral area, ventral (E).
FIG. 13. Oral area, with esophagus shown, lateral (E).
FIG. 14. Posterior edge of labrum (F).
FIG. 15. Exopod of leg 1, anterior, stippled areas indicating sclerotization (E).
FIG. 16. Leg 1, posterior (E).
FIG. 17. Terminal spine on exopod of leg 1 (F).
FIG. 18. Leg 2, anterior (E).
FIG. 19. Leg 3, anterior (E).
FIG. 20. Three spines on exopod of leg 3 (F).
FIG. 21. Leg 4, posterior (E).
FIG. 22. Leg 5, ventral (G).

Same, male

FIG. 23. Dorsal (B).
FIG. 24. Lateral (B).
FIG. 25. Posterior part of body, dorsal (H).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SCALE D. 0.5 MM
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SCALE E. 0.1 MM
SCALE F. 30μ
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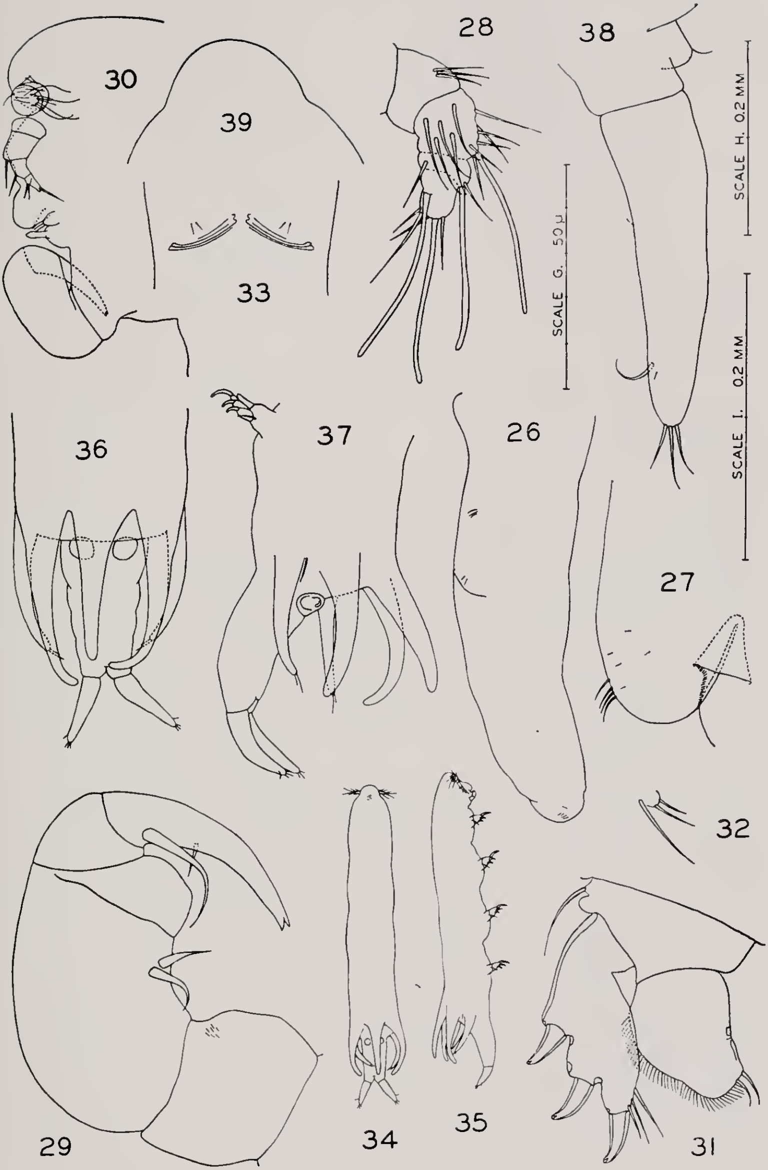
Plate III

Xarifia gerlachi, n. sp., male, continued

Fig. 26. Posterior part of body, lateral (H).
Fig. 27. Caudal ramus, dorsal (E).
Fig. 28. First antenna (F).
Fig. 29. Maxilliped (F).
Fig. 30. Oral area, lateral (E).
Fig. 31. Leg 1, posterior (F).
Fig. 32. Leg 5 (F).
Fig. 33. Leg 6 (I).

Xarifia longipes, n. sp., female

Fig. 34. Dorsal (A).
Fig. 35. Lateral (A).
Fig. 36. Posterior region of body, dorsal (D).
Fig. 37. Posterior region of body, lateral (D).
Fig. 38. Caudal ramus, dorsal (E).
Fig. 39. Outline of rostral area (I).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SCALE H. 0.2 MM
SCALE G. 50µ
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SCALE I. 0.2 MM
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PLATE IV

Xarifia longipes, n. sp., female, continued

FIG. 40. First antenna (G).
FIG. 41. Second antenna (G).
FIG. 42. Mandible (F).
FIG. 43. Maxilliped (F).
FIG. 44. Leg 1, anterior (E).
FIG. 45. Terminal spine on exopod of leg 1, lateral (E).
FIG. 46. Leg 2, posterior (E).
FIG. 47. Leg 3, anterior (E).
FIG. 48. Leg 4, anterior (E).
FIG. 49. Leg 5 (C).

Same, male

FIG. 50. Dorsal (A).
FIG. 51. Lateral (A).
FIG. 52. Posterior part of body, ventral (B).
FIG. 53. Caudal ramus, ventral (E).
FIG. 54. First antenna (G).

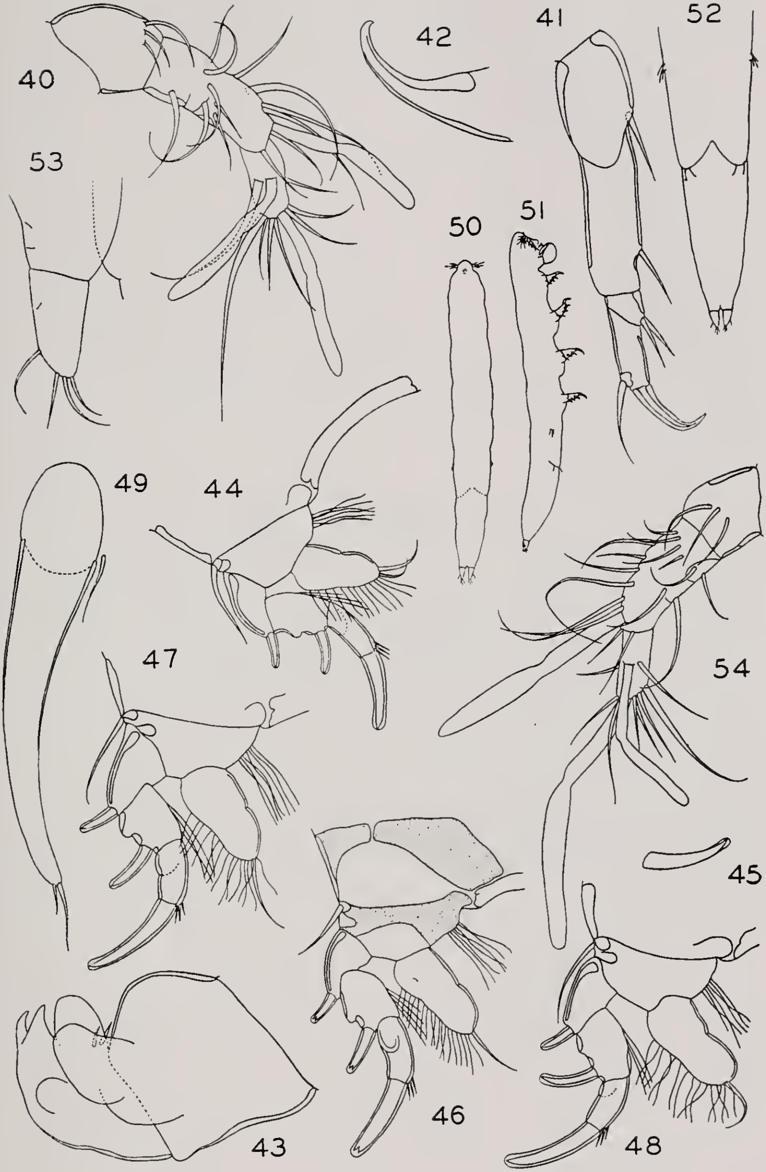
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PLATE V

Xarifia longipes, n sp., male, continued

FIG. 55. Maxilliped (G).
FIG. 56. Leg 5 (F).
FIG. 57. Leg 6 (F).

Xarifia dispar, n. sp., female

FIG. 58. Lateral (A).
FIG. 59. Dorsal (A).
FIG. 60. Posterior part of body, dorsal (D).
FIG. 61. Posterior part of body, lateral (D).
FIG. 62. Caudal ramus, dorsal (E).
FIG. 63. Egg sac attached to posterior part of body, lateral (D).
FIG. 64. First antenna (G).
FIG. 65. Second antenna (E).
FIG. 66. Mandible (F).
FIG. 67. First maxilla (F).
FIG. 68. Second maxilla (F).
FIG. 69. Maxilliped (F).

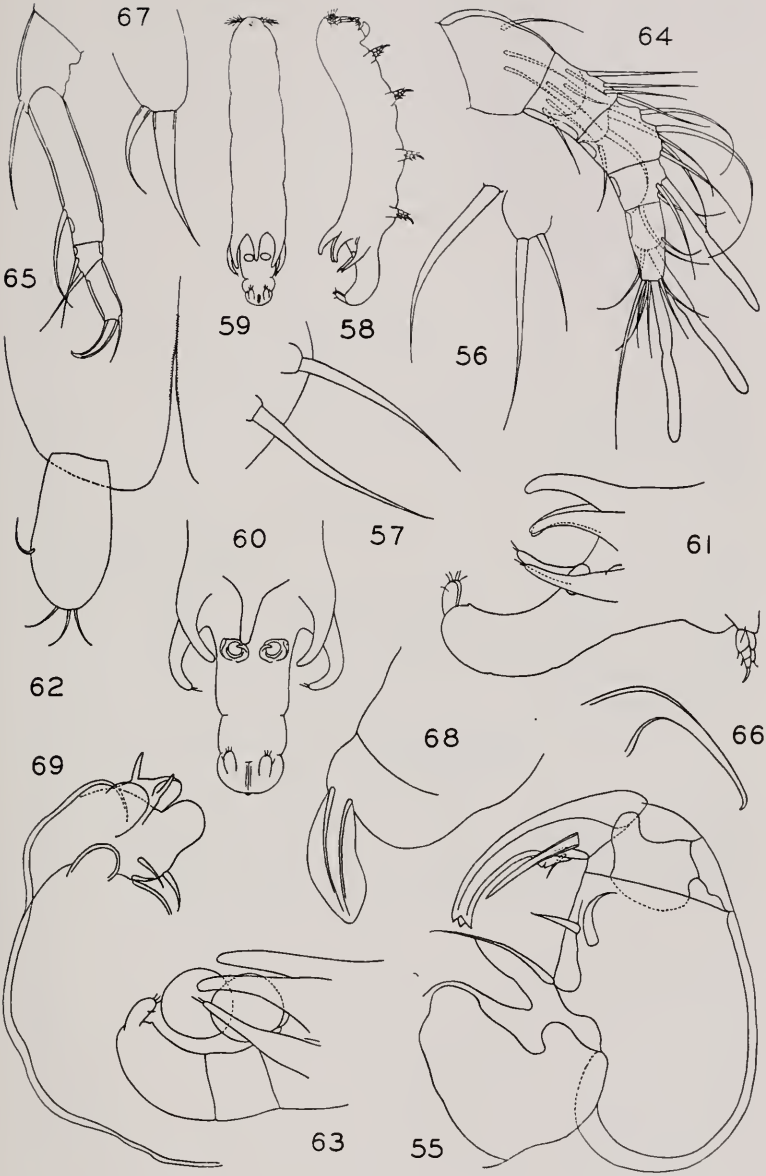
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PLATE VI

Xarifia dispar, n. sp., female, continued

FIG. 70. Outline of rostral area and labrum, lateral (E).
FIG. 71. Leg 1, posterior (E).
FIG. 72. Leg 2, anterior (E).
FIG. 73. Leg 5 (C).

Same, male

FIG. 74. Lateral (A).
FIG. 75. Dorsal (A).
FIG. 76. Posterior part of body, ventral (B).
FIG. 77. Caudal ramus, ventral (F).
FIG. 78. Maxilliped (G).
FIG. 79. Leg 5(F).
FIG. 80. Leg 6 (F).

Xarifia reducta, n. sp., female

FIG. 81. Lateral (B).
FIG. 82. Dorsal (B).
FIG. 83. Posterior part of body with egg sac, dorsal (H).
FIG. 84. Caudal ramus, dorsal (F).

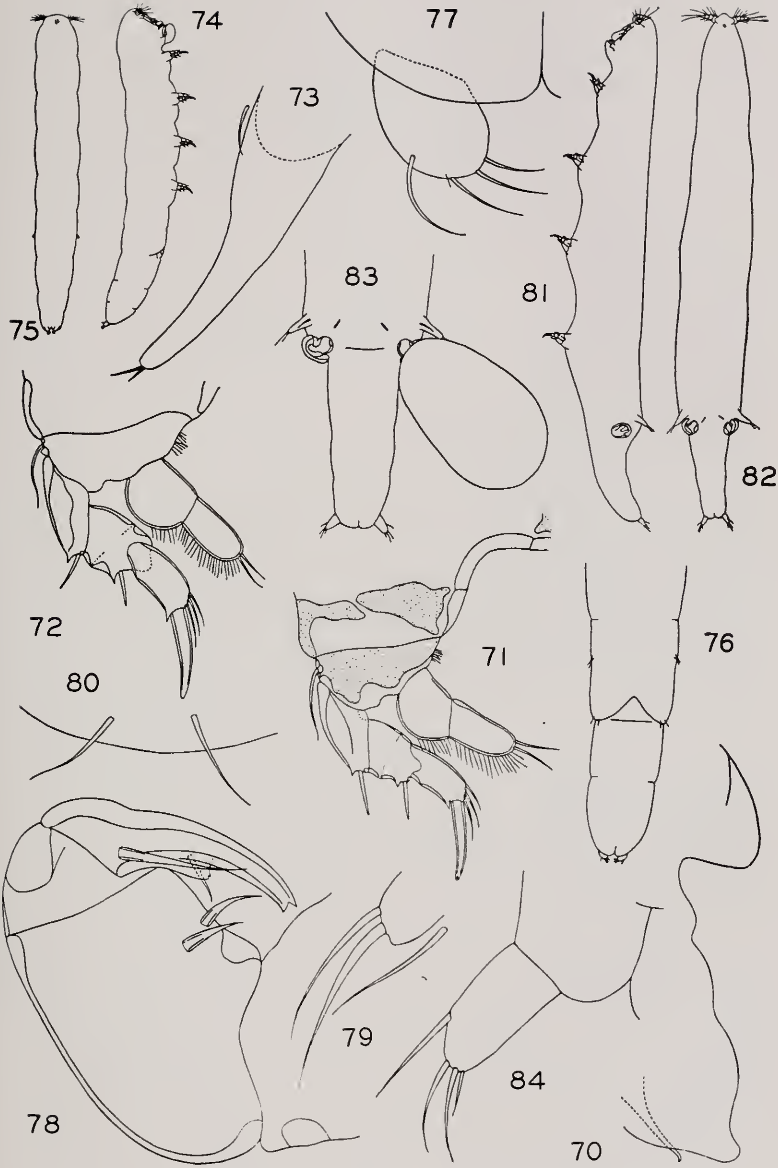
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PLATE VII

Xarifia reducta, n. sp., female, continued

FIG. 85. Egg sac (H).
FIG. 86. Rostral area, dorsal (E).
FIG. 87. First antenna (F).
FIG. 88. Second antenna (F).
FIG. 89. Mandible (F).
FIG. 90. First maxilla (F).
FIG. 91. Second maxilla (F).
FIG. 92. Maxilliped (F).
FIG. 93. Outline of rostral area and labrum, lateral (G).
FIG. 94. Leg 1, posterior (F).
FIG. 95. Leg 3, anterior (F).
FIG. 96. Leg 5 (F).

Same, male

FIG. 97. Lateral (B).
FIG. 98. Dorsal (B).
FIG. 99. Posterior part of body, lateral (H).
FIG. 100. Caudal ramus, dorsal (F).
FIG. 101. Maxilliped (F).

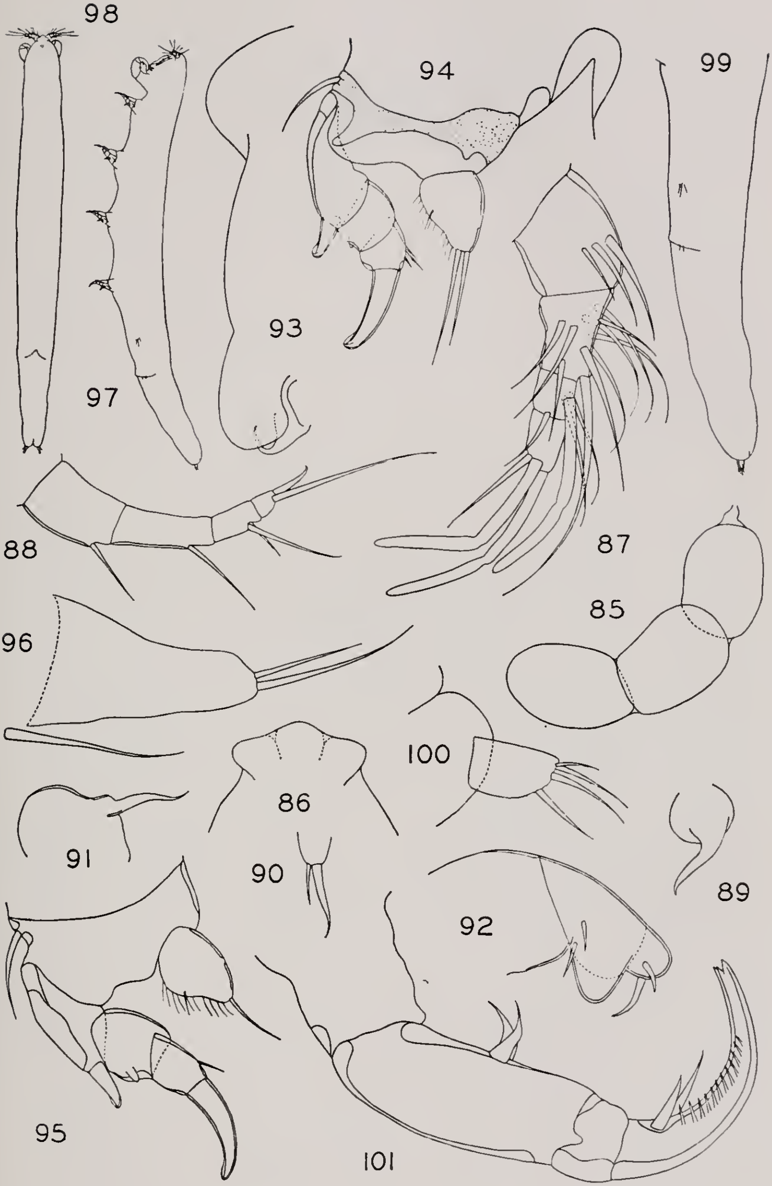
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Plate VIII

Xarifia reducta, n. sp., male, continued

Fig. 102. Leg 5 (F).
Fig. 103. Leg 6 (F).
Fig. 104. Spermatophore (H).

Xarifia serrata, n. sp., female

Fig. 105. Lateral (A).
Fig. 106. Dorsal (A).
Fig. 107. Area of fifth legs, dorsal (H).
Fig. 108. Posterior part of body, dorsal (H).
Fig. 109. Posterior part of body, lateral (D).
Fig. 110. Posterior part of body, lateral (D).
Fig. 111. Caudal ramus, ventral (G).
Fig. 112. Egg sac (B).
Fig. 113. First antenna (G).
Fig. 114. Second antenna (F).
Fig. 115. Mandible (F).
Fig. 116. First maxilla (F).
Fig. 117. Second maxilla (F).
Fig. 118. Maxilliped (G).
Fig. 119. Labrum and mouthparts, lateral (E).

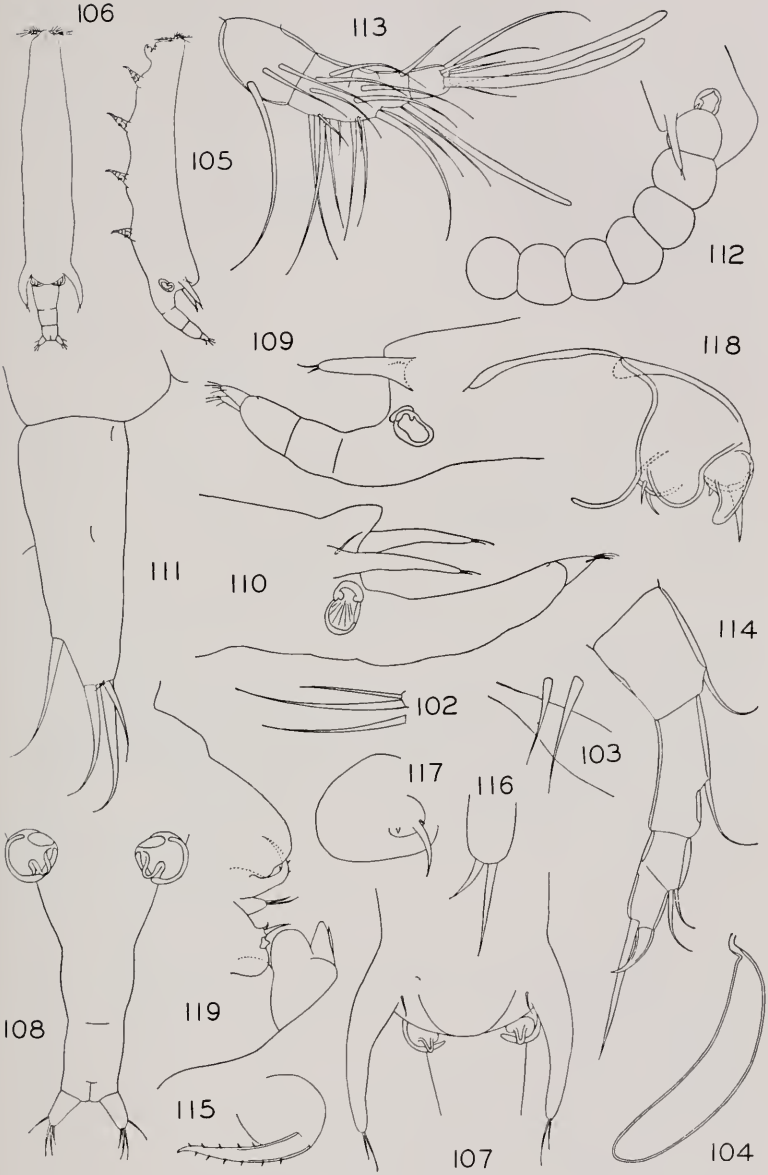
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PLATE IX

Xarifia serrata, n. sp., female, continued

FIG. 120. Labrum and mandibles, ventral (F).
FIG. 121. Leg 1, posterior (G).
FIG. 122. Terminal spine on exopod of leg 1 (F).
FIG. 123. Leg 2, anterior (G).
FIG. 124. Leg 3, anterior (G).
FIG. 125. Leg 5 (C).

Same, male

FIG. 126. Lateral (A).
FIG. 127. Dorsal (A).
FIG. 128. Posterior part of body, ventral (B).
FIG. 129. Caudal ramus, ventral (G).
FIG. 130. Posterior edge of labrum and mandibles, pressed, ventral (F).
FIG. 131. Maxilliped (E).
FIG. 132. Claw of maxilliped (F).
FIG. 133. Claw of maxilliped (F).

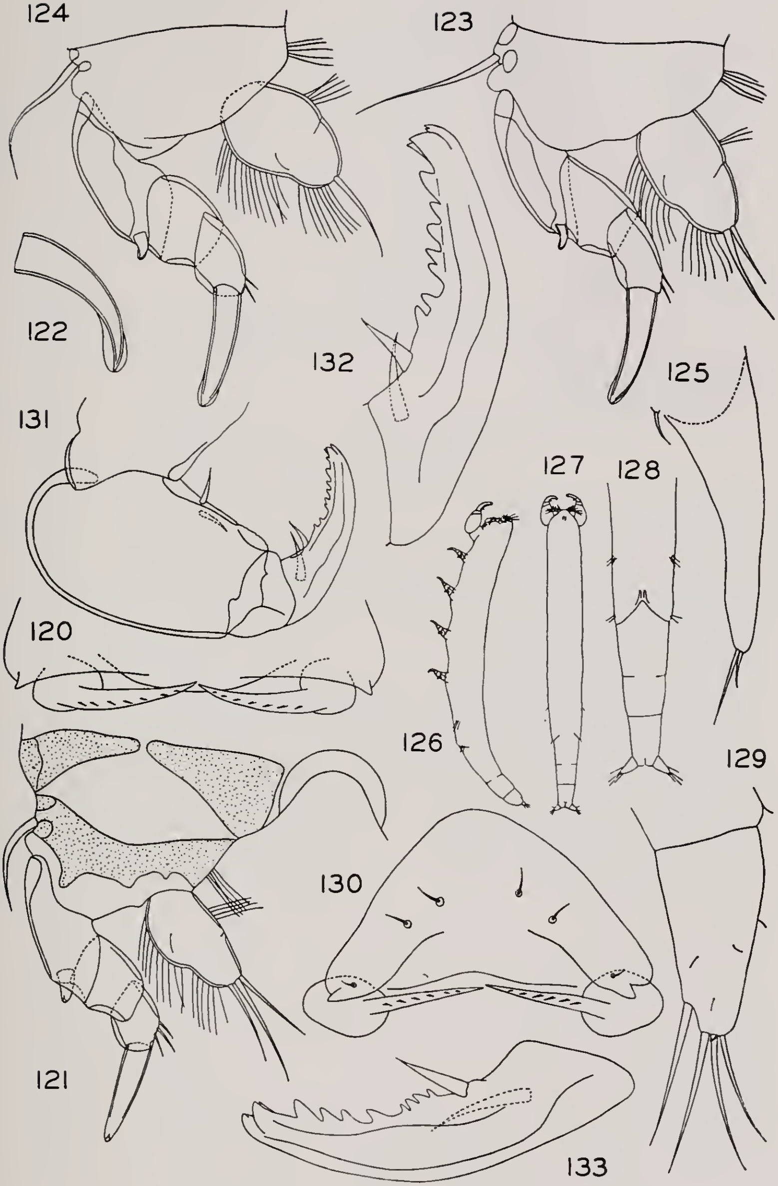
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PLATE X

Xarifia serrata, n. sp., male, continued

FIG. 134. Leg 5 (F).
FIG. 135. Leg 6 (F).
FIG. 136. Spermatophore (D).

Xarifia tenuis, n. sp., female

FIG. 137. Lateral (A).
FIG. 138. Dorsal (A).
FIG. 139. Posterior part of body, dorsal (H).
FIG. 140. Posterior part of body, lateral (H).
FIG. 141. Caudal ramus, ventral (E).
FIG. 142. Egg sac (H).
FIG. 143. First antenna (F).
FIG. 144. Second antenna (F).
FIG. 145. Mandible, first maxilla, and second maxilla (F).
FIG. 146. Maxilliped (F).
FIG. 147. Contour of labrum, lateral (F).
FIG. 148. Leg 1, lateral (E).
FIG. 149. Protuberance behind leg 1, posterior view (F).
FIG. 150. Leg 1, anterior (F).
FIG. 151. Leg 5 (F).

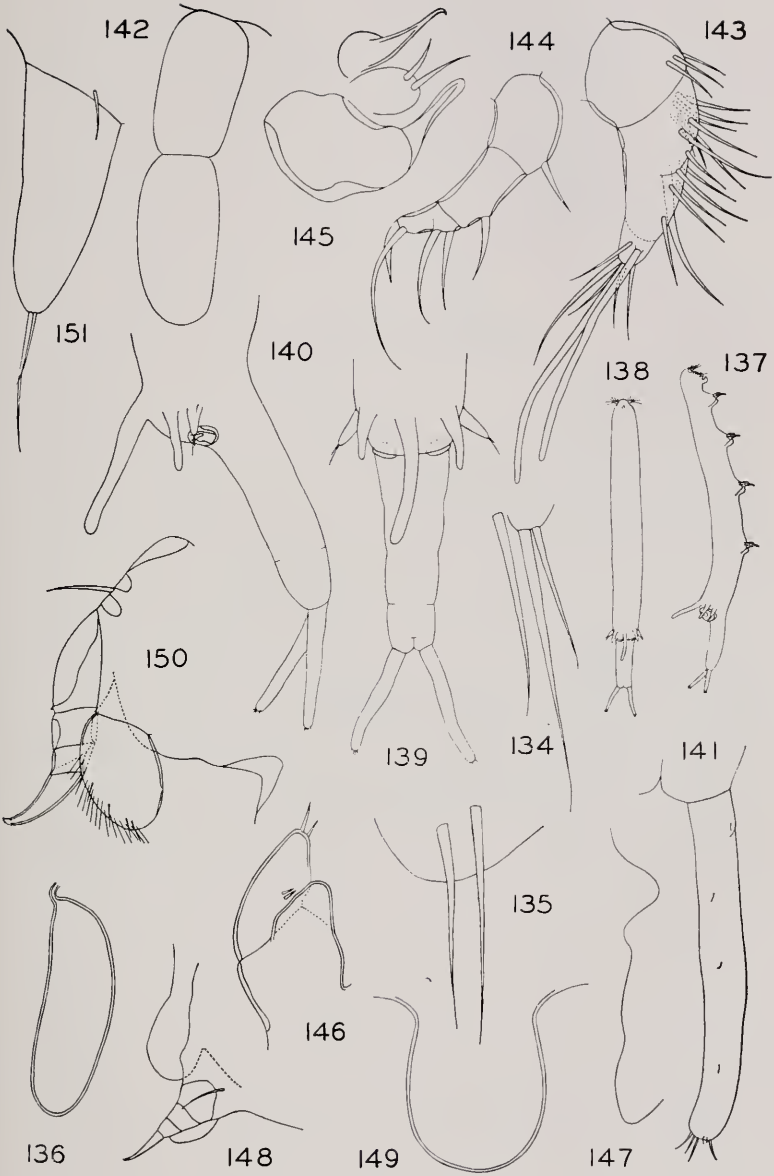
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PLATE XI

Xarifia tenuis, n. sp., male

FIG. 152. Lateral (A).
FIG. 153. Dorsal (A).
FIG. 154. Posterior part of body, dorsal (H).
FIG. 155. Caudal ramus, ventral (F).
FIG. 156. Maxilliped (F).
FIG. 157. Leg 5 (F).
FIG. 158. Leg 6 (F).

Xarifia infrequens, n. sp., female

FIG. 159. Lateral (A).
FIG. 160. Dorsal (A).
FIG. 161. Posterior part of body, dorsal (D).
FIG. 162. Posterior part of body, lateral (D).
FIG. 163. Caudal ramus (E).
FIG. 164. Second antenna (F).
FIG. 165. Contour of labrum, lateral (F).
FIG. 166. Leg 1 and posterior protuberance, posterior view (F).
FIG. 167. Leg 5 (E).


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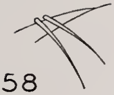
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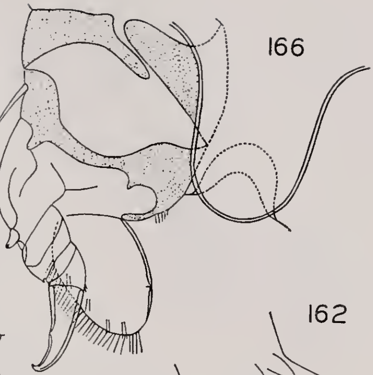
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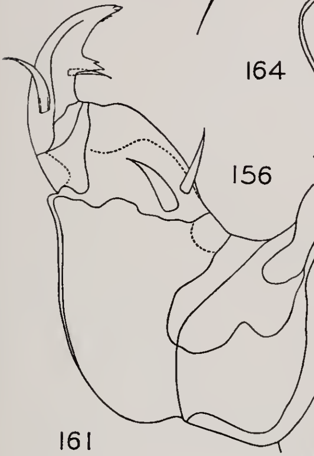
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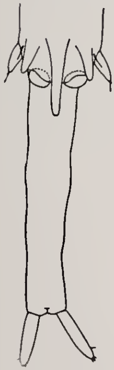
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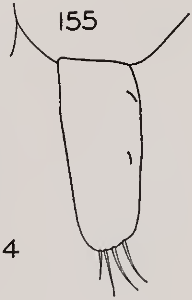
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PLATE XII

Xarifia infrequens, n. sp., male

FIG. 168. Lateral (A).
FIG. 169. Dorsal (A).
FIG. 170. Caudal ramus, dorsal (F).
FIG. 171. Maxilliped (F).

Xarifia comata, n. sp., female

FIG. 172. Lateral (A).
FIG. 173. Dorsal (A).
FIG. 174. Posterior part of body, dorsal (D).
FIG. 175. Posterior part of body, lateral (D).
FIG. 176. Caudal ramus (G).
FIG. 177. Posterior part of body with egg sac, lateral (D).
FIG. 178. Posterior part of body with egg sac, lateral (D). Not drawn from a type specimen.
FIG. 179. Second antenna (F).

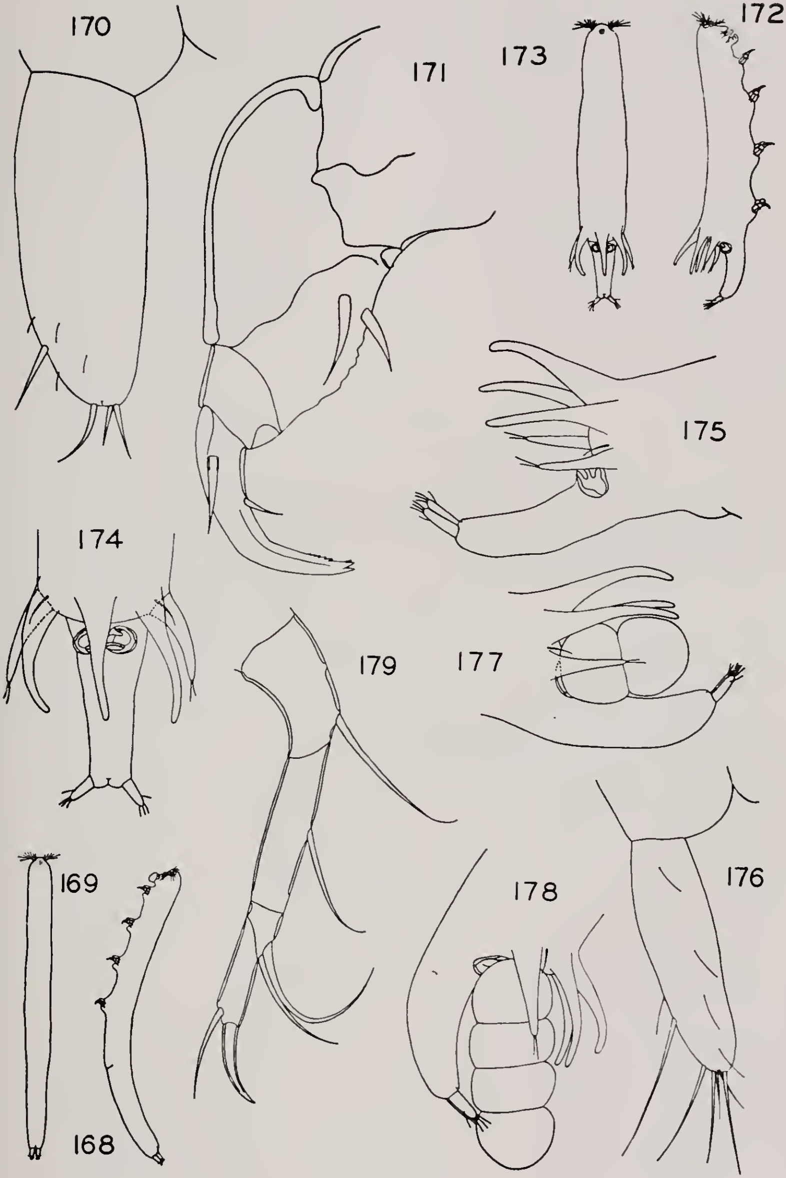
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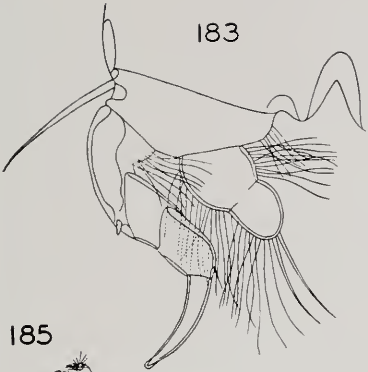
PLATE XIII

Xarifia comata, n. sp., female, continued

FIG. 180. Second maxilla (F).
FIG. 181. Maxilliped (F).
FIG. 182. Contour of rostral area and labrum, lateral (E).
FIG. 183. Leg 1, anterior (G).
FIG. 184. Leg 5 (E).

Same, male

FIG. 185. Lateral (A).
FIG. 186. Dorsal (A).
FIG. 187. Posterior part of body, ventral (D).
FIG. 188. Caudal ramus, dorsal (G).
FIG. 189. Maxilliped (G).
FIG. 190. Leg 5 (F).
FIG. 191. Leg 6 (F).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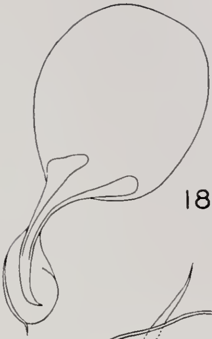
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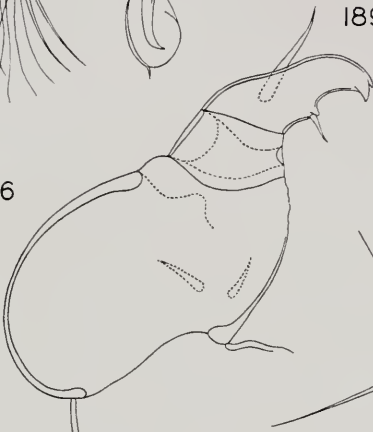
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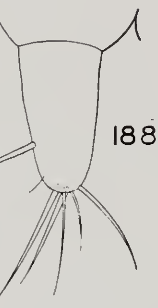
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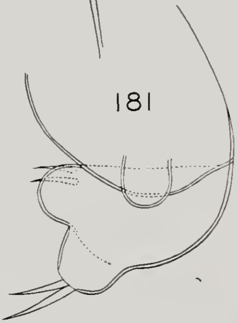
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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 128, No. 3

STUDIES ON AMPHISBAENIDS (AMPHISBAENIA, REPTILIA). 2. ON THE AMPHISBAENIDS OF THE ANTILLES

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and
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With Twelve Plates

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Occasional Papers of the Department of Mollusks (octavo) 1945 — Vol. 2, no. 28 is current.

Proceedings of the New England Zoological Club (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained on application to the Director of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1 and 2, 4 and 6 are out of print; volumes 3, 5, 7, 9, and 15 are sold by the Museum, and future volumes will be published under Museum auspices.

The Proceedings of the First International Symposium on Natural Mammalian Hibernation edited by C. P. Lyman and A. R. Dawe is available as volume 124 of the Museum of Comparative Zoology Bulletin. Published in 1960, it consists of 26 papers and a general discussion, totalling 550 pages. Price $3.00 paper back, $4.50 cloth bound.

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AT HARVARD COLLEGE

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STUDIES ON AMPHISBAENIDS (AMPHISBAENIA, REPTILIA). 2. ON THE AMPHISBAENIDS OF THE ANTILLES

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No. 3 — *Studies on amphisbaenids (Amphisbaenia, Reptilia)* *2. On the amphisbaenids of the Antilles.*

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INTRODUCTION

In his third Antillean checklist, Barbour (1937) recognized two genera and nine species of amphisbaenids on islands of the northern Caribbean. The names of these species and their approximate ranges (see Figs. 1-4 for all localities) were:

Amphisbaena cubana Peters	Cuba
Amphisbaena innocens Weinland	Southwestern Hispaniola
Amphisbaena caudalis Cochran	Grande Cayemite Id., Haiti
Amphisbaena manni Barbour	Hispaniola, except the Southwest
Amphisbaena bakeri Stejneger	Northwestern Puerto Rico
Amphisbaena caeca Cuvier	Puerto Rico
Amphisbaena fenestrata (Cope)	Virgin Islands
Cadea blanoides Stejneger	Western Cuba
Cadea palirostrata Dickerson	Isla de Pinos

In 1951 Vanzolini (1951a) resurrected Cope's genus *Diphalus*, originally based on the species *fenestratus*. Consideration of the status of this supposedly monotypic genus, endemic to a small group of islands midway in the Caribbean, led to our becoming interested in the relations of the other Antillean species of *Amphisbaena*. Besides forming one of a continuing series of studies and notes on the Amphisbaenia, this paper was designed to supply the West Indies discussion group with a summary of yet another group of Caribbean animals. We have included the two species of *Cadea* in keys, maps, and summaries, though the information presented rests in part on the work of Zug and Schwartz (1958), and on some unpublished data kindly made available by the latter.

While two studies of the variation within single species of amphisbaenids have recently been published (Vanzolini, 1951, 1955), there exists no comparison of the range of variation within and between several closely related forms of amphisbaenids. An attempt at such analysis might offer a test of the occasionally stated and often implicit hypothesis that the variation of one common species may serve as a guide to the variability of rarer forms.

No attempt has been made to deal with the broader relationships of the forms discussed, as it is intended to treat this matter jointly for the entire family at a future time. Zoogeographic discussion has also been kept to a minimum, derived primarily from internal evidence. Extended discussion of this topic is best handled for the fauna as a whole, and the zoogeographic scheme then synthesized from a maximum of independent analyses of individual groups.

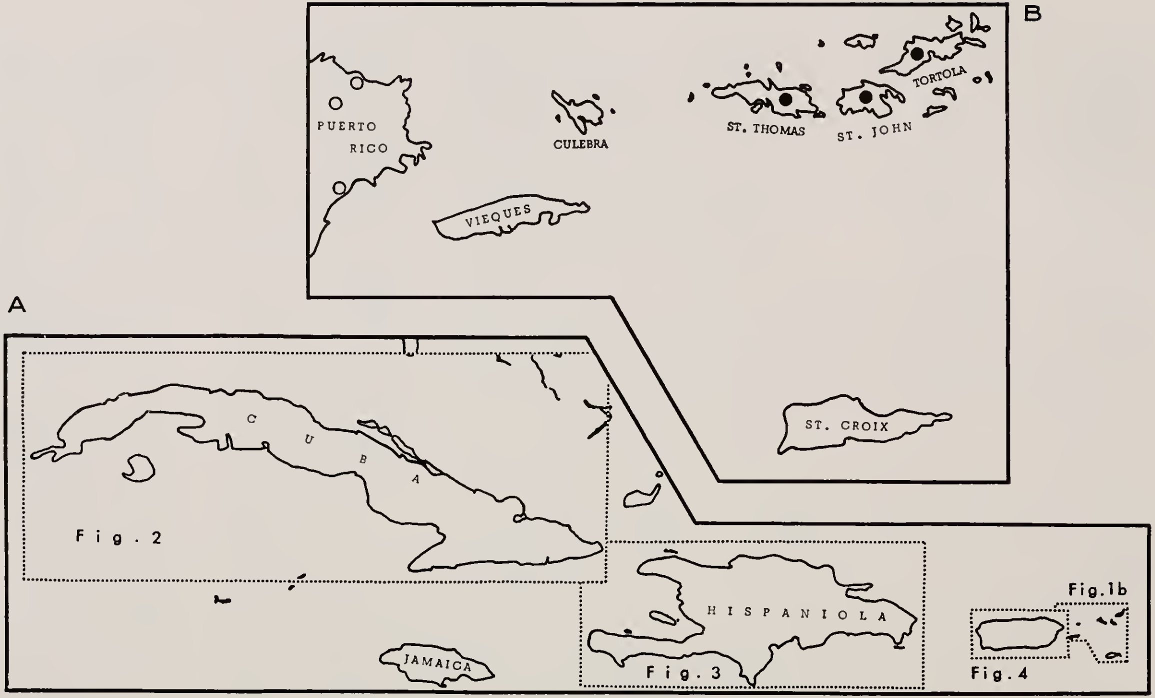

FIG. 1. *A.* Map of the northern Antilles showing the relations of the islands to each other and the relative size of the four detailed maps (Figs. 2 to 4 and 1B). *B.* Localities on eastern Puerto Rico and the Virgin Islands. Solid circles refer to islands (not specific localities) from which *A. fenestrata* has been recorded, open circles to localities of *A. caeca* on Puerto Rico. Dorothea lies on St. John.

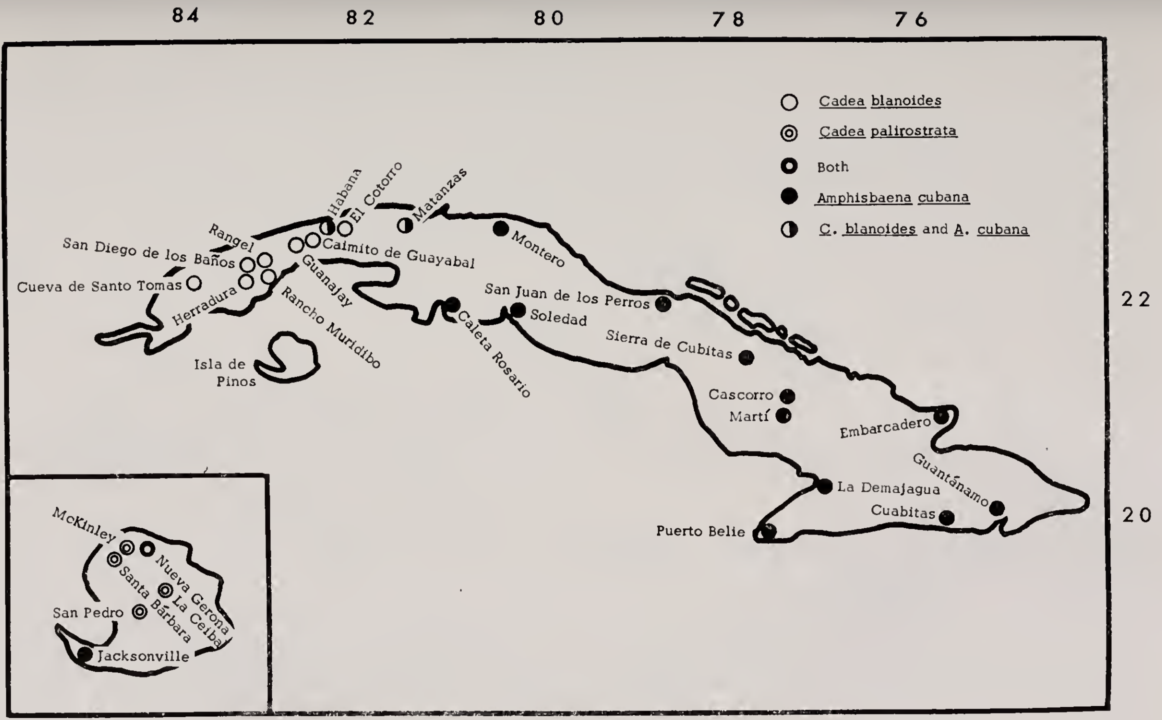

FIG. 2. Localities on Cuba and the Isla de Pinos (in inset). It was not possible to determine which of several Santa Cruz Mountains was the source of our specimen. The Sierra del Anáfe is just north of Guanajay. Marianao, Playa del Chivo and Vedado are near Habana. Puerto Boniato is near Cuabitas. Cienfuegos may refer to the province or the town (just south of Soledad). These specimens were most probably collected in the vicinity of Soledad.

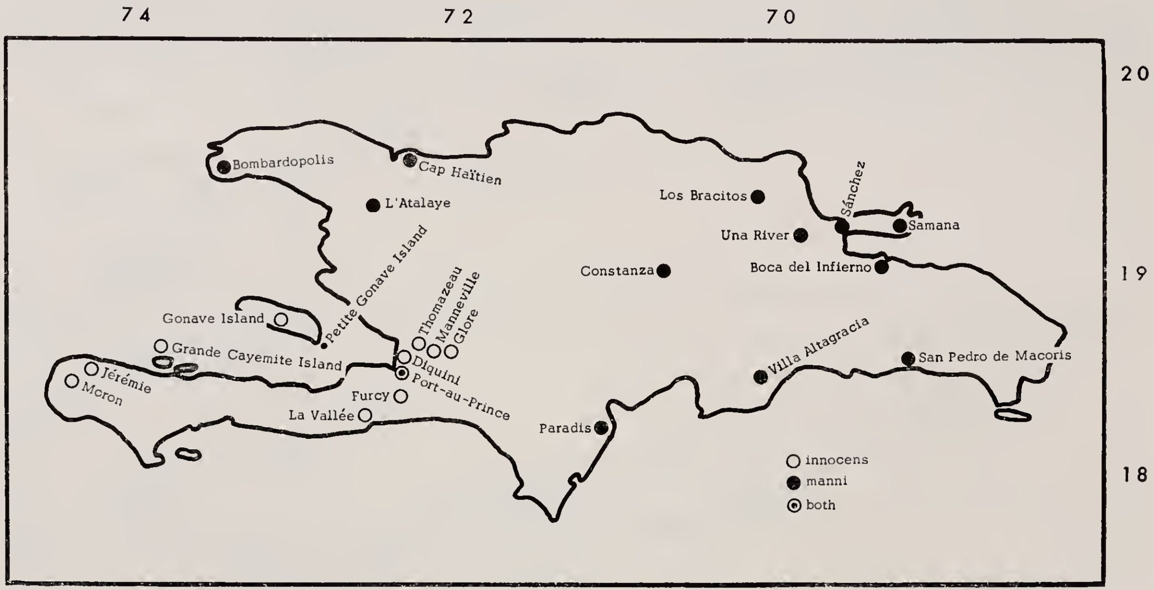

FIG. 3. Localities on Hispaniola. Of the *A. innocens* localities, Morne-à-Cabrits is in the vicinity of Glore, and La Vanneau possibly in the vicinity of La Vallée. The *A. manni* localities of San Francisque, Haiti and Isla de las Flechas, Dominican Republic, were not located. The Río San Juan enters the ocean on the north coast (approximately north of Los Bracitos on the map). Santo Domingo Province (Distrito Santo de Domingo) surrounds Ciudad Trujillo (formerly and now again Santo Domingo) which lies between our localities of Villa Altagracia and San Pedro de Macoris on the south coast.

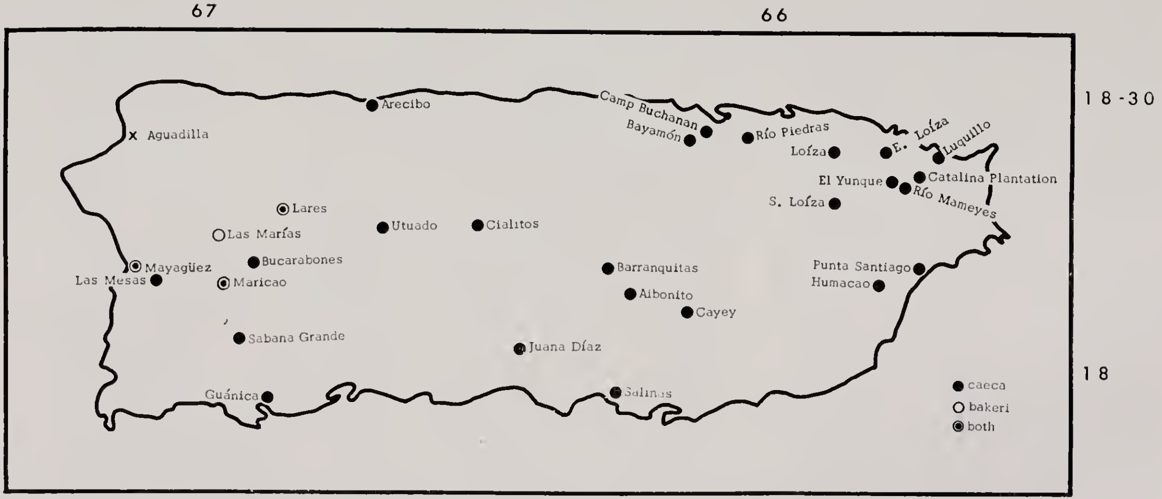

FIG. 4. Localities on Puerto Rico. The x indicates the dubious record from Aguadillo discussed under *A. caeca*.

MATERIAL

The specimens for this study came from the following collections, listed by abbreviations throughout:

AMNH	The American Museum of Natural History, New York, New York
ANSP	The Academy of Natural Sciences of Philadelphia, Pennsylvania
BM	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco, California
CM	Carnegie Museum, Pittsburgh, Pennsylvania
CNHM	Chicago Natural History Museum, Illinois
HM	Zoologisches Museum, Hamburg, Germany
KM	Universitetets Zoologiske Museum, København, Denmark
KUMNH	University of Kansas, Museum of Natural History, Lawrence, Kansas
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts
MHNP	Muséum National d'Histoire Naturelle, Paris, France
MJ	Miguel Jaume collection, Museo y Biblioteca Zoologica de la Habana, Cuba (data from Schwartz)
PM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden, Holland
SMF	Senckenbergische naturforschende Gessellschaft, Frankfurt a. M., Germany
SU	Stanford University Museum, California
UH	Universidad de la Habana (Museo Poey), Cuba, (data from Schwartz)
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
UPR	University of Puerto Rico, Mayagüez, Puerto Rico
USNM	United States National Museum, Washington, D.C.
VM	Naturhistorisches Museum zu Wien, Austria
ZMU	Zoologisches Museum der Universität, Berlin, Germany

Specimens cited, but not seen, have been preceded by an asterisk (*).

PROCEDURES

For the present study we have spot-checked sizeable samples for most characters previously mentioned by authors. We have then reviewed the entire series for those characters found useful for taxonomic discrimination during the initial analysis. Particular attention has been paid to sources of error in data, and differences from values presented in the literature have been reviewed though not necessarily mentioned here. Procedures and comments on the value of certain of these items are given below.

The raw data for most characters are given in the appendix. Their publication eliminates the need for extensive discussions of possible trends in geographic or individual variation. It is hoped that they will also facilitate the assignment and analysis of material that may be collected or become available in the future.

Sex: Amphisbaenid hemipenes are small, encased in layers of fat and connective tissue, and often poorly preserved (Vanzolini, 1955, p. 691). Accurate determination of sex can only be made by dissection of the gonads and associated structures (of which the left always lies slightly anterior to the right). This somewhat destructive technique had to be restricted to the two largest series (57 *A. manni* from Los Bracitos, and 59 *A. caeca* from 10 km. east of Loíza). These demonstrate no significant sexual dimorphism and data from both sexes are lumped here.

Absence of sexual dimorphism is not surprising as only precloacal pore number and size had been shown to vary in other species of amphisbaenids (Gans, 1960, 1961). Zug and Schwartz (1958) had suggested sexual dimorphism in relative tail length and caudal annuli number, but a check of the gonads of specimens examined by them showed sufficient error to invalidate their results.

Annuli and segments: All counts were made along the left side of the ventral surface, from the first postoral annulus up to and including the annulus bearing the precloacal pores (Vanzolini, 1951). Irregularities were recorded.

Graphic analysis of the number of body annuli in samples of *A. caeca* from the vicinity of Loíza suggested that the ratio of odd to even counts differed significantly from 1. This did not seem to be the case for the few large samples of the other species, and the point should be checked when additional specimens become available. Such asymmetry is not surprising from a theoretical viewpoint, as the dermal annuli lie two to a myotome or vertebra (Smalian, 1884, p. 184). Three sources of variation then exist for the counts of dermal body annuli: (1) Variability of myotome number. (2) Variability in the number and position of intercalated half-annuli (which do not receive dermal innervation and may represent supernumerary structures). (3) Variability in the position of the first "body" annulus, which may be more or less advanced onto the head so that it will be the fourth to eighth (?) annulus that corresponds to the first vertebra. These factors may explain the rather platycurtic distribution of body annuli, and may well introduce some complications in more advanced statistical treatment (Klauber, 1941, p. 8 *et seq.*).

Some of the published counts for *A. innocens* differed sufficiently from ours to warrant a recheck. This check disclosed geographic variation in the number of supernumerary dorsal half-annuli. This character, the so-called "difference," has been plotted in some graphs (but omitted from the appendix). It represents the difference between a middorsal and a standard midventral count of body annuli.

The caudal annuli were counted from the first complete (=ventrally not reduced) post-cloacal up to and including the last complete annulus showing regular segments. The half-annuli dorsal and lateral to the patch of modified cloacal scales have been referred to as "laterals." This nomenclature results in counts differing from those occasionally reported in the literature, in which laterals seem to have been included with caudals. Here, as elsewhere, asymmetric observations are written: left/right. Our separation of the lateral from either body or caudal annuli rests upon the observation that the doubling of dermal segments per myotome is a characteristic restricted to the body (Gans, ms.). The dermal segments of the tail occur one to a myotome and the change takes place in the cloacal region.

In the appendix the annuli counts are given as number of body annuli, plus (+) number of laterals (left/right), plus (+) number of caudal annuli. When the tail is autotomized the number of caudal annuli is recorded in parentheses. The problem of caudal autotomy in the amphisbaenids is intended as the subject of a subsequent discussion.

The dermal segmentation of amphisbaenids allows a complete shift of the loosely attached skin "tube" both rostrad and caudad. The slack is taken up by a curving or narrowing of the length of each annulus (Gans, 1960, p. 183). Diametric expansion (thickening of the animal's body) occurs primarily at the lateral grooves or lines. These grooves also seem the preferred site of dropping out of extra dorsal or ventral half-annuli. A secondary site for this is the general middorsal or midventral region, site of grooves in some genera, of a discontinuous suture only in *Cadea*.

The segments of an annulus are far less constant in shape than are the annuli; they vary in proportion both within and between successive annuli. Their sutures may or may not align in longitudinal series on an animal, the frequency of such alignment decreasing from the midventral to the middorsal line. Counts of segments were made at midbody, continuously around a single annulus selected at random, and recorded as dorsals/ventrals.

The relative sizes of dorsal and ventral segments have occasionally been used as species indicators. These relative sizes change (with the number of segments) from front to rear of the animal. The relative longitudinal curvature of an annulus, or the amount of contraction in the region where such measurements are made, influences them decidedly, so that refined measurements are useless. Only approximate estimates are given in the descriptions of the species.

Head scalation: The paucity of landmarks on the amphisbaenid head makes it difficult to compare head scales. Only rostral, labials, nasals, oculars and mental can easily be defined by standard methods. The absence of a parietal organ, foramen or eye does not even permit estimation of head scale relation from the position of the interparietal. The angle of the gape marks the posterior extremity of the large head shields and the anterior level of the clearly defined body annuli, which in *Amphisbaena* extend onto the occiput. Either of the two pairs of large scales following caudad upon the rostral and nasals may be considered the "true" frontals (i.e. those scales between the orbits), as their relative length and with this their position varies intra- and interspecifically within *Amphisbaena*. Decision for either pair makes the other pre- or postfrontals, respectively. Our diagram (Fig. 5) presents a suggested nomenclature that will be followed in the subsequent papers of this series. Its use does not imply homologies with scales called by the same name in other squamate families.

All our species of *Amphisbaena* have three supra- and three infralabials, and this characteristic has not been tabulated. Confusion is occasionally caused by the apparent caudad displacement of the angle of the mouth, because of its coincidence with an intersegmental suture of the first body annulus. Labials

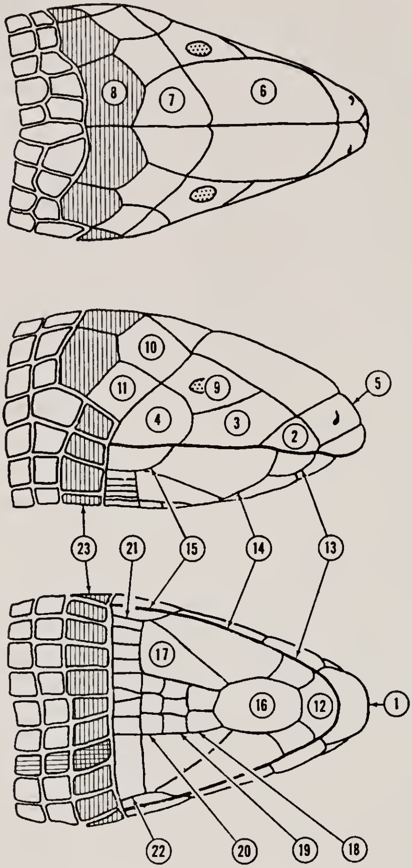

FIG. 5. Diagrammatic dorsal, lateral and ventral views of the head scalation to illustrate nomenclature. 1. Rostral, 2. First supralabial, 3. Second supralabial, 4. Third supralabial, 5. Nasal, 6. Prefrontal (frontal of some authors), 7. Frontal (postfrontal of some authors), 8. Parietal (occipital of some authors), 9. Ocular, 10. Postocular (no, or point contact with supralabials), 11. Temporal (broad contact with second and third supralabials), 12. Mental, 13. First infralabial, 14. Second infralabial, 15. Third infralabial, 16. Postmental (median chin shield of some authors), 17. Malar, 18. First row of postgenials, 19. Second row of postgenials, 20. Third row of postgenials, 21. First row of postmalars (included between last infralabials), 22. Postmalar scale (demonstrating a common kind of asymmetry), 23. First body annulus (the cross-hatched segments indicate start and direction of counts).

should be defined as the scales bordering the actual gape, i.e. those scales that separate when the lower jaw is depressed. Segments caudad to these are not labials, even when they are enlarged.

The constancy of head scale pattern seems to decrease with distance from the rostral. A zone of constant shield arrangement covers the snout of the several species. The gap between this zone and the first body annulus is filled by scales arranged in a more variable pattern which has contributed to nomenclatorial confusion in the description of the head scales (cf. Grant, 1946, p. 61). While variation exists, it is the constancy of certain scales that deserves particular emphasis. Every specimen has the double pair of "frontals" and where large scales exist caudad to these, they are restricted to one or two middorsal pairs of parietals (only *A. caeca* from eastern Puerto Rico suggests some deviation from this). On the chin there is always a single postmental, flanked posteriorly by a single large malar on each side.

The constancy permits the coding of certain exceptions, useful in the discussion of variation. First, there are three items listed as "Major" (and coded by the letters in parentheses under this rubric in the appendix). Deviations from *N*, for normal, as illustrated in Figure 5 are: *C*, for *cubana*, the fusion of the ocular to the second supralabial; *M*, for *manni*, the fusion of the rostral to the nasal with a single suture connecting nostril to first supralabial; and *F*, for *fenestrata*, the caudad projection of the dorsal tip of the rostral which separates the nasals and inserts for some slight distance between the prefrontals.

Analysis suggests that the segmentation back of the region of constant head scalation may best be understood in terms of body annuli. We have defined the first body annulus as the one including the segments back of the angulus oris, even where the postlabial segments are enlarged and seem to form a continuation of the labial series. Using this definition and the concept that accessory dorsal half-annuli may be present in the nuchal region, we can then discuss the several enlarged segments in serial terms. The first series would consist of the temporal(s), postoculars, and possibly the frontals and would represent an accessory half-annulus in the "standard" diagram (Fig. 5). One of the following series would include the first (and another the second) pairs of parietals as middorsal segments. Complications due to the fusions, segmentations, and other abnormalities of the temporal-nuchal region become less disturbing with this approach. Thus the segments of a second dorsal half-annulus, excluded from middorsal contact by an anterior shift along the lateral edges of the frontals, need not be characterized by the undescriptive term of "extra temporals."

The variation in number of intercalated half-annuli reflects to some extent both the length to the back of the frontal and the size of the parietals. This is immediately apparent when comparing such species as *A. cubana* and *A. manni* (Figs. 13 and 24). In *A. cubana* the dorsal halves of the anterior annuli swing forward and only the third body annulus lies in a plane normal to the long axis of the animal. In *A. manni* even the first annulus runs straight dorso-ventrally. Instead of devising a code, we have, in the appendix, recorded measurements (read off a vernier caliper to the nearest .1 mm, under a dissecting scope, and representing the shortest distance between points) from snout tip to back of frontals, and from snout tip to back of parietals (usually equal to back of first body annulus). These measurements are but a few of a somewhat more extensive series made during the course of the study. The remaining ones generally showed differences already indicated by other characters, but did not suggest additional trends. They have been omitted from the appendix, though some are used in graphs. While such head length measurement should theoretically be plotted against snout-vent length minus "head" length, we have omitted this nicety as unjustified at this level of comparison.

It is of interest to note that the species within this group agree much more closely in relative length from snout to back of first (or second) parietals, than in length of snout to back of frontals. It is speculated that this agreement reflects a basic functional pattern. What is measured is the distance along which the snout is covered with enlarged segments. If this segmental enlargement represents an adaptation for friction reduction (Vanzolini, ms.; Gans, 1960), one would expect a correlation of the distance-covered with behavior. It may be that the number of participating segments is less significant than the matter of absolute distance. The several forms would seem to have solved the problem by distinct methods. The idea that enlargement of the head segments is a secondary or phylogenetically advanced development is supported by: (1) the increased size and fusion of shields in various amphisbaenid lines, and (2) the observation that specimens will often regenerate scarred areas as numbers of small segments rather than a single large one. Such evidence for a putative ancestral condition seems to have been accepted by

Camp (1923) and other authors.

The chin shield pattern shows variation in relative length of infralabials and postmentals-malars. This is best indicated by the number of postgenial (between the malars) and postmalar (between the third infralabials) scale rows. Four patterns (coded in appendix under the heading CHIN) exist: (a) two rows of postgenials — no postmalars, (b) two postgenials — one postmalar, (c) two postgenials — two postmalars, and (d) three postgenials — no postmalars. The number of segments in each postgenial and postmalar row have also been listed. The postmalar row often shows considerable asymmetry, with one side appearing to have been separated from the malar by a suture (item 22, Fig. 5) while the other is subdivided into a regular series of segments. The medial edges of the malars often show a similar cutting off of segments, which explains some of the variation in postgenial segment counts.

Cloacal region: The cloaca is surrounded by a ring of segments that project some distance into the proctodeum, and are prolapsed during defecation. Their number and relative shape is subject to considerable variation and asymmetry. A deep transverse fold subdivides the cloacal rim into anterior and posterior portions. The anterior group (precloacal segments) is generally larger and more closely jointed, thus forming a shield for most of the cloacal opening. The shield is slightly scalloped in the center of its posterior margin. The precloacal pores lie on the midventral segments of the last body annulus rather than on the precloacal segments. The pores show some, possibly ontogenetic and sexual, variation in size and pigmentation. Every kind or size of pore was counted and the count has been recorded, followed by the numbers of pre- and postcloacal segments. Counts included all segments regardless of size, though segments lying in line radially from the cloaca were counted as one.

Body proportions: Snout-vent and tail measurements were read by adpressing the specimen to a meter stick. Readings of snout-vent length were recorded to the nearest mm, those of tail length to .5 mm.

Appearance of eye: All amphisbaenids have eyes. As with other cephalic structures there is a decrease in their relative size during life. Observations also suggest a thickening and gradual pigmentation of the overlying skin with age. This, plus the depigmentation of the retina and reduced translucency of the skin due to the vagaries of preservation, is responsible for the comments on "invisible" eyes and "blind" (= *caeca*) forms (cf. Gundlach, 1881).

GENERIC STATUS

Five generic names have been used for one or another of the species discussed here. These are:

Amphisbaena Linné, 1758. Type species: *A. fuliginosa* Linné by first reviser (Fitzinger, 1843).

Typhloblanus Fitzinger, 1843. Type species: *A. coeca* (*sic*) Cuvier 1829 by original designation.

Sarea Gray, 1844. Type species: "*A caeca*" (=*A. ridleyi* Boulenger, 1890) by original designation.

Cadea Gray, 1844. Type species: *Amphisbaena punctata* Bell, 1827 (names preoccupied, replaced by *Cadea blanoides* Stejneger, 1916) by monotypy.

Diphalus Cope, 1861. Type species: *D. fenestratus* Cope by monotypy.

Amphisbaena is the oldest generic name for limbless amphisbaenians. The Antillean forms *caeca* Cuvier, 1829, *innocens* Weinland, 1862, *cubana* Peters, 1878, *bakeri* Stejneger, 1904, *manni* Barbour, 1914, and *caudalis* Cochran, 1928, are customarily referred here.

Typhloblanus belongs in the synonymy of *Amphisbaena*, even though it would be available if it became desirable to distinguish the Antillean species by generic or subgeneric status.

The generic name *Sarea* does not belong in the present assemblage as Boulenger (1890, p. 481; see also Boulenger, 1890a, p. 79; Stejneger, 1904, p. 676) has shown that Gray based it upon a misidentified specimen of *Amphisbaena ridleyi* Boulenger, 1890, from "Porto Bello" (read Fernando Noronha, Brazil). The latter form thus becomes the type species and the generic name belongs in the synonymy of *Amphisbaena*.

Little comment need be made on the genus *Cadea*, clearly distinct from *Amphisbaena* by the unpaired prefrontal scale, by a number of skull characteristics (Vanzolini, 1951a), and by the retention of the hypocentrum of the atlas. It includes the Caribbean species *blanoides* Stejneger, 1916 and *palirostrata* Dickerson, 1916.

The resurrection of *Diphalus* by Vanzolini (1951a, p. 114) made without examining a specimen, stimulated the present study. He listed three distinguishing characters: (1) a pointed rather than a rounded, or flattened snout, (2) the separation of the nasal shields by a narrow process of the rostral, and (3) a dental formula (premaxilla, maxilla, dentary) of 5, 4, 7 rather than 7, 4-5, 7-9.

The first of these characteristics is worthless as the actual difference is minor, and there is considerable evidence of ontogenetic changes in the head shape. The head of *fenestrata* is no more pointed than is that of *innocens.* It might also be argued that this difference is far less striking than that between the Antillean species as a group and such blunt-headed yet congeneric (?) forms as *alba* and *fuliginosa.*

The separation of the nasal shields is clear and constant, but hardly more significant than the fusion of ocular and second labial in *cubana* or of rostral and nasal in *manni.*

Of the characters listed, we should have most confidence in the low number of premaxillary teeth, as this number is usually remarkably constant in amphisbaenids and equals 7 in all species of *Amphisbaena* checked thus far. Vanzolini apparently obtained the counts from Boulenger (1885, p. 449), who must have been misled by an aberrant or poorly prepared specimen. The skulls of the type and of MCZ 36306 both have 7 teeth on the premaxilla.

These two skulls were compared with skulls of each of the Antillean species of *Amphisbaena* (*A. c. cubana,* MCZ 10802; *A. c. barbouri,* MCZ 12135; *A. i. innocens,* MCZ 27596; *A. i. caudalis,* MCZ 25551; *A. manni,* MCZ 44389, plus 5 cleared AMNH specimens; *A. bakeri,* UPR 11; *A. caeca,* CM 36377, 37636, MCZ 36317). The comparison furnished no grounds for generic separation. Plates 1-3 show views of skulls of *A. fenestrata* and *A. caeca.* Differences similar to those shown may be seen between skulls of any pair of the other species. *A. fenestrata* also agrees with the other species of *Amphisbaena,* all of which differ from the two forms of *Cadea,* in lacking the hypocentrum of the atlas. This is a matter to be discussed in a subsequent paper.

KEY TO THE ANTILLEAN AMPHISBAENIDS

1. All median cephalic shields paired, prefrontals in contact with supralabial, precloacal pores in continuous row, sharply defined lateral grooves, color uniform, possibly with uniform markings on (dorsal) segments . . . . (*Amphisbaena*) 2.

First median post-rostral shield azygous, prefrontals kept from labial contact by elongate preocular shield, row of precloacal pores with central gap, poorly marked lateral grooves, segments with irregular spots . . . . (*Cadea*) 9.

2. Nasal scales separated by posterior process of rostral scale (Fig. 6c) .... *A. fenestrata*
   Nasal scales in contact on midline .... 3.
3. Second labial fused to ocular (Fig. 6a) .... *A. cubana* 4.
   Second labial distinct from ocular .... 5.
4. Body annuli less than 218; caudal annuli 14 or less .. *A. cubana cubana*
   Body annuli more than 226; caudal annuli 14 or more .... *A. cubana barbouri* n. ssp.
5. Nasals fused to rostral (Fig. 6b), the nostril connected to the labials by a suture; sixth caudal annulus generally narrower and of smaller diameter so that tail constricted at this point .... *A. manni*
   Nasals distinct from rostral, caudal annuli more or less equal in width, tail generally lacks constriction .... 6.

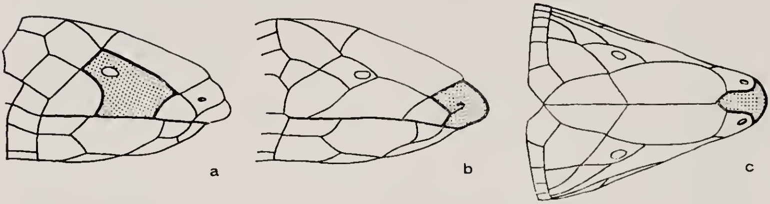

FIG. 6. Major changes in the head scale arrangement. *a*, Fusion of ocular and second labial. *b*, Fusion of rostral to the nasal with a single suture connecting nostril to the first supralabial. *c*. Caudad projection of the dorsal tip of the rostral, which separates the nasals.

6. Two, rarely three, rows of postgenials, the first row with three, rarely four, equal scales; 14-20 ventral segments per midbody annulus; tail with almost no taper, blunt ended .... 7.
   Two or three rows of postgenials; if two rows, then the first with two large scales, occasionally separated by a small element; 18-24 ventral segments per midbody annulus; tail tapering continuously toward the tip .... (*A. innocens*) 8.
7. Body annuli 217-236, tail slightly longer (Fig. 9), internasal suture considerably shorter (Fig. 10) .... *A. caeca*
   Body annuli 239-255, tail slightly shorter (Fig. 9), internasal suture considerably longer (Fig. 10) .... *A. bakeri*
8. Two rows of postgenials, the second row with three scales; one row of postmalars; caudal annuli 10-13; body annuli 214-225 .... *A. innocens gonavensis* n. ssp.
   Three rows of postgenials, the second row with four or more scales; no postmalars; caudal annuli 9-14; body annuli 185-219 .... *A. innocens innocens*
   Three rows of postgenials, the second row with four scales; no postmalars; caudal annuli 18-19; body annuli 200-208 *A. innocens caudalis*

9. Body annuli 175-218 (counted on ventral surface), caudal annuli 10-14, segments in a midbody annulus 25-33, snout rounded, blunt .... *C. blanoides*
   Body annuli 274-320 (counted on ventral surface), caudal annuli 12-17, segments in a midbody annulus 32-39, snout domed, laterally compressed .... *C. palirostrata*

TAXONOMIC DISCUSSIONS

Genus AMPHISBAENA Linné, 1758[1]

Amphisbaena Linné, 1758. Type species: *Amphisbaena fuliginosa* Linné, 1758, by first reviser (Fitzinger, 1843).

Typhloblanus Fitzinger, 1843. Type species: *A. coeca* (*sic*) Cuvier, 1829, by original designation.

Sarea Gray, 1844. Type species: "*A. caeca*" (=*A. ridleyi* Boulenger, 1890), by monotypy.

Diphalus Cope, 1861. Type species: *D. fenestratus* Cope, 1861, by monotypy.

Discrimination of the species: The application of the biological species concept (Mayr, 1942) encounters its greatest difficulty when one is dealing with populations on adjacent islands, populations that may represent either distinct species or races of a single polytypic form. Remnants of a morphological concept inevitably remain, since it is usually necessary to use the degree of phenotypic difference of the allopatric populations as the indicator of some sort of "inter-population fertility potential." The degree of phenotypic difference may furnish but a poor inference of the actual difference between the genotypes (e.g. Zahavi and Wahrmann, 1957, p. 354), yet it remains the only indicator available for museum material.

The present analysis has made use of the fact that two of the forms here recognized as species were polytypic, one of these (*A. cubana*) on a single land mass. Our species differences involve characteristics that remain constant in each of these cases and generally a greater number of differences as well. We also checked for increased similarity of populations from adjacent parts of adjacent islands.

Analysis demonstrated that each of the large islands of the Antilles (Cuba, Hispaniola and Puerto Rico), and the group of small islands known as the Virgin Islands, has a distinct, endemic species of *Amphisbaena*. Hispaniola and Puerto Rico each have a second species of more limited distribution, but sympatric with the first at least over part of its range.

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[1] The generic synonymy is complete only for names based on forms from the Antilles.

The more important reasons for considering the several forms distinct at the species or subspecies level are as follows:

(1) The polytypic species *A. cubana* is found in the eastern two thirds of Cuba and on the Isla de Pinos. From allopatric *A. i. innocens* on the mainland of Haiti and *A. i. caudalis* on Grande Cayemite it differs by fusion of the ocular to the second supralabial, by shorter nasal contact (Fig. 7), by possession of two rather than three rows of postgenials, by a tendency toward a blunt rather than a continuously tapering tail and by the presence of caudal autotomy. Adult specimens of *A. cubana* are slightly smaller (Fig. 8), have a smaller range of body annuli, and a definitely lower mean number of segments to a midbody annulus. The island population of *A. i. gonavensis* is more similar to *A. cubana* in lacking the third row of postgenials and in nasal length (cf. Fig. 7). This suggests that *A. cubana* may be

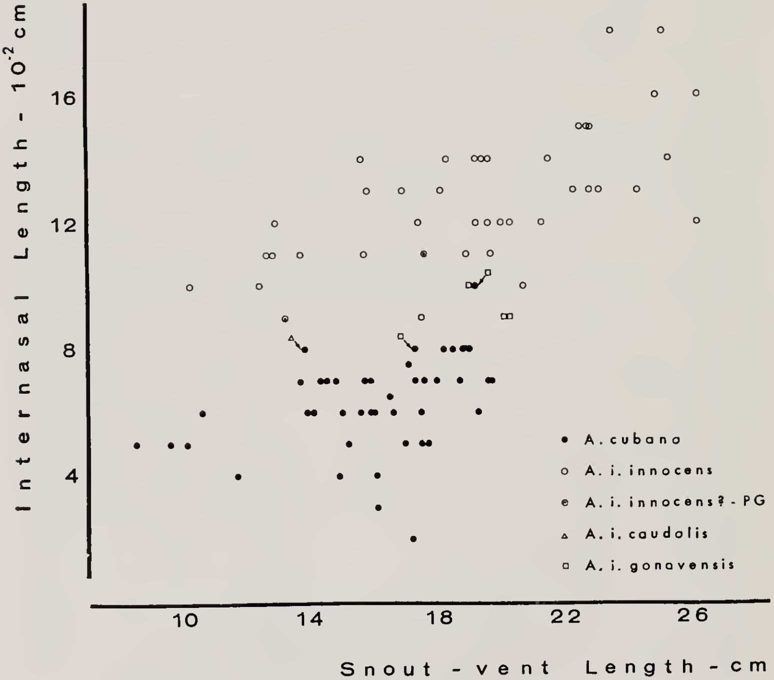

FIG. 7. Scatter diagram of internasal length versus snout-vent length of *A. cubana* and *A. innocens*. The specimens of *A. i. gonavensis* and the single exemplar from Petit Gonave (PG) appear to be intermediate in this characteristic.

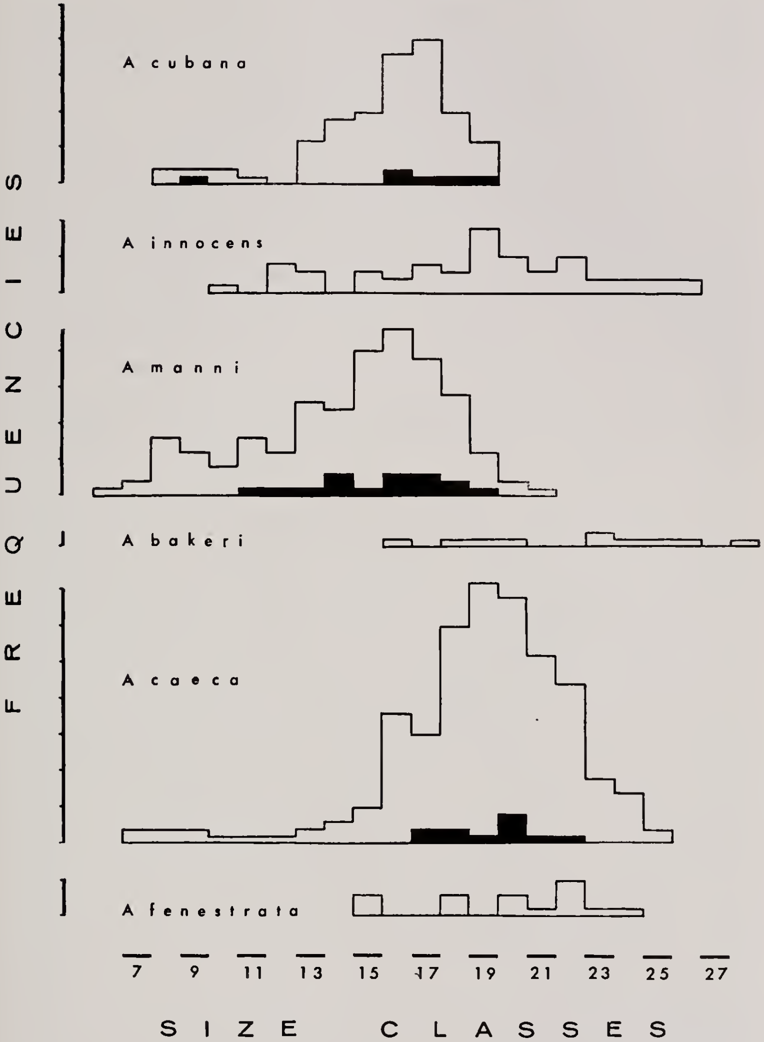

FIG. 8. Histogram to show number of specimens of each species of Antillean *Amphisbaena* in the different size classes. The units of the frequency scale indicate 5 specimens. The numbers on the size class scale indicate centimeters, thus class 7 includes snout-vent measurements from 70 to 79 mm, etc. The solid black rectangles indicate specimens in which caudal autotomy has taken place.

closely related to *A. i. gonavensis,* but the constancy of the other characteristics and the greater difference of *A. i. gonavensis* in number of midbody annuli, plus its possession of a postmalar row, leads us to maintain them as separate species.

A. cubana is even more distinctly different from the allopatric *A. manni,* which inhabits northwestern and eastern Hispaniola. From the latter it differs by fusion of ocular with the second supralabial, by normal rostral segmentation, by lack of caudal constriction, by a lower range of body annuli, by a clearly lower number of caudals, and by a relatively much shorter tail. *A. cubana* also has a lower number of body annuli, a tendency toward a higher number of dorsal segments at midbody, a greater difference between the number of dorsal and ventral segments to a midbody annulus, a tendency to a greater number of postgenials and precloacals, and a much lower number of precloacal pores.

(2) *A. innocens* and *A. manni* are allopatric over most of their ranges (Fig. 3). The only indication of possible sympatry is given by the single record of *A. manni* from the Haitian capital of Port-au-Prince, well within the range of *A. innocens.* The latter species seems to be restricted to the southwestern peninsula of Hispaniola (and the islands of Gonave, Petite Gonave and Grande Cayemite), not extending north much beyond the Cul-de-Sac plain. All Haitian records of *A. manni* come from the northern half of that country. Mainland *A. innocens* is clearly different from *A. manni* in lack of rostro-nasal fusion, in the presence of a third row of postgenials (found in only 2 of 140+ specimens of *A. manni*), in the absence of caudal autotomy and the clear caudal constriction exhibited by *A. manni,* by the relatively shorter tail length, by the lower number of body annuli (the few apparently overlapping counts come from specimens collected at opposite ends of the island), and by the lower number of caudal annuli. *A. innocens* also differs by a tendency to higher ventral, and clearly higher dorsal (and total) counts of segments per midbody annulus, by the presence of mostly 2 instead of 3 postgenials in the first row, by the presence of 4 or fewer precloacal pores (only 3 of 140+ specimens of *A. manni* also have 4), and by the tendency toward a higher number of pre- and postcloacals. *A. manni* from northern Haiti differs more from the mainland *A. innocens* than *A. manni* from the Dominican Republic differs from *A. innocens.* This is apparent in the following characters: number of body annuli, number of caudal

annuli, number of dorsal and of ventral segments per midbody annulus, numbers of segments in the first and second postgenial rows, number of precloacal pores, and number of precloacal shields. No reversals of this trend were encountered.

(3) Only *Amphisbaena manni* occurs in eastern Hispaniola and this species differs from the allopatric *A. caeca* on Puerto Rico by the presence of rostro-nasal fusion, by a greater range of body annuli counts, by a higher number of caudal annuli, by the relatively longer tail, and by the higher number of precloacal pores. *A. manni* also has a lower number of both dorsal and ventral (and total) segments per midbody annulus, but the forms agree in the differences between number of segments in dorsal and ventral half rings. *A. manni* tends to have lower numbers of pre- and postcloacal segments, a somewhat smaller adult size (Fig. 8), and includes only two specimens with a row of postmalar segments (only 7 specimens of *A. caeca* lack this row).

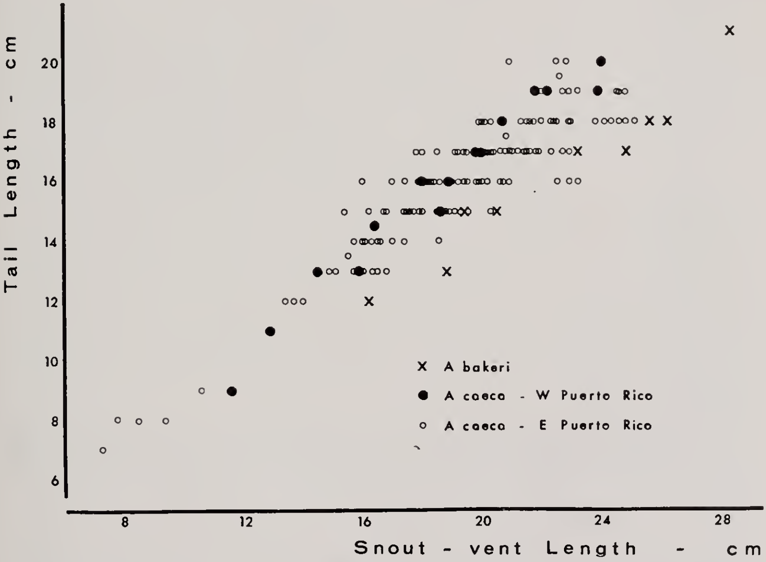

FIG. 9. Scatter diagram of tail length versus snout-vent length of *A. caeca* and *A. bakeri*. Western Puerto Rico refers to the region west of Arecibo which includes the zone of possible sympatry. Material of *A. caeca* from this region is more distinct from *A. bakeri* than eastern *A. caeca* is from *A. bakeri*.

(4) *A. innocens* and *A. caeca* are not directly adjacent in the sense of this comparison. Their differences are quite as clear as those between the preceding pair of forms.

(5) The most difficult and interesting situation involves the status of populations from the northwestern sixth of Puerto Rico. We here retain *A. bakeri* as a good species for the following reasons: (a) both *A. caeca* and *A. bakeri* have been collected in three of the four localities (Fig. 4) from which the latter has been

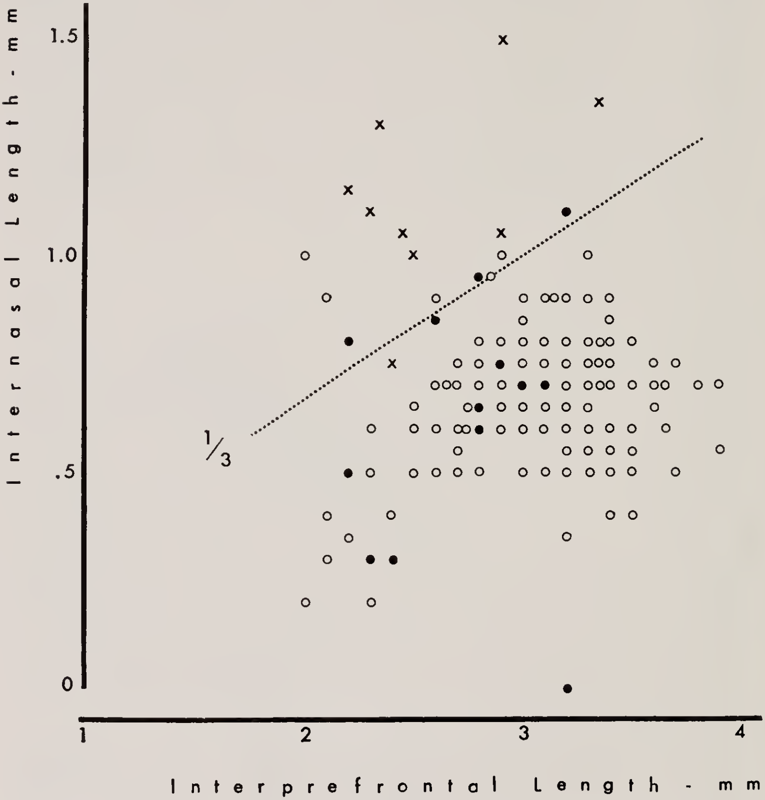

FIG. 10. Scatter diagram of internasal length versus interprefrontal (contact) length of *A. caeca* (○, ●) and *A. bakeri* (x). The line, internasal length = 3 x interprefrontal length, has been dotted in. As in Figure 9, solid circles indicate specimens from west of Arecibo. The specimen with internasal length equal to zero is the anomalous Lares specimen already mentioned by Stejneger (1904), and Grant (1932), and figured by the former.

seen, indicating geographical (though possibly not ecological) sympatry; (b) *A. bakeri* has clearly higher counts of body annuli (range of 239-255, against 217-237 for *A. caeca*); (c) *A. bakeri* has a distinctly shorter tail than have specimens of *A. caeca* from the jointly occupied range (Fig. 9), though the range of measurements of eastern *A. caeca* overlaps them; (This suggests that the relatively shorter tail length is not directly correlated to the increased number of body annuli.) (d) the relatively longer internasal contact length (compared either to snout-vent or to interprefrontal contact length — Fig. 10) of *A. bakeri,* which again is clearer when comparison is made to specimens from sympatric populations of *A. caeca;* and (e) the relatively larger maximum size of *A. bakeri* (Fig. 8).

The presence of such diverse specimens might also be explained in other ways, less probable on the basis of present evidence. Thus no reason exists to suspect ontogenetic change (or ontogenetic selection) for the characters in question. Both sexes are present in each sample, eliminating the idea of sexual dimorphism. Decision for geographical (= ecological?) polymorphism would require detailed collecting data, and for nongeographic polymorphism would require data on broods, both of which are lacking. Reference should here be made to the peculiar low-count specimens from Aguadilla and Salinas which have been discussed in more detail below.

The increased difference in relative tail length in the jointly occupied range might be explained as "character displacement" (Brown and Wilson, 1956), but the data are not as clear for relative length of internasals, while the data on presence of a postmalar row suggest an increased similarity between sympatric rather than allopatric populations. Thus, *A. bakeri* lacks both postmalars and a third row of postgenials; more than 210 specimens of *A. caeca* have postmalars, but 5 of the 7 specimens lacking this row of segments come from western Puerto Rico where the frequency of postmalars drops from 99 to 65 per cent.

(6) The characters differentiating *A. bakeri* from *A. caeca* make it more, rather than less, different than the latter is from both *A. innocens* and *A. manni.*

(7) Only *A. caeca* is found in eastern Puerto Rico. It differs from the allopatric *A. fenestrata* of the Virgin Islands (St. John, St. Thomas, Tortola) by contact between the nasal segments (except for one anomalous specimen from Lares, fig. 131 in Stejneger, 1904), by lower counts of body and higher counts of caudal

annuli, by somewhat greater numbers of dorsal and ventral, and distinctly higher total numbers of segments to a midbody annulus, and by a relatively shorter tail (Fig. 11).

In two of these characteristics (higher number of body annuli and relatively shorter tail) *A. fenestrata* approaches *A. bakeri*. Comparison of Figures 9 and 11 shows different slopes for the growth curves of these two species so that the similarity seems fortuitous.

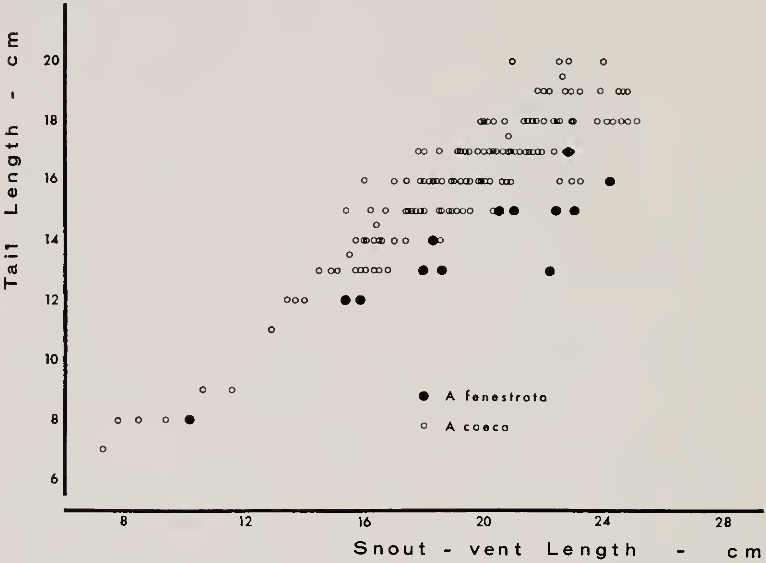

Fig. 11. Scatter diagram of tail length versus snout-vent length of *A. fenestrata* and *A. caeca.*

Interrelationships of the species: The forms under discussion show considerable similarity in general scale arrangement, habitus, and superficial appearance. Preliminary review of a number of internal characteristics did not provide any evidence that would modify this statement.

Granting this similarity, it becomes more difficult to establish any simple pattern or sequence of relationships, particularly since we are ignorant regarding the genetic basis of the observed variation. There is thus no reason for the often implicit assumption that a difference of X units between the ranges of a character in two species implies a greater similarity of genotypes than would a difference of 2X, or of nX. We have chosen to be more impressed by numbers of similarities or differences in divers, possibly non-associated, characters, than by the extent of differences. Trends have been evaluated with this in mind.

Most noticeable is the loss of the postmalar row as well as of the third row of postgenial segments, from east to west (except for the *A. manni* records). Counts of body annuli fall into three groups, *innocens — c. cubana, c. barbouri — manni — caeca,* and *bakeri — fenestrata,* with increasing number. *A. innocens* and *A. manni* differ from all other forms in having a much larger range of body annuli. Caudal annuli drop from *c. barbouri* to *c. cubana — i. innocens — i. gonavensis,* rise to *i. caudalis — manni,* and drop again to *bakeri — caeca,* and further to *fenestrata.* Only *manni* and some specimens of *caeca* have a clear autotomy constriction; *cubana* also shows bobbing of tail but less of the tail seems to be lost and occasional specimens may show severe caudal scarring without autotomy. Dorsal and ventral segment numbers rise from *cubana* to *innocens,* drop sharply to *manni,* rise slightly to *bakeri — caeca,* and drop to *fenestrata.* Only *manni* differs significantly in number of precloacal pores and cloacal segments, and in having a uniform coloration. The major segmental abnormalities show no geographic trends.

The review suggests strongly that 1) *A. manni* is quite distinct from the other forms, and 2) the pattern of variation gives a checkerboard assembly of characters, rather than an east-west sequence. The differentiation of *A. manni* may well reflect an extensive isolation from and adaptation to a different environment than the other forms. Its differences may have been emphasized by the existence of a second form on Hispaniola. It seems logical to assume that this second form (*A. innocens*) obtained its initial diversification south of the Cul-de-Sac plain, at a time when this was inundated by a rise in sea-level. The checkerboard of discrete characteristics might be expected in an assemblage of closely related species. Ignorance of the selective value of the characters does not permit us to discuss the relative importance of selection and genetic drift in the establishment of such pattern, nor does the character pattern of itself permit conclusions regarding the invasion route(s) by which these forms entered the Antillean area.

Discussion of the affinities of the Antillean forms to other amphisbaenids is avoided here as it will form the topic of a subsequent paper. The analysis does not furnish evidence against the hypothesis that the various species of *Amphisbaena* represent a single invasion and subsequent diversification. Amphisbaenids have been found on too many islands to permit us to retain the old idea (Schmidt, 1928, p. 20; Mertens, 1934, p. 31, cf. Rivas, 1958) that their occurrence necessitates the former existence of a land-bridge. Most of the Antillean forms could have arisen by crossing of water gaps and subsequent differentiation in isolation. The races of *A. innocens* suggest that this may occur rapidly, while the lack of island races in *A. fenestrata* may be the result of insufficient time, too small an area,[1] or of the ecological homogeneity — or, alternatively, our sample is too small. Such isolation does not appear to have existed between *A. bakeri* and *A. caeca,* a situation deserving additional scrutiny.

Generic description: The Antillean species of *Amphisbaena* share the following external characteristics:

An azygous rostral followed by three or more pairs of enlarged cephalic shields in contact along the dorsal midline, with the nostrils pierced in the first pair (which may be separated by a process of the rostral). The second pair (prefrontals) are the largest segments of the head. Three supra- and three infralabials, the second by far the largest in each case, and the third the smallest. A varying number of postocular and temporal segments, lying posteriorly to the ocular and generally much smaller than the prefrontal. A large T-shaped mental followed by a much larger postmental often flanked posterolaterally by a pair of large malars.

The snout is pointed, flattened very slightly dorsoventrally, and oval in cross-section. The upper jaw protrudes strongly and the much shorter lower jaw inserts between the projecting supralabials. The shape of the head is strongly affected by the allometric growth pattern of the temporal musculature, which protrudes very much more in adults than in juveniles. This protrusion starts back of the eyes and increases the animal's diameter from snout to neck. There is little external emphasis on the level of the head joint. A very faint constriction and a narrowing of the fourth and fifth body annuli are all that mark this region.

The lateral grooves are generally well defined, starting gradually after the first sixth of the body and ending gradually at the

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[1] The Columbia-Lippincott Gazetteer of the World gives the following areas (in square miles) for the islands involved: Cuba 43,036; Isla de Pinos 1,182; Hispaniola 29,829; Cayemite Islands 17; Grande Gonave 254; Puerto Rico 3,423; St. Thomas 27; St. John 19; Tortola 21. Other islands of the chain might have amphisbaenid populations though none have thus far been reported.

level of the cloaca. The ventral groove is indicated only as a gap between aligned segments. The dorsal groove may be suggested by an alignment alone. Considerable variation exists in segment size, but length to width of dorsals varies from 1 (in embryos) to 1.5, rarely 2, and of ventral segments from .33 (in embryos) to .5 to 1 (in adults).

The precloacal pores lie in a single uninterrupted row of normal sized or elongate segments anterior to the precloacal shield. The tail is circular to oval in cross section and bears no terminal specializations.

AMPHISBAENA CUBANA Gundlach and Peters, 1878

Geographic variation: The available sample for this species numbers 86 specimens, but it is difficult to say much about infraspecific variation as 58 of these come from the immediate vicinity of Soledad (the Harvard Botanical Garden in Cuba) and Cienfuegos, while seven others lack precise locality data.

Eight specimens pose a problem. Of these, two come from Marianao, one from Playa del Chivo, two from Matanzas (city or province?), two from Caleta Rosario and one from Soledad. All

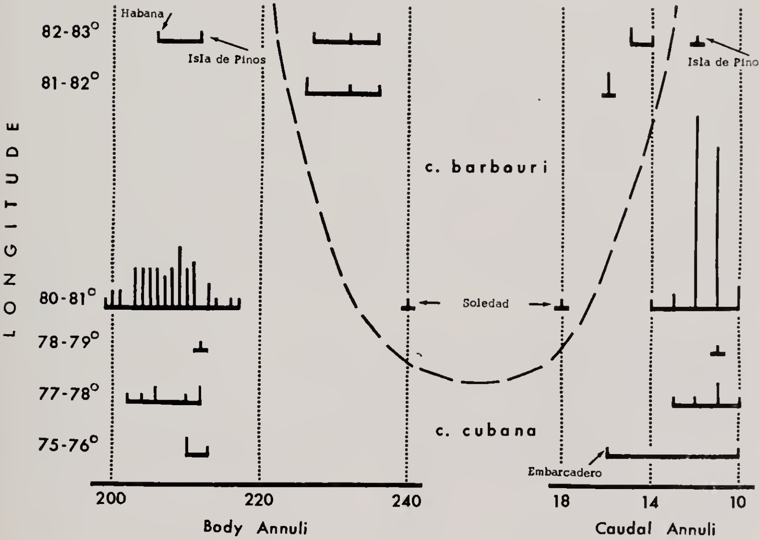

FIG. 12. *A. cubana.* Comparison of counts of body and caudal annuli for samples. See discussion in text.

have significantly high counts of body annuli, 225-240 compared to 199-217, and of caudal annuli, 15-18 compared to 10-14 (omitting the Embarcadero record, of which more below) for the rest of the species (Fig. 12).

With the exception of the Soledad specimen, which may have been collected further to the west, the five localities form a geographic unit. The high-count specimens may thus represent either 1) a distinct allopatric species, or 2) a race, inhabiting the western end of the range, or lowland areas below 250 feet.

The first hypothesis is prejudiced by the similarity of the geographically replacing forms (both of which share the oculolabial fusion otherwise unique in the group) and the lack of evidence for sympatry. The second hypothesis seems on firmer ground, though it requires the explanation of two low-count specimens labelled "Habana" and Jacksonville, Isla de Pinos, respectively. The Habana specimen may have been catalogued under the home address of the donor. That from Jacksonville represents the only record of *A. cubana* from the Isla de Pinos. It has 6 (instead of 4) precloacal pores and differs in other minor ways from mainland specimens.

Also unclear is the possible restriction of the high-count race to lowland areas. Three of the localities are definitely coastal, and the inexactly localized other two specimens may well come from below the 250-foot and possibly below the 100-foot contour. In contrast, all but two eastern (low-count) specimens were definitely collected at or above 250 feet, and this may even hold for the low-count Habana and Jacksonville records. The exceptions are San Juan de los Perros and Embarcadero. The former could not be located on a map (it is missing from Gazetteer 30 of the U.S. Board on Geographic names). The Embarcadero specimen differs from the other eastern specimens by a high count of caudal, though not of body, annuli and by somewhat aberrant head scale proportions. More material from Oriente would seem to be desirable. It is interesting that the distribution of the low-count specimens coincides with the areas of the two eastern islands probably left exposed during various Pleistocene inundations, while the distribution of the high-count form represents an area flooded during the interglacial stages (Rivas, 1958, maps on p. 316).

It seems clear that the high-count material represents a subspecifically distinct population, though it remains to be determined what factors separate the races. Since the holotype of

A. cubana Gundlach and Peters is a low-count specimen, we here propose the name *barbouri*[1] for the high-count western race.

AMPHISBAENA CUBANA CUBANA Gundlach and Peters, 1878

Amphisbaena cubana Gundlach and Peters, *in* Peters, 1878, p. 780. Type locality: ''Cuba.'' HOLOTYPE: ZMU 6904.

Diagnosis: A form of *Amphisbaena* with the ocular fused to the second supralabial. Specimens have 199 to 218 body annuli; 10 to 14 (exceptionally 16) caudal annuli; 12 to 16 dorsal, and 14 to 18 ventral segments per midbody annulus; two postgenial and no postmalar rows of chin shields; and 4 (exceptionally 5 or 6) precloacal pores; caudal autotomy occurs between the sixth and ninth, mostly after the seventh postcloacal annulus.

Description: Meristic characters are summarized in Table 1, and Figures 7, 8 and 12, individual data in the appendix. Figure 13 shows the head scalation, Figure 14 the ventral surface of tail and cloacal zone. Plate 4 shows views of the color pattern and kinds of caudal damage.

Preserved specimens are various shades of brown; the ventral surface has a pink to violet sheen in life. The color is solid on dorsal surface of head and tail; on the rest of the body the rectangular center of each segment is much darker than its margin giving the impression of dark spots. The color is darker dorsally than ventrally. A few specimens show degrees of darkening of the segmental margins approaching the uniform dorsal color of *A. manni*. Most specimens have few white segments randomly scattered over the ventral surface, less than 10 per cent of the sample had most of the ventral surface white. The existence of pigment on a segment appears to be a yes-or-no phenomenon and independent of the general ventral lightening. The color drops out in an irregular manner and not at a given level.

The head scalation is characterized by fusion of the ocular and the second supralabial. Only two specimens show partial separation of these two scales. The first two body annuli correspond to the three dorsal half-annuli. The segments of the anterior half-annulus are customarily referred to as temporal and postocular and abut middorsally on the frontals. The next posterior half-annulus culminates in the enlarged parietals. The third is

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[1] Named after Thomas Barbour who collected most of the available specimens of these two races.

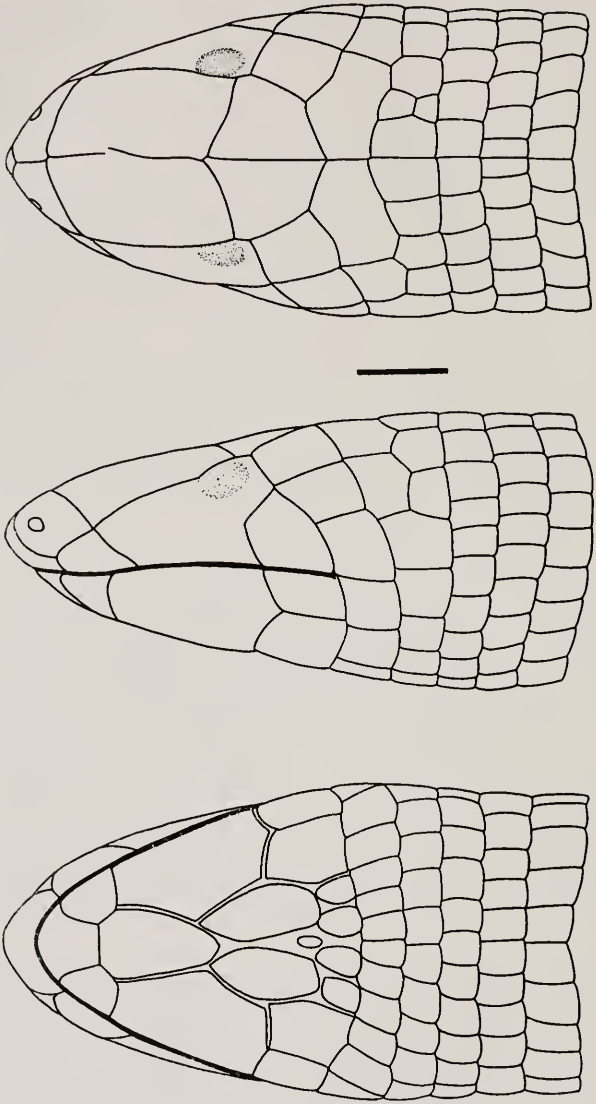

Fig. 13. *A. c. cubana.* Dorsal, lateral and ventral views of head scales of ZMU 6904 (HOLOTYPE). The line equals 1 mm to scale. (V. Cummings, del.)

generally of normal size though the postparietals may be enlarged. Approximately 10 per cent of the specimens have a fourth dorsal half-annulus between the second and third, and another 20 per cent show a few, often asymmetric supplementary segments in the nuchal region. The anterior edge of the third body annulus lies in a plane normal to the long axis of the animal.

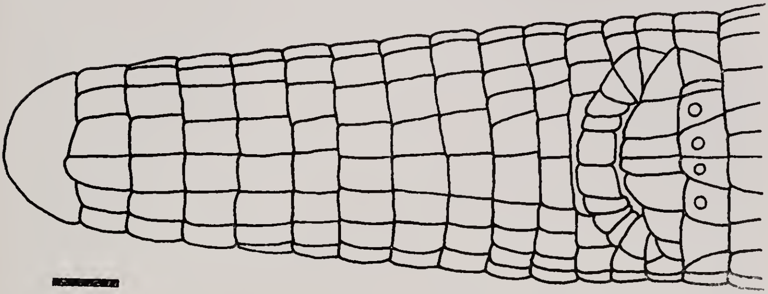

FIG. 14. *A. c. cubana.* Ventral view of cloacal region and tail of MCZ 10790 from Soledad, Cuba. The line equals 1 mm to scale. (M. Franson, del.)

The chin is characterized by an elongate tear-drop shaped postmental flanked posteriorly by a pair of large tear-drop shaped segments of the first postgenial row. One or more extremely elongate segments fill the narrow gap between the enlarged postgenials. These tiny and irregular segments may or may not be in contact with the postmental and often break crossways into two or more segments.

The fourth and fifth body annuli are narrower, mark the end of the bulging temporal musculature and appear to correspond to the position of the atlas.

General observations: The skull has been figured and discussed by Zangerl (1944) and Kesteven (1957). Girdle remnants and vertebrae were commented on by Zangerl (1945). The thyroid was studied by Lynn and Komorowski (1957).

Range: Isla de Pinos; Central and eastern Cuba from Cienfuegos to Oriente.

Locality records (see Fig. 2 for map): ISLA DE PINOS: Jacksonville MCZ 46235. CUBA: —— (Barbour, 1930, 1935, 1937; Boulenger, 1885; Gundlach, 1880; Peters, 1878; Stejneger, 1904; Strauch, 1881); AMNH 58839; HM 367 A—B; MHNP

3120; RMNH 9978; SU R—14634; ZMU 6904 (HOLOTYPE), 9383. Habana Province: Habana? MCZ 35510. Las Villas Province (formerly Santa Clara): Banos del Ciego, Montero AMNH 7312. Soledad (Barbour, 1914; Barbour and Ramsden, 1916, 1919); BM 1912-9-4-3; CAS 39292; MCZ 7936 A—N, 10790-811, 10814, 10817-18, 13525-27, 22722, 32665; USNM 48802-03, 137083. Cienfuegos (Stejneger, 1917); ANSP 16365; BM 1915-10-22-5—8; RMNH 4638; USNM 58747. Camagüey Province: San Juan de los Perros (North Coast) MCZ 13523. Sierra de Cubitas, Paso de Lasca, 5.5 miles northeast of Banao AMNH 77790. Martí UMMZ 70923, 70925-26. Three miles west of Cascorro UMMZ 70924. Santa Cruz Mts. (Cochran, 1934); USNM 75861. Oriente Province: 8 miles south of Puerto Belie, north of Cabo Cruz UMMZ 90720. La Demajagua, near Ramón de las Yaguas (Barbour and Ramsden, 1916). Cuabitas (Alayo, 1951). Puerto Boniato (Alayo, 1951). Embarcadero, Banes Bay (Barbour and Ramsden, 1916, 1919); MCZ 47897. Guantánamo, San Carlos Estate (Barbour and Ramsden, 1916, 1919); MCZ 10712, USNM 63217.

Habitat: One Soledad specimen was taken under stones near a brook (P. J. Darlington, Jr. on field label). Barbour (1914) mentions that 26 specimens were obtained following "plows in the cane fields near Soledad." He later (Barbour and Ramsden, 1919) added that this procedure was not uniformly successful and failed at a plantation in the Cienaga de Zapata on the Rio Hanabana (20 km north of Caleta Rosarío). This may have reflected local absence from a swampy area.

AMPHISBAENA CUBANA BARBOURI subsp. nov.

Diagnosis: A form of *Amphisbaena* with the ocular fused to the second supralabial. Specimens have 226 to 240 body annuli; 14 to 18 caudal annuli; 12 to 14 dorsal and 16 to 18 ventral segments per midbody annulus; two postgenial and no postmalar rows of chin shields; and 4 to 6 precloacal pores. None of our specimens shows caudal autotomy.

Holotype: MCZ 12136, a male collected by Thomas Barbour at Caleta Rosarío on the east shore of the Ensenada de Cochinos, Las Villas Prov., Cuba, in "January, 1917 . . . under stones on the floor of a heavy lowland forest." For data see appendix.

Allotype: USNM 26364, a female collected by J. W. Daniel at Matanzas, Cuba.

Paratypes: MCZ 58788-89, from Marianao; MCZ 12135, from Playa del Chivo; USNM 26363, from Matanzas; MCZ 12137, from Caleta Rosarío; MCZ 13524 from Soledad.

Description: Meristic characters are given in Table 1 and Figures 7, 8 and 12, individual data in the appendix. Plate 5 shows views of the holotype.

The general head scalation and coloration of the form closely follows that described for *A. c. cubana.* All specimens show pairs of enlarged parietals and of postparietals.

Range: Western Cuba from Cienfuegos to Habana.

Locality records (see Fig. 2 for map): CUBA. Habana Province; Marianao MCZ 58788-89 (PARATYPES); Playa del Chivo (Barbour and Ramsden, 1919), MCZ 12135 (PARATYPE). Matanzas Province: Matanzas (Barbour and Ramsden, 1919; Stejneger, 1904, 1917), USNM 26363 (PARATYPE), 26364 (ALLOTYPE). Las Villas Province: Caleta Rosarío, Ensenada de Cochinos (Barbour and Ramsden, 1919), MCZ 12136 (HOLOTYPE), 12137 (PARATYPE); Soledad MCZ 13524 (PARATYPE).

Habitat: "Under stones on the floor of a heavy lowland forest" (Barbour and Ramsden, 1919). "Under cardboard on top of a cliff; surrounded by ants" (B. B. Collette note on MCZ 58788-89).

AMPHISBAENA INNOCENS Weinland, 1862

Geographic variation: The sample numbers 50, including 2 specimens from the island of Grande Cayemite, 1 from Petite Gonave, 7 from Gonave, and 40 from Hispaniola proper. Of the latter, 24 come from the vicinity of Jérémie, and the remaining mainland specimens from a series of scattered localities.

While the geographic range of the species is not particularly extensive, there is a considerable amount of geographic variation. This is probably emphasized by the collecting gaps between the several mainland localities from which we have seen specimens. The variation can best be described by discussing the material in terms of six geographically delimited samples, namely Jérémie (Moron, Jérémie, Place Negre, Carrefour Sanon, Laye, Paroty), Grande Cayemite, Furcy (La Vallée,[1] La Vanneau,[1]

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[1] Note that these two localities may represent another area. Particularly, the data from the La Vanneau specimen representing extreme values (cf. Fig. 15) tend to indicate this. It should also be noted that the present groupings are pragmatic, artificial, and for convenience of description. Thus, Furcy lies at an elevation of 5000′ and Diquini is at sea level.

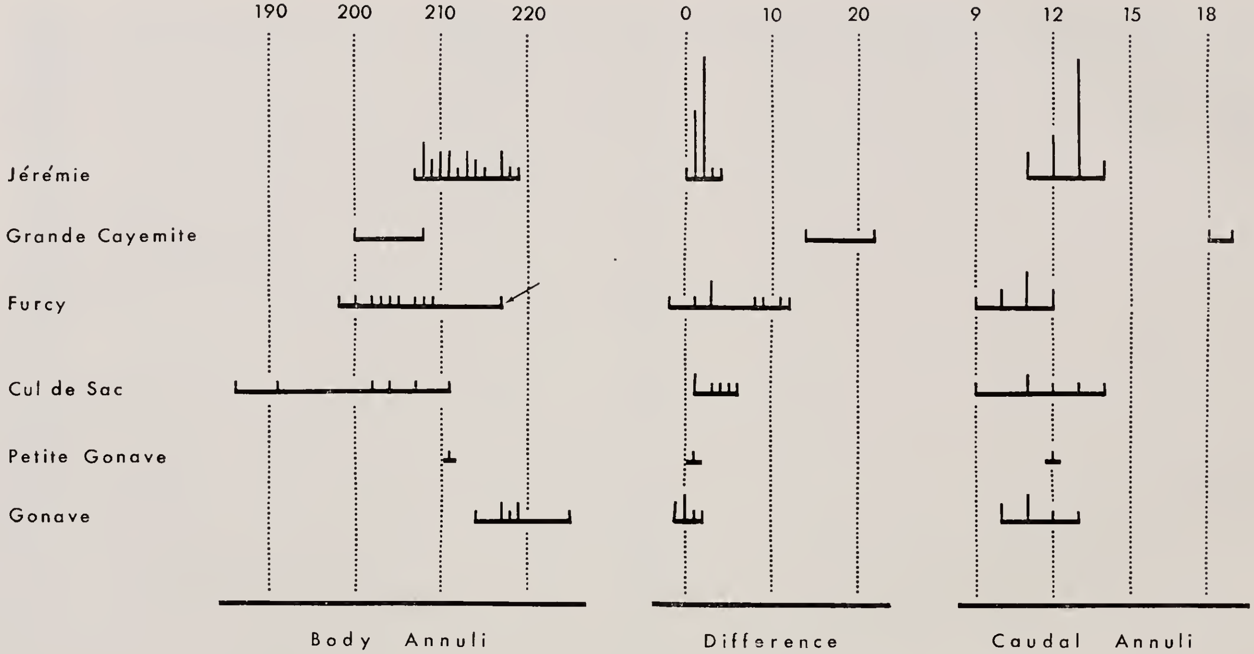

FIG. 15. *A. innocens.* Comparison of the several geographic samples for number of body annuli, difference between dorsal and ventral counts of body annuli, and number of caudal annuli. The arrow indicates the La Vanneau record.

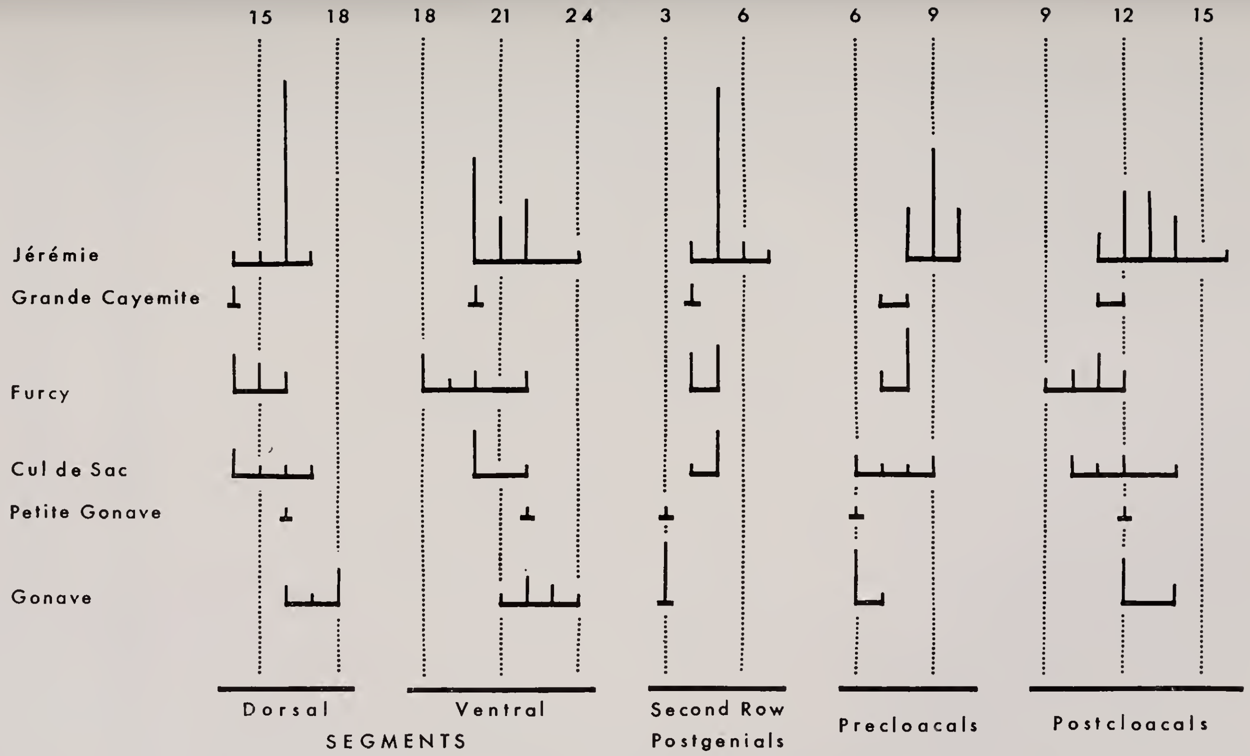

Fig. 16. *A. innocens.* Comparison of the several geographic samples for number of dorsal and of ventral segments to a midbody annulus, number of postgenials in the second row, and numbers of pre- and postcloacals.

Furcy, Port-au-Prince, Diquini), Cul-de-Sac (Thomazeau, Manneville, Morne-à-Cabrits), Petite Gonave Island, and Gonave Island (Point-à-Roquettes). Some of the data has been graphed in Figures 15 to 18.

The graphs and raw data permit the following conclusions: 1) the two specimens from Grande Cayemite differ decidedly from mainland Hispaniolan specimens; 2) the Gonave specimens differ decidedly from the Grande Cayemite specimens and from those of the mainland; 3) the specimen from Petite Gonave is intermediate between those from Gonave and the mainland sample; and 4) the several mainland localities show trends of

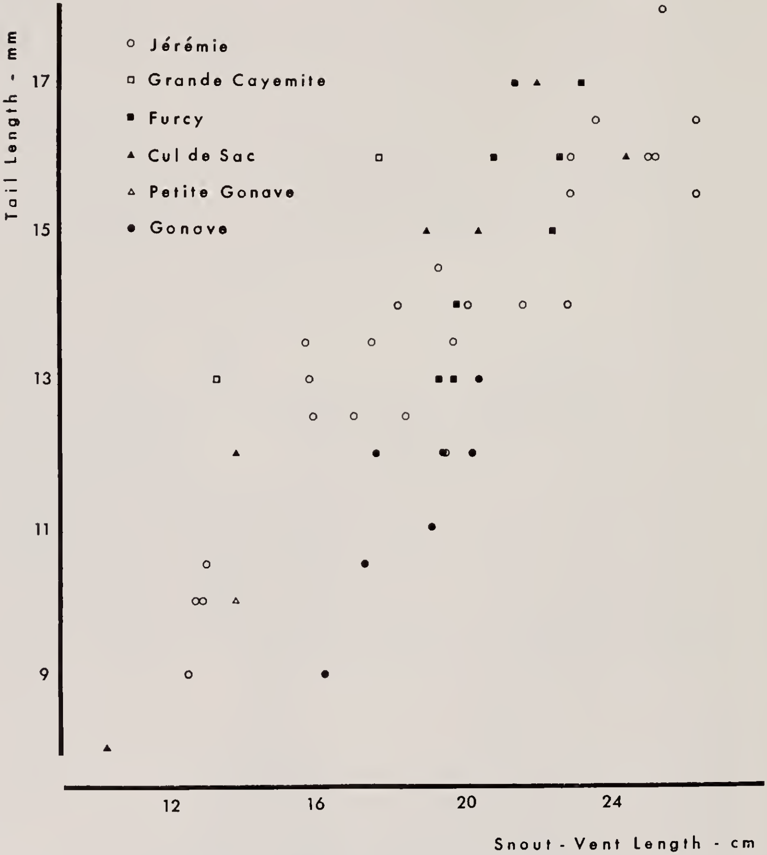

FIG. 17. *A. innocens.* Scatter diagram of tail length versus snout-vent length of the geographic samples.

variation from the Cul-de-Sac region to the tip of the Southwestern Peninsula.

1. The two specimens from Grande Cayemite Island are distinct from the mainland specimens in having the greatest difference (Difference, in Fig. 15) between dorsal and ventral numbers of body annuli, and for that matter are distinct in absolute number of dorsally counted body annuli. They are also distinct in number of caudal annuli, in relative tail length (Fig. 17), and in relative length from snout to back of first parietal (Fig. 18). In number of body annuli (Fig. 15), dorsal and ventral segment counts (Fig. 16), number of postgenials in the second row (Fig. 16), and pre- and postcloacals (Fig. 16), they are more distinct from the adjacent Jérémie sample than

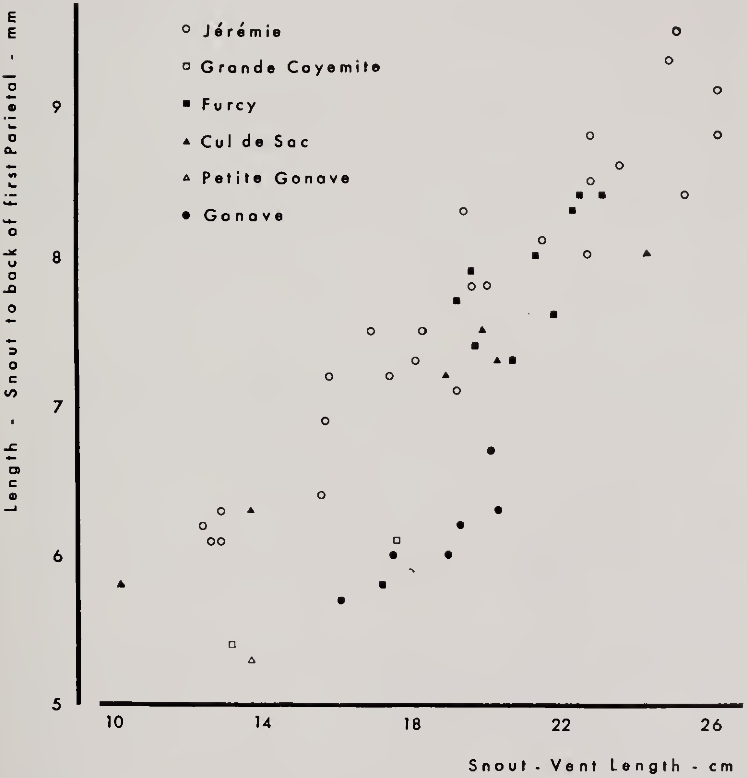

FIG. 18. *A. innocens.* Scatter diagram of length from snout to back of first parietal versus snout-vent length of the several geographic samples.

from the material from the vicinity of Furcy at the base of the Peninsula, though they appear intermediate between these two samples in several of the characteristics.

2. The Gonave series is clearly distinct from all mainland samples by the presence of a row of postmalars (and absence of a third row of postgenials), by a lower number of segments in the second postgenial row (Fig. 16), and by differences in the proportions of the head scales as indicated by a shorter relative distance to back of first parietal (Fig. 18). The several diagrams also suggest differences in body annuli (Fig. 15), dorsal and ventral numbers of body segments (Fig. 16), pre- and postcloacals (Fig. 16), and relative tail length (Fig. 17).

The Gonave series differs from the two specimens from Grande Cayemite by higher number of body annuli (Fig. 15), lower difference between dorsal and ventral counts (Fig. 15), and lower caudal counts (Fig. 15). There are also clear differences in numbers of dorsal and ventral segments (Fig. 16), postgenials in the second row (Fig. 16), the presence of a postmalar and absence of a third postgenial row, and the relatively much shorter tail (Fig. 17). The two populations often represent extremes within this species. While the limited number of specimens does not lend too much certainty to any one of the several characters, this does appear to be another instance of the conspicuous difference of ''peripherally'' isolated populations (Mayr, 1954).

3. The single specimen from Petite Gonave Island represents an interesting case. The island in question is so small (it is omitted on most maps, but shown on the plate opposite page 4 in Wetmore and Swales, 1931) that we suspected that the specimen might have come from Petit-Gôave on the mainland. However, its character pattern is close to or identical with that of the Gonave sample in all of the characters discussed above. Where there is some range in the Gonave values, the Petite Gonave specimen is at that end of the range closest to the Cul-de-Sac sample.

4. A variety of trends is shown between the three mainland samples. It is interesting that these seem continuous for only three characters (body annuli, precloacals, and relative length from snout to back of first parietal, Figs. 15, 16 and 18). A reversing cline is shown for range of difference, ventral segment number, and number of postcloacals, while the other characters do not exhibit any apparent trends.

A matter of possible significance or at least of interest is the position of the several island populations relative to these clines. The island data repeatedly fall closest to those from the immediately adjacent mainland sample (except for the characters that clearly define them). It is tempting, but dangerous, to speculate that this indicates closeness of relation, i.e., that the islands were populated from the adjacent mainland.

Nomenclature: The name *A. innocens* was assigned to three syntypes from Jérémie by Weinland (1862, pp. 132, 137), with the intention of vindicating the beast "von den Indianern . . . für Entsetzlich giftig gehalten." He mentioned that one specimen had been deposited in Berlin (ZMU 1386), and talked of one other in his personal collection. The second and third syntypes were later acquired by the Museum of Comparative Zoology (MCZ 3624-25). The larger of the MCZ specimens (MCZ 3624) shows the best agreement with Weinland's original measurements and is here designated as lectotype of *A. i. innocens.*

It seems clear that the Grande Cayemite and Gonave-Petite Gonave populations may each well be assigned subspecific status. For the first we have Cochran's (1928) name *A. caudalis* based upon just the specimens we have been discussing, and reflecting the increased caudal count and tail length. For the other we here propose the new name *A. i. gonavensis.*

AMPHISBAENA INNOCENS INNOCENS Weinland, 1862

Amphisbaena innocens Weinland, 1862, p. 137. Type locality: "in einem lichten Schlage von Campèche-Holz in der Nähe des Hafen-Städtchens Jérémie." Haiti. LECTOTYPE: MCZ 3624 (by present designation). PARATYPES: MCZ 3625, ZMU 1386.

Amphisbaena weinlandi Schmidt, 1928, p. 29. Lapsus for *A. innocens* Weinland.

Diagnosis: A form of *Amphisbaena* without fusion of head segments; having 186 to 219 body annuli along the ventral line; a difference of dorsal and ventral counts ranging from minus one to plus two; 10 to 15 caudal annuli; 14 to 17 dorsal and 18 to 22 ventral segments per midbody annulus; three postgenial and no postmalar rows of chin shields; and 4 (occasionally 6) precloacal pores. Tail pointed and caudal autonomy absent.

Description: Meristic characters are summarized in Table 1, and Figures 7, 8, 15, 16, 17 and 18; individual data in the appendix. Figure 19 shows the head scalation, Plate 6 various views of Jérémie specimens.

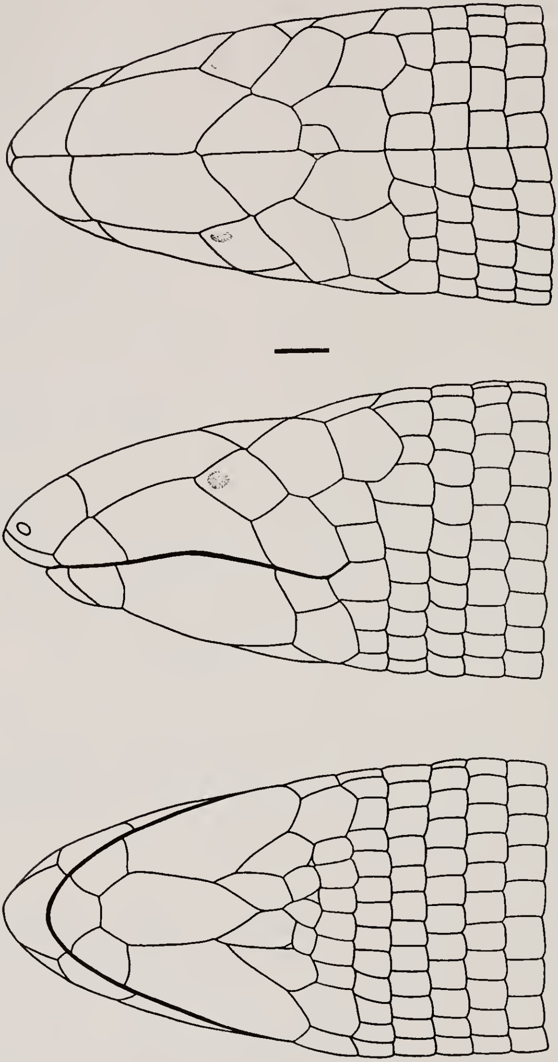

FIG. 19. *A. i. innocens.* Dorsal, lateral and ventral views of the head scales of ZMU 1386, from Jérémie, PARATYPE of *A. innocens* Weinland. The line equals 1 mm to scale. (V. Cummings, del.)

The preserved specimens are various shades of brown, one recently pickled series shows a dark violet-brown head and tail, grading to chocolate-brown on the body. The color is solid on the dorsal surface of the head and tail; on the rest of the body the rectangular center of each segment is much darker than its margin, giving the impression of dark spots. The color is darker dorsally than ventrally, but there are no white segments on which the color has dropped out entirely. One specimen (Manneville, MCZ 8748) has the uniform chocolate-brown dorsal and ventral color normally characteristic of *A. manni.*

The head scalation is characterized by lack of major fusions. The first two body annuli correspond to three dorsal half-annuli. The segments of the first are commonly referred to as temporal and postocular and abut middorsally on the frontals. The next posterior half-annulus culminates in the first of two pairs of enlarged parietals. There is some geographic variation in the point of ventrad penetration of the second half-annulus. This extends lowest in Jérémie specimens, while only the parietals are doubled in some Cul-de-Sac material, thus yielding two pairs of enlarged postfrontal segments.

The chin is characterized by a quite large second infralabial, by a malar segment that lies between this and the third infralabial, often far out of contact with the postmental. The extreme lateral segments of the postgenial rows give the impression of having been separated from the medial edge of the malars.

The fourth and fifth body annuli are narrower than the rest. The body annuli are generally characterized by extensive irregularities and asymmetries.

The tail is short and tends to be pointed and laterally compressed, particularly in Furcy and Jérémie material. The midventral segments of the first postcloacal annulus tend to be enlarged, often to one and a half times their normal length.

General observations: The thyroid of this form has been discussed by Lynn and Komorowski (1957).

Range: Southwestern Hispaniola.

Locality records (see Fig. 3 for map): HAITI:— (Barbour, 1930, 1935, 1937; Gray, 1872; Günther, 1865; Meerwarth, 1901; Stejneger, 1904; Strauch, 1881). Eastern end of San Domingo (=Hispaniola) (Cope, 1869). Moron (Cochran, 1924, 1941); USNM 60620. Jérémie (Barbour, 1914; Barbour and Loveridge, 1929; Cochran, 1941; Peters, 1878; Weinland, 1862); MCZ 3624

(LECTOTYPE), MCZ 3625 (PARATYPE); ZMU 1386 (PARATYPE). Place Negre, near Jérémie, MCZ 63609-20. Carrefour Sanon, near Jérémie, MCZ 63621-24. Laye, near Jérémie, MCZ 63625-27. Paroty, near Jérémie, MCZ 63628-29. La Vallée (Cochran, 1941); RMNH 10008. La Vanneau (Cochran, 1941); USNM 69439. Furcy, MCZ 51417; USNM 117250-51, 118036, 118906. Port-au-Prince (Werner, 1910); HM 2907. Diquini, USNM 118903. Thomazeau (Cochran, 1934a, 1941); MCZ 37595-97. Manneville (Barbour, 1914; Cochran, 1941); MCZ 8748, 62511. Morne-à-Cabrits (Cochran, 1941); USNM 59212.

Habits and habitat: We have no collecting notes, but offer the following items excerpted from a letter dated 10 February 1944 from Anthony Curtis, in Port-au-Prince, to Doris Cochran, and cited with her kind permission: "*Amphisbaena* comes to the surface in the dark, shortly before dawn. I believe they always remain underground or under stones except during this period, unless they meet the stinging ant *Solenopsis geminata*, when, as I have seen by the observation of other, not captive, specimens they are apt to ascend into daylight rather hurriedly."

AMPHISBAENA INNOCENS CAUDALIS Cochran, new comb.

Amphisbaena caudalis Cochran, 1928, p. 58. Type locality: "Grande Cayemite Island, Haiti." HOLOTYPE: MCZ 25550. PARATYPE: MCZ 25551.

Diagnosis: A form of *Amphisbaena* with no fusions of head scales, having 200 to 208 body annuli in ventral count, a difference between dorsal and ventral counts of 14 to 22; 18 to 19 caudal annuli; 14 dorsal and 20 ventral segments per midbody annulus; 3 postgenial and no postmalar rows of chin shields; and 4 precloacal pores. Tail cylindrical and caudal autotomy absent.

Description: Meristic characters are summarized in Table 1 and Figures 15, 16, 17 and 18, individual data in the appendix. Plate 6 shows the tail of the holotype.

The preserved specimens resemble the nominal race in most particulars. Their head scalation reminds one of that of Furcy and Cul-de-Sac samples. Only the two segments closest to the middorsal line are doubled. The midventral segments of the first postcloacal annulus are of normal size in the holotype and slightly enlarged in the paratype. The tail is cylindrical, of circular cross-section, and rounded at the end.

Range: Grande Cayemite Island, off southwestern Haiti.

Locality records (see Fig. 3 for map): HAITI: Grande Cayemite Island (Barbour, 1930, 1935, 1939; Barbour and Loveridge, 1929; Cochran, 1928, 1941); MCZ 25550 (HOLOTYPE), 25551 (PARATYPE).

AMPHISBAENA INNOCENS GONAVENSIS subsp. nov.

Diagnosis: A form of *Amphisbaena* with no fusions of head scales; having 214 to 225 body annuli in ventral count; a difference between dorsal and ventral counts between minus one and plus two; 10 to 13 caudal annuli; 16 to 18 dorsal and 21 to 24 ventral segments per midbody annulus; 2 postgenial and 1 postmalar rows of chin shields; and 4 (exceptionally 3) precloacal pores. Tail pointed, of rounded cross section, and caudal autonomy absent.

Holotype: PM 3384 a male collected by Philip S. Humphreys at Point-à-Roquettes, Gonave Island, Haiti, February-April 1959.

Allotype: PM 3385 a female collected with the holotype.

Paratypes: PM 3389 a male, PM 3386-88 three females collected with the holotype, and USNM 10168 from Gonave; MCZ 25549 from Petite Gonave.

Description: Meristic characters are given in Table 1 and Figures 8, 15, 16, 17 and 18, individual data in the appendix. Figure 20 shows dorsal, lateral and ventral views of the head scalation, Figure 21 a ventral view of the cloaca and tail. Plate 4 shows various views.

The color of preserved specimens resembles that of the nominal race. The head scalation is characterized by lack of major fusions. The first two body annuli correspond to three dorsal half-annuli, but two rather than one of these contact the frontal middorsally and are excluded from contact. The second pair may occasionally achieve point contact just posterior to the frontals, thus confusing the determination of first parietals.

The malars are split with their posterior portions forming the lateralmost segments of the postmalar rows.

The body annuli are similar to those of the nominal race, but show less irregularity. The tail is rounded in cross-section and the midventral segments are not enlarged. The precloacal pores are much larger and more clearly expressed in males than in females.

Range: Petite Gonave, and Gonave islands, Haiti.

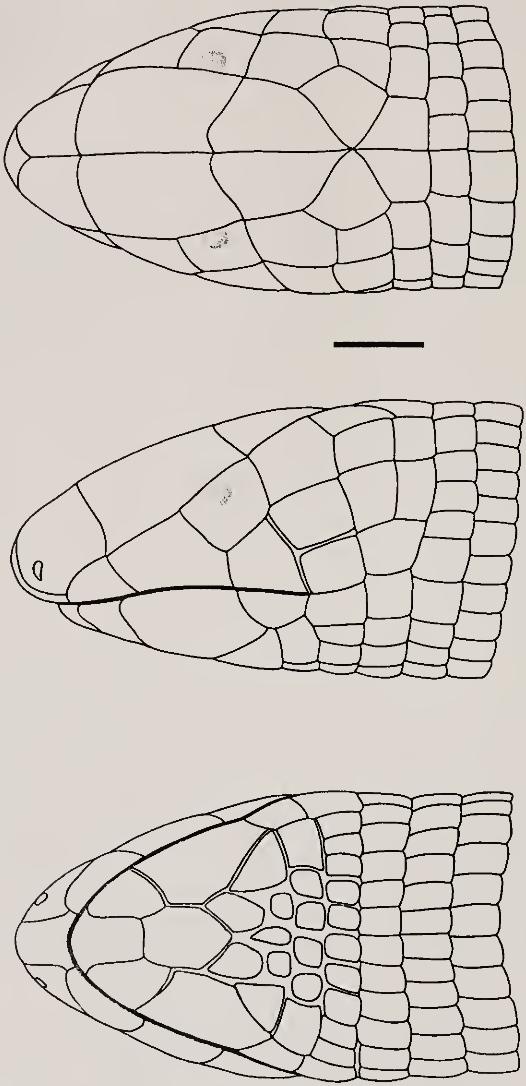

Fig. 20. *A. i. gonavensis.* Dorsal, lateral and ventral views of the head scales of PM 3388, from Point-à-Roquettes, Gonave, Haiti (PARATYPE). The line equals 1 mm to scale. (V. Cummings, del.)

Locality records (see Fig. 3 for map): HAITI: Petite Gonave Island: —— (Cochran, 1941); MCZ 25549 (PARATYPE). Gonave Island: —— (Cochran, 1941; Cope, 1879; Stejneger, 1904); USNM 10168 (PARATYPE). Point-à-Roquettes PM 3386-89 (PARATYPES), 3385 (ALLOTYPE), 3384 (HOLOTYPE).

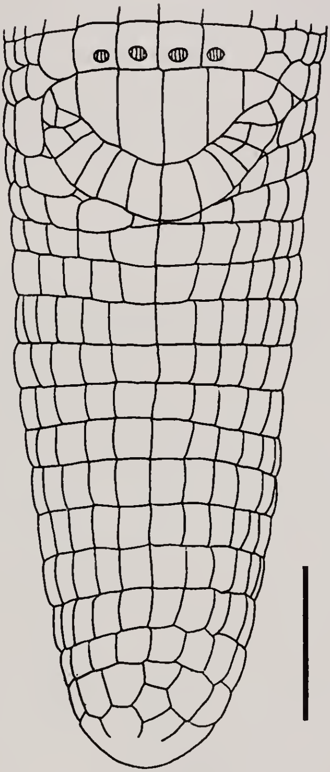

FIG. 21. *A. i. gonavensis.* Ventral view of cloaca and tail of MCZ 25549 from Petite Gonave Island, Haiti. The line equals 1 mm to scale. (M. Franson, del.)

AMPHISBAENA MANNI Barbour, 1914

Amphisbaena manni Barbour, 1914, p. 318. Type locality: "Cape Haitien, Haiti." HOLOTYPE: MCZ 8645. PARATYPES: MCZ 8646-47, USNM 67113.

Diagnosis: A form of *Amphisbaena* with the rostral and nasal fused, a suture connecting the nostril to the anterior suture defining the first supralabial. Specimens have 209 to 243 body annuli, 17 to 22 caudal annuli; 12 to 16 dorsal and 14 to 20 ventral segments per midbody annulus; generally (3 per cent exceptions) 2 postgenial and no postmalar rows of chin shields; and 4 to 9 precloacal pores. The sixth to seventh postcloacal annulus is slightly constricted, narrower, and more darkly pigmented. Caudal autotomy occurs here (between the fifth and seventh caudal annulus).

Geographic variation: This species exhibits a certain amount of minor geographic variation expressed both as a shift in the mean values of several characters between the various samples, and secondly in a general divergence of the sample from the montane portions of Haiti.

Thus, the two largest (if poorly preserved) samples from Los Bracitos and Samana differ in number of body annuli, dorsal segments to a midbody annulus, and precloacal pores (Fig. 22), and in various body proportions as well (Fig. 23). These differences are not sufficient to permit assignment of individual specimens to either locality. Smaller samples from scattered localities (not included in the figures) exhibit a similar pattern of variation. What makes this situation different from those previously discussed is the extreme range of variation shown by the material of the large samples. Table 1 does show that the range of variation (of body annuli) is highest in *A. manni* and *A. i. innocens* among the forms discussed, but this information is prejudiced by the fact that the *A. i. innocens* sample range included a clear case of geographical variation. In contrast the single Los Bracitos sample of *A. manni* has a range almost equivalent to the observed variation of the entire species, far greater than that of any non-Hispaniolan form.

The sample from several Haitian localities (Bombardopolis, L'Atalaye, San Francisque?) shows the only approach to recognizable geographic differentiation. This accounts for most of the species variation range not overlapped by that of the large samples. The illustrations show differences in number of body annuli, dorsal and ventral segments to a midbody annulus, first and second postgenials, and number of precloacal pores (Fig. 22), as well as minor differences in relative tail length and proportions of head shields (Fig. 23).

The Cap Haïtien sample and the single specimen from Port-au-Prince do not differ significantly from Dominican material.

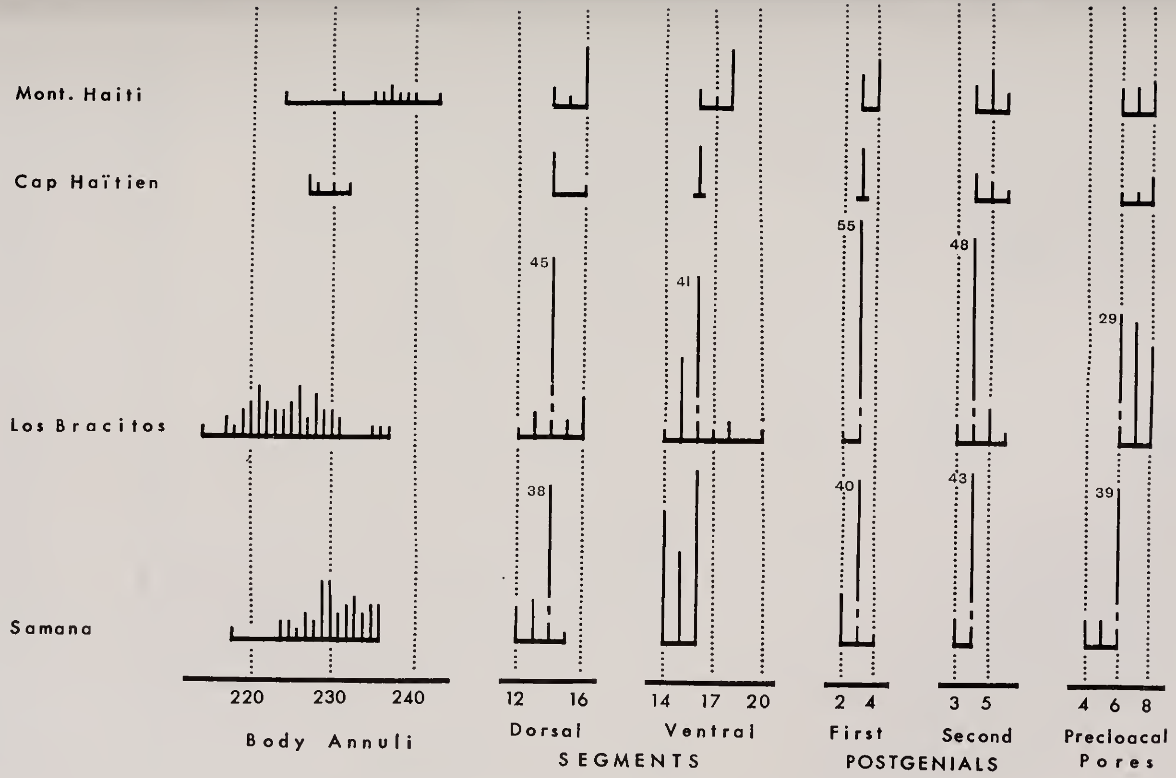

FIG. 22. *A. manni.* Comparison of the several geographic samples for numbers of body annuli, dorsal and ventral segments, numbers of first and second postgenials and number of precloacal pores.

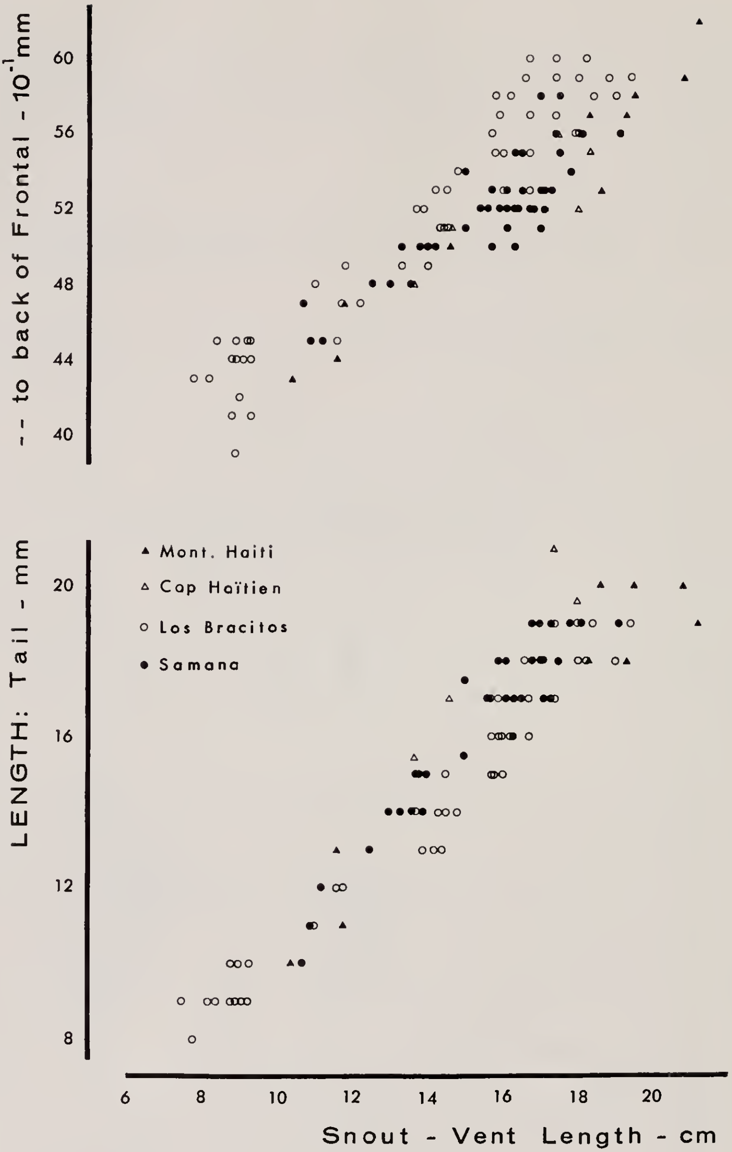

FIG. 23. *A. manni.* Scatter diagrams of tail length and of length of snout to back of frontal segments versus snout-vent length for the several geographic samples.

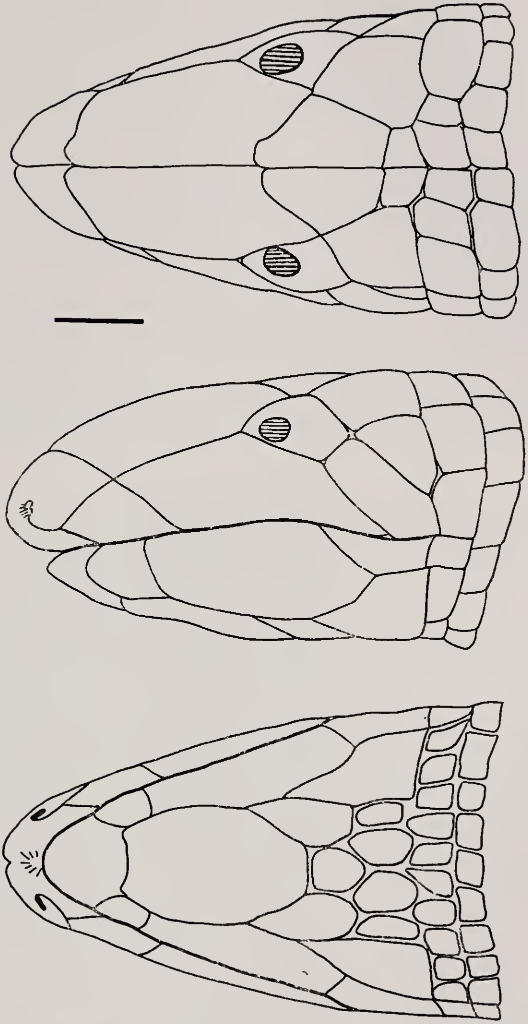

FIG. 24. *A. manni.* Dorsal, lateral and ventral views of the head scales of AMNH 49726 from Port-au-Prince, Haiti. The line equals 1 mm to scale. (M. Franson, del.)

The difference would be greater than here indicated if we are correct in assuming that the separation between populations is primarily altitudinal, because the Bombardopolis material was brought in from various points along the slope.

Description: Meristic characters are summarized in Table 1, and Figures 8, 22 and 23, individual data in the appendix. Figure 24 shows the head scalation, Figure 25 the ventral surface of tail and cloacal zone. Plate 7 presents photographs of color pattern.

Preserved specimens are a uniform brown with only slight darkening of the dorsal surfaces and somewhat more of head and tail. The tendency toward darkening of the rectangular center of each segment may be faintly noted under the microscope, but it is not otherwise apparent.

The head scalation is characterized by fusion of rostral and nasal. A suture connects the nostril to the first supralabial's anterior border. The temporal and postocular lie anterior to the vertically ascending first body annulus. Only in 20 per cent of the specimens do they give the impression of representing an

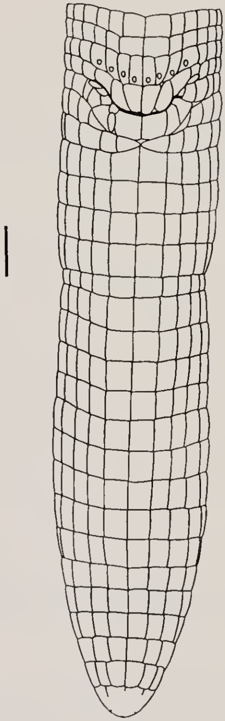

FIG. 25. *A. manni.* Ventral view of cloaca and tail of MCZ 8645 (HOLOTYPE) Cap Haïtien, Haiti. The line equals 1 mm to scale. (V. Cummings, del.)

anterior half-annulus. Here there are often splits in the temporal, and the several segments form a dorsally widening wedge.

The vertically ascending first annulus, which includes the slightly enlarged pair of parietals, may have some of its segments fused with those in line in the second annulus. The segments flanking the parietals are often wider than long, while the parietals are longer than wide, their anterior edge lying between the medial edges of the postoculars. The suture between parietals and frontals is often occupied by a pair of small segments that appear as if broken off the posterior edge of the frontals (Fig. 24). The last infralabials do not end exactly at the angulus oris, but often seem to have fused with or been encroached on by segments of the first body annulus. The fourth to sixth body annuli may be faintly narrowed and mark the turning point of the head on the neck. This rotation seems to be compensated for by the ventral halves of the third to fifth annuli.

The eye is very clearly noticeable through the ocular, which has a circular bulged out area covering its location. The pupil is directed forward and it is possible to see both eyes simultaneously from the front.

The tail is marked by a clear autotomy constriction at the level of the sixth to seventh caudal annulus. Posterior to this it maintains its diameter to within one diameter of the tip, whence it reduces conically toward the tip.

General observations: Two specimens (AMNH 43844 an adult, and 41058 a hatchling) showed everted hemipenes, a character rarely illustrated for amphisbaenids. Figure 26 shows those of the adult. The structures are short, without apparent ornamentation, bilobed with a deeply inserted bifurcate sulcus, and with more or less pointed apices (nomenclature modified from Dowling and Savage, 1960).

Lynn and Komorowski (1957) have discussed and figured the thyroid.

Range: Eastern, central and northwestern Hispaniola.

Locality records (see Fig. 3 for map): HISPANIOLA: —— (Barbour, 1930, 1935, 1937). HAITI: Port-au-Prince AMNH 49726. Bombardopolis MCZ 62534-40. L'Atalaye, near San Michel du Nord (Cochran, 1941); USNM 76656-57. Cap Haïtien (Barbour, 1914; Barbour and Loveridge, 1929; Cochran, 1941); MCZ 8645 (HOLOTYPE), 8646-47 (PARATYPES), 62532-33; USNM 67113 (PARATYPE). San Francisque (Cochran, 1941); USNM 69175. DOMINICAN REPUBLIC: Paradis, Herrmann's

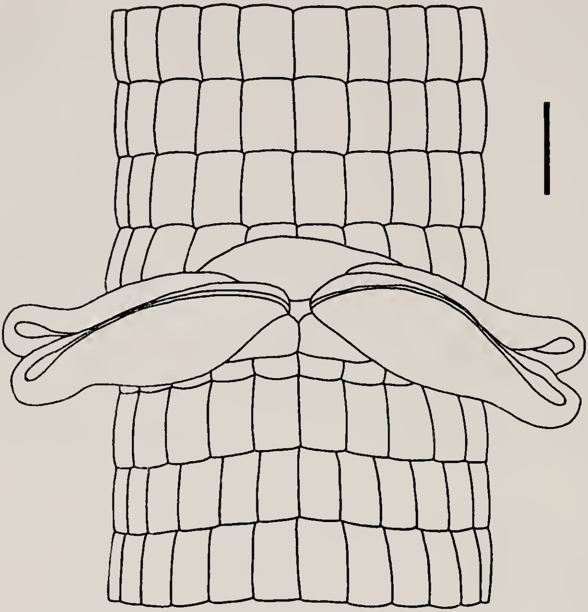

FIG. 26. *A. manni.* Views of the extruded hemipenes of AMNH 43844 from Los Bracitos, Dominican Republic. The line equals 1 mm to scale. (V. Cummings, del.)

Finca ("at least 1800′, near house") AMNH 51279-82. Rio San Juan (Cochran, 1941); RMNH 10010; UMMZ 92180; USNM 74680-83, 74685-87. Constanza (Cochran, 1941); MCZ 44389. Los Bracitos AMNH 41030-36, 41038-84, 41251, 41262-63. Una River AMNH 6341. Sánchez (Cochran, 1941; Schmidt, 1921); CAS 55001, MCZ 44399. Samana, Samana AMNH 40421-27, 40429, 42286, 50264, 63200-01, 63203. Laguna, Samana AMNH 42288-89. Samana District AMNH 40302-05, 43844-52, 44829-30, 50357-73, MCZ 57147. Boca del Infierno (Cochran, 1941); USNM 74978-79. Cordillera Central, Villa Altagracia (Cochran, 1941); MCZ 44390. Santo Domingo Province (Schmidt, 1921); AMNH 5207. San Pedro de Macoris (Schmidt, 1921); AMNH 7557-58. Isla de las Flechas AMNH 42287.

Habits: No collecting data are available; however, the jar containing the Los Bracitos sample also held a vial with two cylindrical eggs measuring 28 x 8.5 and 26.5 x 10.5 mm, respectively. The shorter and stouter egg held an embryo near term, lying in a twice-doubled position, and connected by its umbilical cord to an elongate yolk (?allantoic) mass (see Plate 7). The embryo's estimated length of 100+ mm suggests that some of the other Los Bracitos specimens had only recently hatched.

AMPHISBAENA BAKERI Stejneger, 1904

Amphisbaena bakeri Stejneger, 1904, p. 681. Type locality: "Lares, Porto Rico." HOLOTYPE: USNM 25541. PARATYPES: USNM 25537 (Lares), 27458 (Puerto Rico).

Diagnosis: A form of *Amphisbaena* lacking fusions of head shields; with 239 to 255 body annuli; 14 to 16 caudal annuli; 14 to 16 dorsal and 16 to 17 ventral segments per midbody annulus; two rows of postgenial and no postmalar chin shields; and 4 precloacal pores. Caudal autotomy not present.

Description: Meristic characters are summarized in Table 1, and Figures 8, 9 and 10, individual data in the appendix. Figure 27 shows dorsal, lateral and ventral views of the head scalation, Figure 28 the ventral surface of the tail and cloacal zone. Plate 8 shows various views.

The color of preserved specimens is a light brown, with a darker more uniform coloring of the dorsal surface of head and tail. The rectangular center of each segment is much darker than the margin, giving the impression of a pattern of dark spots. The coloration is darker dorsally than ventrally. The chin and varying portions of the ventral surface are occupied by light-colored segments lacking the dark rectangles, which do not fade but rather drop out suddenly along the margins of these light-colored regions.

The head segmentation of the few available specimens is characterized by striking variability. While there is no pattern of major fusions, there are remarkable differences in the shape of the individual segments from one specimen to another. The first dorsal half-annulus, comprising generally only temporal and postocular, may be followed by a second half-annulus which includes the parietals. Occasionally there is an anterior enlargement of one of its segments, which then wedges in between temporal and postocular. The first body annulus then follows, lying in a plane normal to the long axis of the body.

There are two postgenial and no postmalar rows of segments under the chin.

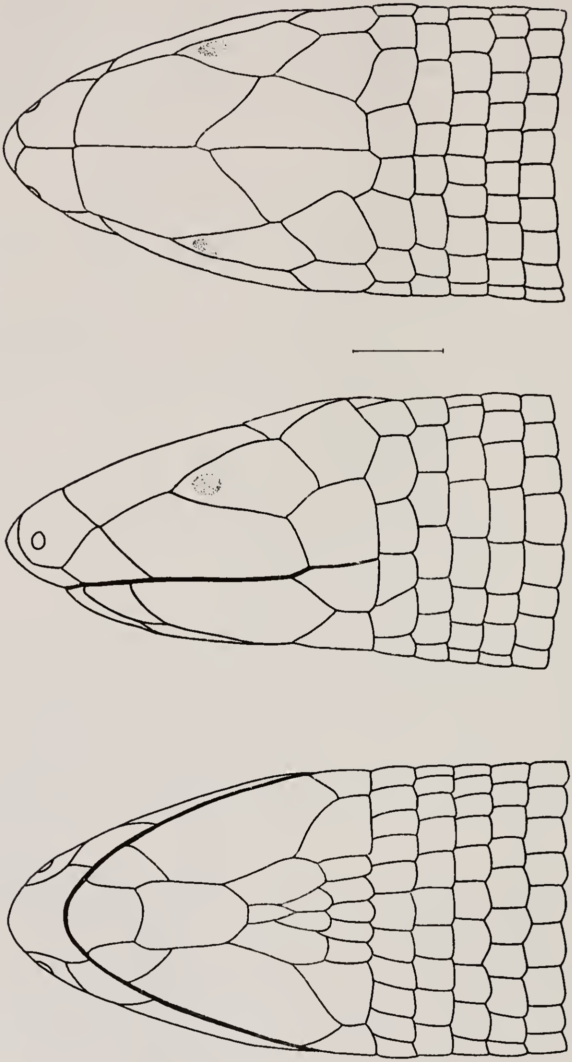

FIG. 27. *A. bakeri.* Dorsal, lateral and ventral views of the head scales of UMMZ 55824 from Mayagüez, Puerto Rico. The line equals 1 mm to scale. (V. Cummings, del.)

The tail is rounded and seems to be slightly flattened dorsoventrally in our material.

Range: Northwestern Puerto Rico.

Locality records (see Fig. 4 for map): PUERTO RICO: —— (Barbour, 1914, 1930, 1935, 1937; Grant, 1932; Stejneger, 1904); UPR 7; USNM 27458 (PARATYPE). Mayagüez (Danforth, 1925); CNHM 12473; UMMZ 55824; UPR 1. Las Marías UPR 2. Maricao UPR 10, 11. Lares (Schmidt, 1928; Stejneger, 1904); USNM 25537 (PARATYPE), 25541 (HOLOTYPE).

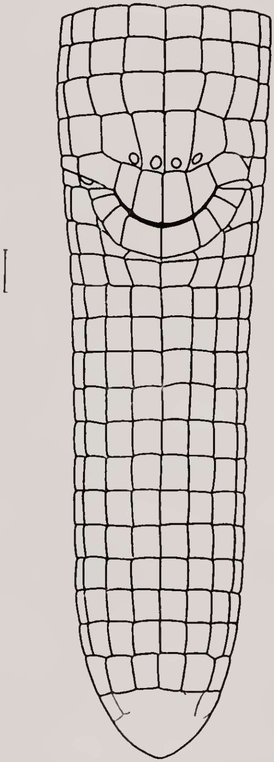

FIG. 28. *A. bakeri.* Ventral view of cloaca and tail of CNHM 12473 from Mayagüez, Puerto Rico. The line equals 1 mm to scale. (V. Cummings, del.)

AMPHISBAENA CAECA Cuvier, 1829

Amphisbaena caeca Cuvier, 1829, p. 73. Type locality: "Martinique," = Puerto Rico (cf. Stejneger, 1904, p. 675). LECTOTYPE: MHNP 550 (Strauch, 1881, p. 80). PARATYPES: MHNP 3114, 3115.

Amphisbaena (*Typhloblanus*) *coeca* Fitzinger, 1843, p. 22. Emendation.

Diagnosis: A form of *Amphisbaena* without fusions of head scales; having 217 to 236 body annuli; 13 to 18 caudal annuli; 13 to 18 dorsal and 14 to 20 ventral segments per midbody annulus; 2 rows of postgenial and 1 row of postmalar chin shields (3 and 0, respectively, in <1 per cent of examined specimens); and 4 (to 6) precloacal pores. The tail is cylindrical and its end rounded. A small number of specimens have a visible autotomy constriction at the sixth annulus, and autotomized tails show the break after the fourth to eighth, mostly after the fifth caudal annulus.

Geographic variation: Most of the observed geographical variation seems to involve a seemingly random variation of adjacent populations in one character or another. If this is disregarded it becomes possible to distinguish four regional groupings, dependent in each case on the existence of adequate samples. Arranged in a geographical sequence these are: 1) western Puerto Rico (Mayagüez, Las Mesas, Maricao, Sabana Grande, Bucarabones, Lares), 2) west-central Puerto Rico (Arecibo, Utuado, Cielitos, Juana Diaz, Salinas), 3) central Puerto Rico (Baranquitas, Aibonito, Cayey), and 4) northeastern Puerto Rico (Río Piedras, Loíza, South of Loíza, East of Loíza).

Figure 29 gives a graphic representation of the confusion of trends between these samples.[1] Only two of the trends continue in the same direction across the island. In three, the break occurs at sample 2, in one at sample 3, while two others show convergence toward samples 2 and 3 from 1 and 4. None of the present differences would justify nomenclatorial recognition of the populations. The western Puerto Rican sample seems to be the most clearly defined, both in terms of degree of difference and of range for the several characters. This was already brought out for body proportions in Figures 9 and 10. It is also true for the variation of head shields in the temporal region, the segment pattern being far more stable in the eastern half of the island. This variability of western *A. caeca* confirms Grant's (1932, p. 155) remarks, without invalidating the specific distinctness of *A. bakeri.*

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[1] We have avoided the application of statistical tests because of the composite nature of the samples. Changes in the relative number of specimens from any of the several here combined localities could in each case affect the steepness, though not the direction, of our trends. Furthermore, the vagaries of collectors, seasonal differences, etc. have often presented us with obviously non-random samples composed either of exceptionally large adults, or groups of recently hatched specimens.

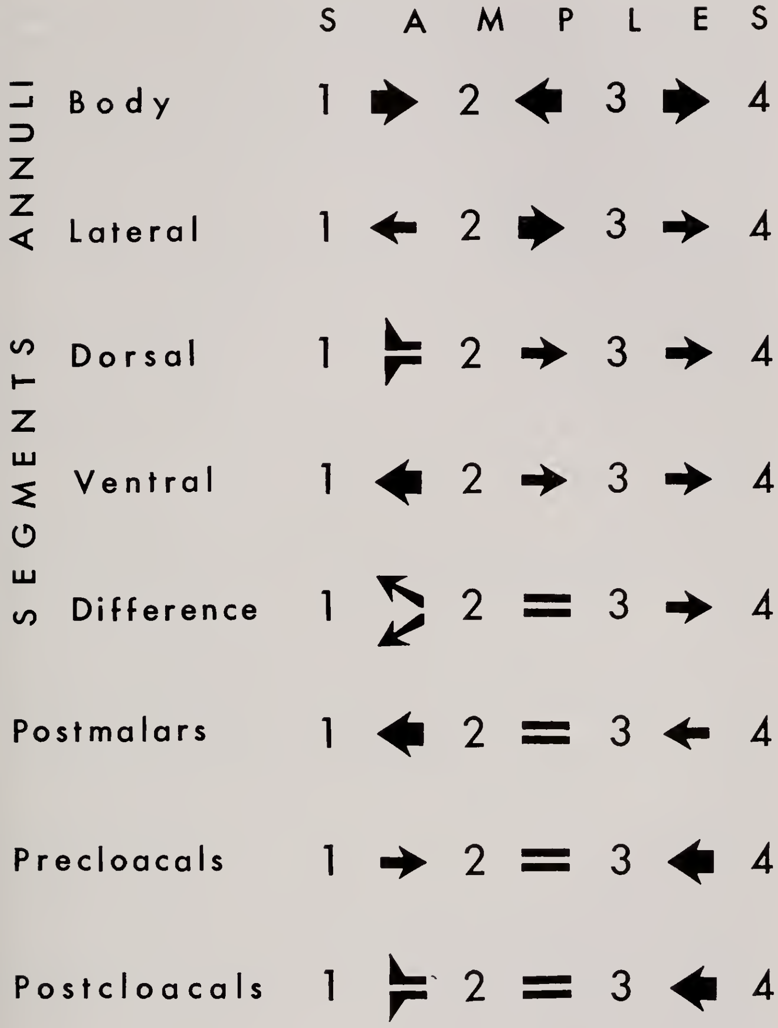

FIG. 29. *A. caeca.* Comparison of trends in a number of characters between the four geographic samples. Equal signs suggest that there is no clear difference. The arrows point from low to high values and their sizes indicate whether the trend is weak or strong. Paired arrows suggest an increase in values as well as in range. A V-shaped equal sign suggests an increase in range for equivalent mean. See text for discussion. The diagram elegantly suggests the confusion of trends between the samples.

A situation that we do not understand at all, but which may have definite bearing on the matter of *A. bakeri,* is posed by two specimens from Aguadilla (from which we lack further material) and one from Salinas. When the former were first examined, their extremely low body annuli (200, 202), high caudal annuli (22, x) counts, odd body proportions, and "uniform" coloration suggested that the locality might be erroneous. Dr. F. W. Braestrup of the København Museum kindly confirmed that the collector (Meinert, the well-known Danish entomologist) had been working at Aguadilla and had been in a position to collect amphisbaenids. The Salinas specimen represents one of an otherwise normal series of *A. cacca,* and did not reach us until this study had been completed. It agrees with the Aguadilla pair in all but color pattern, differing from the rest of the Salinas series (and *A. cacca* in general) in number of body and caudal annuli, relative tail length, and possibly in arrangement of segments in the occipital region.

It is unlikely that these three specimens from two quite distant localities represent geographic variants. The Aguadilla specimens are particularly puzzling, and we here list them as *incertae sedis* in the hope that more material will permit resolution of the matter.

Description: Meristic characters are summarized in Table 1, and Figures 8, 9, 10, and 11, individual data in the appendix. Figure 30 shows the head scalation, Figure 31 the ventral surface of tail and cloacal zone. Plates 8 and 9 present photographic views.

Preserved specimens are various shades of brown, solidly so on the dorsal surface of head and tail. On the rest of the body the rectangular center of each segment is much darker than its margin, giving the impression of dark spots. The color is darker dorsally than ventrally. Some of the specimens have a white ventral stripe, normally ranging from the cloaca anteriorly for one-third to one-half the length of the trunk. Some geographic variation exists in this character, with Aibonito and Cayey specimens having little or no white. The stripe is produced by a dropping out of the pigment on specific segments rather than by a fading of the color pattern.

The head scalation is characterized by lack of major fusions. The first three body annuli correspond to four or sometimes five dorsal half-annuli, of which the temporal-postocular form the first. There may be two, one or no temporals, and asymmetry often exists. This variation of the temporal region seems more pronounced in western Puerto Rico, with variation of the parietal segments independent of geography. The dorsal segments of the second half-annulus (first one after the temporal) may or may not meet at the dorsal midline. All intermediates may be observed from full and broad middorsal contact, to point contact

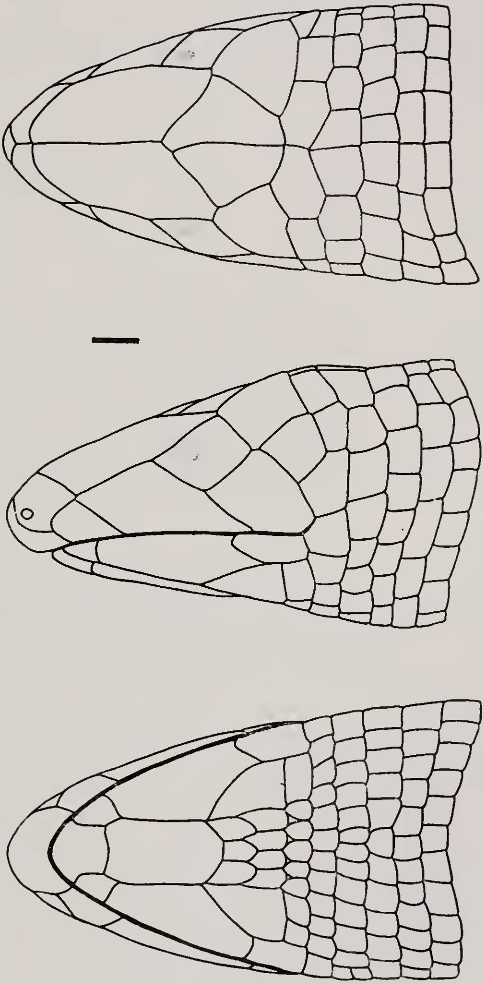

Fig. 30. *A. caeca.* Dorsal, lateral and ventral views of USNM 27223 from Utuado, Puerto Rico. The line equals 1 mm to scale. (V. Cummings, del.)

of two wedge-shaped segments, to complete exclusion of the segments by frontals and parietals. The shift of this second half-annulus is ventrad, but not forward (as in *A. i. gonavensis*). The annulus is displaced, or interrupted, but retains its position in a plane approximately normal to the long axis of the body. Various fusions and irregularities occur along the middorsal line, often affecting the segments of the first four to five annuli.

The chin pattern is adequately shown in Figure 30. Only a few western and west-central specimens show variations therefrom, coupled generally with abnormalities of the pattern of dorsal annuli.

The anterior five to seven body annuli seem narrower, show some ventral curvature, and represent the zone of the head joint. The trunk annuli show few fusions, dorsal half-annuli and the like, except for a zone of irregularity just anterior to the cloaca.

The tail is cylindrical, rounded terminally and bears a poorly marked autotomy constriction. This, the sixth or seventh postcloacal annulus is often narrower and more solidly pigmented.

General observations: The skull of this form was discussed by Kesteven (1957), and is figured on Plates 2 and 3. Camp (1923) discussed and figured the hyoid apparatus of an embryo. The thyroid of this form has been discussed and figured by Lynn and Komorowski (1957). Zavattari (1910) comments on hyoid muscles.

Two specimens, a hatchling AMNH 13237 and an adult male MCZ 58831, have everted hemipenes. Those of the adult are incompletely everted, but show a better preservation of detail (Pl. 9, fig. E). The general shape is similar to that of *A. manni,* short, without ornamentation except for a loose folding (possibly due to the incomplete eversion), bilobed with a deeply inserted bifurcate sulcus (its outside edges reinforced by a ridge of skin), but with less pointed apices (eversion?). The sulci of a hemipenis start at the medial surface of each base, swing to its lateral side and ascend to the level where the apices separate. From here it ascends — the medial base of each apex swinging clockwise around one and counterclockwise around the other in a 180° circle to terminate at the distal extremity. The folding of the free skin of each hemipenis leads to the suspicion that the passage of the sulci is straighter in the turgid organ.

Range: Puerto Rico (with the possible exception of the northwestern corner of the island).

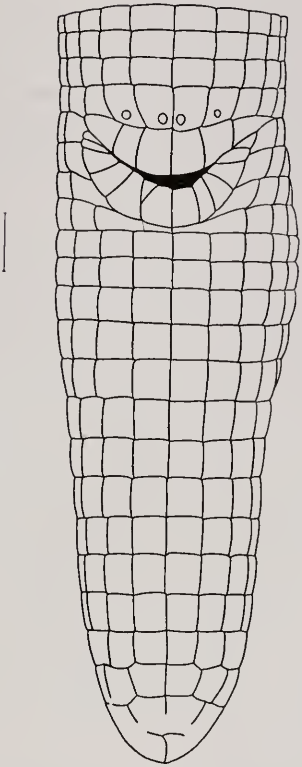

FIG. 31. *A. caeca.* Ventral view of cloaca and tail of USNM 27223 from Utuado, Puerto Rico. The line equals 1 mm to scale. (V. Cummings, del.)

Locality records (see Fig. 4 for map): PUERTO RICO: "Martinique" (Cuvier, 1829; Duméril and Bibron, 1839; Duméril and Duméril, 1851; Duvernois, 1838; Gray, 1831; Griffith and Pidgeon, 1831; Peters, 1878; Reinhardt and Lütken, 1862; Strauch, 1881); MHNP 550 (LECTOTYPE), 3114 (PARATYPE); RMNH 3563. —— (Atiles, 1887 *in* Grant, 1937; Barbour, 1914, 1930, 1935, 1937; Boulenger, 1890a; Grant, 1932, 1946; Gundlach, 1881; Peters, 1876; Stahl, 1882 *in* Grant, 1937; Stejneger, 1904); KM R-4413; UPR 6, 8; ZMU 8949. Mayagüez (Burt and Myers, 1942; Schmidt, 1928); CNHM 102260 (data not listed); SU 7775; UPR 3, 4, 9, 12, A, B. Las Mesas, near Mayagüez MCZ 64133-34. Maricao MCZ 36303; UMMZ 73839.

Sabana Grande UMMZ 73844. Bucarabones MCZ 61500. Guanica (Fowler, 1918). Lares (Schmidt, 1928; Stejneger, 1904); USNM 25538-40. Arecibo HM 2434. Utuado (Schmidt, 1928; Stejneger, 1904); USNM 27223. Cialitos UMMZ 73841. 3 miles east of Juana Díaz UMMZ 73846. 10 miles east of Juana Díaz MCZ 36301. Salinas CM 36276,[1] CM 37636-39. Barranquitas UPR 5. Aibonito (Schmidt, 1920, 1928); AMNH 13103, 13132, 13146-47, 13153, 13237, 13325, 13327-28, 13864-69, 14008; CAS 54858. Cayey MCZ 36311-24; UMMZ 73832 (+A – M), 73835 (6433-40). Bayamón (Schmidt, 1920, 1928; Stejneger, 1904); AMNH 8591; CAS 54861; RMNH 9985; USNM 27320-22. Camp Buchanan UMMZ 73838. Río Piedras (Schmidt, 1920, 1928); MCZ 36304; UMMZ 73840, 73842. 10 kilometers south of Canovenas (=Loíza) MCZ 36325; UMMZ 73830 (3377-82, 3393-96), 73831 (+ A – J), 73833 (2155-59), 73836 (3658-66). Near Canovenas (=Loíza) UMMZ 73834 (+2702-09, 2711). 10 kilometers east of Canovenas (=Loíza) MCZ 36326-50 (+1637-38, 3174-84, 4526, 5046, 6125, 6152, A — H, J — N, P, R — T). Humacao MCZ 36302; UMMZ 73837. Punta Santiago MCZ 58831. El Yunque UMMZ 53253. Luquillo (Ranger's Cabin) (Schmidt, 1928; Stejneger, 1904); MCZ 36307-10; UMMZ 73845 (1091-92); USNM 27005-06. Catalina Plantation, 890 feet, on El Yunque (Schmidt, 1928; Stejneger, 1904); MCZ 7902; USNM 26879-81. Río Mameyes, near headwaters UMMZ 73843. Doubtfully referred specimens: Aguadilla KM R-1414, 1416.[1] Salinas CM 36277.[1]

Habits and habitat: "All of the specimens were found burrowing in the ground, most of them uncovered by cultivation. One was located about three inches beneath an ant's nest, under a log." (Schmidt, 1920, p. 194; 1928, p. 119).

"Three eggs were found — one beneath a termite nest, the other two under a log where the above-mentioned adult was dug up. The largest egg measured 42 x 11 mm." (Schmidt, *op. cit.*). The egg in question (AMNH 13237 from Aibonito) contained a specimen of hatchling size (78 x 8 mm.) and an elongate mass of yolk similar to that described for *A. manni*. The several small Aibonito specimens would then appear to be hatchlings or pre-term embryos and to mark the minimum size of the species.

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[1] Data at end of Appendix.

AMPHISBAENA FENESTRATA (Cope), 1861

Diphalus fenestratus Cope, 1861, p. 76. Type locality: St. Thomas, Virgin Islands (by present restriction). HOLOTYPE: USNM 11715.

Amphisbaena antillensis Reinhardt and Lütken, 1862, p. 224. Type locality: St. John, Virgin Islands (by present restriction). LECTOTYPE: KM R-449. PARATYPES: KM R-4411 (Virgin Islands), ZMU 4346 (St. Thomas).

Notes on the types: Cope (1861, p. 76) described *D. fenestratus* from material discovered by A. H. Riise "in the West Indian Islands of St. Thomas and Santa Cruz," but neglected to name a type. Stejneger (1904, p. 678) believed the type to be USNM 11715. This specimen had initially been catalogued as collected on St. Thomas by A. H. Riise. Stejneger crossed off St. Thomas in the USNM catalog and wrote "St. John" above this. He cited the specimen as from St. John without giving reasons for his action. St. Thomas was the home of the collector and is one of the islands on which this species occurs. Since the inter-island variation of the species is insufficient to allow us to allocate specimens to islands, it seems best to retain the original locality.

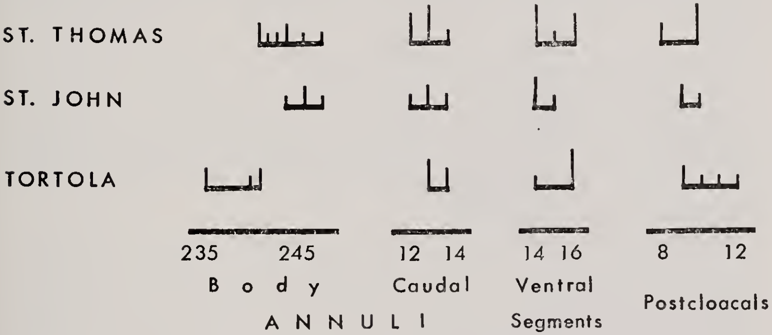

FIG. 32. *A. fenestrata.* Diagram of body annuli, caudal annuli, ventral segments per midbody annulus, and postcloacal segments for specimens from the three Virgin Islands.

Grant, to whom we owe much of the material here discussed, has presented reasons (1937a, p. 512; 1946, p. 60) for the probable absence of this species from "Santa Cruz" (=St. Croix). We here restrict the type locality to "St. Thomas."

Amphisbaena antillensis was described by Reinhardt and Lütken (1862, p. 224) from "St. Thomas og St. Jan." The

Universitetets Zoologiske Museum in København retains two specimens (KM R-449 and R-4411) marked ''Originalexemplarer'' (=Types) in Reinhardt's handwriting. These are the remnants of a type series, part of which was exchanged to other museums (Braestrup, *in litt.*). Neither is in perfect agreement with the original description, which appears to have been composite. We select KM R-449 from ''St. Jan'' as lectotype, because it is closest to the original description and bears a definite locality label. The restricted type locality is then St. John.

Diagnosis: A form of *Amphisbaena* with the nasal scales kept from contact by the ascending process of the rostral which contacts the frontals. Specimens have 236 to 249 body annuli; 12 to 14 caudal annuli; 13 to 14 dorsal and 14 to 16 ventral segments per midbody annulus; 2 postgenial and 1 postmalar rows of chin shields; and 4 precloacal pores. Caudal autotomy not present.

Geographic variation: The sample is too small to justify a long discussion, but Figure 32 suggests that the Tortola sample differs from those collected on St. Thomas and St. John. It is perhaps suggestive that there is a tendency for values approaching those shown by *A. caeca* with increasing distance from Puerto Rico.

The possible occurrence of this species on Virgin Gorda, Culebra and Viques has never been confirmed.

Description: Meristic characters are summarized in Table 1, and Figures 8, 11 and 32, individual data in the appendix. Figure 33 shows the head scalation, Figure 34 the ventral surface of the tail and cloacal zone.

Preserved specimens are various shades of brown, solidly so on the dorsal surface of the head and tail. On the rest of the body the rectangular center of each segment is much darker than its margin, giving the impression of dark spots. The color is darker dorsally than ventrally. Most of the specimens have most of the midventral region white, due to a dropping out of the pigment on a number of the ventral segments.

The head scalation is characterized by the posterior elongation of the rostral which keeps the nasals from contact and inserts for some slight distance between the prefrontals. The first body annulus continues dorsad and includes the slightly enlarged parietals. Only the postocular and temporal lie anterior to it, but occasional specimens show various fusions and complications between segments of the first two body annuli. The first annulus lies in a plane normal to the long axis of the animal's trunk.

The shape of the head and segmentation of the head joint reminds one of *A. caeca,* as does the segmentation pattern of the trunk. The tail shows no autotomy plane.

General observations: The skull of this form is illustrated in Plates 1 and 3.

Range: Virgin Islands, from St. Thomas to Tortola.

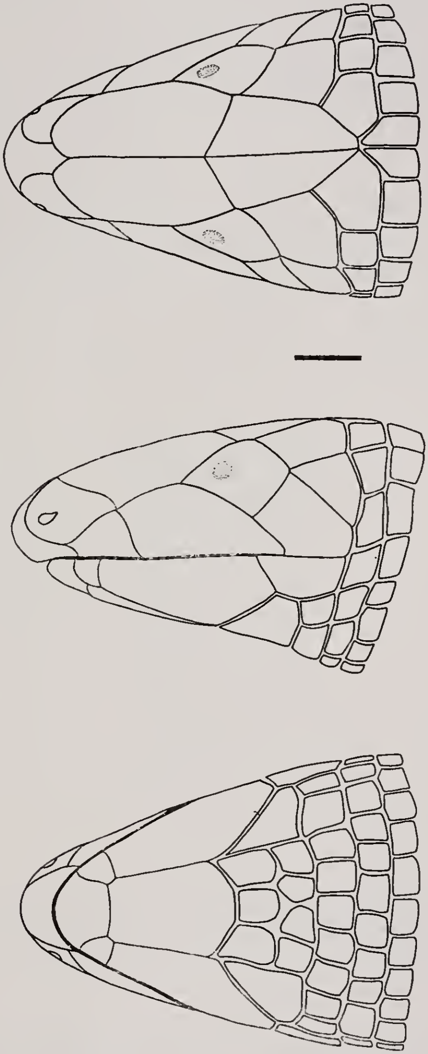

FIG. 33. *A. fenestrata.* Dorsal, lateral and ventral views of MCZ 36305 from Tortola, Virgin Islands. The line equals 1 mm to scale. (V. Cummings, del.)

Locality records (see Fig. 1 for map): VIRGIN ISLANDS: —— (Barbour, 1914, 1930, 1935, 1937; Cope, 1869; Gray, 1872, 1873; Günther, 1865; Stejneger, 1904); KM R-448, R-4411 (PARATYPE *antillensis*). ST. THOMAS: —— (Boulenger, 1885, 1890; Cope, 1861; Grant, 1937a, 1946; Gray, 1865, 1872, 1873; Meerwarth, 1901; Reinhardt and Lütken, 1862; Stejneger, 1904 see NOTES ON THE TYPES; Strauch, 1881); BM 60·4·18·71-72; CNHM 51586 (800′ altitude, on shady hillside); HM 308; KM R-4410; MHNP 1071; USNM 11715 (HOLOTYPE *fenestrata*); ZMU 4346 (PARATYPE *antillensis*). ST. JOHN: —— (Boulenger, 1885; Reinhardt and Lütken, 1862; Stejneger, 1904 see above; Strauch, 1881); BM 65·10·2·11; KM R-449 (LECTOTYPE *antillensis*); VM 12345[1]; KUMNH 45630 (West end Great St. James). Dorothea (Grant, 1946); UMMZ 91436. TORTOLA: —— (Grant, 1932a); MCZ 36305-06; SU 14633; UMMZ 73847 A-B (+C); 80649.

Habitat: "It lives like *Typhlops* and is usually found in St. Jan under dry leaves of sugar cane which are cut off the cane

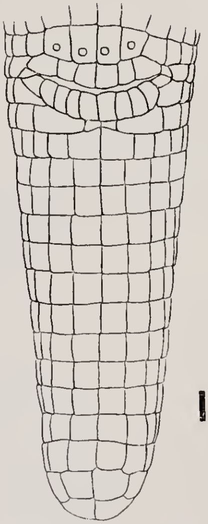

FIG. 34. *A. fenestrata.* Ventral view of cloaca and tail of MCZ 36305 from Tortola, Virgin Islands. The line equals 1 mm to scale. (E. Coogle, del.)

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[1] Data in addendum to Appendix. May have been one of syntypes of *A. antillensis.*

during the harvest. These leaves are left covering the fields for some time. . . . On St. Thomas, where sugar cane is no longer grown, it is found under stones in small holes on moist ground; here it is very rare." (Riise, *in* Reinhardt and Lütken, 1862, translation courtesy of F. W. Braestrup.)

Genus CADEA Gray, 1844

Cadea Gray, 1844, p. 71. Type species: *Amphisbaena punctata* Bell, 1827 (name preoccupied, replaced by *Cadea blanoides* Stejneger, 1916) by monotypy.

Discussion: Vanzolini (1951a, p. 114) diagnosed this genus as follows:

"Snout compressed, pointed, or raised in a small keel. Basipterygoid processes, partes posteriores choanarum and supratemporals present. Quadrate proximally dilated. Meckel's groove

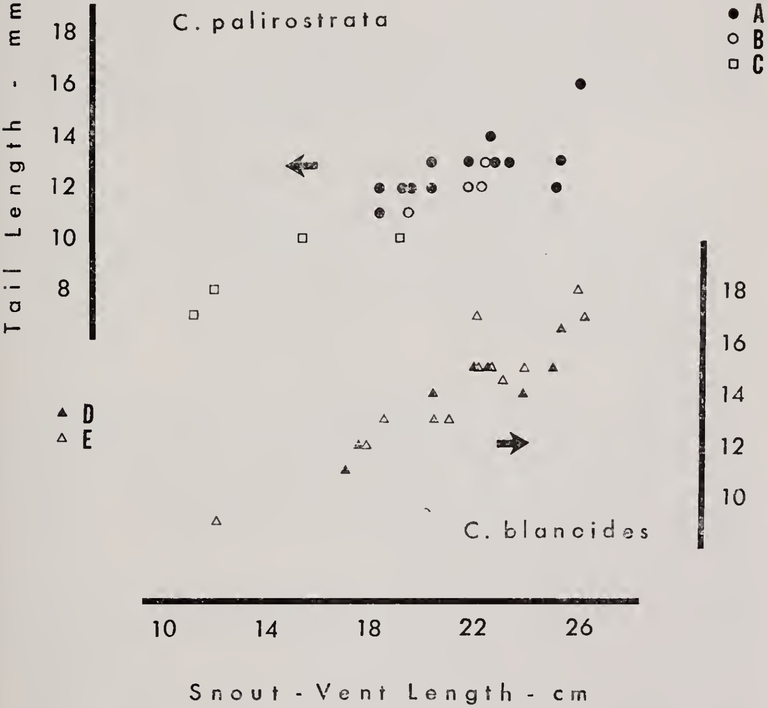

FIG. 35. *Cadea.* Scatter diagram of tail versus snout-vent length demonstrating the absence of sexual dimorphism in relative tail length. Solid symbols indicate males, open circles and triangles females, open squares indeterminate. A-C, *C. palirostrata,* D-E, *C. blanoides.*

open. Dentition 7; 5; 7. One unpaired median shield adjacent to the rostral. Nasal shields separated from first labials.''

This may be amplified to include certain other characters. These are:

A narrow scale separating the azygous prefrontal from the supralabials. Head relatively pointed with quite distinct postcephalic narrowing. Atlas (vertebra) consisting of two neural arch halves plus a hypocentrum. Dorsal and ventral folds (of the integument) absent, lateral folds expressed as a narrow zone in which half-annuli run out, with the division skipping back and forth between often non-aligned segments (Gans, 1960, p. 145, footnote). Dorsal segments rounded instead of rectangular (Plates 11 and 12). No caudal autotomy. Tail short, becoming wider in the immediate postcloacal region, flattened ventrally and domed dorsally. The precloacal pores in two series of very small segments running medially from the lateral edge of the precloacals, interspersed between the precloacals and the last, non-pore bearing, body annulus which often contacts the precloacals at the midline. The dorsal surface has a color pattern that is more or less independent of the segmental arrangement.

CADEA BLANOIDES Stejneger, 1916

Amphisbaena punctata Bell, 1827, p. 236; (? plate 20, fig. 2 — *not seen*). Type locality: ''In Ins. Cubâ.'' HOLOTYPE: BM 1946.8.2.20. Junior homonym of *Amphisbaena punctata* Wied, 1825 (= *Leposternon microcephalum* Wagler, 1824; cf. Wagler, 1833, pl. 16). Also see: Bianconi, 1850.

Cadea blanoides Stejneger, 1916, p. 85. *Nomen novum* for *Amphisbaena punctata*.

Diagnosis: A form of *Cadea* with 175 to 218 body annuli; 10 to 14 caudal annuli; 25 to 33 segments to a midbody annulus; 6 to 8 precloacal segments; and 7 to 9 (occasionally 4) precloacal pores in two series. Head with faint lateral compression. Dorsal surface of body speckled with brown dots which may coalesce into a series of lines on the tail.

General observations: Zug and Schwartz (1958), some of whose data were used for the diagnosis, have discussed the variation of this species. They suggested the possible existence of an eastern race with low precloacal pore counts. This suggestion is not confirmed by the USNM specimen from Matanzas (which has 6 pores). The sexual dimorphism in number of caudal annuli, relative tail length, and smaller size of female specimens (Fig. 35) suggested by them could not be confirmed after the entire sample had been sexed by examination of gonads, rather than hemipenes.

Figure 36 shows the head scalation; Figure 37 is a view of the underside of the tail.

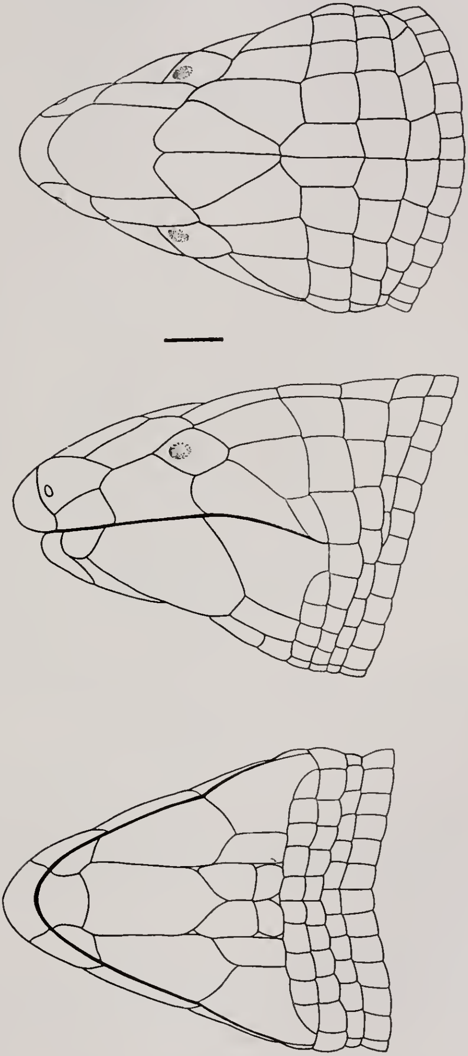

FIG. 36. *Cadea blanoides.* Dorsal, lateral and ventral views of AMNH 78397 from the Sierra de las Casas, just west of Nueva Gerona, Isla de Pinos. The line equals 1 mm to scale. (V. Cummings, del.)

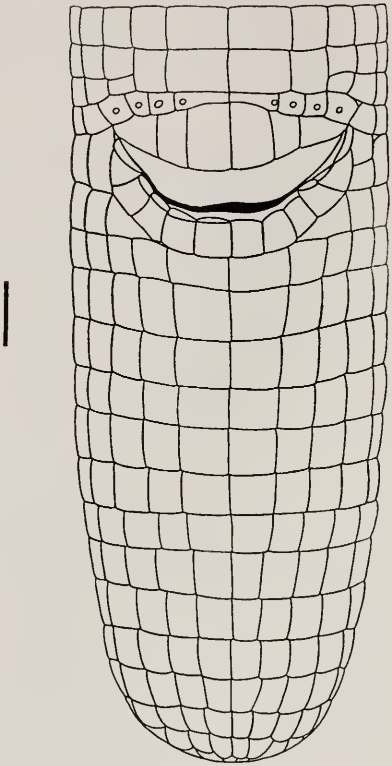

FIG. 37. *C. blanoides.* Ventral view of cloaca and tail of AMNH 78397 from the Sierra de las Casas, just west of Nueva Gerona, Isla de Pinos. The line equals 1 mm to scale. (V. Cummings, del.)

The skull and mandible were figured by Vanzolini (1951, figs. 1-5). The thyroid was studied by Lynn and Komorowski (1957). Payne (1906, and *in* Eigenmann, 1909) described the eye, and this description was commented on by Franz (1934) and Bellairs and Boyd (1947).

Range: Cuba, west of Matanzas; Isla de Pinos.

Locality records: CUBA: —— (Barbour, 1930, 1935, 1939; Barbour and Ramsden, 1916; Bell, 1827; Bianconi, 1850; Boulenger, 1885; Cocteau and Bibron, 1838, 1843; Dickerson, 1916; Duméril and Duméril, 1851; Duméril and Bibron, 1839; Gervais, 1853; Gray, 1831, 1844, 1865, 1872, 1873; Gundlach, 1875, 1880; Lichtenstein, 1856; Mertens, 1926; Payne, 1906; Reinhardt and

Lütken, 1862; Strauch, 1881; Zug and Schwartz, 1958); ANSP 9670; BM 1946·8·2·20 (HOLOTYPE of *A. punctata*); HM 5004; KM R-4412; MHNP 3116-17, 3117A; RMNH 3577, 3821, 9977. UH 545.[1] USNM 5729, 36811-12; ZMU 2635, 4082, 9381, 10496. Pinar del Rio Province: Cueva de Santo Tomas, 10 kilometers north of Cabezas (Zug and Schwartz, 1958); AMNH 77789. San Diego de los Baños (Barbour, 1914; Barbour and Ramsden, 1919; Stejneger, 1917; Zug and Schwartz, 1958); MCZ 7934; USNM 27845. Herradura (Barbour, 1914; Barbour and Ramsden, 1919; Zug and Schwartz, 1958); MCZ 7935. Rangel UH 3. Rancho Muridibo, between San Cristobal and Santa Cruz de los Pinos MJ 48; UH2. Guanajay (Barbour and Ramsden, 1919; Stejneger, 1917; Zug and Schwartz, 1958); USNM 27846. Sierra del Anáfe UH 539. Habana Province: Caimito de Guayabal (Barbour and Ramsden, 1919; Zug and Schwartz, 1958); MCZ 13571-74. Vedado MJ 22; UH 1. Santiago de las Vegas *SMF 21537. El Cotorro (Zug and Schwartz, 1958); AMNH 46678-79. Habana *SMF 26479-80. Matanzas Province: Matanzas USNM 58746. ISLA DE PINOS: Sierra de las Casas, just west of Nueva Gerona (Zug and Schwartz, 1958); AMNH 78397.

Habitat: Barbour (1914) and Barbour and Ramsden (1919) mention that specimens were plowed up. Zug and Schwartz (1958) collected *C. blanoides* from beneath rocks in moist soil, while Gundlach (1875, 1880) mentions their occurrence in manure piles, below planks and rocks, and comments that they are insectivorous.

CADEA PALIROSTRATA Dickerson, 1916

Cadea palirostrata Dickerson, 1916, p. 659. Type locality: ''San Pedro, Isle of Pines, Cuba.'' HOLOTYPE: AMNH 2717. PARATYPES: AMNH 2718; MCZ 12052 (ex AMNH 2719); USNM 54379 (ex AMNH 2718?).

Diagnosis: A form of *Cadea* with 274 to 302 body annuli; 12 to 17 caudal annuli; 32 to 39 segments to a midbody annulus; 6 to 10 precloacal segments and 6 to 11 precloacal pores in two series. Head with strong lateral compression and prominent rostral projection. Dorsal surface of body speckled with brown; head with a central light stripe from prefrontal onto nape, often diversified by a pair of lateral bars.

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[1] This specimen bears the astonishing label "Oriente Province, Holguín, Calabazas." Schwartz, who examined it, kindly informed us (*in litt.*) that this collection contains a number of other specimens of west Cuban forms so that it is most likely that the citation represents an error.

General observations: The remarks on Zug and Schwartz (under *C. blanoides*) apply here as well.

Figure 38 shows the head scalation, Figure 39 is a view of the underside of tail.

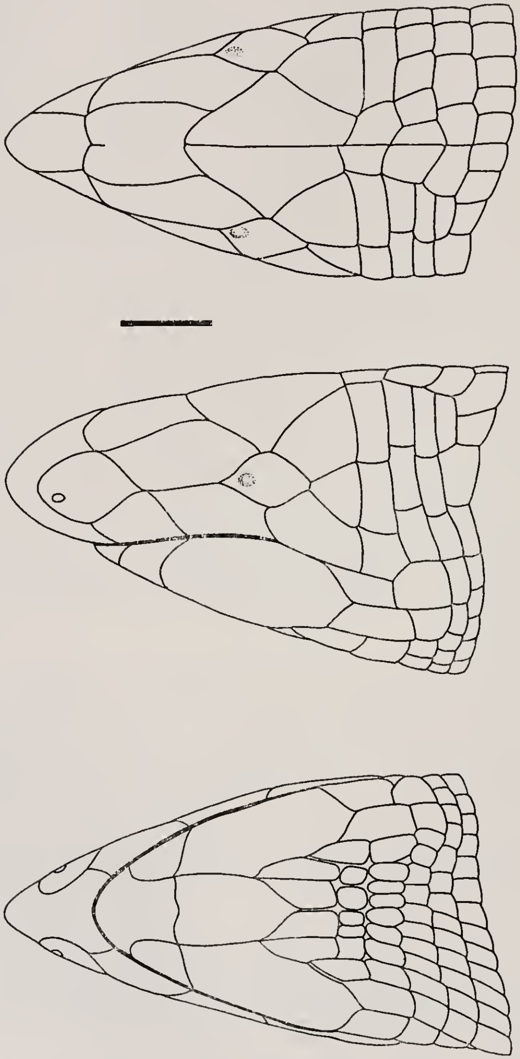

FIG. 38. *C. palirostrata.* Dorsal, lateral and ventral views of AMNH 12809 from La Ceiba, Isla de Pinos. The line equals 1 mm to scale. (V. Cummings, del.)

Range: Isla de Pinos, Cuba.

Locality records: CUBA: ISLA DE PINOS: —— (Barbour, 1930, 1935, 1939; Barbour and Ramsden, 1919; Mertens, 1926). La Ceiba (Barbour and Ramsden, 1919; Zug and Schwartz, 1958); AMNH 12809-10; MCZ 12331-33; USNM 61176. San Pedro (Barbour and Loveridge, 1929; Dickerson, 1916; Zug and Schwartz, 1958); AMNH 2717 (HOLOTYPE), 2718 (PARATYPE); MCZ 12052 (PARATYPE); USNM 54379 (PARATYPE?). McKinley (Barbour and Ramsden, 1919; Zug and Schwartz, 1958); MCZ 12088. Santa Bárbara (Barbour and Ramsden, 1919; Zug and Schwartz, 1958); MCZ 12448-54; *SMF 21539. Nueva Gerona (Zug and Schwartz, 1958); CM 4422; MCZ 13506-12, 13514-16; *SMF 21535-36; ZMU 30768.

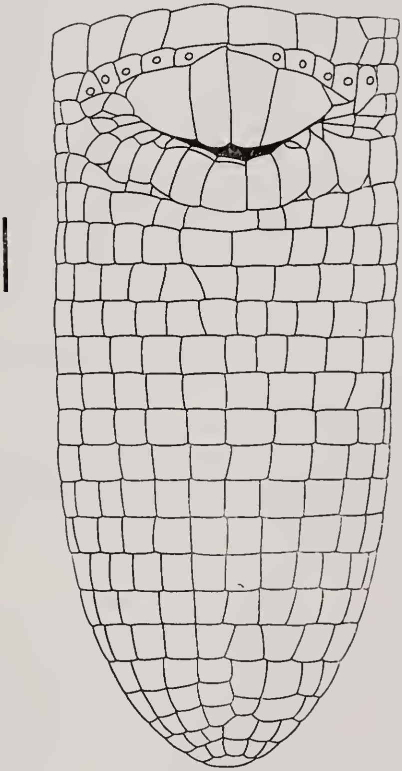

FIG. 39. *C. palirostrata.* Ventral view of cloaca and tail of AMNH 12809 from La Ceiba, Isla de Pinos. The line equals 1 mm to scale. (V. Cummings, del.)

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The artists have been acknowledged in the captions of figures prepared by them. The American Geographical Society assisted with a copy of the Index to the Map of Hispanic America.

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[1] This paper is variously cited as 1881, 1882, and 1883. Dr. Joseph Eiselt has kindly informed one of us that the Vienna Museum separate of this paper is marked 1881 in print and seems to have been published in that year.

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TABLE 1.

	LENGTH		ANNULI		ANNULAR SEGMENTS				POSTGENIALS			POST-MALARS	CLOACA		
	Snout-vent	Tail	Body	Caudal	Dorsals	Ventrals	Ventrals-dorsals	Ventrals+dorsals	First row	Second row	Third row		Pores	Precloacals	Postcloacals
A. c. cubana	88-197	6-15	209 199-217 (?218)	11,12 10-14 (16)	14 12-16	18 14-18	4 2-6	32 28-32	2,3 2-5	5 3-6	-	-	4 4-6	8 4-10	11 9-14
A. c. barbouri	85-177	7-13.5	232,236 226-240	16 14-18	14 12-14	16 16-18	2 2-6	30 26-34	3	5 4-5	-	-	4 4-6	8 4-8	11 9-14
A. i. innocens	102-262	8-17	208 186-219	13 9-15	16 14-17	20 18-24	4 3-8	36 32-40	2 2-3	5 4-7	6 5-7	-	4 (6)	8,9 6-10	12 10-14 (?9)
A. i. caudalis	132-176	13-16	200-208	18-19	14	20	6	34	2	4	5	-	4	7-8	11-12
A. i. gonavensis	137-203	9-13	217 211-225	11 10-13	16,18 16-18	22 21-24	6 4-6	40 37-42	2	3	-	6,7 6-7	4 3-4	6 6-7	12 12-14
A. manni	75-212 (?66)	8-21.5	229 209-243	19 17-21 (?22)	14 12-16	16 14-20	2 0-4	30 26-36	3 2-4	4 3-6	*	*	6 4-9	6 4-9	10,11 6-13
A. bakeri	162-283	12-21	252,255 239-255	15 14-16	16 14-17	16 15-18	2 (-1)-2	32,33 29-34	3	4 4-5	-	-	4	6 6-9	10,11 10-12
A. caeca	73-251	7-20	230 221-236 (217)	15 13-17	16 13-18	18 14-20	2 0-4	34 28-38	3 (4)	4 3-5	*	9 7-11	4 4-6	6 3-9	11,12 9-15
A. fenestrata	102-242	9-17	242 236-247	13 12-14	14 12-14	16 14-16	2 0-2	30 26-30	3	4	-	9,10 9-10	4	6 4-8	10 8-12

The data represent range limits; underscored figures the mode(s) within the range; figures preceded by a question mark (?) and parenthesized ( ) stand for questionable counts on specimens of poor condition; parenthesized figures not preceded by a question mark refer to exceptional specimens generally commented on in the text.

APPENDIX

MUSEUM NUMBER	ANNULI			SEGMENTS		HEAD									CLOACA			LENGTH	
						Dorsal			Ventral										
	Body	Lateral	Caudal	Dorsal	Ventral	MAJOR	Snout-frontal	Snout-parietal	CHIN		Postgenials			Postmalars	Pores	Precloacals	Postcloacals	Snout-vent	Tail
A. cubana																			
MCZ 46235	212	3	12	12	18	C	0.50	0.58	a	2	5	-	-	-	6	7	10	160	11
AMNH 58839	216	3	14	12	16	C	0.50	0.56	a	3	5	-	-	-	4	8	11	159	12
HM 367A	204	4	11	12	18	C	0.49	0.58	a	3	4	-	-	-	4	8	12	?152	12
HM 3678	?218	3	12	12	16	C	0.38	0.44	a	2	4	-	-	-	?	6	12	88	6
MHNP 3120	213	3	13	14	17	C	0.50	0.67	a	3	4	-	-	-	4	7	10	159	12
RMNH 9978	205	4/3	11	14	18	C	0.54	0.72	a	2	5	-	-	-	4	?6	12	187	15
SU R14634	209	4	13	12	18	C	0.40	0.48	a	3	4	-	-	-	4	7	12	96	8
ZMU 6904	209	3	12	14	18	C	0.60	0.64	a	3	4	-	-	-	4	7	12	175	13
ZMU 9383	212	3	13	13	17	C	0.57	0.63	a	2	4	-	-	-	4	8	11	193	14
MCZ 35510	206	4	(7)	14	18	C	0.52	0.61	a	3	5	-	-	-	4	8	10	165	x
AMNH 7312	210	3	12	14	16	C	0.48	0.56	a	3	4	-	-	-	4	7	11	150	11
BM 1912.9.4.3	204	3	14	14	18	C	0.60	0.70	a	4	5	-	-	-	5	10	12	196	16
CAS 39292	203	3/2	12	14	18	C	0.62	0.67	a	3	5	-	-	-	4	8	14	182	13
MCZ 7936A	210	3	10	14	16	C	0.57	0.69	a	2	5	-	-	-	4	8	10	185	13
MCZ 7936B	203	4	12	14	18	C	0.57	0.66	a	3	4	-	-	-	5	8	12	189	14
MCZ 7936C	204	3	12	14	18	C	0.61	0.67	a	4	5	-	-	-	4	9	13	188	15
MCZ 7936D	217	3	12	13	17	C	0.56	0.63	a	2	4	-	-	-	4	9	11	175	13.5
MCZ 7936E	210	3	12	14	18	C	0.48	0.56	a	2	5	-	-	-	4	8	11	137	10
MCZ 7936F	204	3	12	14	18	C	0.42	0.50	a	2	5	-	-	-	4	6	10	106	8.5
MCZ 7936G	201	3	11	14	18	C	0.56	0.70	a	2	5	-	-	-	4	7	12	172	13
MCZ 7936H	209	4	11	14	18	C	0.50	0.58	a	2	5	-	-	-	4	8	11	145	11
MCZ 7936I	208	2	11	14	18	C	0.56	0.67	a	5	5	-	-	-	5	8	12	175	12
MCZ 7936J	213	4	11	13	16	C	0.60	0.67	a	2	4	-	-	-	4	6	10	197	15
MCZ 7936K	213	3	11	14	18	C	0.46	0.55	a	2	4	-	-	-	4	8	10	139	11
MCZ 7936L	209	3	11	14	16	C	0.48	0.56	a	2	5	-	-	-	4	6	12	138	10
MCZ 7936M	207	3	11	12	18	C	0.48	0.56	a	4	5	-	-	-	4	8	12	143	10
MCZ 7936N	203	3	10	14	18	C	0.55	0.60	a	2	5	-	-	-	4	8	11	156	10
MCZ 10790	210	3	11	14	18	C	0.52	0.60	a	3	5	-	-	-	4	7	11	170	12
MCZ 10791	204	3	12	14	16	C	0.57	0.63	a	2	5	-	-	-	5	7	11	?173	13
MCZ 10792	209	3	11	14	18	C	0.56	0.66	a	2	3	-	-	-	4	8	11	?185	12
MCZ 10793	208	3	12	14	17	C	0.55	0.63	a	3	5	-	-	-	6	6	12	?168	13
MCZ 10794	206	3	11	14	18	C	0.57	0.68	a	3	5	-	-	-	4	8	13	?190	13
MCZ 10795	204	4	11	14	16	C	0.54	0.61	a	2	5	-	-	-	4	6	10	?165	12
MCZ 10796	211	3	11	14	18	C	0.51	0.57	a	2	4	-	-	-	4	8	12	?143	10
MCZ 10797	208	3	12	14	18	C	0.54	0.65	a	3	5	-	-	-	4	7	11	?173	13
MCZ 10798	211	3	(6)	14	18	C	0.54	0.65	a	4	5	-	-	-	4	8	11	?177	x
MCZ 10799	208	3	12	12	16	C	0.62	0.66	a	2	5	-	-	-	4	8	11	?185	14
MCZ 10800	205	3	12	12	16	C	0.56	0.62	a	3	5	-	-	-	4	8	11	?166	12
MCZ 10801	206	2	11	14	18	C	0.48	0.57	a	3	5	-	-	-	4	7	12	?134	10
MCZ 10802	206	3	11	14	18	C	0.54	0.63	a	2	5	-	-	-	4	6	11	?173	12
MCZ 10803	214	4	12	14	18	C	0.52	0.62	a	2	4	-	-	-	4	8	10	?168	12
MCZ 10804	209	3	12	14	18	C	0.59	0.65	a	2	5	-	-	-	4	7	12	?178	13
MCZ 10805	211	3	11	12	16	C	0.57	0.67	a	2	4	-	-	-	4	7	11	?183	13
MCZ 10806	207	3	11	15	18	C	0.54	0.59	a	4	6	-	-	-	5	8	12	?175	13
MCZ 10807	211	4/3	12	14	18	C	0.54	0.62	a	3	5	-	-	-	5	7	11	?166	12?
MCZ 10808	203	3	12	14	16	C	0.57	0.64	a	2	5	-	-	-	4	7	11	?167	13
MCZ 10809	200	4	11	12	16	C	0.52	0.61	a	2	5	-	-	-	4	7	11	?154	12
MCZ 10810	205	3	12	14	17	C	0.60	0.68	a	2	5	-	-	-	4	8	12	?171	13
MCZ 10811	203	3	12	14	18	C	0.53	0.61	a	4	5	-	-	-	4	9	12	?152	12
MCZ 10814	206	3/4	11	14	18	C	0.55	0.60	a	2	5	-	-	-	4	8	10	?162	12
MCZ 10817	210	2	12	14	18	C	0.54	0.63	a	3	5	-	-	-	6	7	14	?165	13
MCZ 10818	207	3	12	14	17	C	0.51	0.59	a	3	5	-	-	-	4	8	11	?151	11
MCZ 13525	209	2/3	12	14	18	C	0.54	0.62	a	3	4	-	-	-	5	6	10	?173	11
MCZ 13526	216	3	12	16	18	C	0.54	0.61	a	2	5	-	-	-	4	8	10	?165	12
MCZ 13527	211	3	8?	14	16	C	0.57	0.64	a	4	5	-	-	-	4	8	10	?180	?

MCZ 22722	209+ 2 +12	12+16	C	0.49	0.56	a	2	4	-	-	-	4	8	9	?141+11
MCZ 32665	205+3/4+11	14+18	C	0.50	0.59	a	3	4	-	-	-	4	7	11	?165+12
USNM 48802	209+ 3 +11	14+16	C	0.55	0.62	a	3	5	-	-	-	4	8	11	176+12
USNM 48803	208+ 3 +12	14+18	C	0.52	0.61	a	4	6	-	-	-	4	7	12	173+11.5
USNM 137083	200+ 4 +11	12+16	C	0.42	0.48	a	2	4	-	-	-	5	7	11	101+8
ANSP 16365	199+ 3 +10	14+18	C	0.48	0.57	a	?3	?5	-	-	-	4	8	12	141+10
BM 1915.10.22.5	206+ 3 +12	14+16	C	0.53	0.62	a	2	4	-	-	-	4	7	12	166+12
BM 1915.10.22.6	207+ 3 +13	14+17	C	0.51	0.60	a	2	4	-	-	-	4	8	12	173+13
BM 1915.10.22.7	201+ 3 +11	14+17	C	0.51	0.58	a	4	5	-	-	-	4	7	10	141+11
BM 1915.10.22.8	?205+ 3 +(9)	14+18	C	0.45	0.49	a	3	5	-	-	-	?0	4	13	96+x
RMNH 4638	209+ 3 +12	14+18	C	0.62	0.76	a	2	6	-	-	-	4	6	11	188+15
USNM 58747	211+ 2 +13	14+16	C	0.51	0.59	a	3	5	-	-	-	4	8	11	148+12
MCZ 13523	215+ 3 +11	14+16	C	0.43	0.52	a	3	4	-	-	-	4	8	12	117+9
AMNH 77790	212+ 3 +13	14+16	C	0.52	0.65	a	3	4	-	-	-	4	5	11	177+12
UMMZ 70923	206+ 3 +10	12+16	C	0.55	0.61	a	3	4	-	-	-	4	8	12	172+11
UMMZ 70925	204+ 4 +11	12+16	C	0.53	0 59	a	2	4	-	-	-	4	8	11	161+12
UMMZ 70926	206+ 3 +11	12+14	C	0.52	0.57	a	2	4	-	-	-	4	8	10	161+12
UMMZ 70924	210+ 3 +11	12+14	C	0.50	0.58	a	2	3	-	-	-	4	8	11	?143+10
USNM 75861	202+ 3 +(7)	12+16	C	0.53	0.59	a	3	4	-	-	-	4	6	11	161+x
UMMZ 90720	212+4/3+14	14+17	C	0.50	0.55	a	3	5	-	-	-	4	8	12	157+14
MCZ 47897	213+ 3 +16	14+17	C	0.43	0.47	a	3	4	-	-	-	4	9	12	149+13
MCZ 10712	210+ 3 +(7)	14+18	C	0.64	0.72	a	4	5	-	-	-	4	6	11	190+x
USNM 63217	210+ 4 +10	14+16	C	0.64	0.78	a	3	4	-	-	-	4	8	11	192+14
MCZ 58788	227+ 2 +15	14+16	C	0.48	0.51	a	3	4	-	-	-	4	8	9	?137+9
MCZ 58789	232+ 3 +14	12+18	C	0.49	0.52	a	3	5	-	-	-	4	7	11	177+12
MCZ 12135	236+ 4 +15	12+16	C	?	?	a	3	4	-	-	-	4	6	14	?165+12
USNM 26363	232+ 3 +?	14+16	C	0.50	0.55	a	3	5	-	-	-	4	8	11	155+?
USNM 26364	236+ 2 +16	14+16	C	0.47	?0.64	a	3	5	-	-	-	4	8	13	138+11
MCZ 12136	226+ 3 +16	14+18	C	0.53	0.58	a	3	5	-	-	-	5	6	12	171+13
MCZ 12137	226+ 3 +16	? +?	C	0.40	0.43	a	3	5	-	-	-	6	4	12	85+7
MCZ 13524	240+ 3 +18	14+17	C	0.53	0.57	a	3	5	-	-	-	4	8	11	161+13.5

A. *innocens*

USNM 60620	210+ 4 +11	16+22	N	0.69	0.78	d	2	5	5	-	-	4	10	14	200+14
MCZ 3624	211+ 3 +15	16+20	N	0.63	0.73	d	2	5	6	-	-	4	10	14	181+14
MCZ 3625	208+ 3 +13	16+20	N	0.56	0.69	d	2	5	6	-	-	4	8	14	157+13
ZMU 1386	213+ 3 +13?	16+21	N	0.65	0.83	d	2	5	6	-	-	4	10	13	194+12
MCZ 63609	213+4/3+13	16+22	N	0.73	0.88	d	2	5	6	-	-	4	8	13	228+16
MCZ 63610	208+4/3+13	16+21	N	0.62	0.72	d	3	7	7	-	-	4	9	13	158+12.5
MCZ 63611	214+ 4 +13	16+20	N	0.72	0.84	d	2	5	6	-	-	4	9	13	253+18
MCZ 63612	207+ 4 +13	16+21	N	0.75	0.88	d	2	5	6	-	-	4	9	12	262+16.5
MCZ 63613	208+ 4 +12	16+20	N	0.81	0.95	d	2	5	6	-	-	4	9	12	251+16
MCZ 63614	219+ 3 +12	16+24	N	0.78	0.91	d	2	4	5	-	-	4	10	16	262+15.5
MCZ 63615	218+ 3 +14	16+20	N	0.73	0.86	d	2	5	7	-	-	4	8	12	235+16.5
MCZ 63616	214+ 4 +11	15+20	N	0.68	0.80	d	2	5	6	-	-	4	8	11	227+14
MCZ 63617	209+ 4 +13	16+20	N	0.72	0.85	d	2	5	6	-	-	4	9	12	228+15.5
MCZ 63618	217+3/4+13	16+21	N	0.56	0.64	d	2	5	6	-	-	4	8	12	156+13.5
MCZ 63619	209+ 3 +13	16+20	N	0.63	0.75	d	2	5	6	-	-	4	8	13	183+12.5
MCZ 63620	213+4/3+13	16+20	N	0.53	0.63	d	2	5	7	-	-	4	10	12	129+10.5
MCZ 63621	215+ 4 +12	16+22	N	0.70	0.81	d	2	6	6	-	-	4	9	11	215+14
MCZ 63622	208+ 4 +13	16+21	N	0.53	0.61	d	2	5	6	-	-	4	10	12	128+10
MCZ 63623	217+ 3 +13	16+20	N	0.61	0.72	d	2	5	6	-	-	4	9	13	174+13.5
MCZ 63624	210+ 3 +11	16+22	N	0.53	0.62	d	2	5	6	-	-	4	9	11	124+9
MCZ 63625	212+ 4 +?	16+20	N	?0.76	0.93	d	2	4	6	-	-	?4	9	14	249+16
MCZ 63626	217+ 4 +12	16+22	N	0.65	0.78	d	2	5	6	-	-	6	9	13	196+13.5
MCZ 63627	211+ 4 +13	14+22	N	0.61	0.71	d	2	5	6	-	-	4	9	12	192+14.5
MCZ 63628	210+ 4 +13	16+20	N	0.52	0.61	d	2	5	6	-	-	4	9	14	126+10
MCZ 63629	211+3/4+13	17+22	N	0.63	0.75	d	2	6	7	-	-	4	9	13	169+12.5
RMNH 10008	203+ 4 +12	14+22	N	0.67	0.74	d	2	5	6	-	-	4	?8	?9	197+14
USNM 69439	217+ 4 +12	16+22	N	0.67	0.76	d	2	5	5	-	-	4	8	11	?218+14
MCZ 51417	205+3/4+11	15+18	N	0.72	0.84	d	2	5	6	-	-	4	8	12	225+16
USNM 117250	202+ 5 +10	15+18	N	0.65	0.73	d	?2	?4	?6	-	-	4	8	11	207+16
USNM 117251	209+ 5 +9	14+19	N	0.69	0.79	d	2	4	6	-	-	4	8	11	196+13
USNM 118036	204+ 4 +10	15+18	N	0.66	0.77	d	2	4	5	-	-	4	8	10	192+13
USNM 118906	198+ 4 +11	14+18	N	0.73	0.84	d	2	4	6	-	-	4	7	11	231+17
HM 2907	208+ 4 +11	16+20	N	0.72	0.80	d	2	5	6	-	-	4	7	12	213+17
USNM 118903	207+ 4 +11	14+20	N	0.74	0.83	d	3	5	6	-	-	4	8	10	223+15
MCZ 37595	186+4/3+11	14+20	N	0.65	0.73	d	2	5?7		-	-	4	7	10	203+15
MCZ 37596	207+ 3 +14	16+20	N	?0.63	?0.75	d	2	5	6	-	-	4	9	14	?199+17
MCZ 37597	204+ 3 +13	17+20	N	0.53	0.63	d	3	5	7	-	-	4	9	12	137+12
MCZ 8748	191+ 3 +12	14+20	N	0.52	0.58	d	2	5	6	-	-	4	8	11	102+8
MCZ 62511	211+ 4 +9	14+22	N	0.71	0.80	d	2	4	6	-	-	4	6	10	243+16
USNM 59212	202+ 4 +11	15+20	N	0.66	0.72	d	3	5	5	-	-	4	6	12	189+15

MCZ 25550	208+4/3+19	14+20	N	0.48	0.54	d	2	4	5	-	-	4	7	12	132+13
MCZ 25551	200+ 3 +18	14+20	N	?0.54	?0.61	d	2	4	5	-	-	4	8	11	176+16
MCZ 25549	211+ 4 +12	16+22	N	0.53	0.65	b	2	3	-	6	-	4	6	12	137+10
USNM 10168	219+ 4 +10	18+23	N	0.57	0.72	b	2	3	-	7	-	?	7	12	?161+9
PM A925	217+ 4 +12	16+22	N	0.60	0.72	b	2	3	-	7	-	4	6	12	175+12
PM A933	219+4/3+11	18+24	N	0.62	0.77	b	2	3	-	6	-	4	6	12	193+12
PM A934	214+ 4 +10	18+22	N	0.60	0.73	b	2	3	-	6	-	4	6	12	190+11
PM A935	225+ 3 +13	18+22	N	0.58	0.75	b	2	3	-	7	-	?4	6	14	172+10.5
PM A936	217+ 3 +11	17+23	N	0.63	0.76	b	2	3	-	7	-	4	6	?12	203+13
PM A937	218+ 4 +11	16+21	N	0.67	0.79	b	2	3	-	6	-	3	6	14	201+12
A. manni															
AMNH 49726	229+ 4 +19	16+16	M	0.54	0.67	a	3	4	-	-	-	9	6	13	159+14
MCZ 62534	224+ 4 +17	16+18	M	0.41	0.62	a	3	5	-	-	-	7	6	12	212+19
MCZ 62535	235+ 3 +21	16+18	M	0.35	0.53	a	3	4	-	-	-	8	6	10	186+20
MCZ 62536	237+3/4+18	16+18	M	0.39	0.59	a	4	5	-	-	-	7	6	9	208+20
MCZ 62537	238+ 4 +18	16+18	M	0.37	0.57	a	4	5	-	-	-	7	6	8	193+18
MCZ 62538	240+ 3 +20	16+18	M	0.38	0.58	a	4	5	-	-	-	6	6	11	195+20
MCZ 62539	231+ 4 +19	16+18	M	0.31	0.47	a	4	6	-	-	-	8	6	11	118+11
MCZ 62540	236+ 4 +19	14+16	M	0.29	0.43	a	4	5	-	-	-	6	6	11	104+10
USNM 76656	239+ 3 +19	15+18	M	0.57	0.65	a	3	4	-	-	-	8	8	10	183+18
USNM 76657	243+ 3 +21	14+16	M	0.44	0.50	a	4	6	-	-	-	6	6	12	116+13
MCZ 8645	227+ 4 +19	16+16	M	0.56	0.63	a	3	4	-	-	-	8	8	9	174+21
MCZ 8646	232+ 3 +(6)	14+16	M	0.55	0.63	a	3	5	-	-	-	7	6	11	183+x
MCZ 8647	227+ 3 +20	14+16	M	0.51	0.61	a	3	6	-	-	-	8	7	10	146+17
MCZ 62532	228+ 3 +21	14+16	M	0.29	0.48	a	3	5	-	-	-	6	6	10	137+15.5
MCZ 62533	230+ 3 +20	14+16	M	0.32	0.52	a	3	4	-	-	-	8	8	8	180+19.5
USNM 67113	? ? ?	14+16	M	?	?	a	3	4	-	-	-	?	?	?	? ?
USNM 69175	237+ 3 +(6)	16+17	M	0.50	0.56	a	3	4	-	-	-	8	6	?	146+x
AMNH 51279	225+ 3 +19	14+16	M	0.49	0.58	a	3	4	-	-	-	8	6	10	127+13
AMNH 51280	228+ 3 +18	16+16	M	0.60	0.65	a	3	4	-	-	-	8	6	10	180+18
AMNH 51281	228+ 3 +18	14+16	M	0.60	0.70	a	3	5	-	-	-	7	6	11	200+21
AMNH 51282	229+ 3 +19	14+16	M	0.50	0.59	a	3	4	-	-	-	8	6	11	134+13
RMNH 10010	233+ 3 +19	14+16	M	0.57	0.63	a	3	4	-	-	-	6	6	9	175+18
UMMZ 92180	227+ 4 +17	14+16	M	?	?	a	3	5	-	-	-	6	6	10	150+14
USNM 74680	224+ 3 +18	12+16	M	?	?	a	3	4	-	-	-	6	6	11	159+16
USNM 74681	229+ 3 +20	14+14	M	0.52	0.67	a	3	4	-	-	-	6	6	10	170+17
USNM 74682	230+ 3 +19	14+14	M	0.52	0.58	a	3	4	-	-	-	6	6	12	156+17
USNM 74683	225+ 2 +19	13+16	M	0.48	0.56	a	3	5	-	-	-	6	6	10	125+13
USNM 74685	226+2/3+20	14+16	M	0.51	0.54	a	3	4	-	-	-	6	6	12	136+14
USNM 74686	228+ 2 +19	14+16	M	0.47	0.51	a	3	4	-	-	-	6	6	11	111+10
USNM 74687	236+ 3 +(5)	14+16	M	0.50	?	a	2	4	-	-	-	6	6	11	164+x
MCZ 44389	235+ 3 +19	14+16	M	?	?	a	3	4	-	-	-	8	6	12	?182+21
AMNH 41030	226+ 3 +(6)	14+17	M	0.56	0.65	a	3	4	-	-	-	8	7	12	179+x
AMNH 41031	222+ 3 +17	14+16	M	0.55	0.62	a	3	4	-	-	-	8	6	8	160+15
AMNH 41032	222+2/3+18	14+16	M	0.57	0.65	a	3	4	-	-	-	6	6	7	167+16
AMNH 41033	224+ 3 +18	14+16	M	0.60	0.66	a	3	4	-	-	-	6	6	11	182+18
AMNH 41034	220+ 3 +18	14+16	M	0.58	'0.68	a	3	4	-	-	-	6	6	10	184+19
AMNH 41035	221+ 3 +18	14+15	M	0.54	0.61	a	3	5	-	-	-	8	6	9	148+14
AMNH 41036	218+ 3 +17	14+15	M	0.58	0.62	a	3	3	-	-	-	7	6	11	162+16
AMNH 41038	221+ 3 +18	14+16	M	0.44	0.53	a	3	4	-	-	-	8	6	9	? 91+9
AMNH 41039	226+ 3 +20	14+16	M	0.51	0.59	a	3	4	-	-	-	6	6	10	145+15
AMNH 41040	222+ 3 +18	14+16	M	0.57	0.63	a	3	4	-	-	-	?7	6	12	159+16
AMNH 41041	217+ 3 +18	14+16	M	0.58	0.68	a	3	4	-	-	-	?8	6	11	190+18
AMNH 41042	226+ 3 +19	14+16	M	0.48	0.54	a	3	4	-	-	-	6	6	13	110+11
AMNH 41043	228+ 2 +20	14+16	M	0.41	0.51	d	3	4	5	-	-	7	6	11	933+10
AMNH 41044	226+3/4+20	13+15	M	0.45	0.48	a	3	4	-	-	-	6	6	11	82+9
AMNH 41045	221+ 2 +(7)	14+15	M	0.47	0.55	a	3	4	-	-	-	7	6	9	117+x
AMNH 41046	222+ 3 +19	14+16	M	0.51	0.56	a	3	5	-	-	-	6	6	10	143+14
AMNH 41047	230+ 3 +19	?14+16?	M	0.45	0.48	a	3	4	-	-	-	7	6	9	89+9
AMNH 41048	225+ 3 +19	14+16	M	0.39	0.49	a	3	4	-	-	-	8	6	11	89+9
AMNH 41049	228+4/3+19	14+16	M	0.45	0.51	a	3	4	-	-	-	6	6	10	92+9
AMNH 41050	229+ 3 +20	14+15	M	0.44	0.48	a	3	5	-	-	-	7	6	9	93+10
AMNH 41051	235+ 4 +(5)	14+16	M	0.49	?0.56	a	3	4	-	-	-	6	5	12	140+x
AMNH 41052	217+ 3 +19	14+15	M	0.59	0.64	a	3	4	-	-	-	6	6	9	166+18
AMNH 41053	221+ 2 +19	14+16	M	0.57	0.64	a	3	4	-	-	-	6	6	10	159+17
AMNH 41054	219+ 2 +18	16+16	M	0.49	0.56	a	3	4	-	-	-	?6	6	9	118+12
AMNH 41055	229+ 3 +19	14+16	M	0.53	0.60	a	2	4	-	-	-	6	6	8	160+16
AMNH 41056	227+ 3 +19	14+16	M	0.55	0.62	a	3	4	-	-	-	8	6	11	158+15
AMNH 41057	220+ 3 +17	14+16	M	0.53	0.60	a	3	4	-	-	-	8	6	9	145+14
AMNH 41058	? + 3 +21	? ?	M	?	?	?	?	?	?	?	?	?	?	?	75+9
AMNH 41059	227+ 3 +19	13+15	M	0.52	0.58	a	3	4	-	-	-	6	6	11	139+13

AMNH 41060	223+ 3 +19	14+16	M	0.52	0.56	a	3	4	-	-	-	7	6	10	137+14
AMNH 41061	220+4/3+18	13+15	M	0.44	0.49	a	3	6	-	-	-	6	6	9	88+9
AMNH 41062	225+ 3 +18	14+15	M	0.45	0.53	a	3	4	-	-	-	7	6	11	116+12
AMNH 41063	221+ 3 +18	14+16	M	0.53	0.61	a	3	4	-	-	-	7	6	9	142+13
AMNH 41064	229+ 3 +18	14+16	M	0.56	0.61	a	3	4	-	-	-	6	6	10	157+15
AMNH 41065	237+ 3 +19	16+18	M	0.60	0.68	a	3	4	-	-	-	6	6	10	174+17
AMNH 41066	230+3/4+(6)	14+16	M	0.56	0.63	a	3	4	-	-	-	6	6	8	191+x
AMNH 41067	225+ 3 +18	14+14	M	0.59	0.67	a	3	4	-	-	-	6	6	8	174+17
AMNH 41068	225+ 2 +(7)	14+16	M	0.53	0.60	a	3	3	-	-	-	6	6	6	167+x
AMNH 41069	230+ 3 +18	14+16	M	0.59	?	a	3	4	-	-	-	7	6	11	194+19
AMNH 41070	228+ 4 +(6)	14+16	M	0.59	0.67	a	3	4	-	-	-	7	6	9	188+x
AMNH 41071	236+ 3 +19	16+20	M	0.55	0.62	a	3	4	-	-	-	6	4	11	167+16
AMNH 41072	221+ 2 +20	15+16	M	0.57	0.64	a	3	4	-	-	-	6	6	7	174+19
AMNH 41073	226+ 3 +19	15+16	M	0.56	0.67	a	3	4	-	-	-	8	6	9	180+19
AMNH 41074	220+ 3 +18	16+16	M	0.60	0.72	a	3	5	-	-	-	7	6	11	167+17
AMNH 41075	?219+4/3+19	14+16	M	0.45	0.55	a	3	4	-	-	-	7	7	10	84+9
AMNH 41076	219+ 3 +18	14+16	M	0.59	0.67	a	3	4	-	-	-	8	6	10	180+18
AMNH 41077	214+ 3 +18	14+16	M	0.58	0.66	a	3	4	-	-	-	6	6	10	158+16
AMNH 41078	225+ 2 +(6)	14+16	M	0.49	0.58	a	3	4	-	-	-	8	6	9	133+x
AMNH 41079	224+ 3 +18?	14+16	M	0.47	0.50	a	3	4	-	-	-	6	6	10	122+14?
AMNH 41080	231+ 3 +20	14+16	M	0.45	0.49	a	3	4	-	-	-	6	6	11	93+9?
AMNH 41081	?231+2/3+19	14+16	M	0.42	0.47	a	3	4	-	-	-	6	6	11	?66+9?
AMNH 41082	228+ 3 +19	14+16	M	0.48	0.54	a	3	4	-	-	-	7	6	11	125+13
AMNH 41083	224+3/2+19	16+18	M	0.51	0.59	a	3	4	-	-	-	7	6	7	144+13
AMNH 41084	226+ 3 +19	12+16	M	0.41	0.45	a	3	4	-	-	-	6	6	11	88+10
AMNH 41251	?223+ 3 +18	14+15	M	0.43	0.46	a	3	4	-	-	-	6	6	10	78+8
AMNH 41262	223+ 3 +18	14+16	M	0.44	?0.50	a	3	4	-	-	-	8	6	12	89+9
AMNH 41263	228+ 3 +19	14+16	M	0.42	0.48	a	3	4	-	-	-	6	6	9	90+10
AMNH 6341	226+ 3 +17	14+15	M	0.44	0.49	a	3	5	-	-	-	8	6	12	83+8
CAS 55001	223+ 3 +19	14+16	M	0.54	0.62	a	3	4	-	-	-	8	7	10	?150+15
MCZ 44399	225+ 3 +18	14+16	M	0.58	0.64	a	3	4	-	-	-	8	6	11	159+16
AMNH 40421	229+ 3 +19	12+14	M	?0.51	?	a	2	4	-	-	-	6	6	10	139+14
AMNH 40422	229+ 3 +18	14+16	M	0.45	0.52	a	3	4	-	-	-	6	6	7	112+12
AMNH 40423	231+ 3 +18	14+15	M	0.55	0.62	a	3	4	-	-	-	6	6	12	163+17
AMNH 40424	230+ 3 +21	13+14	M	0.52	0.56	a	3	4	-	-	-	6	6	12	159+18
AMNH 40425	228+3/4+19	12+14	M	0.50	0.57	a	3	4	-	-	-	6	6	11	157+17
AMNH 40426	234+ 3 +19	13+16	M	0.48	?	a	3	4	-	-	-	5	6	12	137+15
AMNH 40427	232+2/3+20	13+14	M	0.50	0.55	a	3	4	-	-	-	?4	6	8	133+14
AMNH 40429	229+ 3 +18	14+16	M	?	?	a	3	4	-	-	-	6	6	11	168+18
AMNH 42286	226+ 3 +19	14+15	M	0.54	0.61	a	4	4	-	-	-	6	6	10	150+17.5
AMNH 50264	236+ 3 +(5)	14+15	M	0.53	0.60	a	3	4	-	-	-	?	?	?	?170+x
AMNH 63200	234+ 3 +19	14+14	M	0.51	0.55	a	3	4	-	-	-	6	6	9	150+15.5
AMNH 63201	235+ 3 +18	14+14	M	0.52	0.59	a	2	4	-	-	-	5	6	10	164+17
AMNH 63203	230+ 3 +20	14+15	M	0.51	0.57	a	3	4	-	-	-	6	6	10	170+18
AMNH 42288	236+ 3 +19	14+14	M	0.53	0.58	a	3	4	-	-	-	6	6	10	173+19
AMNH 42289	225+ 3 +20	14+14	M	0.53	0.61	a	3	4	-	-	-	6	6	11	161+18
AMNH 40302	233+ 3 +20	14+16	M	0.55	0.59	a	3	4	-	-	-	6	6	11	165+17
AMNH 40303	235+ 3 +19	14+14	M	0.54	0.57	a	3	4	-	-	-	6	6	10	178+19
AMNH 40304	233+ 3 +19	?12+14?	M	0.48	?0.54	a	3	4	-	-	-	?6	6	9	125+13
AMNH 40305	224+ 3 +(6)	14+16	M	0.50	0.58	a	3	4	-	-	-	6	6	11	163+x
AMNH 43844	229+ 3 +19	14+15	M	0.52	0.58	a	3	4	-	-	-	6	6	12	168+19
AMNH 43845	230+ 2 +19	14+14	M	0.52	0.55	a	3	4	-	-	-	5	6	10	161+18
AMNH 43846	230+ 3 +19	14+14	M	0.56	0.64	a	3	4	-	-	-	6	6	12	191+19
AMNH 43847	224+ 3 +(5)	14+16	M	0.52	0.58	a	3	4	-	-	-	6	7	10	154+x
AMNH 43848	233+ 3 +19	14+14	M	0.51	0.56	a	?	?	-	-	-	6	6	10	170+18
AMNH 43849	227+ 3 +19	15+15	M	0.53	0.61	a	3	4	-	-	-	6	6	11	171+18
AMNH 43850	225+ 3 +18	14+16	M	0.56	0.62	a	3	4	-	-	-	6	6	11	173+17
AMNH 43851	231+ 3 +20	14+16	M	0.50	0.56	a	3	4	-	-	-	6	6	11	138+15
AMNH 43852	233+ 3 +(6)	14+16	M	0.55	0.62	a	3	4	-	-	-	6	6	11	175+x
AMNH 44829	229+ 3 +19	14+16	M	0.52	0.63	a	2	4	-	-	-	6	6	12	156+17
AMNH 44830	236+ 3 +19	14+14	M	0.53	0.59	a	3	4	-	-	-	?	?	?	157+17
AMNH 50357	234+ 3 +18	14+16	M	0.53	0.62	a	3	4	-	-	-	?	?	?	165+18
AMNH 50358	233+ 3 +19	14+16	M	0.58	0.65	a	3	4	-	-	-	6	6	12	175+18
AMNH 50359	230+3/4+18	14+15	M	0.45	0.52	a	2	4	-	-	-	6	6	9	?106+11
AMNH 50360	227+3/4+19	14+16	M	0.52	0.58	a	3	3	-	-	-	6	6	10	163+16
AMNH 50361	230+ 3 +19	13+15	M	0.52	0.58	a	3	4	-	-	-	6	6	12	167+18
AMNH 50362	231+ 4 +19	14+16	M	0.50	0.55	a	3	4	-	-	-	6	6	12	161+17
AMNH 50363	228+ 3 +20	12+14	M	0.49	0.57	a	3	4	-	-	-	6	6	10	?154+17
AMNH 50364	229+ 3 +(6)	14+15	M	0.50	0.53	a	3	4	-	-	-	6	6	8	142+x
AMNH 50365	232+ 3 +19	14+16	M	0.50	0.56	a	3	4	-	-	-	6	7	11	140+15

AMNH 50366	235+ 3 +19	14+16	M	0.53	0.61	a	3 4 -	-	-	6	8	10	186+20
AMNH 50367	230+ 3 +18	14+15	M	0.47	0.55	a	3 4 -	-	-	6	6	10	107+10
AMNH 50368	232+ 3 +19	14+14	M	0.56	0.61	a	3 4 -	-	-	6	6	9	181+19
AMNH 50369	236+ 3 +(6)	14+16	M	0.48	0.55	a	3 3 -	-	-	4	6	10	126+x
AMNH 50370	229+ 3 +19	14+15	M	0.48	?0.53	a	2 4 -	-	-	4	6	10	136+14
AMNH 50371	227+ 3 +20	13+16	M	0.48	0.53	a	3 4 -	-	-	6	6	10	130+14
AMNH 50372	218+ 3 +18	14+16	M	0.58	0.64	a	3 4 -	-	-	6	6	11	170+19
AMNH 50373	235+ 3 +19	14+16	M	?0.45	?0.51	a	3 3 -	-	-	6	6	11	109+11
MCZ 57147	232+ 3 +19	14+16	M	0.32	0.52	b	3 4 -	(9)	-	6	7	10	171+17
USNM 74978	219+ 2 +21	14+16	M	0.50	0.57	d	3 4 5	-	-	8	6	10	140+16
USNM 74979	209+ 3 +19	14+16	M	0.46	0.56	a	3 4 -	-	-	8	6	10	130+14
MCZ 44390	232+ 3 +18	15+16	M	0.59	0.67	a	3 4 -	-	-	8	6	10	172+18
AMNH 5207	227+2/3+19	14+16	M	0.54	0.63	b	3 4 -	(10)	-	6	9	12	166+18
AMNH 7557	223+ 2 +22?	14+16	M	0.57	0.65	a	3 4 -	-	-	6	8	9	184+21.5
AMNH 7558	226+ 3 +21	14+15	M	0.55	0.60	a	3 4 -	-	-	8	8	8	163+19
AMNH 42287	226+2/3+20	15+15	M	0.49	0.55	a	3 4 -	-	-	6	6	11	156+16
A. bakeri													
UPR 7	239+ 3 +15	14+15	N	0.56	0.68	a	3 4 -	-	-	4	6	11	196+15
USNM 27458	251+ 4 +15	16+18	N	0.72	0.81	a	3 5 -	-	-	4	9	12	232+17
CNHM 12473	240+ 3 +14?	14+16	N	0.56	0.65	a	3 5 -	-	-	4	6	10	162+12
UMMZ 55824	252+ 4 +15	16+16	N	0.65	0.71	a	3 5 -	-	-	4	6	10	188+13
UPR 1	255+3/4+15	15+17	N	0.67	?0.69	a	3 4 -	-	-	4	7	11	?205+15
UPR 2	254+ 3 +15	14+16	N	0.72	0.79	a	3 4 -	-	-	4	6	11	248+17
USNM 27458	245+ 3 +15	16+17	N	0.82	0.99	a	3 5 -	-	-	4	8	11	283+21
CNHM 12473	247+ 3 +16	16+17	N	0.78	0.87	?a	3 5 -	(9)	-	4	6	10	?237+20
UMMZ 55824	254+ 3 +15	17+16	N	?0.68	?0.82	a	3 5 -	-	-	4	7	11	256+18
UPR 1	251+ 3 +15	16+16	N	0.72	0.90	a	3 5 -	-	-	4	6	10	262+18
A. caeca													
MHNP 550	227+ 3 +15	14+16	N	-	-	-	- - -	-	-	4	6	12	224+18
MHNP 3114	230+ 3 +14	16+18	N	0.65	0.78	b	3 4 -	9	-	4	6	12	160+16
RMNH 3565	231+ 3 +15	16+18	N	0.62	0.73	b	3 4 -	8	-	4	6	10	163+14
KM R4413	226+ 4 +14	16+16	N	0.65	0.72	b	3 4 -	8	-	4	6	11	?195+15
UPR 6	229+ 3 +17	14+16	N	0.63	0.71	b	3 4 -	9	(10)	4	8	12	195+17
UPR 8	234+ 2 +17	?14+14?	N	0.65	0.74	a	3 4 -	-	-	4	6	11	227+19
ZMU 8949	232+ 3 +15	16+18	N	0.72	0.84	b	3(3)-	9	-	4	6	12	209+16
SU 7775	?227+3/4+15	13+17	N	?0.63	?0.77	?d	4 4(5)	-	-	4	6	13	239+19
UPR 3	221+2/3+15	14+16	N	0.55	0.63	a	3 4 -	-	-	4	8	10	164+14.5
UPR 4	224+ 4 +14	16+16	N	0.65	0.73	?d	4(2)5	-	-	4	6	10	207+18
UPR 9	?225+ 3 +(6)	16+18	N	0.62	0.68	b	3 4 -	9	-	4	8	12	?175+x
UPR 12	223+ 3 +16	16+16	N	0.62	0.66	b	4 5 -	10	-	4	6	13	183+15
UPR A	224+2/3+14	14+15	N	?0.67	0.75	d	3 4 4	-	-	4	8	11	220+20
UPR 8	227+ 3 +16	16+18	N	0.65	0.73	b	3 4 -	8	-	4	6	12	186+15
MCZ 64133	225+ 3 +17	16+18	N	0.64	0.71	b	3 5 -	11	-	4	8	12	180+16
MCZ 64134	224+ 4 +16	15+18	N	0.65	0.71	b	3 4 -	9	-	4	7	12	189+16
MCZ 36303	228+ 3 +16	18+18	N	?0.60	?0.73	b	3 5 -	9	-	4	6	14	198+17
UMMZ 73839	229+ 4 +16	17+18	N	0.61	0.67	?c	3 4 -	10(11)		4	8	10	199+17
UMMZ 73844	225+ 3 +15	14+16	N	0.63	0.74	a	3 4 -	-	-	4	6	11	218+19
USNM 25538	229+ 3 +16	14+18	N	0.52	0.58	b	3 4 -	9	-	5	6	12	129+11
USNM 25539	230+ 3 +16	17+18	N	0.58	0.67	b	3 4 -	9	-	4	6	12	?145+13
USNM 25540	225+ 3 +17	14+17	?N	0.74	0.78	b	3 4 -	9	-	4	6	11	222+19
MCZ 61500	233+ 3 +15	16+18	N	0.32	0.52	b	3 4 -	10	-	4	6	11	116+9
HM 2434	230+ 2 +(6)	16+16	N	0.63	0.71	b	3 4 -	9	-	4	7	11	171+x
USNM 27223	228+ 3 +16	16+18	N	0.65	0.70	b	3 4 -	8	-	4	7	13	183+16
UMMZ 73841	231+ 3 +15	15+17	N	0.72	0.86	b	3 4 -	9	-	4	8	11	207+16
UMMZ 73846	235+ 3 +15	14+16	N	0.50	0.56	a	3 5 -	-	-	4	8	11	137+12
MCZ 36301	230+ 3 +14	14+14	N	0.58	0.62	a	3 4 -	-	-	4	7	12	174+14
CM 37636	227+ 3 +16	14+16	N	?0.63	?0.72	b	3 4 -	8	-	4	6	12	?184+16
CM 37637	235+ 3 +15	14+16	N	0.67	0.74	b	3 4 -	9	-	4	5	12	206+17
CM 37638	234+2/3+16	16+16	N	0.63	0.74	b	3 4 -	9	-	4	8	12	178+17
CM 37639	228+ 3 +16	15+16	N	0.60	0.72	b	3 4 -	9	-	4	6	12	168+13
UPR 5	225+ 3 +16	16+18	N	0.62	0.69	b	3 4 -	8	-	6	8	10	168+15
AMNH 13103	228+ 4 +14	15+18	N	0.72	0.74	b	3 4 -	9	-	4	6	11	208+17
AMNH 13132	224+ 3 +13	16+18	N	0.69	0.71	b	3?4 -	8	-	4	6	12	194+17
AMNH 13146	?226+ 3 +14	? +?	N	0.51	0.58	b	3 4 -	8	-	?	?	?	73+7
AMNH 13147	?227+3/4+14	? +?	N	0.53	0.61	b	3 4 -	9	-	4	8	9	85+8
AMNH 13153	228+ 3 +15	16+18	N	0.61	0.67	b	3 5 -	9	-	4	7	12	174+15
AMNH 13237	227+3/4+14	? +?	N	0.53	0.56	b	3?3 -	8	-	?	6	12	78+8
AMNH 13325	223+ 4 +14	15+16?	N	0.58	0.69	b	3 4 -	9	-	4	6	10	151+13

AMNH 13327	223+ 3 +14	14+16	N	0.51	0.58	b	3 4 -	9	-	4	6	12	85+8
AMNH 13328	225+ 3 +15	16+18	N	0.52	0.62	b	3 4 -	9	-	4	7	12	94+8
AMNH 13864	225+ 3 +14	16+18	N	0.64	0.71	b	3 4 -	8	-	4	7	11	185+14
AMNH 13865	228+ 3 +14	16+18	N	0.68	0.73	b	3 4 -	9	-	4	6	11	195+16
AMNH 13866	225+ 3 +14	15+16	N	0.70	0.75	b	3 4 -	9	-	4	6	12	213+18
AMNH 13867	227+ 3 +14	16+18	N	0.67	0.82	b	3 4 -	9	-	4	6	12	193+15
AMNH 13868	222+3/4+15	16+17	N	0.73	0.89	b	3 4 -	9	-	4	6	11	216+17
AMNH 13869	231+ 3 +15	16+18	N	0.61	0.66	b	3 4 -	9	-	4	8	10	177+15
AMNH 14008	229+ 3 +14	16+18	N	0.66	0.71	b	3 4 -	8	-	4	6	12	186+15
CAS 54858	217+ 4 +14	? +?	N	?0.46	?0.50	b	3 4 -	8	-	?4	?6	?14	?95+7?
AMNH 8591	222+ 3 +14	16+16	N	0.67	0.80	b	3 4 -	9	-	4	6	12	194+17
CAS 54861	226+ 4 +17	15+17	N	0.61	0.66	b	3 4 -	8	-	4	6	12	176+15
RMNH 9985	223+ 4 +14	16+16	N	0.63	0.70	b	3?4 -	8	-	4	6	10	170+16
USNM 27320	222+ 3 +16	18+18	N	0.78	0.90	b	3 4 -	9	-	4	6	11	225+20
USNM 27321	226+ 3 +16	17+18	N	0.64	0.78	b	3 4 -	8	-	4	6	11	179+16
USNM 27322	227+ 3 +16	16+16	N	0.70	0.79	b	3 4 -	7	-	4	6	12	202+18
UMMZ 73838	225+2/3+(6)	16+19	N	0.66	0.80	b	3 4 -	9	-	4	6	12	187+x
MCZ 36304	? + 3 +14	16+16	N	0.64	0.67	b	3 4 -	8	-	4	6	12	?185+16
UMMZ 73840	229+ 3 +15	16+16	N	0.72	0.86	b	3 4 -	9	-	4	6	10	201+17
UMMZ 73842	234+ 4 +14	16+18	N	0.67	0.82	b	3 4 -	8	-	4	6	11	191+15
MCZ 36311	226+2/3+15	17+18	N	0.77	0.88	b	3 5 -	10	-	4	9	12	227+17
MCZ 36312	228+3/4+15	16+17	N	0.74	0.85	b	3 4 -	10	-	4	8	13	200+16
MCZ 36313	227+ 3 +15	16+16	N	0.86	0.98	b	3 4 -	9	-	4	7	12	248+19
MCZ 36314	225+ 3 +15	16+17	N	0.77	0.91	b	3 4 -	9	-	4	8	12	215+17
MCZ 36315	225+ 3 +16	16+16	N	0.77	0.90	b	3 4 -	9	-	4	6	12	?209+18
MCZ 36316	229+2/3+14	16+17	N	0.84	0.97	b	3 4 -	9	-	4	9	12	246+18
MCZ 36317	225+ 3 +14	16+18	N	0.81	0.93	b	3 4 -	9	-	4	8	11	?230+18
MCZ 36318	232+ 4 +15	16+16	N	0.83	0.95	b	3 4 -	9	-	4	8	13	229+18
MCZ 36319	227+ 3 +14	16+18	N	0.74	0.90	b	3 4 -	9	-	4	7	13	210+17
MCZ 36320	228+ 3 +15	16+16	N	0.80	0.90	b	3 4 -	8	-	4	7	12	231+17
MCZ 36321	228+ 3 +16	18+18	N	0.75	0.88	b	3 4 -	9	-	4	7	12	214+18
MCZ 36322	231+ 3 +15	16+16	N	0.73	0.81	b	3 4 -	9	-	4	8	13	216+18
MCZ 36323	233+ 3 +15	16+18	N	0.82	?0.93	b	3 4 -	10	-	4	8	12	243+18
MCZ 36324	227+ 4 +15	14+15	N	0.78	0.93	b	3 5 -	8	-	4	6	14	227+17
UMMZ 73832	226+ 3 +15	16+16	N	0.78	0.89	b	3 4 -	10	-	4	8	12	217+18
UMMZ 73832A	231+ 3 +15	16+18	N	0.80	0.95	b	3 4 -	9	-	4	8	10	238+18
UMMZ 73832B	225+ 3 +17	16+18	N	0.84	1.00	b	3 4 -	10	-	6	6	14	251+18
UMMZ 73832C	230+3/4+15	16+17	N	0.83	0.95	b	3 4 -	8	-	4	8	13	241+18
UMMZ 73832D	231+ 3 +14	16+18	N	0.77	0.91	b	3 4 -	9	-	4	6	12	229+16
UMMZ 73832E	223+3/4+14	17+18	N	0.74	0.86	b	3 4 -	9	-	4	6	11	214+17
UMMZ 73832F	225+ 3 +15	16+18	N	0.81	0.88	b	3 4 -	9	-	4	6	12	230+19
UMMZ 73832G	222+ 3 +15	16+17	N	0.80	0.90	b	3 4 -	10	-	4	8	11	219+17
UMMZ 73832H	230+ 3 +15	16+16	N	0.77	0.87	b	3 4 -	10	-	4	8	11	225+16
UMMZ 73832I	226+ 3 +15	16+16	N	0.71	0.84	b	3 4 -	10	-	4	9	11	224+18
UMMZ 73832J	232+ 3 +14	16+18	N	0.83	0.95	b	3 4 -	9	-	4	8	12	248+18
UMMZ 73832K	229+ 3 +16	16+16	N	0.76	0.89	b	3 5 -	9	-	4	8	12	?215+18
UMMZ 73832L	227+ 3 +15	16+16	N	0.85	0.97	b	3 4 -	10	-	4	8	13	245+19
UMMZ 73832M	229+ 3 +15	16+18	N	0.78	0.89	b	3 4 -	8	-	5	6	11	219+17
UMMZ 73835-6433	227+ 3 +15	16+16	N	0.59	0.72	b	3 4 -	8	-	4	8	12	106+9
UMMZ 73835-6434	227+ 3 +15	17+18	N	0.73	0.84	b	3 4 -	9	-	4	8	12	210+17
UMMZ 73835-6435	230+ 3 +15	16+16	N	0.86	0.98	b	3 4 -	9	-	4	6	12	243+18
UMMZ 73835-6436	228+ 3 +15	16+16	N	0.78	0.84	b	4 4 -	10	-	4	8	13	204+17
UMMZ 73835-6437	231+2/3+15	15+18	N	0.76	0.88	b	3 4 -	9	-	4	8	12	217+18
UMMZ 73835-6438	226+ 4 +14	16+18	N	0.86	0.99	b	3 4 -	9	-	4	8	12	250+19
UMMZ 73835-6439	228+ 4 +(5)	16+18	N	0.77	0.91	b	3 4 -	8	-	4	8	12	227+x
UMMZ 73835-6440	229+ 3 +14	16+18	N	0.77	0.85	b	3 4 -	9	-	4	8	12	209+17
MCZ 36325	230+ 4 +15	16+18	N	0.77	0.83	b	3 4 -	8	-	4	7	11	228+20
UMMZ 73830-3377	232+ 4 +15	16+19	N	0.67	0.83	b	3 4 -	8	-	4	6	11	190+16
UMMZ 73830-3378	234+ 3 +14	17+20	N	0.73	0.78	b	3 4 -	7	-	4	6	11	200+16
UMMZ 73830-3379	232+ 4 +15	16+18	N	0.71	0.76	b	3 4 -	10	-	4	8	10	223+17
UMMZ 73830-3380	230+ 4 +16	16+19	N	0.65	0.77	b	3 4 -	8	-	4	7	12	179+15
UMMZ 73830-3381	227+ 3 +16	16+18	N	0.59	0.69	b	3 4 -	7	-	4	6	10	155+13.5
UMMZ 73830-3382	230+ 4 +15	17+18	M	0.65	0.73	b	3 4 -	8	-	4	6	10	185+15
UMMZ 73830-3393	231+3/4+16	16+18	N	0.73	0.88	b	3 4 -	7	-	4	6	12	?220+17
UMMZ 73830-3394	230+ 4 +16	16+18	N	0.67	0.71	b	3 4 -	8	-	4	4	12	177+15
UMMZ 73830-3395	234+ 3 +16	16+18	N	0.66	0.73	b	3 4 -	8	-	4	6	12	198+16
UMMZ 73830-3396	227+4/3+15	16+18	N	0.70	0.75	b	3 4 -	9	-	4	6	11	198+16
UMMZ 73831	229+ 4 +13	17+18	N	0.72	0.76	b	3 4 -	9	-	4	8	11	215+17
UMMZ 73831A	230+ 3 +15	16+18	N	0.72	0.77	b	3 4 -	8	-	4	6	13	208+18
UMMZ 738318	232+ 3 +14	16+18	N	0.68	0.82	b	3 4 -	8	-	4	7	11	202+17

UMMZ 73831C	231+ 3 +16	16+18	N	0.69	0.75	b	3	4	-	9	-	4	8	12	201+18
UMMZ 73831D	230+ 4 +14	16+18	N	0.65	0.73	b	3	4	-	8	-	4	8	12	182+16
UMMZ 73831E	234+ 4 +14	16+17	N	0.71	0.74	b	3	4	-	7	-	4	8	12	199+17
UMMZ 73831F	226+3/4+14	16+18	N	0.63	0.69	b	3	4	-	9	-	4	8	12	188+15
UMMZ 73831G	232+3/4+14	16+18	N	0.71	0.78	b	3	4	-	9	-	4	6	12	219+17
UMMZ 73831H	232+3/4+14	18+18	N	0.72	0.79	b	3	4	-	8	-	4	8	10	220+19
UMMZ 73831I	232+ 3 +14	16+18	N	0.65	0.72	b	3	4	-	8	-	4	6	12	199+16
UMMZ 73831J	231+ 4 +(5)	16+18	N	0.68	0.72	b	3	4	-	8	-	4	7	11	193+x
UMMZ 73833-2155	229+ 4 +16	16+18	N	0.67	0.80	b	3	4	-	9	-	4	6	12	186+16
UMMZ 73833-2156	236+ 4 +16	16+17	N	0.71	0.85	b	3	4	-	9	-	4	6	13	?202+18
UMMZ 73833-2157	.230+ 4 +16	17+18	N	0.62	0.65	b	3	4	-	8	-	4	7	12	162+15
UMMZ 73833-2158	234+3/4+16	18+19	N	0.74	0.82	b	3	4	-	7	-	4	6	11	209+20
UMMZ 73833-2159	232+ 4 +16	18+20	N	0.72	0.78	b	3	4	-	7	-	4	7	10	210+17
UMMZ 73836-3658	232+ 4 +(6)	15+18	N	?	?	b	3	4	-	7	-	4	7	12	186+x
UMMZ 73836-3659	234+ 3 +16	16+18	N	0.67	0.80	b	3	4	-	9	-	4	7	10	198+17
UMMZ 73836-3660	232+ 3 +16	16+18	N	0.66	0.69	b	3	4	-	9	-	4	7	11	185+15
UMMZ 73836-3661	230+ 3 +16	16+18	N	0.65	0.67	b	3	4	-	7	-	4	7	11	180+15
UMMZ 73836-3662	234+ 4 +16	16+17	N	0.65	0.75	b	3	4	-	7	-	4	6	11	183+15
UMMZ 73836-3663	?227+ 4 +15	16+18	N	0.61	0.74	b	3	4	-	8	-	4	8	11	?174+16
UMMZ 73836-3664	228+ 4 +16	16+18	N	0.59	0.67	b	3	3	-	8	-	4	7	11	149+13
UMMZ 73836-3665	231+ 4 +16	16+18	N	0.68	0.72	b	3	4	-	9	-	4	7	11	191+17
UMMZ 73836-3666	229+ 3 +17	16+18	N	0.65	0.78	b	3	4	-	9	-	4	6	11	183+15
UMMZ 73834	231+2/3+15	16+18	N	0.74	0.84	b	3	4	-	8	-	4	6	10	230+18
UMMZ 73834-2702	225+2/3+17	16+18	N	0.72	0.85	b	3	4	-	8	-	4	6	11	199+18
UMMZ 73834-2703	228+ 4 +(5)	16+17	N	0.73	0.75	b	3	4	-	7	-	4	6	11	205+x
UMMZ 73834-2704	230+ 4 +(8)	16+17	N	0.76	0.91	b	3	4	-	8	-	4	6	11	214+x
UMMZ 73834-2705	228+ 4 +15	16+19	N	0.68	0.74	b	3	4	-	8	-	4	6	12	215+18
UMMZ 73834-2706	231+ 4 +(4)	16+18	N	0.75	0.88	b	3	4	-	8	-	4	6	13	202+x
UMMZ 73834-2707	231+ 4 +14	16+18	N	0.75	0.88	b	3	4	-	8	-	4	8	11	212+17
UMMZ 73834-2708	231+3/4+16	16+18	N	0.65	0.78	b	3	4	-	9	-	4	6	11	192+17
UMMZ 73834-2709	229+3/4+16	16+17	N	0.74	0.89	b	3	4	-	8	-	4	6	11	200+17
UMMZ 73834-2711	224+ 3 +15	15+18	N	0.72	0.79	b	3	4	-	7	-	4	6	10	206+16
MCZ 36326	233+ 3 +14	16+18	N	0.61	0.72	b	3	4	-	8	-	4	6	12	157+13
MCZ 36327	228+ 3 +15	16+18	N	0.64	0.68	b	3	4	-	9	-	4	7	11	179+15
MCZ 36328	226+ 4 +15	16+18	N	0.70	0.79	b	3	4	-	9	-	4	7	12	?215+17
MCZ 36329	228+ 3 +15	16+18	N	0.59	0.63	b	3	4	-	8	-	4	9	10	154+15
MCZ 36330	226+ 4 +14	16+18	N	0.63	0.66	b	3	4	-	7	-	4	7	10	163+14
MCZ 36331	226+ 3 +15	16+18	N	0.74	0.89	b	3	4	-	9	-	4	6	11	?214+18
MCZ 36332	231+3/4+14	16+18	N	0.71	0.76	b	3	4	-	6	-	4	6	13	196+16
MCZ 36333	223+2/3+15	16+18	N	0.66	0.71	b	3	4	-	9	-	4	8	10	183+16
MCZ 36334	230+ 3 +16	16+19	N	?0.66	0.74	b	3	4	-	9	-	4	6	12	192+17
MCZ 36335	228+3/4+14	16+18	N	0.58	0.65	b	3	4	-	9	-	4	8	11	165+14
MCZ 36336	228+3/4+15	16+18	N	0.60	0.70	b	3	4	-	9	-	4	8	12	157+14
MCZ 36337	229+2/3+15	16+18	N	0.67	0.74	b	3	4	-	8	-	4	6	11	186+16
MCZ 36338	233+2/3+15	16+18	N	0.67	0.70	b	3	4	-	8	-	4	8	11	192+16
MCZ 36339	227+3/4+15	16+18	N	0.66	0.71	b	3	4	-	8	-	4	8	12	189+15
MCZ 36340	232+3/4+15	16+18	N	0.67	0.75	b	3	4	-	7	-	4	8	10	194+16
MCZ 36341	233+3/4+15	16+18	N	0.69	0.76	b	3	4	-	9	-	4	6	11	220+18
MCZ 36342	233+ 3 +15	17+19	N	0.67	0.74	b	3	4	-	7	-	4	7	12	192+16
MCZ 36343	227+ 3 +15	16+18	N	0.68	0.71	b	3	4	-	9	-	4	6	11	188+15
MCZ 36344	233+ 3 +15	16+18	N	0.60	0.64	b	3	4	-	9	-	4	7	11	170+14
MCZ 36345	227+ 4 +14	16+18	N	0.71	0.81	b	3	4	-	9	-	4	8	12	202+17
MCZ 36346	233+ 3 +15	16+18	N	0.58	0.64	b	3	4	-	9	-	4	6	11	160+14
MCZ 36347	232+ 3 +15	16+18	N	0.69	0.77	b	3	4	-	7	-	4	6	11	213+18
MCZ 36348	231+ 3 +15	16+18	N	0.66	0.74	b	3	4	-	7	-	4	6	12	194+17
MCZ 36349	234+3/4+15	18+18	N	0.66	0.83	b	3	4	-	9	-	4	6	12	203+17
MCZ 36350	236+2/3+15	16+18	N	0.74	0.92	b	3	4	-	8	-	4	6	10	230+18
MCZ 36350-1637	230+ 4 +15	16+18	N	0.74	0.90	b	3	4	-	8	-	4	7	12	198+17
MCZ 36350-1638	225+3/4+14	16+18	N	0.73	0.87	b	3	4	-	7	-	4	5	12	200+18
MCZ 36350-3174	232+ 4 +15	18+19	N	0.73	0.79	b	3	4	-	8	-	4	7	10	203+18
MCZ 36350-3175	232+3/4+14	16+17	N	0.72	0.76	b	3	4	-	9	-	4	6	12	202+16
MCZ 36350-3176	232+2/4+15	17+18	N	0.62	0.74	b	3	4	-	8	-	4	6	12	169+13
MCZ 36350-3177	230+ 3 +15	18+19	N	0.60	0.65	b	3	?	-	8	-	4	8	12	163+13
MCZ 36350-3178	232+3/4+14	18+18	N	0.58	0.70	b	3	4	-	7	-	4	8	11	165+13
MCZ 36350-3179	233+ 3 +15	17+20	N	0.66	0.80	b	3	3	-	7	-	4	6	10	189+16
MCZ 36350-3180	232+ 4 +14	18+19	N	0.64	0.67	b	3	3	-	8	-	4	7	10	163+14
MCZ 36350-3181	232+2/3+15	16+18	N	0.63	0.67	b	3	4	-	7	-	4	6	12	167+15
MCZ 36350-3182	226+3/4+15	16+19	N	0.67	0.81	b	3	4	-	9	-	?4	7	11	?191+17
MCZ 36350-3183	228+ 3 +(6)	16+18	N	0.70	0.74	b	3	4	-	9	-	4	8	11	?200+x
MCZ 36350-3184	229+3/4+14	16+18	N	0.58	0.67	b	3	4	-	8	-	4	8	10	168+14

MCZ	36350-4526	229+ 3 +14	16+18	N	0.71	0.79	b	3 4 -	9	-	4	7	10	218+17
MCZ	36350-5046	226+ 3 +15	16+18	N	0.70	0.74	b	3 4 -	8	-	4	7	10	206+18
MCZ	36350-6125	230+ 4 +15	16+18	N	0.60	0.69	b	3 4 -	9	-	4	7	11	161+14
MCZ	36350-6152	231+3/4+14	17+19	N	0.67	0.72	b	3 4 -	9	-	4	7	11	192+17
MCZ	36350A	233+3/4+17	16+18	N	0.64	0.72	b	3 4 -	8	-	4	6	11	180+17
MCZ	36350B	230+ 4 +16	16+17	N	0.78	0.95	b	3 4 -	8	-	4	6	12	225+18
MCZ	36350C	228+ 3 +16	16+18	N	0.70	0.80	b	3 4 -	9	-	4	8	11	190+16
MCZ	36350D	?230+3/4+17	17+18	N	?	?	b	3 4 -	8	-	4	6	11	?160+14
MCZ	36350E	230+3/4+16	16+18	N	0.66	0.76	b	3 4 -	8	-	4	8	10	181+16
MCZ	36350F	228+ 4 +16	18+20	N	0.68	0.79	b	3 4 -	9	-	4	8	11	185+17
MCZ	36350G	229+2/3+15	16+19	N	0.78	0.83	b	3 4 -	8	-	4	3	12	223+18
MCZ	36350H	236+ 4 +15	18+20	N	0.73	0.87	b	3 4 -	9	-	4	6	12	216+18
MCZ	36350J	233+ 4 +15	16+18	N	0.73	0.90	b	3 4 -	9	-	4	6	12	220+18
MCZ	36350K	229+3/4+16	16+17	N	0.67	0.80	b	3 4 -	7	-	4	7	11	192+17
MCZ	36350L	226 +3 +16	14+16	N	?0.53	?0.64	b	3 4 -	8	-	4	7	11	134+12
MCZ	36350M	233+ 3 +(6)	17+18	N	0.71	0.75	b	3 4 -	9	-	4	6	12	201+x
MCZ	36350N	232+2/3+16	16+18	N	0.55	0.68	b	3 4 -	7	-	4	6	11	140+12
MCZ	36350P	230+ 4 +16	16+18	N	0.65	0.69	b	3 4 -	8	-	4	6	11	191+17
MCZ	36350R	230+3/4+16	16+18	N	0.70	0.69	b	3 4 -	7	-	4	6	9	201+17
MCZ	36350S	231+ 4 +15?	15+17	N	0.63	0.74	b	3 4 -	7	-	4	6	12	160+13
MCZ	36350T	222+ 4 +15	16+18	N	0.69	0.74	b	3 4 -	8	-	4	6	13	185+17
MCZ	36302	231+ 2 +17	16+17	N	0.70	0.80	b	3 4 -	8	-	4	6	11	209+17
UMMZ	73837	227+ 3 +14	17+18	N	0.81	0.98	b	3 4 -	7	-	4	8	11	231+19
MCZ	58831	231+3/4+15	16+18	N	0.71	0.81	b	3 4 -	8	-	4	6	15	?228+17
UMMZ	53253	229+ 3 +15	15+18	N	0.63	0.77	b	3 3 -	8	-	4	6	11	170+14
MCZ	36307	232+ 4 +14	15+18	N	?	0.77	b	? ? ?	?	?	4	7	11	202+16
MCZ	36308	232+ 3 +15	16+18	N	0.72	0.83	b	3 3 -	8	-	4	8	11	208+17.5
MCZ	36309	231+3/4+14	15+18	N	0.72	0.78	b	3 3 -	9	-	4	8	12	203+15
MCZ	36310	230+3/4+14	16+18	N	0.78	0.83	b	3 4 -	8	-	4	8	12	232+16
UMMZ	73845-1091	233+ 3 +16	16+18	N	0.76	0.81	b	3 4 -	10	-	4	8	12	212+17
UMMZ	73845-1092	228+ 4 +15	15+18	N	0.70	0.81	b	3 4 -	9	-	4	8	11	189+16
USNM	27005	228+3/4+14	16+18	N	0.65	0.78	b	3 4 -	9	-	4	6	12	195+16
USNM	27006	231+2/3+16	14+18	N	0.63	0.75	b	3 4 -	8	-	4	8	11	181+16
MCZ	7902	232+ 4 +14	14+18	N	0.66	0.77	b	3 5 -	7	-	4	8	10	195+15
USNM	26879	230+ 3 +16	16+18	N	0.65	0.70	b	3 4 -	9	-	4	6	12	195+16
USNM	26880	233+ 3 +16	16+18	N	0.68	0.80	b	3 4 -	8	-	4	8	11	192+16
USNM	26881	232+2/3+14	14+18	N	0.73	0.84	b	3 3 -	7	-	4	6	12	194+15
UMMZ	73843	229+ 3 +16	16+18	N	?0.82	0.93	b	3 4 -	9	-	4	9	11	226+20

A. fenestrata

KM	R448	244+ 2 +13	14+16	F	0.58	0.63	b	3 4 -	9	-	4	6	10	205+15
KM	R4411	244+ 2 +14	13+14	F	0.56	0.65	b	3 4 -	10	-	4	6	10	224+15
BM	60.4.18.71	?249+ 3 +13	14+14	F	0.57	0.67	b	3 4 -	9	-	4	8	8	?205+14
BM	60.4.18.72	?247+ 2 +13	14+14	F	0.57	0.65	b	3 4 -	9	-	4	4	10	?220+13
CNHM	51586	244+ 2 +12	14+14	F	-	-	-	- - -	-	-	-	-	-	180+13
HM	308	243+ 2 +13	14+16	F	0.64	0.66	b	3 4 -	10	-	4	6	10	230+15
KM	R4410	242+ 3 +12	14+15	F	0.57	0.67	b	3 4 -	9	-	4	6	10	205+15
MHNP	1071	245+ 2 +14	14+16	F	0.56	-	-	- - -	-	-	4	6	8	224+15
USNM	11715	245+ 2 +13	13+14	F	-	-	-	- - -	-	-	-	-	-	222+13
ZMU	4346	242+ 2 +12	14+16	F	0.50	0.57	b	3 4 -	10	-	4	6	10	154+12
BM	65.10.2.11	247+ 3 +14	14+15	F	0.64	0.72	b	3 4 -	10	-	4	6	10	228+17
KM	R449	247+ 3 +13	14+14	F	0.64	0.72	b	3 4 -	9	-	4	6	9	242+16
UMMZ	91436	245+ 2 +12	14+16	F	0.56	0.63	b	3 4 -	10	-	4	?	?	210+15
MCZ	36305	241+ 3 +13	14+16	F	0.60	0.72	b	3 4 -	9	-	4	6	10	183+14
MCZ	36306	242+ 3 +13	14+16	F	-	-	b	3 4 -	10	-	4	6	9	186+13
SU	14633	242+ 2 +13	14+14	F	0.49	0.54	b	3 4 -	10	-	4	6	11	159+13
UMMZ	73847A	236+ 2 +14	14+16	F	0.55	0.62	b	3 4 -	9	-	4	6	12	159+11.5
UMMZ	738478	236+ 2 +14	14+16	F	0.51	?0.63	b	3 4 -	10	-	4	6	9	102+9

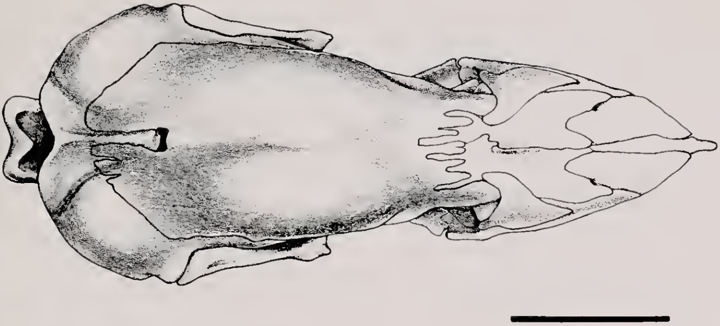
Addendum

KM	R4414	202+ 3 +(7)	14+16	N	0.48	0.56	b	2 3 -	7	-	4	8	7	117+x
KM	R4416	200+ 3 +22	14+16	N	0.59	0.70	b	2 3 -	7	-	4	8	10	163+23
CM	36276	234+4/3+16	15+18	N	0.64	0.68	b	3 4 -	9	-	4	8	12	?211+18
CM	36277	198+3/4+21	14+16	N	0.63	0.78	b	3 4 -	6	-	4	8	10	?173+21?
VM	12345	249+ 3 +12	12+14	F	0.53	0.62	b	3 4 -	9	-	4	6	9	? +14

PLATES

PLATE 1

Amphisbaena fenestrata. Dorsal, lateral and ventral views of the skull of MCZ 36306. The line equals .2 cm to scale. (M. Franson, del.)



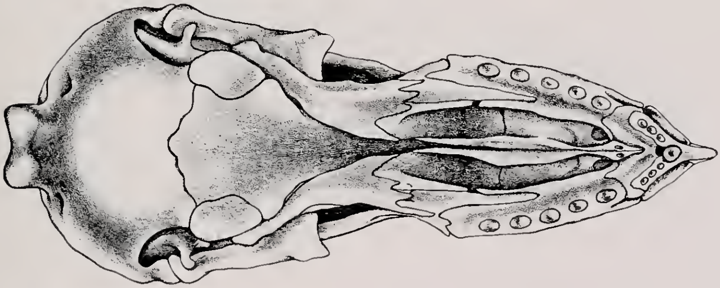


PLATE 2

Amphisbaena caeca. Dorsal, lateral and ventral views of the skull of MCZ 36317. The line equals .5 cm to scale. (M. Franson, del.)

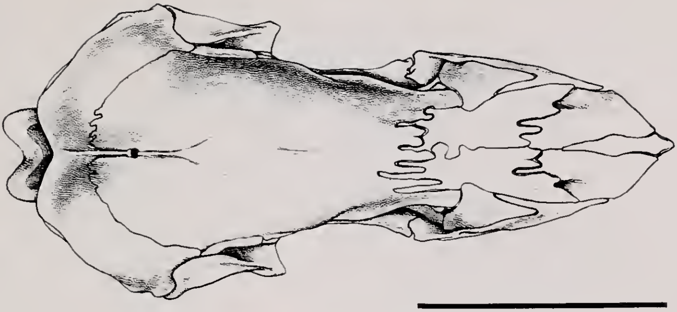
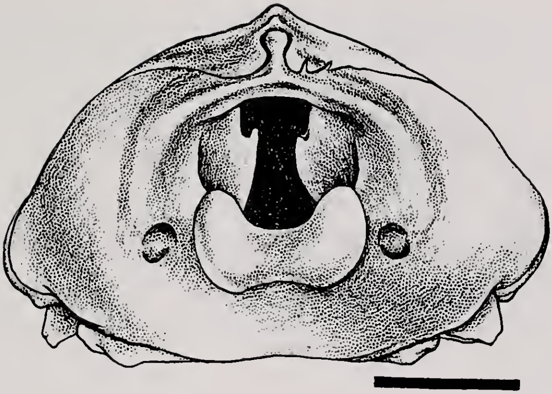


PLATE 3

Occipital aspect of amphisbaenid skulls. Upper, *Amphisbaena fenestrata,* MCZ 36306. Lower, *Amphisbaena caeca,* MCZ 36317. The lines equal 1 mm to scale. (M. Franson, del.)



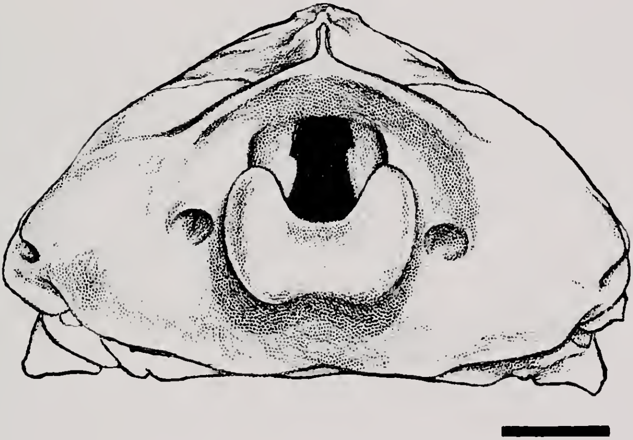


PLATE 4

Amphisbaena c. cubana. *A.* View of dorsum at midbody of AMNH 77790. *B.* View of ventrum of same specimen. *C.* Ventral view of entire tail of same specimen. Note absence of autotomy constriction. *D.* Same view of the badly scarred tail of MCZ 13527. This indicates the extent of damage possible without loss of the terminal portion of the tail. *E.* Same view of the tail of MCZ 35510, truncated after the seventh caudal annulus.

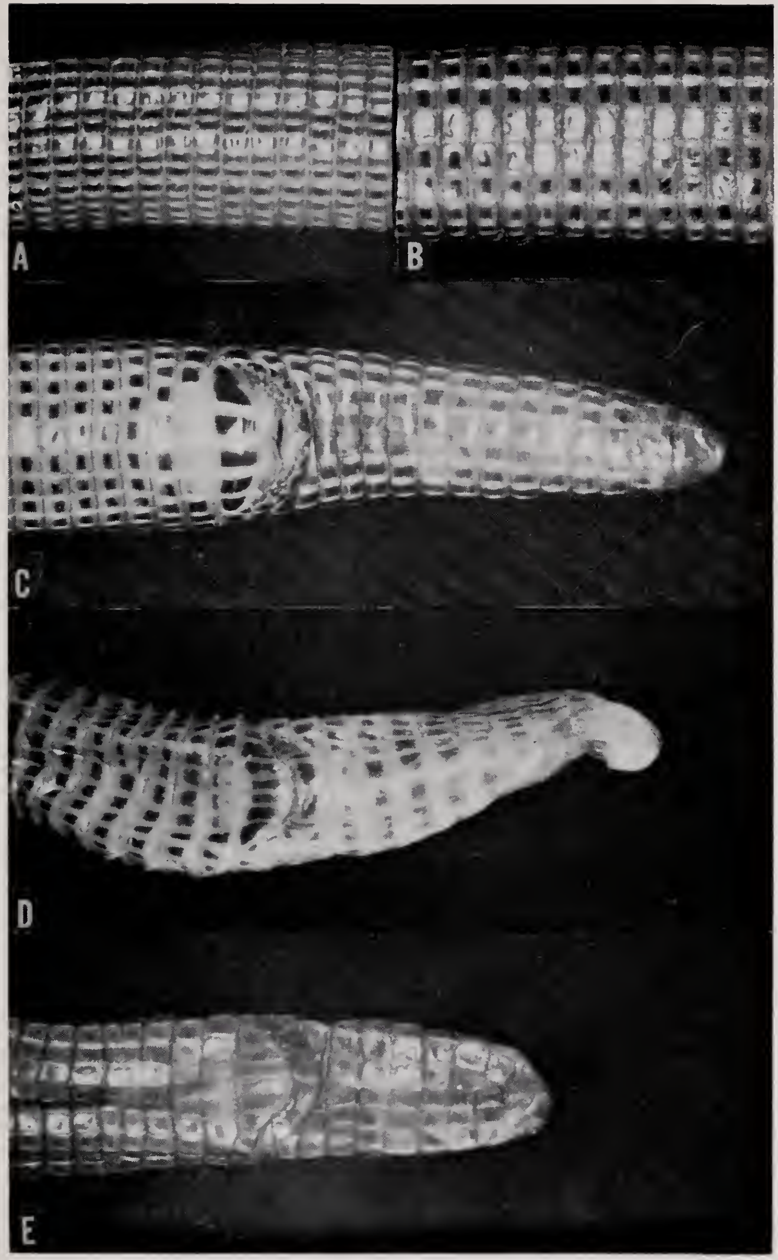

A
B
C
D
E

PLATE 5

Amphisbaena cubana barbouri. A-C. Dorsal, lateral and ventral views of the head and anterior body of the holotype, MCZ 12136. *D.* Ventral view of the tail of the same specimen.

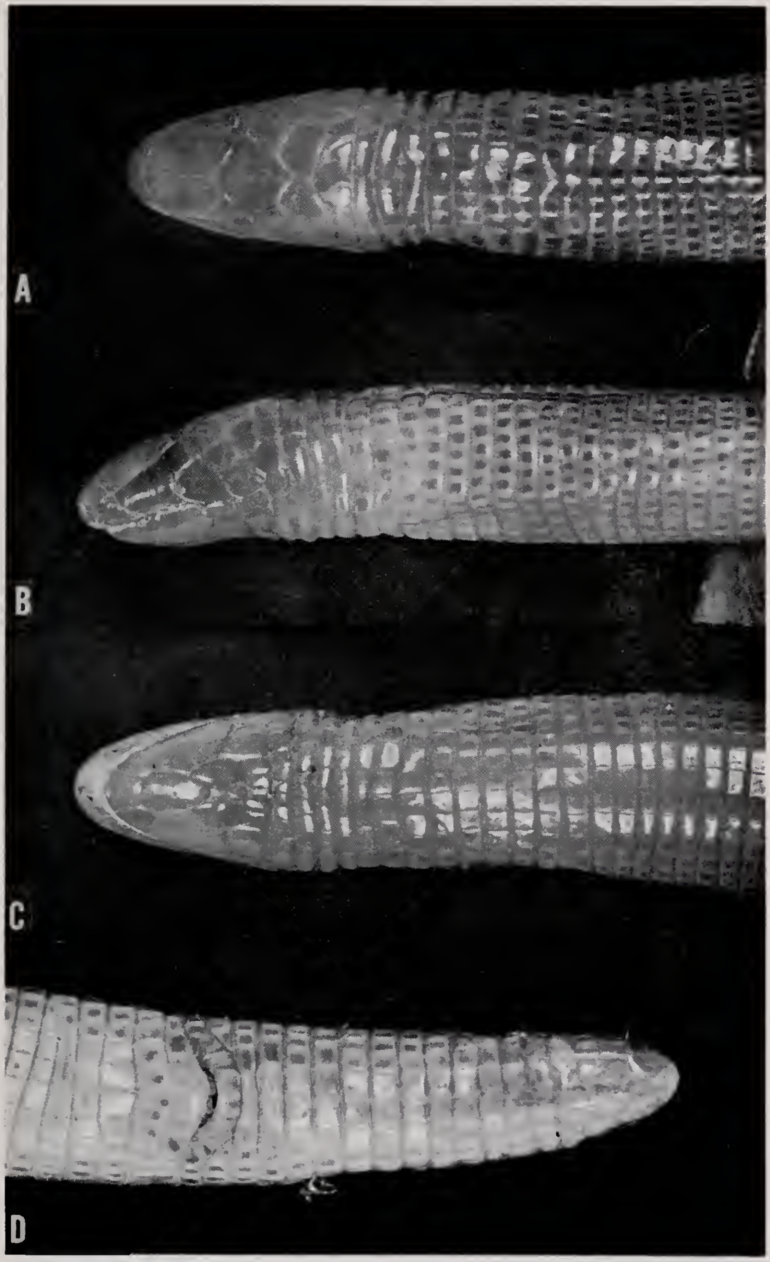

A
B
C
D

PLATE 6

Amphisbaena innocens. *A*. View of dorsum at midbody of MCZ 63618 (*A. i. innocens*). *B*. Lateral view at midbody of the same specimen. *C-D*. Lateral and ventral views of the tail of MCZ 63611 (*A. i. innocens*) showing its conical shape. *E*. Ventral view of the tail of the *A. i. caudalis* holotype (MCZ 25550), showing the relatively elongate, cylindrical shape.

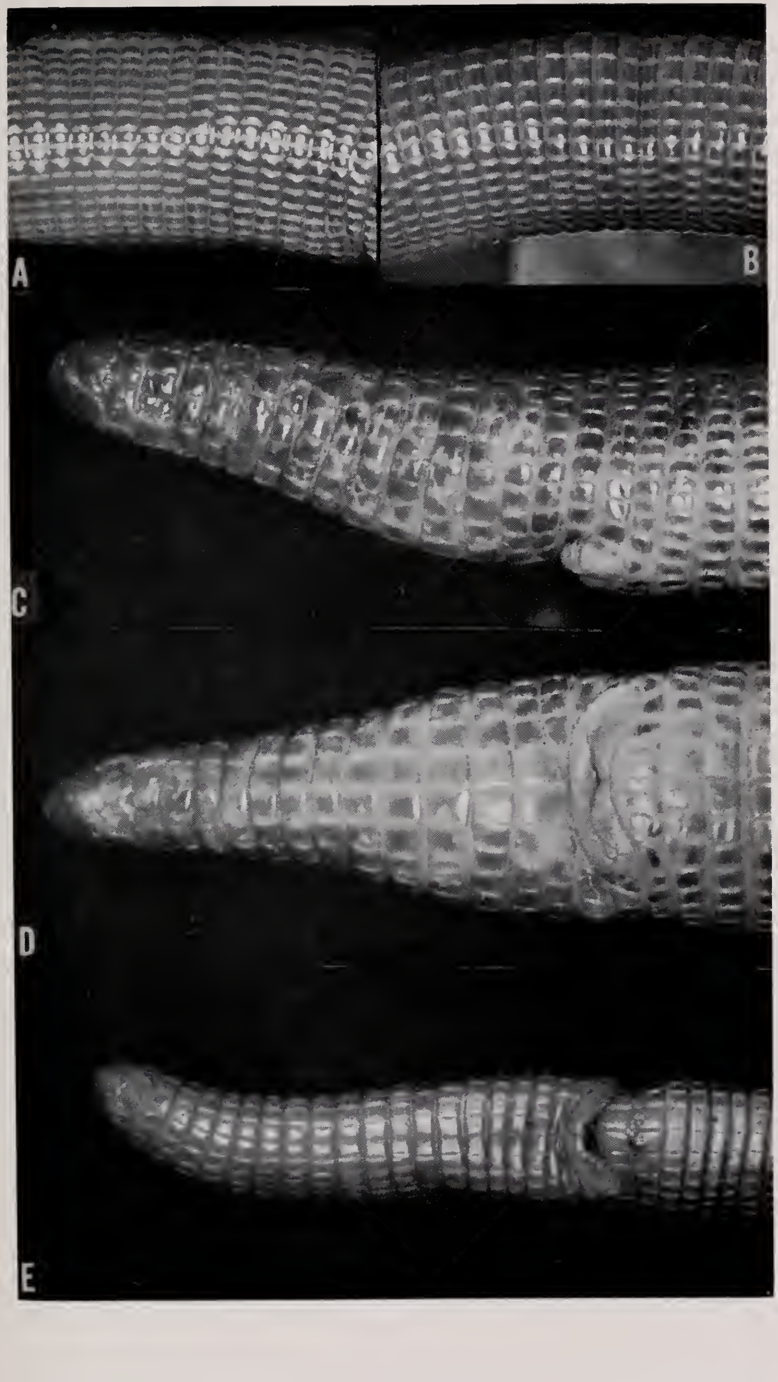

A
B
C
D
E

PLATE 7

Amphisbaena manni. *A-B*. Views of dorsum and ventrum at midbody of MCZ 62533 showing the uniform coloration of the segments. *C*. Ventral view of the cloaca and tail of the same specimen showing the characteristic constriction representing the preferred level of autotomy. *D*. Embryo (with AMNH 41030-84) showing the peculiar yolk or allantoic mass stretching from end to end of the egg.

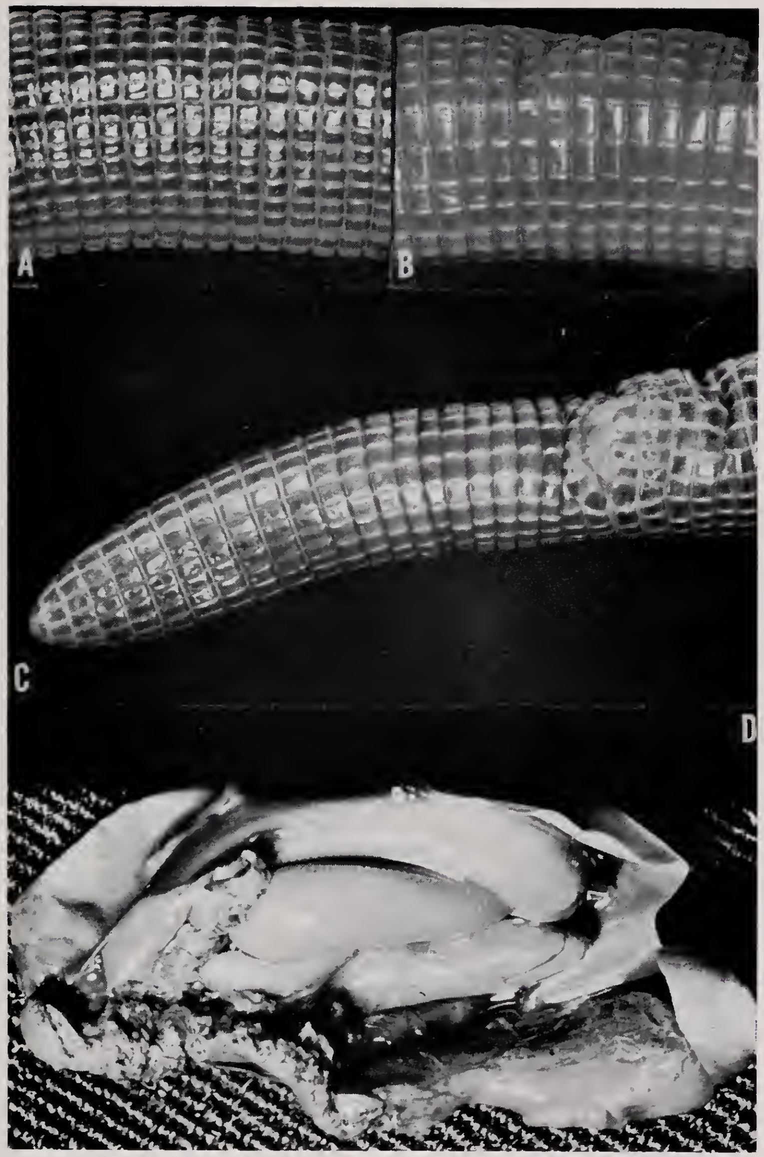

A
B
C
D

PLATE 8

Amphisbaena. *A-B*. Views of the dorsum and ventrum at midbody of CNHM 12473 (*A. bakeri*). The color is somewhat faded. *C*. Ventral view of the cloaca and tail of same specimen showing lack of autotomy level. *D*. Same view of MCZ 64133 (*A. caeca*) with clear autotomy level.

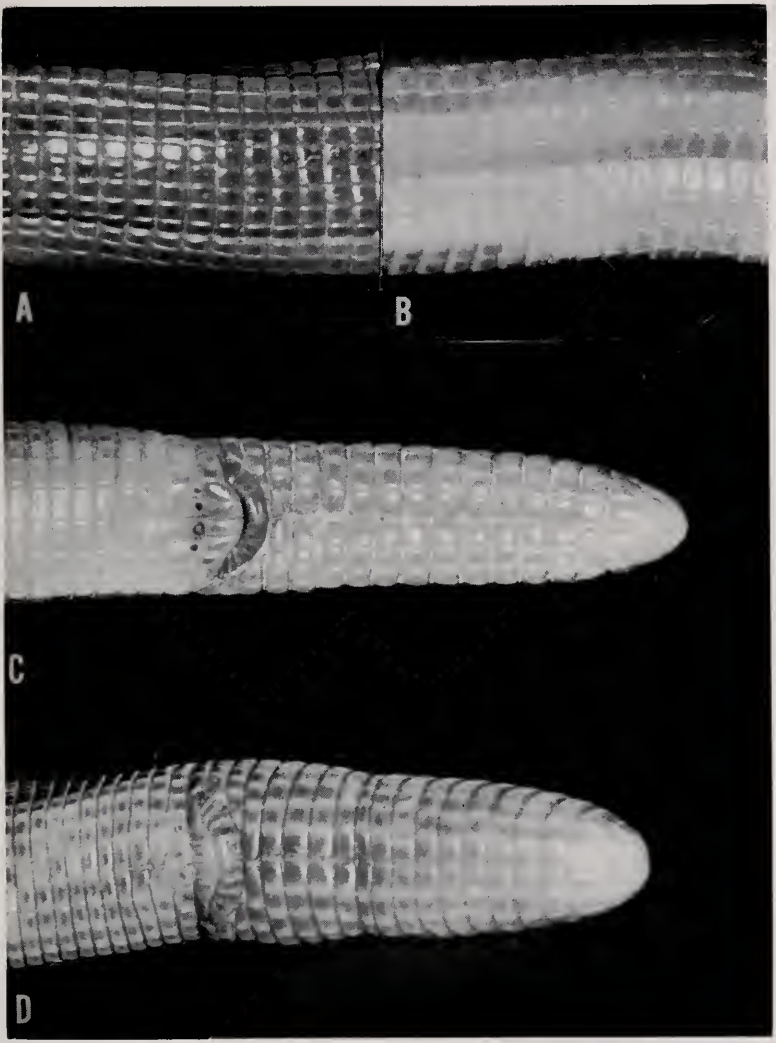

A
B
C
D

PLATE 9

Amphisbaena caeca. *A.* Lateral view of the head of UMMZ 73831-G, showing the general color pattern and the excessive subdivision of segments following injury. *B-C.* Views of dorsum and ventrum at midbody, and *D.* view of ventrum in the precloacal region of the same specimen. Note that the dorsal color drops out by segments, with more light area posteriorly. The fusion of the midventral, precloacal segments into pairs is an anomaly. *E.* View of cloaca of MCZ 58831 with partially everted hemipenes. *F.* Same view with outlines and sulci traced in. Arrow (1) points to the right and (2) to the left sulcus spermaticus.

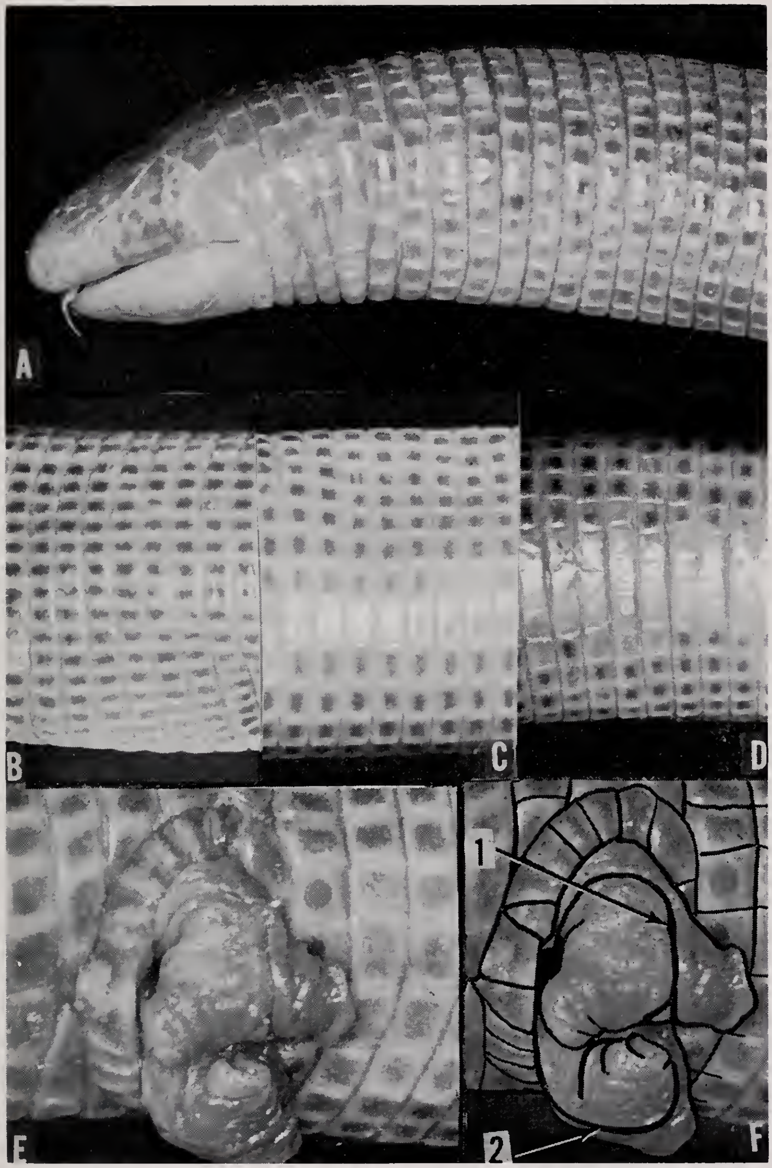

A
B
C
D
E
F
1
2

PLATE 10

Amphisbaena. *A*. Dorsal view of the head of an embryo at term (AMNH 13147). *B*. Same view of a large adult (UMMZ 73840). These views suggest the drastic ontogenetic change in head shape, caused primarily by the enlargement of the cephalic musculature. *C-D*. Views of dorsum and ventrum at midbody of *A. fenestrata* (SU 14633).

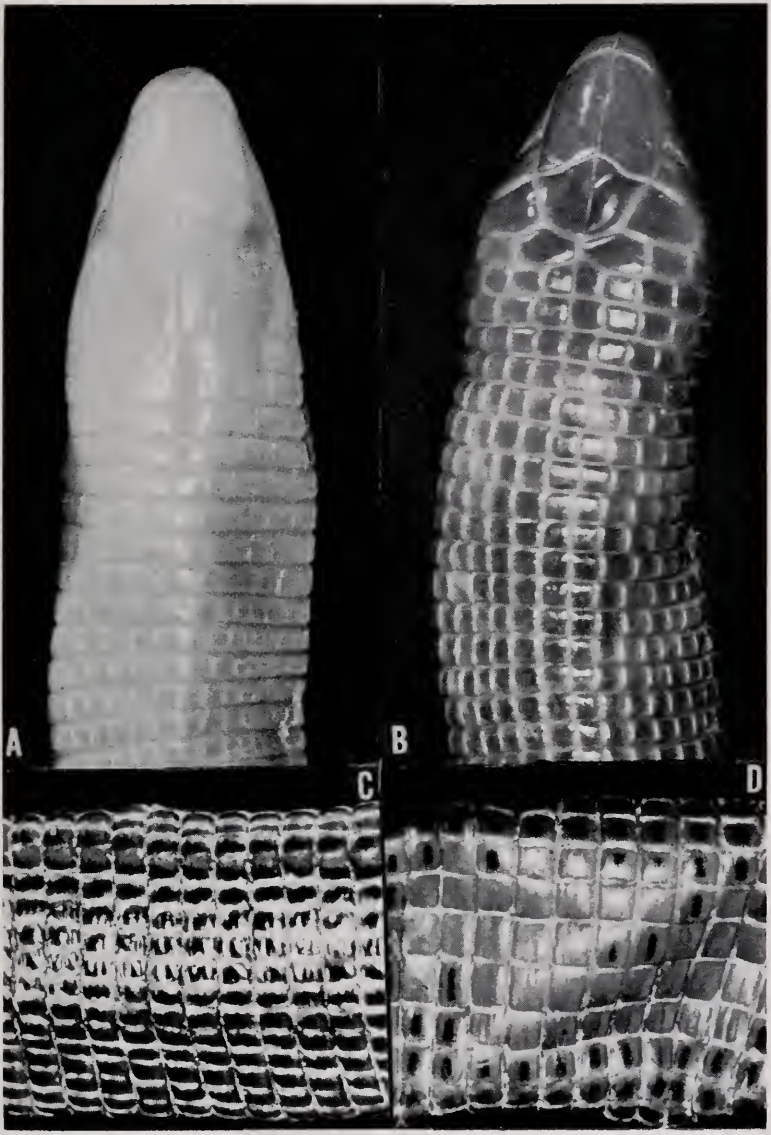

A
B
C
D

PLATE 11

Cadea blanoides (AMNH 77789). *A*. Dorsal view of the head. The light color of the segments surrounding the rostral is an artifact. *B-D*. Views of dorsum, side and ventrum at midbody. This sequence shows the rounding of the dorsal segments and the non-concordance of segment arrangement and color pattern. *E*. View of dorsal, and *F*. ventral surfaces of the cloacal and caudal regions. Note the short, blunt tail, the characteristic color pattern, absence of autotomy constriction, and arrangement of precloacal pores in two series.

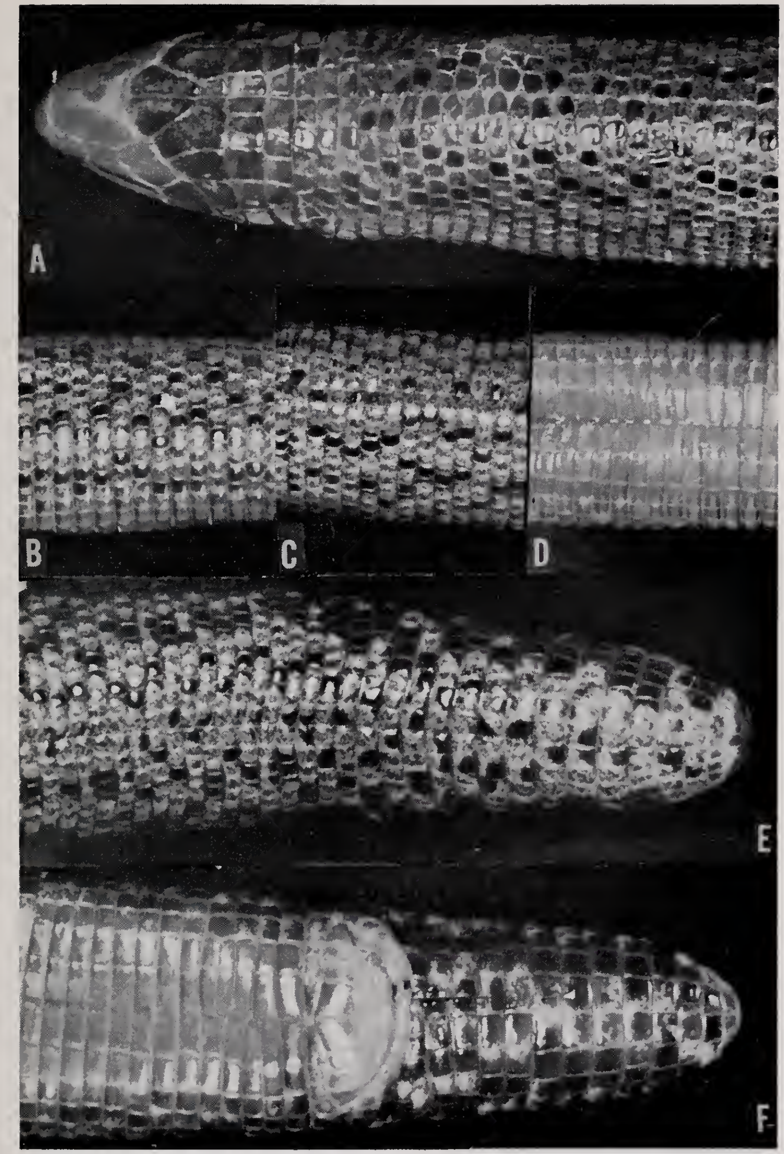

A
B
C
D
E
F

PLATE 12

Cadea palirostrata (AMNH 12810). *A*. Dorsal view of the head. Note the remarkable design extending forward from the nuchal region. *B-D*. Views of dorsum, side and ventrum at midbody. This sequence shows the characteristic rounding of the dorsal segments, non-concordance of segments and color blotches and greater number of dorsal than ventral half-annuli. Here again the lateral sulcus is most poorly defined. *E*. Ventral view of the cloacal region and tail.


A
B
C
D
E

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 128, No. 4

NEW AND LITTLE KNOWN BATOID FISHES FROM THE WESTERN ATLANTIC

By Henry B. Bigelow and William C. Schroeder

With One Plate

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
December 31, 1962

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No. 4 — *New and Little Known Batoid Fishes from the Western Atlantic*

By Henry B. Bigelow and William C. Schroeder

CONTENTS

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[1] Contribution No. 1204 from the Woods Hole Oceanographic Institution.

INTRODUCTION

During the last five or six years, we have received for study a number of interesting batoids trawled by the U.S. Fish and Wildlife Service vessels ''Oregon,'' ''Combat,'' ''Silver Bay,'' ''Pelican,'' and ''George M. Bowers.'' Most of these were taken in the Gulf of Mexico, the Caribbean and along the coast of South America to as far south as Lat. 01°49′N, off the mouth of the Amazon, but a few were trawled along our eastern coast, to the southward of Cape Hatteras. The catches were made chiefly in depths between 100 and 500 fathoms, with a few shoaler. Eight new species are here described, together with notes on other species. We are indebted to Harvey R. Bullis, Jr., of the U.S. Fish and Wildlife Service, for placing these specimens at our disposal.

Included also is an account of the first western Atlantic record of the pelagic ray *Dasyatis violacea*, captured by the U.S. Fish and Wildlife exploratory vessel ''Delaware.'' For this specimen we thank Ernest D. McRae, Jr., Field Party Chief on the ''Delaware'' and Frank J. Mather III of the Woods Hole Oceanographic Institution. Drawings are by Jessie H. Sawyer except as otherwise noted.

SYSTEMATIC DESCRIPTIONS

ORDER BATOIDEI

Suborder TORPEDINOIDEA

FAMILY TORPEDINIDAE

Torpedo nobiliana Bonaparte 1835

This species has long been known from both sides of the Atlantic. In the western side it occurs regularly from southern Nova Scotia to northern North Carolina and it has also been reported. on what appeared to be somewhat doubtful evidence, from the Florida Keys, Cuba, and the Gulf of Mexico.[1] We can now report that it is widespread in southern waters, although perhaps in smaller numbers than to the northward, for the present collection includes the following: a female of 330 mm in total length trawled about 85 miles northwest of Trinidad, Lat. 11°36′N, Long. 62°52′W, in 215-230 fathoms, ''Oregon'' station 2780; another female of 290 mm taken nearby in 290 fathoms, ''Oregon'' station 2777; also 2 from off the Mississippi Delta, a male of 215 mm in 10 fathoms, and a female of 613 mm in 250 fathoms, ''Oregon'' stations 1567 and 2285; a female of 450 mm from off the northwest coast of Florida (Cape San Blas) in 11-12 fathoms, ''Silver Bay'' station 32; a female of 211 mm from off Cape Romain, South Carolina, in 125 fathoms, ''Combat'' station 284; and 2 females, 300-336 mm from off Cape Fear, North Carolina, in 200 fathoms, ''Combat'' stations 290 and 356.

This electric ray is the only member of its genus thus far known from the western North Atlantic. Among its relatives in the eastern North Atlantic the typical plain dark chocolate or purplish brown coloration of its upper surface (occasionally with a few obscure darker spots) and the smooth margins of its spiracles distinguish it from *marmorata* Risso 1810 which is prominently spotted above and has long papillae around the margins of the spiracles; and it is marked off from *torpedo* by invariably lacking spiracular papillae, in a much wider caudal fin (21.5-26.0 per cent of total length on 8 specimens of *nobiliana,* 13.3-15.6 per cent on 3 specimens of *torpedo*) and a shorter distance from the origin of the first dorsal to the origin of the caudal fin (17.2-20.7 per cent for *nobiliana,* 22.4-23.7 per cent for *torpedo*).

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[1] For discussion of its occurrence in southern waters up until that time, see Bigelow and Schroeder, 1953, p. 105.

Previously recorded from near shore out to about 60 fathoms, its known depth range is now considerably extended, to 290 fathoms, and its range southward to the offing of Trinidad.

Genus DIPLOBATIS Bigelow and Schroeder 1948

The outstanding feature of this genus is that each nostril is subdivided into two separate apertures by a cross bridge of stiff tissue. We state also, in our original diagnosis, that the teeth are entirely concealed when the mouth is retracted and closed. However, this statement must now be modified, for on a number of our specimens of *Diplobatis pictus,* listed below, from one to several rows of teeth in the upper jaw are exposed when the mouth is tightly closed, although on others none are exposed.

DIPLOBATIS PICTUS Palmer 1950

Plate I

Study material. Twenty-four specimens, males and females, 77-164 mm in total length, trawled off the coasts of Brazil, French Guiana and British Guiana, between Lat. 02°29′N, Long. 48°58′W, and Lat. 09°31′N, Long. 60°36′W, in 9-50 fathoms, "Oregon" stations 2001, 2037, 2058, 2213, 2215, 2236, 2263, 2267.

D. pictus differs from its close relative *D. guamachensis* Martin 1957 in its relatively narrower and shorter disc, in narrower expanse of pelvics, in location of the folds along sides of tail, and in coloration. Thus in 21 of our specimens of *pictus* the width of disc ranges from 38.8 to 50.0 per cent, the length of disc from 38.8 to 48.0 per cent, and the breadth of pelvics from 28.7 to 36.6 per cent (the smaller specimens having the narrower pelvics) of total length, whereas these proportions for the few *guamachensis* thus far examined are 53.0-58.1, 50.3-54.5, and 36.7-40.0 per cent, respectively.[1] The lateral tail folds originate between the rear end of the first dorsal base and the origin of second dorsal on *pictus* whereas they originate immediately behind the origin of the first dorsal in *guamachensis.* None of the color varieties of *pictus* thus far seen show the narrow elongate markings that are present on the holotype of *guamachensis.*

The color varies considerably in this species, if we are correct in assigning all our specimens to *pictus,* falling into two major

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[1] Personal communication from Felipe Martin S., based on 4 specimens, 3 females and 1 male, 56.5-70.9 mm in total length.

patterns which can be termed the freckled form and the non-freckled form.

Fifteen non-freckled specimens, 77-156 mm long, were taken at 3 stations at the extremes of the above given latitudes, in depths of 9-26 fathoms while 9 freckled ones, 87-133 mm long, were taken at 5 stations between Lat. 05°51′ and 08°09′ in 19-28 fathoms (1 specimen in 50 fathoms).

The upper surface of the freckled form is pale brown, densely sprinkled in advance of the first dorsal with irregular dark brown spots ranging in size from smaller than the spiracle to about 1-2 times as large; also with a larger dark blotch or spot aside each dorsal and one or more on the dorsals and caudal but lacks the prominent blotch in advance of the first dorsal that is present on the type specimen; other markings agree with those of the type. There is also a series of white spots, as large as or a little smaller than the spiracle and surrounded by small dark brown markings arranged in 5 pairs in nearly straight lines from a little posterior to the spiracles to opposite the middle part of the pelvics, with a single spot (usually smaller than the others) in the midline opposite the second pair and another on one or both sides between the second and third pairs and about in line with axils of pectorals. On some specimens one or more of the white spots are missing. One specimen also has about 20 dark brown spots, about as large as the spiracle, scattered across the disc in front of the orbits, replacing several of the blotches present in that area on other specimens.

The non-freckled form ranges from plain light brown with a few vague darker blotches here and there, to others in which the blotches are prominent, especially those aside and on the dorsals, the dark bar in front of the first dorsal present on the type of *pictus* being clear on some, vague on others. On only one specimen are white spots present (faintly) arranged as on the freckled form.

The under surface of both color varieties is plain whitish.

The fins vary in shape in both color phases. Thus the tips of the two dorsals and the upper caudal lobe all are rounded on some specimens while on others the second dorsal is pointed, as are both dorsals on a few, although not quite as sharply so as is pictured for the type specimen (Palmer 1950, fig. 1 reproduced by Bigelow and Schroeder 1953, fig. 25 α). The upper caudal lobe is somewhat pointed on a few specimens. Dr. Giles Mead who kindly examined for us the type in the British Museum found that the two dorsals are indeed as pointed as illustrated, the caudal a little less so and, on two larger specimens, these fins are not quite as pointed as those of the type.

In both color varieties the width of the disc is the same as the vertical length in some cases but in others it is either a little greater, or a trifle less. The widest divergence found in the one direction was a width of 50 per cent compared with a length of 44.7 per cent of total length of the specimen, and in the other a width of 42.8 per cent compared with a length of 45.1 per cent, among specimens greater than 100 mm long. On one abnormal male, 111 mm long, the width of disc is only 38.7 per cent of total length, a condition similar to that found by Palmer and Wheeler (1958, p. 450) for abnormal specimens of *Torpedo nobiliana*.

The longest diameter of orbit is greater than the interorbital width on most of the small and medium-sized specimens but less on the largest. Thus the orbit ranges from 0.8 to 1.7 (average 1.2) times the interorbital on 14 specimens 100-140 mm long and 0.7-0.8 (average 0.76) times on 5 specimens 150-164 mm long, the latter all females and of the non-freckled variety.

The teeth of both sexes, small to large, are in a triangular patch in both jaws, arranged in quincunx, in about 14-16 rows counting inward from center of jaw, the outermost row with 1 or 2 teeth and each succeeding row with an added tooth or two, making a series of 16-20 teeth in the innermost row, the anterior few rows of teeth usually without cusps, except on mature males, the succeeding teeth with a small triangular cusp which becomes increasingly long, narrow, and canine-like on the most posterior teeth, all the cusps pointing inward.

The claspers of mature or nearly mature specimens of 120-126 mm are short and stubby and scarcely reach, or extend but little, beyond the tips of the pelvics.

Proportional dimensions in per cent of total length of a female 122 mm in total length from Lat. 07°12′N, Long. 56°47′W (freckled variety) and of a female of 155 mm from Lat. 02°29′N, Long. 48°58′W (non-freckled variety) are as follows: —

Disc. — Extreme breadth 46.8; 46.1; vertical length 44.3; 45.4.

Snout length. — In front of orbits 10.7; 12.2; in front of mouth 13.2; 13.6.

Orbits. — Horizontal diameter 5.3; 4.1; distance between 4.1; 5.5.

Spiracles. — Length 3.6; 3.2; distance between 6.2; 6.5.

Mouth. — Breadth 6.2; 4.2.

Exposed nostrils. — Distance between inner ends 6.6; 5.5.

Gill openings. — Length, 1st 2.9; 2.5; 3rd 2.9; 2.5; 5th 2.5; 1.9.

First dorsal fin. — Vertical height 7.0; 7.1; length of base 6.3; 6.5.

Second dorsal fin. — Vertical height 7.8; 7.1; length of base 6.3; 5.8.

Caudal fin. — Upper margin 15.7; 16.1; lower margin 12.5; 12.9.

Pelvics. — Origin to tip 26.4; 27.7.

Distance. — From tip of snout to center of cloaca 52.8; 52.8; to 1st dorsal 66.0; 66.7; from center of cloaca to tip of tail 47.2; 47.2; from 2nd dorsal to origin of caudal 4.1; 3.2.

Interspace. — 1st and 2nd dorsals 3.3; 2.9.

Known from off the mouth of the Amazon to British Guiana in 9-50 fathoms.

Suborder RAJOIDEA

Since the publication of Fishes of the Western North Atlantic, Part 2 (Bigelow and Schroeder 1953), in which the suborder Rajoidea included three families, the Rajidae, Arhynchobatidae and Anacanthobatidae, a fourth has been added, the Pseudorajidae Bigelow and Schroeder 1954. A revised key to families follows.

Key to Families

1 Two dorsal fins . . . . Rajidae p. 168
Only one dorsal fin, or none 2
2 One dorsal fin . . . . Arhynchobatidae, New Zealand.
No dorsal fin 3
3 Upper surface with prickles, or prickles and thorns; pelvic fins wing-like, not divided into lobes . . . . Pseudorajidae[1] p. 209
Upper surface smooth; pelvic fins divided into two distinct lobes, the anterior lobe limb-like . . . . Anacanthobatiade p. 216

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[1] The characters on which the family Gurgesiellidae De Buen 1959 are based appear to fall within the Pseudorajidae.

Family RAJIDAE

RAJA BULLISI sp. nov.

Figure 1

Study material. An immature male, 400 mm in total length, holotype, U. S. Nat. Mus. No. 196442, from about 30 miles SW of Dry Tortugas, Florida, Lat. 24°18'N, Long. 83°18'W, in 200 fathoms, ''Silver Bay'' station 1199. Also a male of 296 mm, paratype, M. C. Z. No. 40673, from the same station; and 16 specimens, males and females, 168-371 mm long, from nearby, ''Oregon'' stations 1324, 1326, 1328, 1329, in 200-300 fathoms.

Comparison with previously known species. The dark pores present on the under surface of *bullisi* are so small and inconspicuous that this species is not likely to be confused with other western Atlantic skates on which these pores are more obvious (p. 173). However, while it falls in line with these species with its sharp snout, its persistent nuchal thorn sets it apart from *floridana*, *laevis* and *oregoni* all of which lack this thorn. Absence of thorns between the scapular region and axils of pectorals distinguishes it from *garricki* which has a continuous row of thorns along the disc; its single row of thorns on its tail separates it from *olseni* which has several rows except on young specimens and these lack a nuchal thorn; and it differs from half grown and larger *flavirostris* in its longer tail (45.7-50.3 per cent of total length contrasted with 41.8-42.5 per cent in the half grown *flavirostris* with which we have compared it), also in its single row of tail thorns, *flavirostris* having lateral thorns as well.

Bullisi resembles several species of *Raja* known from Japanese waters (p. 176) in its sharp snout, nuchal thorn, and dark pores on the lower surface. But its narrower tail sets it apart from *R. gigas* and *R. macracauda* which have a robust tail, its plain or nearly plain colored upper surface (except the young) from *pulcra* which is mottled with dark brown and has an ocellus on each pectoral, and its single uniform row of tail thorns both from *kenojei* which has a staggered row, and from *acutispina*, *hollandi* and *macropthalma* which have 3 or more rows of tail thorns. The presence of two widely spaced thorns along the anterior margin of each orbit distinguishes young and half grown *bullisi* from *tengu* at similar stages of growth on which the anterior orbital thorns are close together.

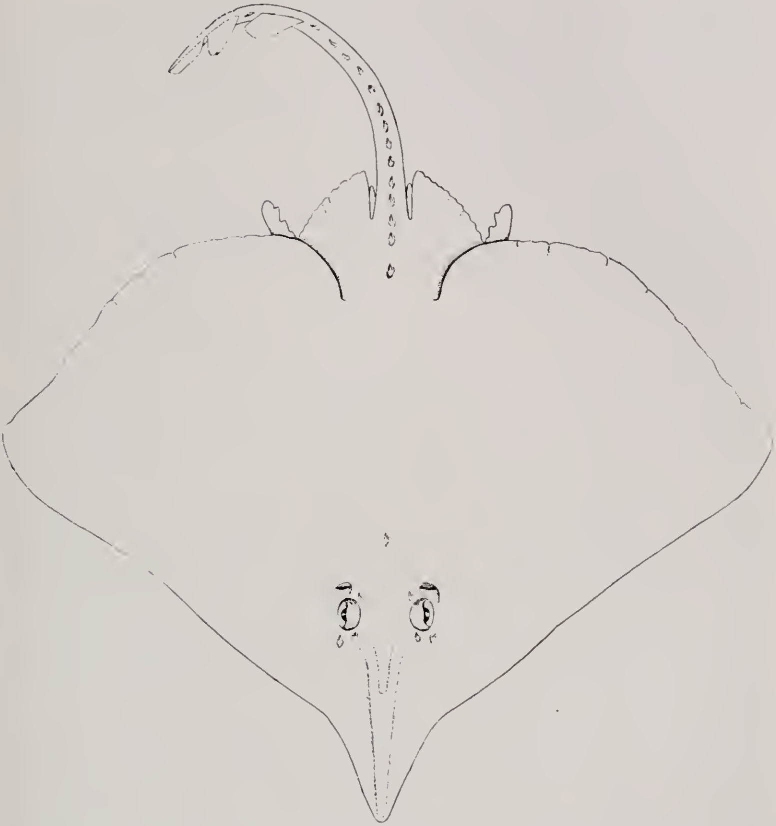

Figure 1. *Raja bullisi,* dorsal view of type, immature male 400 mm long.

Description of holotype. Proportional dimensions in per cent of total length:

Disc. — Extreme breadth 80.0; vertical length 59.5.

Snout length. — In front of orbits 19.0; in front of mouth 20.2.

Orbits. — Horizontal diameter 4.1; distance between 4.5.

Spiracles. — Length 2.7; distance between 7.5.

Mouth. — Breadth 8.8.

Exposed nostrils. — Distance between inner ends 9.2.

Gill openings. — Length, 1st 1.8; 3rd 1.8; 5th 1.3; distance between inner ends, 1st 16.2; 5th 9.1.

First dorsal fin. — Vertical height 3.0; length of base 4.0.

Second dorsal fin. — Vertical height 2.5; length of base 3.9.

Pelvics. — Anterior margin 12.0.

Distance. — From tip of snout to center of cloaca 54.3; from center of cloaca to 1st dorsal 30.7; to tip of tail 45.7; from rear end of 2nd dorsal to tip of tail 5.5.

Interspace. — 1st and 2nd dorsals 1.6.

Disc 1.34 times as broad as long; maximum angle in front of spiracles 90°; anterior margins of disc sinuous, outer corners narrowly rounded; posterior and inner margins gently rounded. Axis of greatest breadth 74 per cent of distance back from tip of snout to axils of pectorals. Tail with a narrow lateral fold, low down on each side, beginning just beyond axils of pelvics, widening posteriorly, widest opposite dorsals and reaching almost to extreme tip of tail. Length of tail from center of cloaca to origin of first dorsal fin 0.57 times as great and to its tip 0.84 times as great as distance from center of cloaca to tip of snout.

Two widely spaced anterior thorns, and 1 posterior, along the margin of each orbit and 1 thorn in the nuchal region. A single row of 14 prominent thorns along the midline of tail, beginning a little posterior to axils of pectorals and extending nearly to first dorsal fin; 1 thorn between the dorsals; rest of disc and tail, fins, and skin over eyes, smooth. Lower surface with coarse prickles on end of snout and in a narrow band along anterior margin of disc, running out about 3/5 the distance to outer angle; rest of disc and tail smooth.

Snout in front of orbits 4.6 times as long as orbit, its length in front of mouth 2.2 times as great as distance between exposed nostrils. Distance between orbits 1.1 times as great as length of orbit. Orbit 1.5 times as long as spiracle. Nasal curtain with a fine fringe; the outer flap of one nostril with a smooth margin; the other with a few minute knobs. Upper and lower jaws moderately arched. Teeth $\frac{33}{32}$, arranged in quincunx, ovate with a nearly flat crown and a low triangular cusp along the posterior margin.

Distance between first gill openings 1.8 as great as between exposed nostrils; between fifth openings 1.0 times; first to fourth openings about 2/5 as long as orbit, fifth opening a little shorter than the others. First and second dorsals similar in size and shape, with convex upper margin; the space between the dorsals is about 3/8 as great as the length of either dorsal base. Second dorsal confluent with caudal fin the base of which is nearly 1½ times as long as dorsal base. Pelvics with concave outer margin which is deeply scalloped anteriorly, weakly so posteriorly; anterior lobe about $\frac{4}{5}$ as long as from its own origin to rear tip of pelvics; posterior lobe with convex margin, its tip sharply rounded, reaching about $\frac{3}{8}$ the distance from axils of pectorals to origin of first dorsal.

Rostral cartilage firm and narrow, reaching nearly to tip of snout. Tips of anterior radials of pectorals reaching about $\frac{2}{5}$ the distance from axis through front of orbits to end of snout.

Color. Upper surface plain light brown. Lower surface of disc, pelvics, and tail, dark brown. Small, inconspicuous dark pores present, chiefly anterior to axis through mouth and directly under lower jaw.

Variations. Other specimens vary as follows. On 7 males 168-335 mm in total length and 3 females of 268-341 mm the disc ranges from 1.35 to 1.46 times as broad as long and the maximum angle in front of spiracles from 85° to 92°. The length of tail from the center of the cloaca is 0.88 to 1.01 times as great as the distance from center of cloaca to the tip of the snout. The ocular thorns show but little variation with growth for while the smallest specimen has 1 anterior and 1 posterior thorn at each orbit all the others have 2 anterior (widely spaced) and 1 posterior. All have 1 nuchal thorn and the tail thorns range in number from 12 to 15, the usual number being 13 or 14. One small thorn is present between the dorsals and some specimens also have a minute thorn at the origin of the second dorsal.

On the lower surface prickles appear on the snout at a very early stage for a specimen of 183 mm (186 mm with embryonic tail) already has a narrow band of prickles along the edge of the disc extending from the tip of the snout half way to a point opposite the mouth.

The snout in front of the orbits ranges from 3.7 to 4.5 times as long as the orbit, its length in front of mouth 2.1 to 2.4 times (1.9 on the 183 mm specimen) as great as the distance between the exposed nostrils. The width of the interorbital space varies from a little less to a little more than the length of the orbit. There are 31 to 36 teeth in the upper jaw and either the same in the lower jaw or 1 or 2 less on a given specimen.

The dorsal bases are about equal in length; the space between is 0.23 to 0.45 as great as the length of either dorsal base and on all the specimens the caudal fin is confluent with the dorsal fin, its base being from 1.3 to 1.8 times as long.

The color above of a newly hatched specimen, 168 mm long, or 157 mm minus its embryonic tail, is light brown marked with irregular dark brown spots, ranging in size from about one-fourth to as large as the orbit, on the disc and extending onto the tail where the markings coalesce to form 9 or 10 irregular crossbars to as far as the second dorsal fin. The dorsals are dark brown except for the posterior part which is pale; caudal dark, and the outer angles of disc are edged with dark brown. The lower surface is whitish, the posterior part of tail slightly dusky. The next largest specimen, 186 mm long, is similarly colored but the markings are less prominent. Specimens up to about 300 mm still have vague dark spots on the disc but larger ones are plain brown above, dark below.

Known from the vicinity of Dry Tortugas, Florida, in depths ranging from 200 to 300 fathoms.

Named after Harvey R. Bullis, Jr., in recognition of his kindness in making available to us for study the batoid fishes collected during the recent exploratory cruises of the U. S. Fish and Wildlife Service vessels in the Gulf of Mexico, Caribbean and southward along the South American coast.

RAJA CLARKII Bigelow and Schroeder 1958

Our description of this species is based on three specimens 580-747 mm long, two males and a female, trawled in the northern part of the Gulf of Mexico, in 260 fathoms, "Oregon" station 1277. The diagnostic features setting it off from all other known members of the Rajidae include the presence of 1 to 3 pairs of prominent white roundish or barlike markings on the upper surface of disc in combination with a broad snout and a band of formidable and very sharp thorns extending along the lower surface from the tip of the snout almost to the extreme outer margin of the pectorals.

Two more specimens have been taken, both females, one of 255 mm in total length from Lat. 12°50′N, Long. 82°12′ W, in 275 fathoms, "Oregon" station 1924, and the other, of 364 mm from Lat. 13°22′N, Long. 82°04′W, in 300 fathoms, "Oregon" station 1929, both from off the coast of Nicaragua.

Neither of these small specimens have the white roundish or barlike markings that characterize the several larger specimens mentioned above, but otherwise their color agrees closely in that the upper surface is pale brown with numerous darker punctulations scattered over the disc, over the pelvics, and on the tail, and in that the white lower surface has a wide irregular grayish band along the posterior and inner margins of the disc and along the rear margin of the pelvics. Also, the pattern of thorns is essentially the same, there being 38 thorns in the median row from the nuchal region to the first dorsal on each of the two smaller skates, of which 25 and 26, respectively, are posterior to the axils of the pectorals, compared with 34-40 on the three larger specimens of which 23-28 are posterior.

The proportional dimensions of all five known specimens are in close agreement excepting that the vertical length and the width of the disc of the 364 mm skate are 50.8 and 58.5 per cent, respectively, of the total length, compared with 54.4-55.0 and 65.0-68.7 on the three larger ones. Also, the two dorsals are virtually confluent on the two smaller ones whereas on the three larger there is 1 thorn directly on the midline within an interspace equal to about $\frac{1}{7}$ the base of first dorsal. This condition of either no interspace between the dorsals, or a very small one, has been found on certain other species of rajids.

The tooth count on the 364 mm specimen is $\frac{62}{63}$ and on the one of 255 mm 62 in the upper jaw, the lower jaw being imperfect, while on the three previously described, it is (580 mm) $\frac{61}{59}$, (665 mm) $\frac{63}{61}$, and (747 mm) $\frac{60}{60}$.

Raja floridana sp. nov.

Figures 2, 3

Study material. An immature male, 772 mm in total length and 593 mm in disc width, the holotype, U. S. Nat. Mus. No. 196441, and a male and two females, 383-448 mm long, disc width 294-363 mm, paratypes M. C. Z. Nos. 40723, 40724, 40725, all from the offing of Jacksonville, Florida, Lat. 29°43′N, Long. 80°10′W, in 195 fathoms, "Silver Bay" station 1605. Also 26 specimens, males and females 158-428 mm long from between the offings of Cape Lookout, North Carolina and Dry Tortugas, Florida, Lats. 34°21′ to 24°17′N, in depths of 170-225 fathoms, taken at 12 "Combat" and 2 "Oregon" stations. In addition, one of 165 mm trawled[1] by the "Albatross III" off South Carolina, Lat. 32°59′N, Long. 77°10′W, in 200 fathoms.

Comparison with previously known species. Western Atlantic skates with a sharp snout and with conspicuous dark pores on

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[1] May 28, 1949.

the under surface include *laevis, oregoni, garricki, olseni, platana,* and *flavirostris.* Among these, *floridana* most closely resembles *laevis,* Mitchill 1817, the common barn-door skate of the northeastern American coast but it differs from *laevis* in a proportionately longer snout, wider disc, shorter tail and smaller dorsal fins. Thus on 7 small to medium-sized males and females of *floridana* 314-772 mm in total length, the distance from the tip of snout to the mouth is 19.5-24.9 per cent, the width of disc 73.3-81.2 per cent, the length of tail from center of cloaca 44.0-47.4 per cent and the distance from origin of first dorsal fin

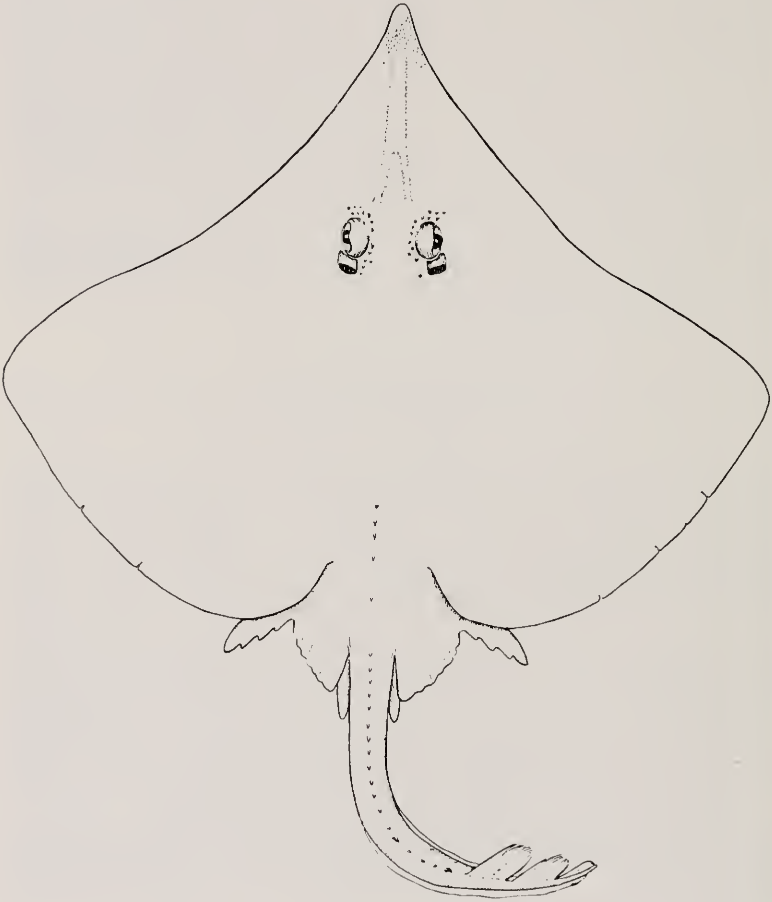

Figure 2. *Raja floridana,* dorsal view of type, immature male 772 mm long.

to the rear end of base of the second dorsal 8.4-12.1 per cent of the total length. These proportions on 2 males and a female *laevis,* 506-542 mm long, are 17.0-18.0 per cent, 68.0-71.0 per cent, 49.7-51.7 per cent and 14.5-14.8 per cent, respectively. We have not yet seen a mature *floridana* but our largest, the 772 mm male, lacks the row of thorns on either side of the midrow on the tail, that is present on *laevis* upwards of about 500 mm in total length, or with a disc width of about 350 mm. On 7 very young *floridana,* 158-240 mm in total length, the distance from snout to mouth is 18.0-21.1 per cent and length of tail 46.2-50.5 per cent of total length and there are only 8 to 10 thorns along the midline of the tail whereas on 5 *laevis* 177-195 mm long these percentages are 14.1-17.8 and 54.2-58.7, respectively, and the tail thorns range from 13 to 18 (see Figs. 3 and 4 for comparison of young of both species). *Floridana* is plain brown or grayish brown on the upper surface (except very small ones, p. 180) while *laevis* is marked with scattered dark brown spots except for some of the newly hatched which may lack spots.

The single row of rather inconspicuous thorns on the tail sets *floridana* apart from *oregoni* Bigelow and Schroeder 1958 which is armed with three rows of formidable tail thorns; absence of thorns along the midline of the disc distinguishes it from *garricki* Bigelow and Schroeder 1958 which has an uninterrupted row of large thorns from the nape to the first dorsal fin; its single row of tail thorns also identifies it from *olseni* as well as its unfringed nostril flap and the absence of conspicuous whitish mucous pores on upper surface of disc (*olseni* has a more less interrupted row of tail thorns each side of the midrow, a fringed nostril flap and conspicuous whitish mucous pores on the upper surface of disc, arranged in various designs). The more or less haphazard arrangement of the dark mucous pores on the under side of its disc, and their paucity over the posterior half, distinguishes *floridana* from *platana* Günther 1880 which is profusely covered with prominent, symmetrically arranged, black pores over the lower surface of its disc[1]; and the absence of thorns on its disc, together with a single row on the tail, marks it off from *flavirostris* Philippi 1892 which has a persistent and prominent nuchal thorn and (except in the very young) an irregular row of spines on each side of the median series on the tail.

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[1] Based on original description and illustration of a specimen 25 inches long (Günther 1880, p. 11, pl. 3) and a specimen 22 inches long in The Museum of Comparative Zoology taken off Rio de Janeiro by the Thayer Expedition in 1872.

Several species of *Raja,* with a sharp snout and with dark pores on the lower surface, bearing a close resemblance to *floridana,* are known from Japanese waters and are described, or discussed, by Ishiyama (1958). Through the kindness of Dr. Ishiyama, the Museum of Comparative Zoology collection includes representatives of all of these. They comprise *Raja macracauda* Ishiyama 1955, *R. gigas* Ishiyama 1958, *R. macropthalma* Ishiyama 1958, *R. acutispina* Ishiyama 1958, *R. hollandi* Jordan and Richardson 1909, *R. tengu* Jordan and Fowler 1903, *R. pulcra* Lui 1932 and *R. kenojei* Müller and Henle 1841.

In spite of the fact that we have this material for comparison, as well as the recently published accounts by Ishiyama, we find it difficult to present reliable characters that might distinguish

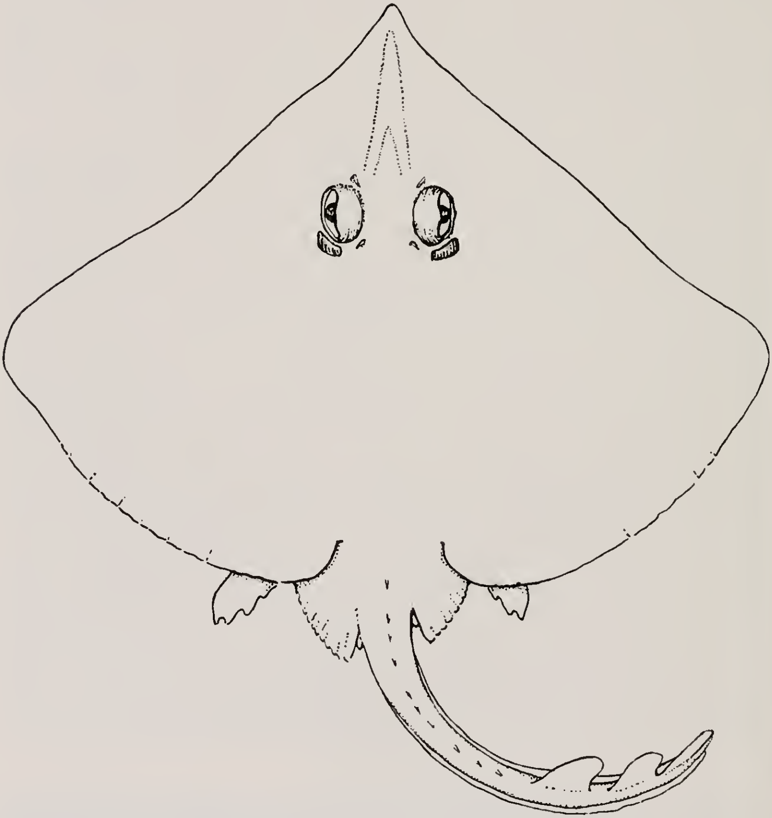

Figure 3. *Raja floridana,* juvenile male 158 mm long.

floridana from the above inasmuch as our only relatively large specimen (the holotype) is immature and all the others are juveniles. However, the lack of a nuchal thorn on all our specimens of *floridana* seems to assume importance, for all of the above Japanese species have one or more nuchals except possibly mature *gigas*, on which this thorn may be obscure or "worn out" (Ishiyama 1958, p. 386).

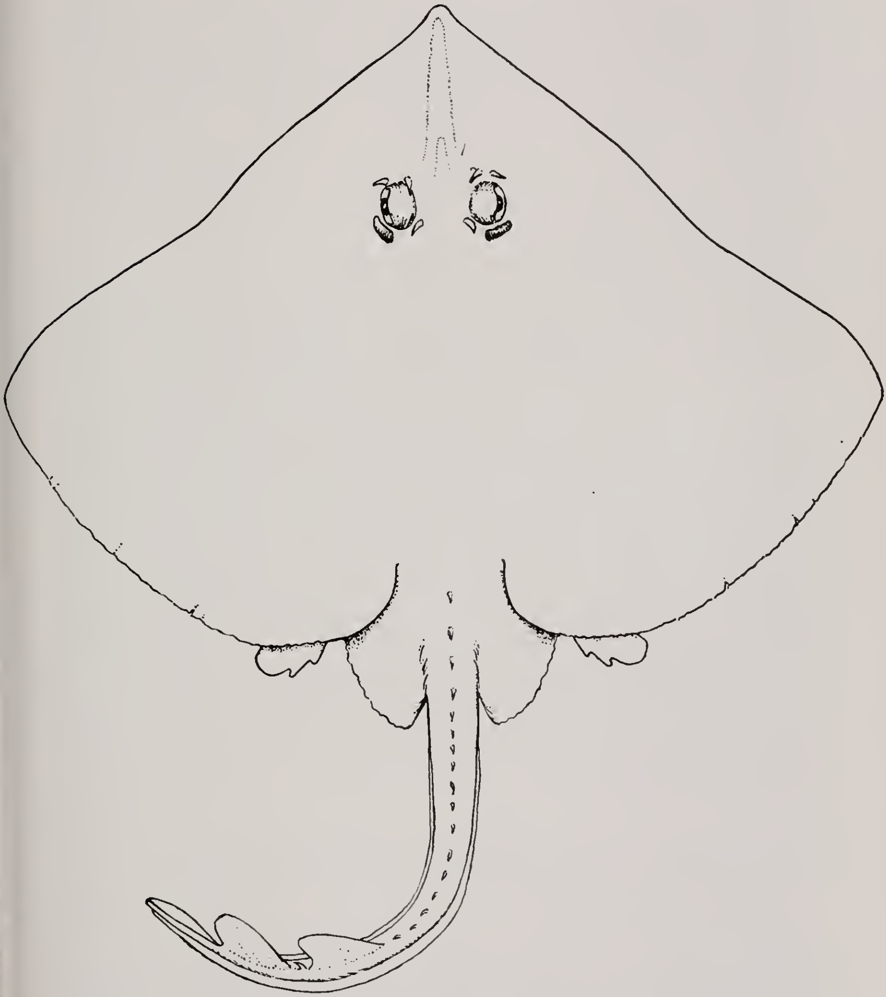

Figure 4. *Raja laevis,* juvenile female 225 mm long.

Description of holotype. Proportional dimensions in per cent of total length:

Disc. — Extreme breadth 76.8; vertical length 62.0.

Snout length. — In front of orbits 22.2; in front of mouth 24.9.

Orbits. — Horizontal diameter 4.0; distance between 4.5.

Spiracles. — Length 2.6; distance between 6.4.

Mouth. — Breadth 8.3.

Exposed nostrils. — Distance between inner ends 9.6.

Gill openings. — Length 1st 1.8; 3rd 1.8; 5th 1.3; distance between inner ends, 1st 13.6; 5th 10.1.

First dorsal fin. — Vertical height 3.0; length of base 4.0.

Second dorsal fin. — Vertical height 3.0; length of base 4.1.

Pelvics. — Anterior margin 12.4.

Distance. — From tip of snout to center of cloaca 56.0; from center of cloaca to 1st dorsal 31.6; to tip of tail 44.0; from rear end of 2nd dorsal base to tip of tail 4.0.

Interspace. — 1st and 2nd dorsals 0.3.

Disc 1.24 times as broad as long, maximum angle in front of spiracles 74°; snout pointed; anterior margins of disc sinuous, the outer corners abruptly rounded; posterior margins gently convex, as are the inner margins. Axis of greatest breadth about 70 per cent of distance back from tip of snout to axils of pectorals. Tail with a narrow lateral fold, low down on each side, beginning about an eye's diameter posterior to axils of pelvics, widening posteriorly but relatively narrower rearward than on most rajids, its width opposite origin of first dorsal only about $\frac{1}{7}$ the width of tail at this point, the fold ending opposite about middle of caudal fin. Tail short and considerably flattened, its length from center of cloaca 79 per cent of the distance from cloaca to tip of snout and 57.3 per cent the width of disc, sides of tail nearly parallel until approaching the first dorsal fin, its width being 3.9 per cent of total length of specimen at axils of pelvics, 3.8 per cent midway between the latter and tip of tail, 3.2 per cent opposite origin of first dorsal and 2.2 per cent opposite second dorsal.

A row of 12 small thorns along anterior and inner margins of each orbit with 3 very small thorns in advance of these. End of snout densely covered with coarse prickles and small thorns, with points directed upward or forward, blending into minute prickles rearward to about opposite spiracles, and with a few prickles in nape region; remainder of disc smooth except for sparse prickles near base of tail in advance of axils of pectorals and continuing more numerous all along upper surface of tail, to about opposite second dorsal fin. A midrow of 25 small thorns of assorted sizes, with a few rather large ones, beginning about an eye's diameter in advance of axils of pectorals and continuing to first dorsal fin. No side thorns on tail; no thorn between dorsals. Pelvics smooth; a few minute prickles on dorsals; caudal fin and skin over eyes smooth. A short row of 9 mucous pores on one side, 11 on the other, in nuchal region. Lower surface densely prickly in advance of axis through mouth, except for a nearly smooth area immediately in front of mouth; a band of prickles extending along margin of disc from snout to about opposite 4th or 5th gill openings; remainder of lower surface, including tail, virtually smooth.

Snout in front of orbits 5.5 times as long as orbit; its length in front of mouth 2.5 times as great as distance between exposed nostrils. Distance between orbits 1.1 times as great as length of orbit. Orbit 1.5 times as long as spiracle. Nasal curtain fringed; expanded outer margin of nostrils smooth. Upper and lower jaws moderately arched. Teeth $\frac{35}{35}$, arranged chiefly in quincunx, with ovate base and a prominent triangular cusp pointing obliquely inward.

Distance between first gill openings 1.4 times as great as between exposed nostrils; between 5th openings 1.1 times; first gill openings 1.4 times as long as fifth and about 0.45 times as long as longest diameter of orbit. Dorsals similar in size and shape, the interspace very short, only 0.07 as long as base of first dorsal. Second dorsal confluent with caudal fin the base of which is equal in length to that of the first dorsal. Pelvics concave, strongly scalloped along anterior side of excavation, weakly so rearward; anterior margin 0.75 times as long as distance from its own origin to rear tip of pelvic; posterior lobe moderately convex, with a narrowly rounded tip, extending about two-fifths the distance from axil of pectorals toward first dorsal. Claspers reaching beyond tips of pelvics by a distance equal to about diameter of orbit.

Color. Plain brown above, the under surface of disc and tail grayish, the disc with dark-ringed mucous pores, most numerous anterior to axis through mouth and immediately below lower jaw.

About 20 of the other specimens examined, 158-448 mm in total length, have the following characteristics. The disc is 1.32-1.43 times as broad as long and the maximum angle in front of spiracles 85°-94°. On sizes ranging from 158-273 mm the tail, from center of cloaca, is 86-100 per cent as long as the distance from cloaca to the tip of the snout, while on those of 305-448 mm its length is 80-90 per cent. There is only 1 anterior and 1 posterior orbital thorn on lengths up to nearly 300 mm, 2 anterior and 1 posterior at 300-400 mm, beyond which size they increase in number, one of 448 mm having 8 or 9 along the margin of each orbit. The number of thorns on the midline of the tail, on 18 specimens, ranges from 8 to 14, in most cases 8 or 9, with as many as 13 on a male as small as 330 mm and as few as 9 on a male of 428 mm. But while a 432 mm female has only 3 tail thorns (there is evidence that some thorns were shed) a 448 mm male has 21. In the interdorsal space 6 specimens lack thorns, 11 have 1 thorn and 3 have 2 thorns. Otherwise, all the specimens, other than the much larger holotype (772 mm), are smooth.

The length of the snout in front of the orbits is 3.8-4.4 times as great as diameter of orbit, its length in front of mouth 2.0-2.2 times as great as the distance between the nostrils while the interorbital space is 0.9-1.2 times as great as the length of orbit. There are from 27 to 38 series of teeth in each jaw, with a low triangular cusp, even on the smallest specimens of both sexes. The space between the dorsals, though short, is relatively greater than that on the holotype being 0.23-0.60 times as long as the base of the first dorsal and the base of the caudal fin is 1.0-1.5 times as long as the dorsal base.

The smallest specimens are light brown above with vague dark brown irregular spots about half as large to as large as the orbit and the tail has 5 dark bars about equally spaced. Lower surface whitish with a narrow dusky margin on outer angles of disc. Our larger specimens lack the spots and below are usually plain grayish white, some of them partly brownish.

Known from the offings of Cape Lookout, North Carolina to Dry Tortugas, Florida, in 170-225 fathoms.

RAJA LENTIGINOSA Bigelow and Schroeder 1951

This skate has heretofore been recorded from the northern part of the Gulf of Mexico in the offings of Pensacola and Cape San Blas, Florida, and in the southern part on Campeche Bank in various depths ranging from 29 to 305 fathoms (Bigelow and Schroeder 1953, p. 228). Our present collection extends its known range to the Atlantic coast of Central America where it was taken off Honduras at 7 "Oregon" stations (1868, 1869, 1870, 1871, 1879, 1883, 1891) and off Nicaragua at 2 stations (1902, 1903), the most southerly at Lat. 11°27'N, Long. 83°11'W.

It apparently is widespread in the Gulf of Mexico for additional records, besides 2 more from off Cape San Blas ("Oregon" stations 945, 953), include 2 stations (550, 1514) in the northwest part and 1 (1054) in the southwest at Lat. 19°37'N, Long. 92°40'W. In all, the above series consists of 20 specimens, males and females, 80-435 mm in total length, from depths of 67-250 fathoms.

There appears to be no significant difference in color, or otherwise, between the specimens taken in the northern part of their range and those taken in the southern part. The smallest mature male, with clasper hooks exposed, is 345 mm in total length.

RAJA OLSENI Bigelow and Schroeder 1951

Earlier descriptions of this species (Bigelow and Schroeder 1951, p. 386; 1953, p. 251) were based on 8 specimens, 280-310 mm in total length, trawled in 64-76 fathoms, from the northern and northwestern part of the Gulf of Mexico. Our present series consists of 7 more, 151-568 mm long, taken in 53-130 fathoms, from the same general locality, "Oregon" stations 602, 847, 1419, 1514 and 2827; also "Silver Bay" station 316.

Raja olseni resembles *R. laevis* Mitchill 1817 in general appearance but differs in having an interspace between the dorsal fins nearly or quite as long as the base of the first dorsal (only 0.1-0.3 that long in *laevis*), a much greater distance between the rear end of the second dorsal base and tip of tail (7.1-9.0 per cent of total length on *olseni*, 2.8-3.8 per cent on *laevis*), in its fringe on the expanded outer margin of nostril (smooth on *laevis*); also the lateral folds along the tail extend only to the anterior third of the caudal fin, whereas on *laevis* they extend almost or quite to the extreme tip of the tail. The original specimens, also, of *olseni* when first described were jet black below, leading to our earlier statement (1951: 386) that "its mucous pores are not marked with black as they are in *laevis*." However, the paratype, in the Museum of Comparative Zoology, has faded by now to a brownish-cream, the pores being darker, while some of the recent "Oregon" specimens are pale below with the pores conspicuously black around and anterior to the mouth. Consequently, the pigmentation, or the reverse, of the mucous pores on the lower surface is not reliably diagnostic between *olseni* and *laevis*.

The proportions of the disc vary within a narrow range, the extreme width being 67.5-74.8 per cent and the vertical length 54.0-60.3 per cent of the total length of the specimens, and the width is 1.21-1.28 times the length save on the smallest one (151 mm) on which it is 1.37 times. The maximum anterior angle in front of spiracles is 110° on a 151 mm female, 88°-97° on females of 241-568 mm and on males of 235-343 mm but only 78° on a male of 506 mm. The axis of greatest breadth ranges from 62 to 72 per cent of the distance back from the snout toward axils of pectorals, on 9 specimens. The length of the tail from the center of cloaca to the origin of the first dorsal fin is 0.51-0.62 times as great and to its tip 0.91-1.06 times as great as the distance from the center of cloaca to the tip of snout on specimens of 235-568 mm; these lengths on the smallest (151 mm) being 0.71 and 1.2, respectively.

Excluding the orbital thorns, the upper surface of the disc is smooth on all our specimens except the two largest, a male of 506 mm and a female of 568 mm in total length. On the male there are prickles over the end of the rostral process and these extend to the orbits on the female; a narrow band of small thorns extends along the edge of disc from tip of snout to about three-fourths the distance to outer angle, on the male, and a little further than this on the female, the thorns being more crowded posteriorly. Also, there is 1 small nuchal thorn on the male and 4 on the large female. The alars on the 506 mm specimen are in 1 to 2 rows, the exposed thorns 11 in number on one side, 14 on the other, the length of the longest row equal to the distance between the spiracles. The thorns along the margin of the orbits tend to increase in number along with the growth of this skate. Thus on the smallest specimen, of 151 mm, there is 1 thorn at the inner anterior margin and 1 at the posterior margin of each orbit; on one of 235 mm, 1 anterior and 2 posteriors; on two specimens of 241-267 mm, 2 along the anterior margin and 1 on the posterior; on four specimens of 313-506 mm there are 2 to 4 thorns along the anterior margin, 2 or 3 along the central and posterior margin, and usually 1 thorn immediately adjacent to each spiracle, and on the 568 mm female there are 6 along the anterior margin and 12 along the inner margin to opposite the spiracles. Along the midline of the tail from a little in advance of the axils of the pelvics to the first dorsal fin there are 12 to 36 thorns, alternating large and small, the number largest on the largest specimens, but the increase in number does not always parallel the size of the skate. There is a single row of from 2 to 6 thorns along the midline between the dorsal fins, the greatest numbers (5 and 6) being on the three largest specimens; there is also an additional row of thorns, usually widely and unevenly spaced, on each side of the mid row, most numerous posteriorly. These first appear on specimens of 235-267 mm and are most conspicuous on the largest, which, in addition, have a few small thorns low down along the sides of the tail. On the 568 mm female the side rows have but few interruptions beginning about opposite the rear margin of the pectorals and developing into 2 rows on each side posteriorly ending at the first dorsal fin beyond which there are a few scattered side thorns. The dorsals, the caudal fin, and the skin over the eyes are smooth.

The lower surface of the disc is smooth on our smallest specimen, but on others of 235-313 mm, of both sexes, and on a female of 401 mm, there are prickles and small thorns on the rostrum and in a narrow band along the margin of the disc from the tip of snout to the level of the nostrils or of the mouth. On a male of 343 mm, the end of the snout in advance of the nostrils is covered with small sharp thorns and prickles, and on the 506 mm male and the 568 mm female these extend to the level of the mouth.

The claspers of the largest male reach beyond the tips of the pelvics by a distance equal to that between the spiracles.

The tooth count ranges from 34 to 42 in both jaws. The jaws of the 506 mm male are strongly arched centrally, those of the other specimens moderately so. The space between the dorsals ranges from 0.82 to 1.40 times the base of first dorsal on all the specimens except the smallest (151 mm) on which it is only 0.62 times. The second dorsal and caudal are confluent on most of the specimens with a barely perceptible interspace on two of them. The caudal base is 1.5-2.1 times as long as the first dorsal base on our specimens of 235-568 mm.

The color of the upper surface varies from light to dark brown. Some specimens have numerous obscure spots, darker than the ground color, scattered over the disc, about half the size of the spiracle opening. An account of the small whitish pores is given in the type description, but it should be added that there is consistently one pair of pores, larger than most of the others, located between and a little posterior to the spiracles followed by two rows of about 10 to 16 close-set pores, diverging anteriorly and posteriorly. The tail and fins are light to dark brownish. The lower surface of some specimens is pale creamy brown while on others it is dark brown everywhere except the fringes on nasal flap and curtain, edges of gill openings, and immediate vicinity of cloaca. Probably most, if not all, *olseni* are much darker in life, for the types are described as jet black below. The pores are conspicuously darker than the ground color on specimens that are pale enough below for this feature to be apparent.

As our largest male (506 mm) has large claspers and our largest female is 568 mm long, it is probable that this species reaches a length somewhat greater than 600 mm.

All the specimens thus far taken are from the northern part of the Gulf of Mexico between the offings of Cape San Blas and Corpus Christi, in 53-130 fathoms.

RAJA PURPURI-VENTRALIS sp. nov.

Figures 5, 6

Study material. One female 510 mm in total length, holotype, U. S. Nat. Mus. No. 196440, from the northern part of the Gulf of Mexico, Lat. 27°48'N, Long. 88°45'W, in 850-1100 fathoms, ''Oregon'' station 2577.

Distinctive characters. Characters in combination which distinguish *purpuri-ventralis* from other species of *Raja* known from the Atlantic Ocean and Gulf of Mexico are: upper surface of disc, tail, and pelvics, covered with sharp, closely set prickles; a continuous row of about 40 thorns along midline of disc and tail from nape to first dorsal fin; 3 thorns on each side of midrow in scapular region; an additional row of large thorns each side of midrow on anterior two-thirds of tail; and in its color which was purplish black both above and below at the time of capture. *Purpuri-ventralis* bears some resemblance to *R. macloviana* Norman 1937 and *R. magellanica* Steindachner 1903 from the Patagonian-Falkland region and Strait of Magellan but these species differ in that the prickles are sparsely distributed; in that they have only 1 or 2 scapular thorns (occasionally 3) on each side, with not more than about 30 thorns in the midrow of disc and tail; in that there are no side rows of thorns on the tail; and in color, both of these species being brownish or grayish above and yellow or white below.

Description of holotype. Proportional dimensions in per cent of total length.

Disc. — Extreme breadth 53.7; length 49.6.

Snout length. — In front of orbits 16.4; in front of mouth 18.8.

Orbits. — Horizontal diameter 2.9; distance between 4.2.

Spiracles. — Length 1.8; distance between 7.4.

Mouth. — Breadth 7.3.

Exposed nostrils. — Distance between inner ends 8.2.

Gill openings. — Length, 1st 1.3; 3rd 1.3; 5th 1.1; distance between inner ends 1st 13.9; 5th 8.3.

First dorsal fin. — Vertical height 1.8; length of base 4.5.

Second dorsal fin. — Vertical height 1.8; length of base 3.7.

Pelvics. — Anterior margin 11.8.

Distance. — From tip of snout to center of cloaca 46.7; from center of cloaca to 1st dorsal 41.9; to tip of tail 53.3; from rear end of 2nd dorsal to tip of tail 2.2.

Interspace. — 1st dorsal and 2nd dorsal 0.0.

Disc 1.08 times as broad as long; tip of snout narrowly rounded; maximum angle in front of spiracles 85°; anterior margins of disc very slightly concave; outer corners, posterior margins and inner margins broadly rounded. Axis of greatest breadth 74 per cent backward from tip of snout toward axils of pectorals. Tail moderately robust anteriorly becoming very slender posteriorly; the lateral folds, low down, originating in advance of first dorsal by a distance equal to that between spiracles (far rearward as compared with other rajids), scarcely perceptible at their origin but widening opposite second dorsal and continuing almost to extreme tip of tail; length of tail from center of cloaca to origin of first dorsal fin 0.90 times as great, and to its tip 1.14 times as great as distance from center of cloaca to tip of snout.

Upper surface of disc, tail, and pelvics closely covered with small, sharp prickles, most of them with the tip bent rearward, the base with 4 radii; dorsal and caudal fins and skin over eyes also with prickles. A single stout thorn at the inner anterior margin of each orbit, with another at the posterior margin, and a smaller thorn inward and behind the latter, in line with rear margin of the spiracles. A row of 43 sharp, prominent and rather widely spaced, thorns along the midline, 3 of them from nape to scapular region, followed by 40 smaller, closely spaced

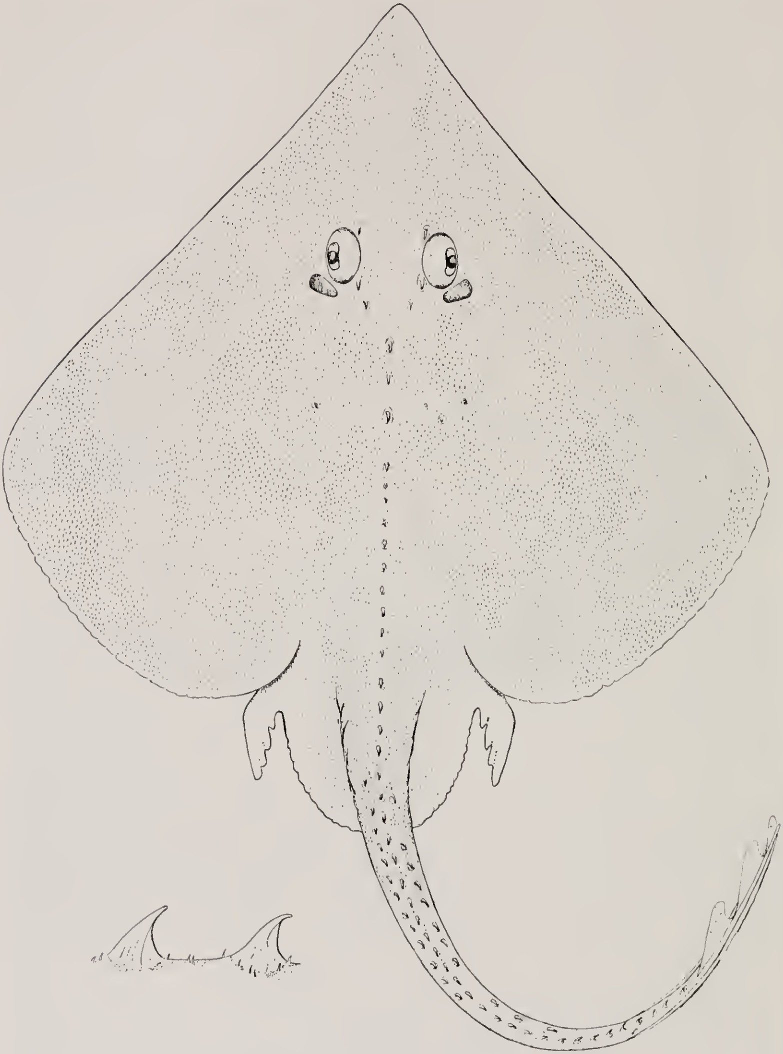

Figure 5. *Raja purpuri-ventralis,* dorsal view of type, female 510 mm long. Lower left, side view of thorns along the midline, about x3.

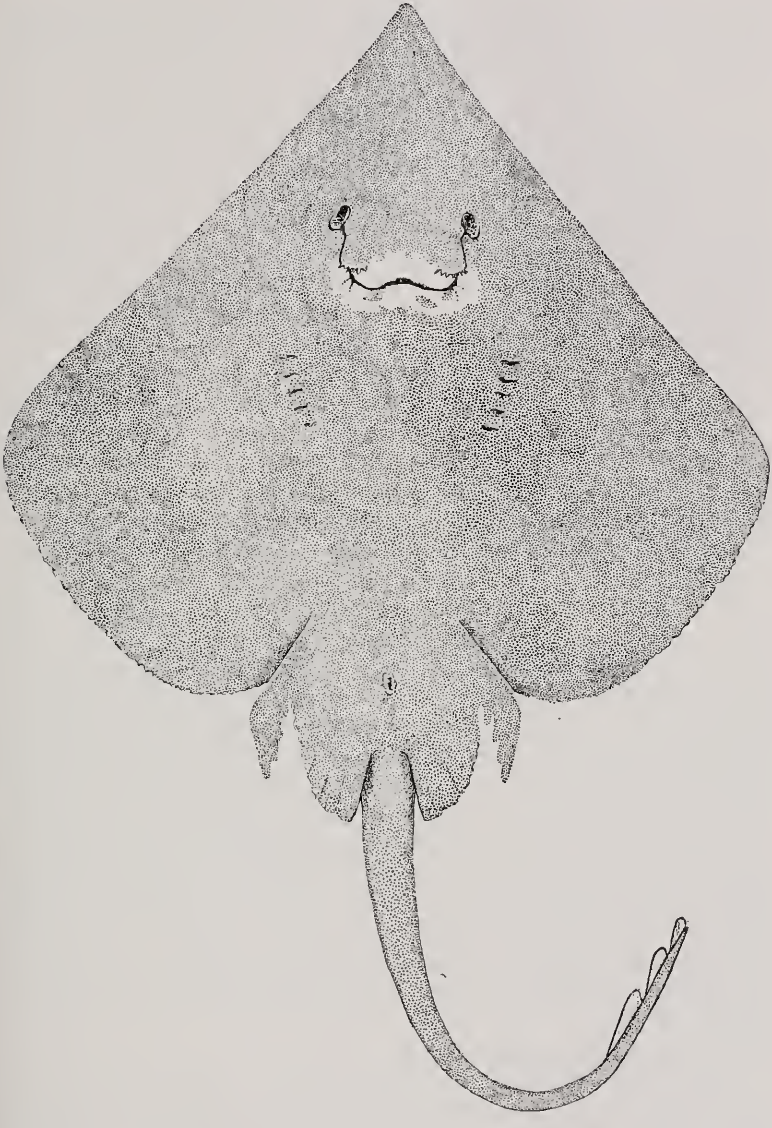

Figure 6. *Raja purpuri-ventralis*, ventral view of type.

thorns along disc and tail, ending at first dorsal fin; an additional row of large thorns on each side of midrow, originating slightly in advance of tips of pelvics, and running out posteriorly; scapular region with a small triangular patch of 3 thorns of unequal size, on each side of midline. Mucous pores are distributed variously on upper surface, including a row of 10 on right side and 11 on left, diverging anteriorly and posteriorly, aside the first and second nuchal thorns; also a small irregular patch of 7 or 8 pores in advance of each anterior orbital thorn. Lower surface of disc and midzone of tail smooth, sides of tail prickly, also edges of lower surface anteriorly and its entire breadth posteriorly.

Snout in front of orbits 5.6 times as long as orbit, its length in front of mouth 2.3 times as great as distance between exposed nostrils. Distance between orbits 1.44 times as great as length of orbit. Orbit 1.7 times as long as spiracle. Nasal curtain fringed; expanded outer margin of nostrils smooth. Upper and lower jaws slightly arched centrally. Teeth $\frac{42}{42}$, in quincunx arrangement, with ovate base and flat crown.

Distance between first gill openings 1.7 times as great as between exposed nostrils; between fifth openings 1.0 times; first gill openings slightly longer than fifth and about 0.4 times as long as longest diameter of orbit. First dorsal slightly larger than second and perhaps similar in shape (both dorsals damaged), its base slightly longer than interorbital space, the fins confluent. Second dorsal confluent with the very small caudal the base of which is about three-fourths as long as that of the second dorsal, very low anteriorly and rising rearward. Pelvics deeply concave, strongly scalloped along anterior side of excavation, weakly so rearward; anterior lobe slender, with 4 radial cartilages besides the first stout one, about 0.8 times as long as distance from its own origin to rear tip of pelvic, its basal part connected by skin with the inner margin of disc.

Rostral cartilage firm, narrow, extending nearly to tip of snout. Anterior pectoral rays reaching about three-fifths distance from mouth toward tip of snout.

Color in preservative dark gray above, blackish everywhere below, except white around mouth and rear edge of nasal curtain. When fresh from the water, this specimen was purplish above and below.

Known only from the type, taken in the northern part of the

Gulf of Mexico in a trawl haul made on bottom at a depth of 850-1100 fathoms.

Breviraja atripinna Bigelow and Schroeder 1950

Previous accounts of this species (Bigelow and Schroeder 1950, p. 390; 1953, p. 286) are based on three specimens trawled off the north central coast of Cuba, in 250-500 fathoms. Our present collection includes two more, a female 291 mm in total length, M. C. Z. No. 40110, from Santaren Channel, west of Great Bahama Bank, Lat. 23°59′N, Long. 79°43′W, in 350 fathoms, "Combat" station 450; and a male 215 mm long, M. C. Z. No. 39865 from Lat. 33°51′N, Long. 76°18′W, in 225 fathoms, "Combat" station 178, extending the range north to the offing of Cape Fear, North Carolina. Another specimen, from the north coast of Cuba, was taken by the "Oregon" in 280 fathoms.[1]

The nasal curtain and flap are usually smooth, or with several tiny lobelets, but on some specimens one or the other, or both, may have a short fringe. The tooth count on both specimens is $\frac{44}{44}$.

Breviraja colesi Bigelow and Schroeder 1948

Originally recorded from off the north and south coasts of Cuba, in 220-285 fathoms,[2] *colesi* has recently been taken off the northwest part of Little Bahama Bank. Eight specimens 132-330 mm in total length were trawled by the "Silver Bay" at Lat. 27°39′N, Long. 79°15′W, at station 441 in 275-300 fathoms and 4 specimens of 138-251 mm at Lat. 27°53′N, Long. 79°09′W, at station 442 in 375-415 fathoms. While the length of tail, as measured from the axils of pelvics to origin of the second dorsal fin, has been given as at least no longer than distance from axils of pelvics to tip of snout, a character, in combination, used to distinguish *colesi* from other members of its genus, we have found several specimens on which this distance is slightly longer.

Breviraja cubensis Bigelow and Schroeder 1950

Previously taken only from off the north central coast of Cuba, in 235-405 fathoms, the known range of this species is now

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[1] Springer and Bullis 1956, p. 43, "Oregon" station 1342.

[2] It was again taken off the north coast of Cuba by the "Oregon" at stations 1341, 1344 and 1345. (Springer and Bullis, 1956, p. 44)

extended northward to the offing of the northwest part of Little Bahama Bank, Lat. 27°53′N, Long. 79°09′W, "Silver Bay" station 442 where a male 150 mm long and a female of 212 mm were trawled in 375-415 fathoms; two others were taken nearby at station 441 in 275-300 fathoms. It was also trawled by the "Combat" (3 males 192-210 mm long) at stations 449 and 450 in Santaren Channel, between Cay Sal and Great Bahama Banks in 350 fathoms, and at station 436 about 20 miles to the southward of Key West, in 300 fathoms.

BREVIRAJA ISHIYAMAI sp. nov.

Figures 7, 8

Study material. A female 338 mm in total length, holotype, U. S. Nat. Mus. No. 196447, from Lat. 13°18′N, Long. 82°12′W, in 350 fathoms, "Oregon" station 1916, and a male of 226 mm, M. C. Z. No. 40097, from Lat. 13°56′N, Long. 81°50′W, in 275 fathoms, "Oregon" station 1931, both from off the Atlantic coast of Nicaragua; a female of 362 mm, M. C. Z. No. 40665, from Lat. 24°11′N, Long. 83°21′W, in 400 fathoms, "Silver Bay" station 1196, about 35 miles to the southwestward of Dry Tortugas, Florida, and a female of 296 mm, paratype, M. C. Z. No. 40389, from Lat. 28°03′N, Long. 78°44′W, in 500-520 fathoms, "Silver Bay" station 445, off Cape Canaveral, Florida.

Comparison with previously known species. Ishiyamai differs as follows from other western Atlantic species of *Breviraja:* from *atripinna* by a very short space between the dorsal fins which also may be confluent (on *atripinna* the dorsals are widely separated); from *colesi* in its plain coloration, smooth nasal flap and curtain, in the presence of a space between the second dorsal fin and the caudal fin and perhaps in a fewer series (about 34-38) of teeth in the upper jaw (upper surface of disc mottled with irregular spots and blotches, nasal flap and curtain with fringes, second dorsal and caudal confluent, about 40-50 series of teeth, on *colesi*); from *cubensis* by its plain coloration, and by the presence of a space between the second dorsal and caudal fins (disc with spots and blotches, tail with dark cross bars, second dorsal and caudal confluent, on *cubensis*); from *plutonia* in its plain coloration, in shape of disc and in the presence of a space between the second dorsal fin and the caudal (disc with spots and blotches, tail with bars, anterior margin of disc sinuous in both sexes, dorsal and caudal confluent, on *plutonia*);

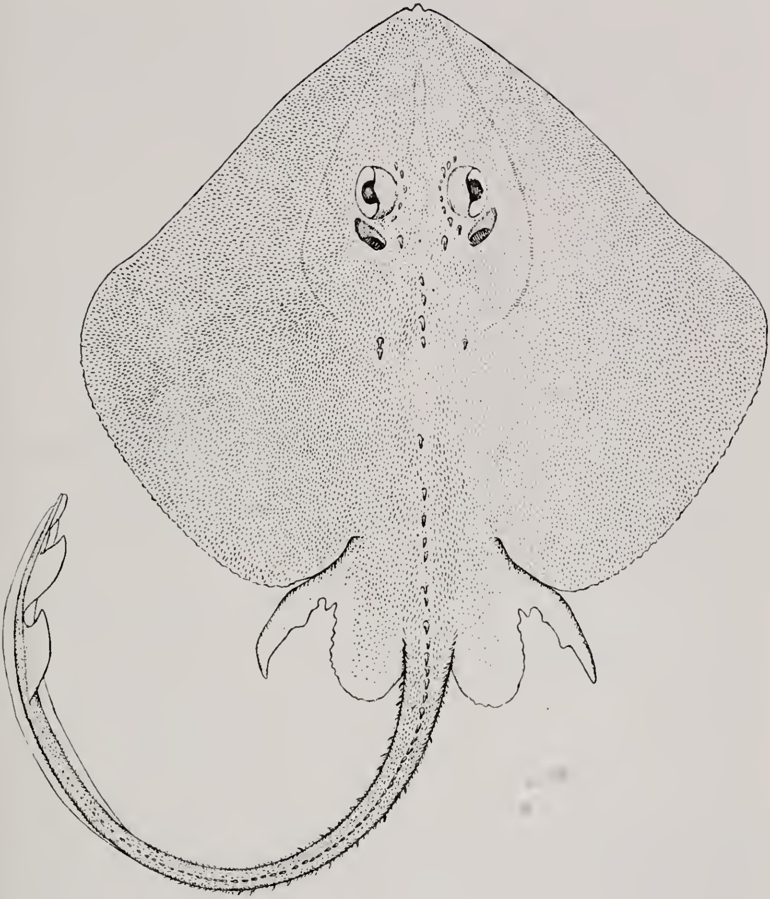

Figure 7. *Breviraja ishiyamai*, dorsal view of type, female 338 mm long.

from *sinus-mexicanus* in the arrangement of the thorns and prickles on the upper surface of its disc and tail, in its smooth nasal flap and curtain, and in its relatively long narrow rostral cartilage (three rows of formidable thorns on tail extending on to disc, fringed nasal flap and curtain and short triangular rostral cartilage, on *sinus-mexicanus*); from *spinosa* in its slender tail, in the presence of a single row of small thorns along the midline of its disc and tail, in its smooth nasal curtain, in the presence of a space between the dorsal fin and the caudal, and in its narrower rostral cartilage (robust tail, 4-5 rows of thorns along back and on tail, fringed nasal curtain, confluent dorsal and caudal, and short triangular rostral cartilage on *spinosa*); and from *yucatanensis* Bigelow and Schroeder 1950 in its plain coloration and smooth nasal flap and curtain (disc and tail freckled with brown dots, nasal curtain and flap fringed on *yucatanensis*).

Description of holotype. Proportional dimensions in per cent of total length:

Disc. — Extreme breadth 49.2; vertical length 40.7.

Snout length. — In front of orbits 11.1; in front of mouth 13.6.

Orbits. — Horizontal diameter 3.5; distance between 3.3.

Spiracles. — Length 2.5; distance between 6.5.

Mouth. — Breadth 5.3.

Exposed nostrils. — Distance between inner ends 5.9.

Gill openings. — Length, 1st 1.2; 3rd 1.2; 5th 0.9; distance between inner ends, 1st 11.8; 5th 6.8.

First dorsal fin. — Vertical height 2.4; length of base 5.0.

Second dorsal fin. — Vertical height 2.4; length of base 4.5.

Pelvics. — Anterior margin 12.1.

Distance. — From tip of snout to center of cloaca 37.9; from center of cloaca to 1st dorsal 47.3; to tip of tail 62.1; from rear end of 2nd dorsal base to tip of tail 5.0.

Interspace. — 1st and 2nd dorsals 0.3; second dorsal and caudal 2.1.

Disc 1.2 times as broad as long, tip of snout with a very small projection, maximum angle in front of spiracles about 115°; anterior margins slightly convex in front of orbits, thence about straight to outer corners which are broadly rounded; rear margins gently rounded, as are inner margins. Axis of greatest breadth about 70 per cent of distance rearward from tip of snout to axils of pectorals. Tail very slender, with a lateral fold low down on each side, beginning almost imperceptibly beyond level of tips of pelvics by a distance equal to that between spiracles and continuing almost to extreme tip of tail, widening posteriorly, being widest opposite dorsal fins where its width is about equal to that of tail at that point; length of tail from center of cloaca to origin of first dorsal 1.25 times and to its tip 1.64 times as great as from center of cloaca to tip of snout.

A row of 5 small thorns along inner margin of one orbit and 9 along the other with a single thorn inward from these and opposite rear margin of spiracle. Extreme tip of snout smooth,

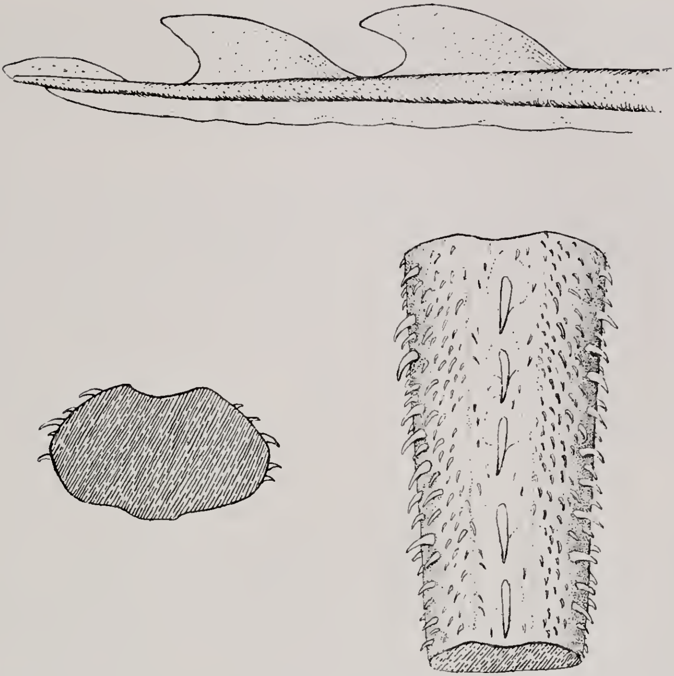

Figure 8. *Breviraja ishiyamai,* end of tail showing dorsal fins and caudal fin about x1.5; section of tail from near tips of pelvics and cross-section of same about x2.

remainder of disc uniformly covered with small, slender prickles, very close set, their tips bent rearward. A median row of 4 small thorns from nape to scapular region a little beyond which the row resumes with about 54 thorns of varying sizes extending on to tail and ending before first dorsal fin by a distance about equal to that from tip of snout to orbits. One or two scapular thorns on each side of median row. Tail, in addition to the thorns in midrow, densely prickly, some of the prickles being coarser than those on disc, with a row of smaller thorns varying in size, low down on each side, ending a little posterior to midrow. Posterior lobe of pelvics, skin over eyes, and dorsals, covered with prickles, with a few on caudal fin and lateral folds. Lower surface smooth.

Snout in front of orbits 3.2 times as long as orbit, its length in front of mouth 2.3 times as great as distance between exposed nostrils. Distance between orbits about 0.9 times as great as length of orbit. Orbit 1.4 times as long as spiracle. Nasal curtain smooth except for 1 or 2 tiny knobs; margin of outer nostril flap without a fringe. Upper and lower jaws weakly arched. Teeth $\frac{34}{33}$, mostly in quincunx, with ovate base and a very small, low triangular cusp.

Distance between first gill openings twice as great as between exposed nostrils; between fifth openings about 1.2 times; first to fourth gill openings about ⅓ as long as orbit, fifth opening slightly shorter than the others. First and second dorsals similar in height and shape with convex upper margin, the tips rather pointed, the base of first about equal to width of mouth, the base of second slightly shorter; virtually no space between dorsals. Second dorsal not confluent with caudal fin, the length of interspace about equal to half the second dorsal base. Caudal fin base equal to half the internarial space. Pelvics deeply concave, weakly scalloped, anterior lobe slender, as long as from its own origin to rear tip of pelvics; posterior lobe with slightly convex outer and rear margins, reaching one-fourth of the distance from axils of pectorals to origin of first dorsal.

Rostral cartilage narrow, extending about ⅔ the distance from front of cranium toward tip of snout. Tips of anterior radials of pectorals close together reaching nearly to tip of snout.

Color. Upper surface plain grayish brown without spots or other markings. Lower surface pale pinkish white, the pectorals darker posterior to the first gill openings.

The paratype, a female of 269 mm, agrees closely with the holotype in proportional dimensions.

The 362 mm female has a somewhat sharper and longer snout than the holotype, the anterior angle being 99°; the distance from snout to orbit 13.3 per cent and from snout to mouth 16.6 per cent of the total length while the disc width is proportionately greater, 52.1 per cent of the total length, and longer, 45.8 per cent. Also, the length of its tail measured from center of cloaca, 57.3 per cent, is shorter than that of the holotype (62.1 per cent).

The male, 226 mm long, has a strongly arched mouth, a relatively shorter snout, its length to orbit being 9.3 and to mouth 10.2 per cent of total length, and a longer tail which is 66.8 per cent. However, the longer tail might prove to be a juvenile character.

On two of the specimens mentioned above, the dorsals are confluent but on one, the male, there is an interspace about ⅓ as long as the first dorsal base. The space between the second dorsal and caudal fin, on these three specimens, ranges from ⅕ to ⅐ the first dorsal base. The small thorns along the inner margin of each orbit vary in number from 4 to 7. The disc and tail are densely covered with small prickles, but prickles are lacking on the posterior lobe of the pelvics on the 269 mm female and on its tail the row of very small thorns along the midline continues to the origin of the first dorsal. There are 36 to 38 series of teeth in the upper jaw, about the same in the lower. The color above is plain grayish or light brownish, the dorsals and caudal fin a little darker; below, plain whitish.

Known from off the Atlantic coast of Nicaragua, and the offings of Dry Tortugas and Cape Canaveral, Florida, in 275-520 fathoms.

Named for Reizo Ishiyama in recognition of his work on Japanese batoids.

BREVIRAJA PLUTONIA (Garman) 1881

Since our last published account of this species (Bigelow and Schroeder 1953, pp. 297-302) in which it is recorded from off the northern coast of North Carolina,[1] the offings of South Carolina and Georgia, and of Jacksonville, Florida, in 230-333 fathoms, more than one hundred additional specimens, 62-270 mm long, have been received from many localities ranging from off Cape Lookout, North Carolina, to an area centering about 30 miles southwest of Dry Tortugas, Florida, within the Gulf of Mexico.[2] They were taken on 7 "Oregon," 18 "Combat," 7 "Silver Bay" and 4 "Pelican" stations in depths of 160-400 fathoms.

A recently hatched specimen 64 mm in total length with a disc 28 mm wide, and one of 84 mm, disc 34 mm, are densely prickly everywhere above on disc and tail, with a few prickles on pelvics, skin over eyes, and on dorsals. There are 2 thorns along anterior margin of orbits and 2 or 3 along posterior margin. The midline row of thorns on disc and tail have not yet appeared. The embryonic tail is present. A specimen of 101 mm has a few thorns in the scapular region, some midline thorns on the tail and a few in the side rows, a total of 8 orbital thorns,

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[1] The precise locality for this record, from the winter trawl fishery (Pearson 1932, p. 18), was not given. If the identification be correct, the capture was probably made at a depth of less than 100 fathoms.

[2] These Dry Tortugas specimens were taken at "Oregon" stations 1010, 1538 and 1542 and "Silver Bay" stations 1195 and 1196.

and it has lost its embryonic tail. On a specimen of 134 mm the midline row of thorns is starting to fill in on the disc. On these young specimens the thorns are very small; the anterior margin of disc is evenly rounded, not concave as it is on older specimens of both sexes; the upper surface of the disc is marked with small dark spots and bars, including one bar across the scapular region, one extending outward and forward from each orbit, and one from the axil of each pectoral, while the tail has from 7 to 9 cross bars.

In our previous account of this species it is stated that the pelvics are naked, but a patch of prickles is present on the posterior pelvic lobes of both sexes, from the smallest to the largest sizes. The number of teeth on 10 specimens counted ranges from $\frac{28}{26}$ on a male of 219 mm to $\frac{34}{34}$ on a female of 225 mm, but young specimens of both sexes as small as 110-133 mm may have as many as $\frac{30}{30}$ teeth.

A female of 234 mm had an egg capsule which protruded for nearly half its length from the cloaca, the opening of which was distended to a width of 11.5 mm. The capsule, yellow brown and with a smooth surface, is 13 mm wide and 24 mm long, with very slender flexible horns 30 mm long at its straight end and stouter horns 8 or 9 mm long at its concave end.

BREVIRAJA SINUS-MEXICANUS Bigelow and Schroeder 1950

Since the publication of Fishes of the Western North Atlantic, No. 1, Part 2 (Bigelow and Schroeder 1953), which records 94 specimens, 117-355 mm long, trawled along the northeastern part of the Gulf of Mexico in depths of 170-347 fathoms, the "Oregon" has again taken *sinus-mexicanus* in this general region and also in the northwest Gulf (Lat. 26°46'N, Long. 96° 20'W) and in the southwest (in the Gulf of Campeche, Lat. 19°37', Long. 92°40'), within the above depth range and down to 400 fathoms.

BREVIRAJA SPINOSA Bigelow and Schroeder 1950

At the time of the last published account (Bigelow and Schroeder 1953, p. 306) of this species, based on 7 specimens, its known distribution was limited to the offings of northern Florida, North Carolina and Delaware Bay. Recently a large series was trawled by the "Oregon" (26 stations), "Combat" (11 stations), and "Pelican" (1 station) from the offing of Cape Fear, North Carolina, off the coast of Georgia, along the east coast of Florida, in the Florida Straits, and off the coasts of Honduras, Nicaragua and the Guianas, between N Lats. 32°58′ and 07°05′, in 150-400 fathoms. The specimens in this collection range from 77 to 424 mm in total length, with both sexes well represented.

These additional specimens show that there is a wide variation in size and number of thorns and prickles on the disc and the tail and in the color above and below. Thus, the upper surface of disc and tail may be densely covered with small prickles, or these may be sparse or virtually absent. The pelvics may be partly prickled or smooth. The thorns along the midbelt of back are conspicuous on some specimens, rather feeble on others, those in nape-scapular region in a triangular patch followed by from 4-5 to 6-7 more or less irregular rows along disc, to 3-4 or 4-5 rows on tail, the latter thorns usually being the larger. The thorns which line the inner margins of the orbits are in a continuous series on some specimens and may number as many as 10-12 but more often are interrupted and number about 5 to 8. The disc is smooth below, also the tail except for a few prickles along the outer edges on some specimens.

The color above ranges from pale grayish or grayish brown to dark gray or brown, sometimes of marbled appearance and, among the pale varieties, some are indistinctly marked with a few whitish blotches, often in pairs, arranged symmetrically on either side of the median line. The small protuberance at tip of snout is dark-edged on some, plain on others. The dorsals and caudal are either brownish or plain on specimens which are pale above, or black on those which are dark brown above. The lower surface may be pale throughout, grayish on the outer part of the pectorals, variously mottled with blackish brown, or entirely blackish excepting for pale areas immediately around the nasal apertures, around the mouth, around the gill openings and around the cloaca.

The mouth is moderately arched on small specimens, more strongly so on large. The number of teeth, on about a dozen specimens small to large, fell within the range of $\frac{36-46}{36-44}$ already given. The first and second dorsal fins are confluent at the base on most specimens but on an occasional one there is a very short interspace.

A mature male had not previously been seen. A specimen 332 mm in total length, from Lat. 29°34′N, Long. 80°23′W, has a disc obtusely rounded in front, thence concave opposite the spiracles, with broadly rounded outer corners and rear margins. The jaws are strongly arched. The teeth in the mid sector are arranged in quincunx, with a slender cusp, those toward outer corners tending to be in oblique rows and with a triangular cusp. The claspers extend beyond the axils of pelvics for a distance equal to that from the tip of the snout to the rear margins of the spiracles. The alar thorns are in 2 to 3 rows, the longest row as long as the distance from the tip of the snout to the rear margin of the orbits. The disc has very few prickles, and the thorns, excepting those on the tail, are relatively feeble. This specimen is pale brownish above and mostly blackish brown below.

The smallest three specimens, 77-83 mm in total length, with discs 42-46 mm wide, have a large yolk and an embryonic tail, one 89 mm long with a disc 48 mm wide has a small yolk and has lost its embryonic tail, while the yolk has been absorbed on a specimen of 105 mm, with disc 54 mm wide. Specimens 77 and 130 mm long are covered with prickles and small thorns; the triangular patch of thorns in the nape-scapular region is present followed by 3 rows along the mid zone of the disc and along the tail. The color is pale brown above, whitish below.

Genus CRURIRAJA Bigelow and Schroeder 1948

In this genus the outer margin of the pelvic fins is so deeply notched that the anterior division is entirely cut off from the remainder of the fin, thus forming a separate limb-like structure arising independently from the lower surface of the disc some little distance inward from the edge of the disc, with the inner posterior margin of the pectoral continuous with the anterior margin of the posterior division of the pelvic. *C. rugosa* and the new species *cadenati* necessitate the following modification of the characters of the genus. The slender anterior division of the pelvic, described as tapering toward the tip, does not taper on *cadenati* but is blunt at the tip (Fig. 9) and while the posterior division of the pelvic of *cadenati* has 18 radials, there are 11-14 radials on *atlantis, poeyi* and *rugosa*.

Key to known species of *Cruriraja*

1. Interspace between 1st and 2nd dorsal fins at least 1.5 times as long as base of 1st dorsal . . . . *atlantis*
Bigelow and Schroeder 1948. North coast of Cuba.

Interspace between 1st and 2nd dorsal fins not more than about half as long as base of 1st dorsal 2

2\. No thorns in the nuchal region . . . . *poeyi*
Bigelow and Schroeder 1948. Cuba and east coast of Florida. p. 204

Thorns present in the nuchal region 3

3\. Thorns in a broken series along midline of back 4

Thorns in an unbroken series along midline of back from close behind level of spiracles rearward along disc and tail 5

4\. Midzone of tail with a single row of thorns . . . . *rugosa*
Bigelow and Schroeder 1958. Gulf of Mexico; Atlantic coast of Central America. p. 204

Midzone of tail with 2 or more rows of thorns . . . . *cadenati*
new species, off Anguilla, Leeward Islands and east coast of Florida. p. 199

5\. A group of thorns on tip of snout, others along anterior half of rostral ridge, and 2 thorns in the space between the two dorsal fins . . .
parcomaculata von Bonde and Swart, 1924. Off Natal Coast, South Africa; 298 fathoms.

No thorns on tip of snout, along rostral ridge, or in the space between the two dorsals . . . .
durbanensis von Bonde and Swart, 1924. Off Natal Coast, South Africa; 420 fathoms.

CRURIRAJA CADENATI sp. nov.

Figure 9

Study material. Female, 376 mm in total length, holotype, U. S. Nat. Mus. No. 196443 from off the western coast of Puerto Rico, Lat. 18°16.5′N, Long. 67°17′W, in 250 fathoms, "Oregon" station 2650, and a mature male of 347 mm, paratype, M. C. Z. No. 40240 from the offing of Cape Canaveral, Florida, Lat. 27°59′N, Long. 78°56′W, in 480-490 fathoms, "Silver Bay" station 443.

Distinctive characters. Cruriraja cadenati differs from *C. rugosa* in the arrangement and number of thorns, there being 11 evenly spaced along the inner margin of each orbit, 5 in nuchal region, 11-12 immediately in advance of axils of pectorals, followed by 1 to 2 or more rows along the top of tail, and in lacking prickles on its under surface (*rugosa* has 2 to 8 orbital thorns, not evenly spaced, 0-3 nuchal thorns, 0-5 immediately in advance of axils of pectorals, only 1 row on the top of the tail, and prickles on the under surface of the tail on specimens larger than about 250 mm). It differs from *atlantis* in that the space between its dorsal fins is not more than about half as long as the first dorsal base (about 2.5 times dorsal base on *atlantis*); from *poeyi* in a more generally prickly disc, and in the presence of several nuchal thorns (disc without prickles, except along part of the midzone posterior to the pectoral girdle, no nuchal thorns, on *poeyi*); from *parcomaculata* and from *durbanensis* in lacking thorns along part of the midzone of the disc.

Description of holotype. Proportional dimensions in per cent of total length:

Disc. — Extreme breadth 62.0; vertical length 46.1.

Snout length. — In front of orbits 11.0; in front of mouth 14.1.

Orbits. — Horizontal diameter 5.3; distance between 3.5.

Spiracles. — Length 2.0; distance between 6.9.

Mouth. — Breadth 6.1.

Exposed nostrils. — Distance between inner ends 6.1.

Gill openings. — Length 1st 1.9; 3rd 1.9; 5th 1.2; distance between inner ends 1st 13.1; 5th 8.0.

First dorsal fin. — Vertical height 2.5; length of base 3.7.

Second dorsal fin. — Vertical height 2.5; length of base 3.5.

Pelvics. — Length of limb 12.2.

Distance. — From tip of snout to center of cloaca 42.1; from center of cloaca to 1st dorsal 47.8, to tip of tail 57.9; from rear end of 2nd dorsal base to tip of tail 2.4.

Interspace. — 1st and 2nd dorsals 0.5.

Disc. — 1.35 times as broad as long; maximum angle in front of spiracles 105°; anterior margins from snout to outer corners of pectorals slightly sinuous, the corners abruptly rounded; posterior and inner margins very gently rounded. Axis of greatest breadth 72 per cent of distance back from tip of snout to axils of pectorals. Tail with a lateral fold, low down on each side beginning a little posterior to tips of pelvics, very narrow anteriorly but widening on approaching tip of tail; length of tail from center of cloaca to origin of first dorsal 1.13 times as great, and to its tip 1.38 times as great as distance from center of cloaca to tip of snout.

Inner margin of orbits with 11 thorns, evenly spaced, with 2 or 3 in addition inward from the most posterior ones. A staggered row of about 10 thorns on anterior part of rostral process.

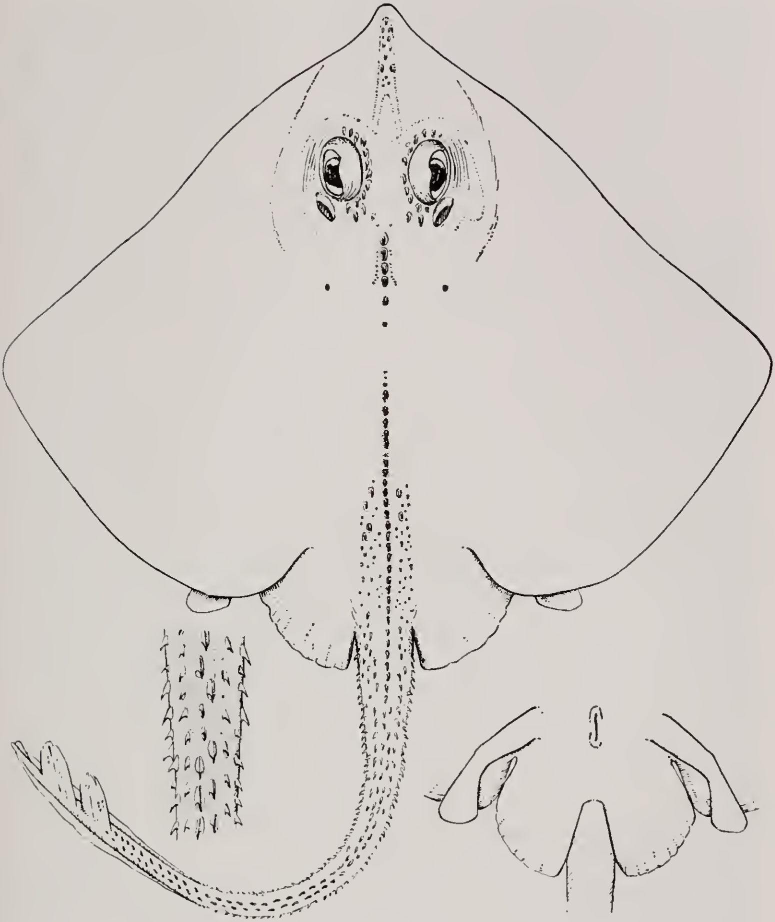

Figure 9. *Cruriraja cadenati,* dorsal view of type, female 376 mm long; ventral view of pelvics about x0.4; section of tail from near tips of pelvics about x0.7.

Five prominent thorns in midline from nuchal to scapular region followed by a space equal to 1⅓ eye's diameter lacking thorns, then a single row of 27 closely spaced thorns, of which 11 are in advance of axils of pectorals, merging a little posterior to tips of pelvics into a double row of 35 thorns, many of them opposite each other, extending to dorsal fin; 2-3 rows of small thorns on each side of midrow beginning a little in advance of axils of pectorals, becoming 2 rows opposite tips of pelvics, then 1-2 rows and running out approaching dorsal fin, the outer row outlasting the inner row; all the thorns pointing strongly rearward; a minute thorn between dorsals; a single very small scapular thorn on each side. Upper surface of disc and tail densely covered with minute prickles, sparse or lacking only along the edge of the posterior margins; prickles also present on dorsals, pelvics, and skin over eyes. Lower surface of disc smooth; tail smooth except for an occasional prickle along outer edges.

Snout in front of orbits 2.1 times as long as orbit, its length in front of mouth 2.3 times as great as distance between exposed nostrils. Distance between orbits 0.7 times as great as length of orbit. Orbit 2.7 times as long as spiracle. Nasal curtain and expanded outer margin of nostrils each with a few very short blunt fringes. Upper and lower jaws virtually straight. Teeth 46 in upper jaw, about the same in lower, chiefly in quincunx arrangement, with ovate base and a low triangular cusp.

Distance between first gill openings 2.1 times as great as between exposed nostrils; between fifth openings 1.3 times; first to third gill openings 1.6 times as long as fifth, the fourth about 1.3 times. First and second dorsals similar in size and shape. Space between dorsals 0.15 as long as base of first dorsal. Caudal fin base about 0.6 as long as second dorsal base, the fins not confluent, the interspace about 0.3 as long as caudal base. Anterior division of pelvics not tapering, wide at tip, failing to reach (when pulled back) tip of posterior lobe by a distance equal to three-fourths the diameter of orbit; posterior lobe with 18 rays, of shape shown in Figure 9.

Rostral cartilage firm, narrow, extending nearly to tip of snout. Anterior pectoral rays reaching about three-fifths the distance from front of orbits toward tip of snout.

Color. Upper surface of disc light brown with numerous dark brown rather vague irregular spots ranging in size from about one-fourth to as large as the area of the orbit, the spots extending along tail, where they are more intense, nearly to dorsal fin. Pelvics pale brown, unspotted: dorsals pale without prominent markings. Below, the disc is marked with a broad irregular band of grayish along its margins from outer angles rearward, otherwise whitish. Pelvics with gray along their posterior margin; tail white.

The male has a somewhat sharper snout than the female, the maximum angle in front of spiracles being 90°. The anterior margins of disc are more strongly sinuous and the axis of greatest breadth somewhat more anterior, being 68 per cent of distance back from tip of snout to axils of pectorals. The tail is relatively longer, the distance from center of cloaca to origin of first dorsal 1.21 times, and to its tip 1.58 times, as great as distance from center of cloaca to tip of snout.

The rostral, orbital and nuchal thorns are in about the same number and arrangement as on the female but there are 2 small scapular thorns on one side and 3 on the other, instead of only one. Behind the scapular region, following the short space lacking armature, there is a single row of 30 thorns of which 12 are in advance of axils of pectorals, merging along tail into a staggered double row of about 32 thorns extending to the dorsal fin. A band of prickles is present each side of the mid row of thorns on the disc, beginning posterior to the scapular region and ending about opposite the tips of the pelvics from where a row of small thorns, low down on tail, continues to near the first dorsal. A patch of prominent thorns is present opposite the orbits and spiracles continuing, with thorns of smaller size, in a narrow band almost to the outer angles of the disc. The alar thorns are in 5-6 rows, the length of each patch about equal to the distance from the eyes to the tip of snout, the width about one-third this distance. The rest of the disc, including the interorbital space, is smooth except for an area of small thorns on the inner posterior part of the pectorals. The dorsals and the caudal fin have a few prickles but the skin over eyes and the pelvics are smooth. Lower surface smooth.

The disc width of the male is 58.3 per cent and the disc length 43.3 per cent of the total length of the specimen, compared with 62.0 and 46.1 per cent, respectively, on the female. However, the longer tail of the male is responsible for much of this difference in proportions as the disc width is 1.50 times and the length 1.11 times the distance from tip of snout to the center of the cloaca, or virtually the same as that of the female on which these proportions are 1.47 and 1.10, respectively. The dorsal interspace is greater, being half the length of the first dorsal base but only one-seventh on the female. The posterior lobe of the pelvics has only 12 rays and is pointed at the tip. The claspers are well developed reaching a little more than half the distance from axils of pectorals to the first dorsal fin. There are 44 series of teeth in the upper jaw, 40 in the lower, arranged in oblique rows, those in the mid sector of the jaws with a prominent conical cusp, those in the outer sectors with a triangular cusp. Color above light brown, the vague spots present on the female not apparent. Dorsals, caudal, and posterior section of tail fold dusky. Lower surface whitish in advance of gill openings, pale brownish posteriorly.

Known only from the holotype, a female 376 mm in total length, trawled in 250 fathoms off the western coast of Puerto Rico, and the paratype, a mature male of 347 mm taken off Cape Canaveral, Florida, in 480-490 fathoms. Named for Dr. J. Cadenat of the University of Dakar in recognition of his work on elasmobranchs of the west coast of Africa.

CRURIRAJA POEYI Bigelow and Schroeder 1948

Four specimens, all females, 235-343 mm in total length, were trawled off the northwest edge of Great Bahama Bank by the "Combat," stations 446 and 447, in 250-300 fathoms. This species has previously been reported from off the south central and north central coasts of Cuba and off St. Augustine, Florida, in 210-475 fathoms.

CRURIRAJA RUGOSA Bigelow and Schroeder 1958

Figure 10

The original account of this species is based on a single specimen, an immature male 367 mm in total length, taken in the northeastern part of the Gulf of Mexico in 200-300 fathoms. We can now amplify our description from a large series of specimens, as follows.

Study material. Thirty-nine specimens, males and females, 90 to 465 mm in total length, taken at 19 "Oregon" stations off the Atlantic coasts of Nicaragua and Honduras, ranging in North Latitude from 12°50′ to 16°46′ and in West Longitude from 81°25′ to 82°44′, in 200-350 fathoms.

Distinctive characters. Cruriraja rugosa was described as differing from all other known members of its genus in that the under side of its tail is covered with minute prickles, this area being smooth in the other species. Our additional material shows that while these prickles are present on specimens larger than about 250 mm in total length, of both sexes, on some specimens being sparse in distribution, on others dense, the prickles are entirely lacking on small individuals. Young and half-grown *rugosa* (larger ones as well) may be distinguished from other western Atlantic *Cruriraja* as follows: from *atlantis* by a short space between the dorsal fins, about 0.2-0.4 times the length of first dorsal base (about 2.5 times the dorsal base on *atlantis*); from *poeyi* by the prickles that cover the disc, the presence of

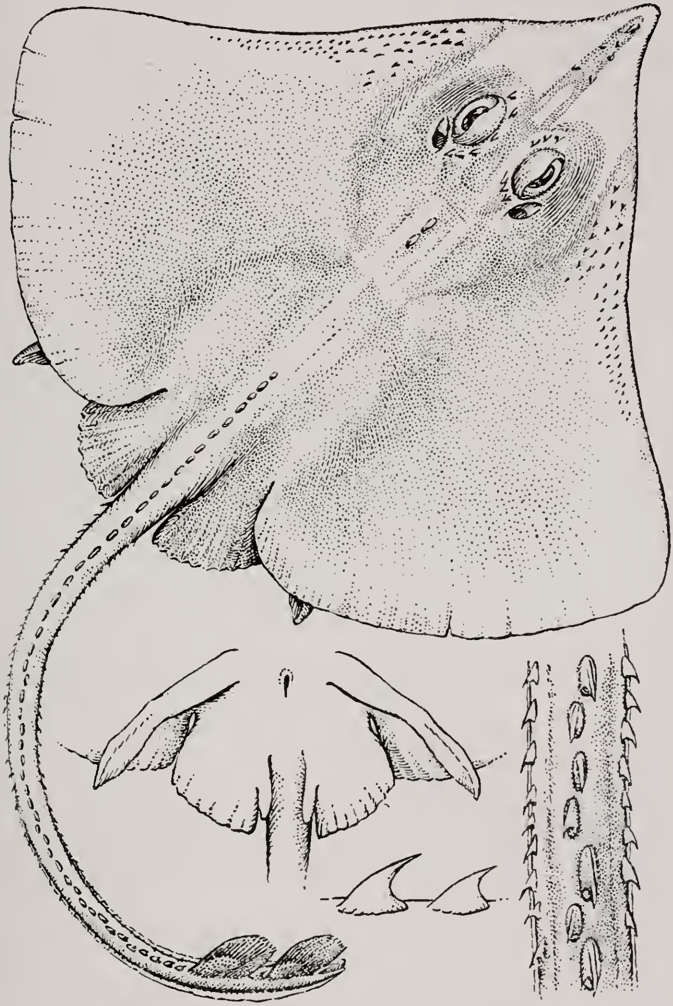

Figure 10. *Cruriraja rugosa*, type, immature male 367 mm long; pelvic fins about x0.5; section of tail about x2; first 2 thorns in front of dorsal fin about x3. (After Bigelow and Schroeder 1958.)

one or more nuchal thorns (occasionally absent) and a single row of thorns along the midline of the tail (disc without prickles, except along part of the midzone posterior to the pectoral girdle, no nuchal thorns, midline of thorns on tail divides into two rows posteriorly, on *pocyi*); from *cadenati* in the number and arrangement of thorns along the inner margin of the orbits, on the midline of the disc, and on the tail, and in differing in several of its proportional dimensions (p. 200). *Rugosa* differs from the two species of *Cruriraja* known from South Africa as follows: from *parcomaculata* in having a wide space lacking thorns along the midzone of the disc between the nuchal thorn or thorns and a point a little in advance of the axils of the pectorals, and by its plain coloration (*parcomaculata* described from a young specimen 181 mm in total length, has a continuous row of thorns from the nuchal region to the first dorsal and 14-18 blackish brown spots of varying sizes on the disc). Absence of thorns along part of the midzone of its disc also sets *rugosa* apart from *durbanensis,* a male, 232 mm long, having a continuous row of thorns along the midline from the nuchal region to the first dorsal fin, and a female, of 311 mm, with this row ending about half-way along the tail, leaving a wide thornless space before the first dorsal.

Proportional dimensions in per cent of total length of a male of 381 mm from Lat. 16°42′N. Long. 82°36′W and of a female of 318 mm, taken nearby, follow:

Disc. — Extreme breadth 58.5; 56.7; length 42.8; 42.5.

Snout length. — In front of orbits 11.8; 11.6; in front of mouth 13.0; 14.2.

Orbits. — Horizontal diameter 4.7; 3.8; distance between 3.2; 3.2.

Spiracles. — Length 2.1; 2.0; distance between 6.7; 6.3.

Mouth — Breadth 6.3; 5.5.

Exposed nostrils. — Distance between inner ends 5.5; 5.5.

Gill openings. — Length 1st 1.3; 1.5; 3rd 1.0; 1.6; 5th 0.9; 1.3; distance between inner ends 1st 10.8; 11.5; 5th 6.1; 6.1.

First dorsal fin. — Vertical height 2.9; 2.5; length of base 3.9; 3.8.

Second dorsal fin. — Vertical height 2.9; 2.8; length of base 4.2; 4.1.

Pelvics. — Length of limb 13.1: 12.0.

Distance. — From tip of snout to center of cloaca 38.9; 37.1; from center of cloaca to 1st dorsal 46.9; 49.3; to tip of tail 61.1; 62.9; from rear end of 2nd dorsal base to tip of tail 4.8; 4.4.

Interspace. — 1st and 2nd dorsals 1.3; 1.3.

A dozen or so males and females have the following characteristics. Maximum angle in front of the spiracles 75°-90° with no apparent difference between the sexes. Axis of greatest breadth 62-77 per cent of the distance back from tip of snout to axils of the pectorals. Tail with a lateral fold, low down on each side, beginning at about 45-55 per cent of the distance from axils of the pelvics toward tip of tail, very narrow anteriorly, widening posteriorly and reaching nearly to tip of tail. The length of the tail from the center of the cloaca is 1.66-1.83 times as great as the distance from the center of the cloaca to the tip of the snout on specimens less than about 200 mm long and 1.50-1.73 times on those of larger size.

There are from 1 to 3 thorns, both anteriorly and posteriorly, along the margin of each orbit, with a space between lacking thorns, on specimens up to 420 mm long. The largest, of 465 mm, has 5 anterior and 3 posterior at one orbit and 3 and 3 at the other.

The number of thorns on the anterior half of the rostrum ranges from 1 to 8, but an occasional specimen lacks these thorns. The patch of thorns along the outer part of the disc opposite the orbits and nuchal region, illustrated on the holotype (Fig. 10), is present on all our smaller specimens but lacking on some of the larger. There is usually 1 prominent nuchal thorn (15 specimens) but two specimens have none, two have 2, and two have 3 nuchal thorns. A scapular thorn is present on each side on sizes up to 186 mm; one of 250 mm has a thorn on one side only, and all the larger specimens lack them.

The midrow of thorns, usually beginning 1 to 2 eyes' diameter in advance of the axils of the pectorals and continuing uninterrupted along the tail to the first dorsal fin, range in number from 24 to 61, of which from 1 to 8 thorns are in advance of the axil of the pectorals except on two specimens where the first thorn is opposite the axil. While the larger specimens on the average have more thorns than the smaller, one of 186 mm has 50, while another, 420 mm long, has only 39. The row of smaller thorns, low down on the tail, on each side of the midrow, begins to appear on specimens as small as about 130 mm but these thorns, except for an occasional one, may be absent on much larger sizes. They are generally spaced unevenly and run out a little in advance of the first dorsal fin, in some cases not extending rearward beyond the anterior half of the tail. There are from 1 to 3 thorns between the dorsals.

The upper surface of the disc, including the smallest specimens, is covered with minute prickles, as described for the holotype. Prickles are present on the dorsals, on skin over eyes, and on the pelvics but are usually absent on specimens smaller than about 170 mm long. The lower surface of the disc is smooth but the tail is more or less prickly on sizes larger than about 250 mm (p. 204).

The teeth are in series from 34 to 44 in the upper jaw and about the same in the lower, arranged chiefly in quincunx with a low triangular cusp, except on mature males on which they are more in a straight series than in quincunx and have a slender sharp cusp. The mouth of females and immature males is slightly arched but is moderately arched on mature males.[1]

The space between the dorsals ranges from about ⅕ to ⅖ as long as the base of the first dorsal on most specimens but on one is only ⅛ as long. The space between the second dorsal and caudal fins is equal to about ¼ to ⅓ the base of the first dorsal. The base of the caudal is a little shorter than the base of the first dorsal. The anterior pectoral rays reach about 55 per cent of the distance from the front of the orbits toward the tip of the snout.[2]

A nearly mature male of 390 mm has well developed claspers which reach beyond the tips of pelvics a distance equal to about that from tip of snout to mouth, and there are 9 exposed alar thorns on the left side and 10 on the right, but on one of 415 mm, fully mature with clasper hooks exposed, the alars are in a patch of about 40 on each side, the thorns slender and pointing obliquely inward and rearward.

The upper surface of the disc is plain brownish, the dorsals and caudal ranging from somewhat darker brownish to dusky. Below pale, some specimens with brownish mottlings on the pectorals.

All the specimens were taken within a depth range of 200-350 fathoms. Although the ''Oregon'' has made many hauls within these depths throughout the Gulf of Mexico and southward to about Lat. 7° N, with a few to Lat. 01°45'N, *rugosa* was taken at only 1 station within the Gulf (type locality) and only along the Atlantic coasts of Nicaragua and Honduras.

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[1] In the original published account (Bigelow and Schroeder 1958, p. 229) the description of teeth and shape of mouth was scrambled in printing. It should have read, "Upper and lower jaws nearly straight. Teeth $\frac{43}{42}$, arranged in quincunx, with ovate base and short triangular cusp."

[2] This was erroneously given as 22 per cent in the original published account.

Family PSEUDORAJIDAE Bigelow and Schroeder 1954

Rajoidea without dorsal fins; tail with a lateral fold low down on each side; with a well developed upper and lower caudal fin, not quite confluent around tip of tail, supported by a great number of very slender raylike strands, apparently cartilaginous; with outer margins of pelvics pointed or rounded and posterior margin straight or slightly convex if spread widely; anterior wall of spiracles with a transverse row of low vertical ridges, representing the vestiges of the embryonic gill filaments; pelvis with transverse element nearly straight, each of its outer corners with a short projection directed forward.

Genus PSEUDORAJA

Pseudorajidae with shape of disc, and of tail relative to disc, as in skates of the family Rajidae; tip of snout with a short protuberance; pelvic fins very large, wing-like, with anterior outline about transverse to main axis of disc; front of cranium with a rostral projection, longer or shorter; a pit on ventral surface of head on either side, close posterior to nostril but entirely separate from the latter. Other characters those of the family Pseudorajidae.

Key to Species

1a Pelvics with outer margins broadly rounded; tip of snout with a short fusiform protuberance .... *fischeri* p. 216

1b Pelvics with outer margins pointed; tip of snout with a short flat protuberance .... *atlantica* n. sp. p. 209

PSEUDORAJA ATLANTICA sp. nov.

Figures 11-13

Study material. Female, 450 mm in total length, holotype, U. S. Nat. Mus. No. 196444, from Lat. 13°20'N, Long. 82°02'W in 325 fathoms, "Oregon" station 1917, and 2 males, 421-435 mm, paratypes, M. C. Z. Nos. 40167, 40168, from Lat. 13°31'N, Long. 81°54'W in 300 fathoms, "Oregon" station 1920, both from off the Atlantic coast of Nicaragua. Also 57 others, males and females, taken at 18 "Oregon" stations as follows: 12 specimens, 230-447 mm, from 8 stations off Nicaragua (12°33'-13°34') in 275-350 fathoms; 20 specimens, 170-481 mm, from 9 stations made SW of Grenada (11°31'-11°40') in 185-290 fathoms; and

23 specimens, 190-375 mm, from 8 stations off British Guiana (07°05′-07°38′) in 135-275 fathoms; also 2 abnormal specimens (p. 215), 250-349 mm, from 2 stations off the mouth of the Amazon River (Lat. 01°45′-01°49′N) in 225-275 fathoms.

Distinctive characters. This species differs further from *fischeri,* its only known genus mate, in lacking enlarged thorns along the margin of orbits and in the scapular region and in having the prickles on the tail sparsely distributed and minute in size while on *fischeri* there are prominent orbital and scapular thorns and the prickles on the tail are densely distributed and large in size. Also, the pelvic fins have 12 to 15 radials, in addition to the first stout one, whereas *fischeri* has 18 to 20.

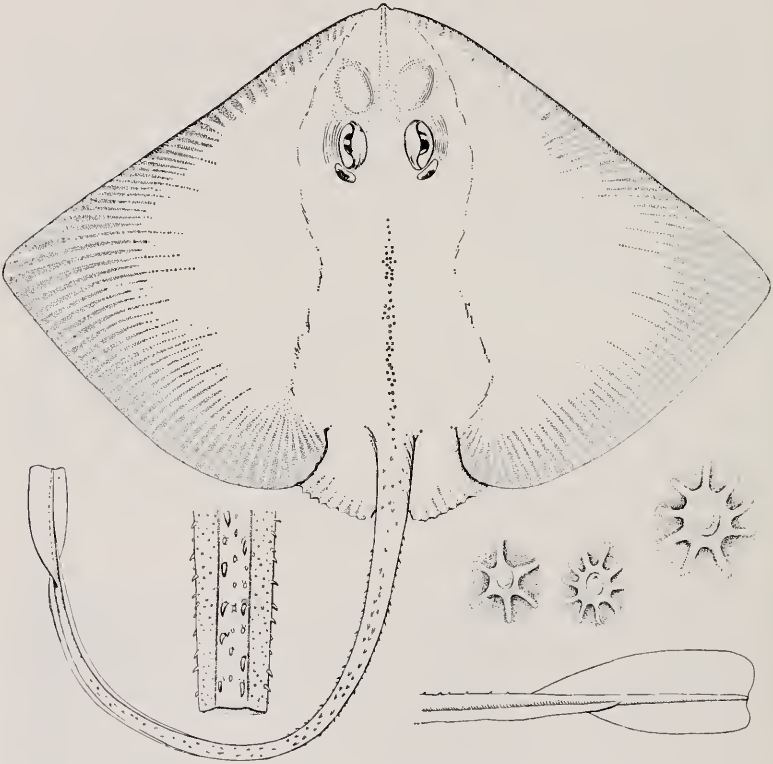

Figure 11. *Pseudoraja atlantica,* dorsal view of type, female 450 mm long; section of tail about x1.8; thorns from along middle of disc, about x12; caudal fin and ending of tail fold, about x1.

Description of holotype. Proportional dimensions in per cent of total length:

Disc. — Extreme breadth 61.8; vertical length 36.7.

Snout length. — In front of orbits 9.9; in front of mouth 10.4.

Orbits. — Horizontal diameter 3.6; distance between 3.1.

Spiracles. — Length 2.0; distance between 5.9.

Mouth. — Breadth 6.0.

Exposed nostrils. — Distance between inner ends 4.9.

Gill openings. — Length, 1st 1.1; 3rd 1.1; 5th 0.9; distance between inner ends, 1st 10.4; 5th 6.9.

Pelvics. — Length of anterior margin 12.7.

Caudal fin. — Length of base, upper 10.0; lower 8.0.

Distance. — From tip of snout to center of cloaca 33.8; from center of cloaca to tip of tail 66.2.

Disc 1.68 times as broad as long, maximum angle in front of spiracles 148°; margins from tip of snout to about opposite orbits slightly convex thence slightly concave to outer corners of disc which are sharply rounded; posterior margins beginning straight and then gently rounded to very short inner margin.

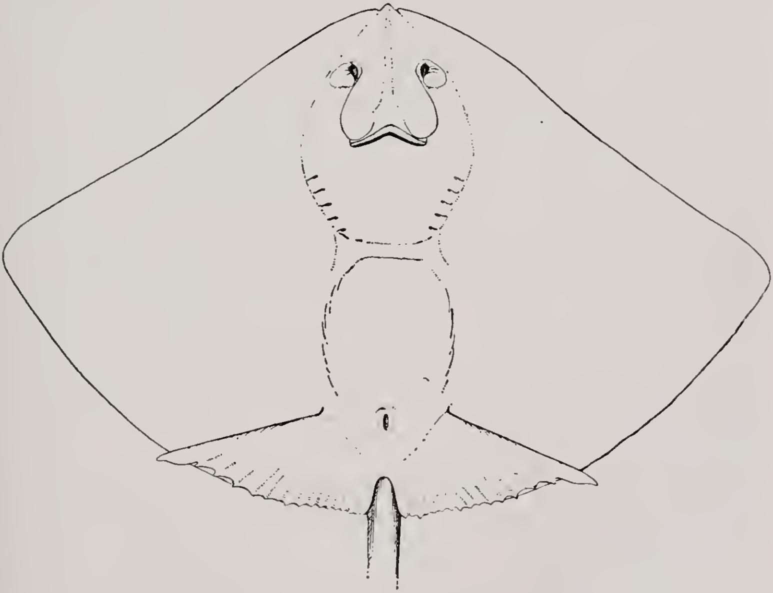

Figure 12. *Pseudoraja atlantica,* ventral view of type, with pelvics spread out.

Axis of greatest breadth about 66 per cent of distance back from tip of snout to axil of pectorals. Tail very slender, its width, about midway between cloaca and its tip, only one-fourth the diameter of eye; a lateral fold low down on each side, beginning almost imperceptibly beyond level of tips of pelvics by a distance equal to about twice diameter of eye and ending an eye's diameter beyond origin of upper caudal fin, very narrow anteriorly but gradually widening rearward until, a little in advance of caudal fin, the fold on each side is nearly as wide as tail at that point; length of tail from center of cloaca 1.96 times distance from tip of snout to center of cloaca.

Upper surface of disc covered everywhere with very small sharp prickles, on stellate bases, somewhat more dense and a trifle larger between and in advance of orbits than posteriorly. Several irregular rows of very small bluntish thorns, with an occasional sharp one, forming a narrow band along midzone of disc from nape to origin of tail from which 2 to 3 interrupted rows of larger thorns, sharp pointed and directed rearward, reduced to 1 or 2 rows posteriorly, extend to a little in advance of caudal; prickles on pelvics, on skin over eyes, and on caudal fin. No enlarged thorns around orbits. Lower surface prickly in advance of pectoral arch and over abdominal region, but virtually smooth on posterior half of pectorals. Lower surface of tail with minute prickles throughout its length.

Snout in front of orbits 2.8 times as long as orbit, its length in front of mouth 2.1 times as great as distance between exposed nostrils, its tip with a very short protuberance. Distance between orbits about 0.9 times as great as length of orbit. Orbit 1.8 times as long as spiracle. Nasal curtain without fringes; expanded (outer) margin of nostrils fringed; nasal pockets large and conspicuous. Upper and lower jaws moderately arched. Teeth $\frac{38}{38}$, with circular or ovate base and a low triangular cusp; upper teeth smallest and in vertical rows at and near center of mouth, becoming larger and the rows increasingly oblique toward corner of mouth; lowers similar to the uppers in shape and arrangement, but all of about the same size.

Distance between first gill openings 2.1 times as great as between exposed nostrils; between fifth gill openings 1.4 times; first gill openings about 1.3 times as long as fifth and 0.2 as long as breadth of mouth. No dorsal fins. Upper caudal fin rising very gradually, its base about as long as distance from tip of snout to orbits, its margin convex and its maximum width about

0.4 times diameter of eye; lower caudal fin originating a little posterior to upper, its base 0.8 times as long and its width 0.6 as great as upper, the fins not confluent although reaching tip of tail. Pelvics with rear margins about straight when spread except for short lobe formed by first ray which is stout and 4-jointed; anterior margin 1.3 times as long as distance from its own origin to rear margin of pelvics.

Rostral cartilage very narrow, extending to tip of snout, firm along the first three-fifths of its length in front of cranium, thence flexible to tip. Pectoral rays reaching anterior part of edge of disc, close together at tip of snout.

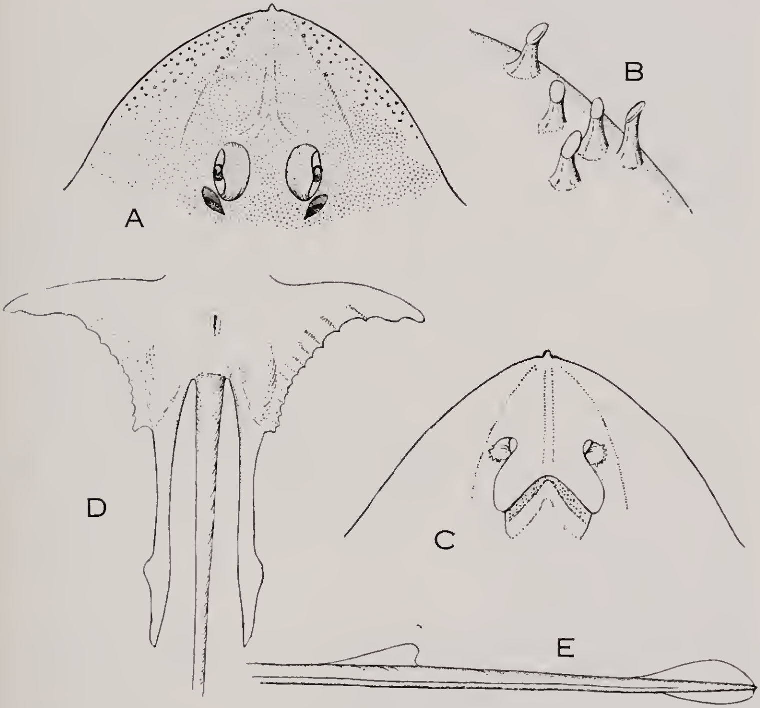

Figure 13. *Pseudoraja atlantica*, mature male 421 mm long, M. C. Z. No. 40168, *A*, Anterior part of disc to show distribution of knob-like thorns, about x0.5. *B*, Thorns enlarged about x6. *C*, Ventral surface to show shape of mouth. *D*, Pelvic fins and claspers about x0.5. *E*, Male 349 mm long, M. C. Z. No. 40406, end of tail to show position of dorsal fin, about x1.

Color. Upper surface of disc pale brownish without distinctive markings in preserved state; tail brownish. Lower surface of disc pale pinkish and brownish, tail mottled with brownish or dusky markings; caudal fin black.

A mature male 421 mm long (the paratype) differs from the holotype chiefly as follows: breadth of disc 1.45 times its length; breadth across anterior edge of orbits 21.8 per cent of total length of specimen (33 per cent on holotype); maximum angle in front of spiracles 123°; margins from opposite orbits to outer corners more strongly concave; axis of greatest breadth about 74 per cent back from tip of snout to axil of pectorals. The thorns along the midline of the disc and tail are fewer than on the female, and there are none on the anterior sixth of the tail. A more striking difference between the sexes is the presence on the male of a patch of 5-6 uneven rows of prominent thorns, with smooth roundish tips (Fig. 13A-B), along the pectorals from the end of the snout to a little in advance of a line through the orbits. The upper and lower jaws are very much more strongly arched in the male than in the female (Figs. 12, 13C).

Teeth only $\frac{26}{26}$, uppers with a narrow sharp cusp, except near corner of mouth where the cusps become low triangular, smallest at center of jaw where they are in vertical rows, the rows becoming increasingly oblique outwardly; lower teeth all of about the same size, those in center in 7-8 functional rows, arranged vertically, the succeeding rows oblique matching those of upper jaw, with sharp inward pointing cusps, except near corner of mouth. Alar thorns in 2-3 rows, length of patch about equal to length of snout, width about ½-⅔ diameter of eye. The claspers are very long and slender, reaching beyond rear tip of pelvics a distance about equal to that from tip of snout to posterior margin of spiracles, or about one-fifth the length of tail from center of cloaca.

The disc width of both sexes usually is proportionally less on small and medium-sized individuals than on large. Thus on 15 examined, 191-379 mm long, the width ranges from 47.2 to 55.4 per cent of total length and, of these, 9 males average 49.1 and 6 females 53.1 per cent. On 3 mature males, 421-432 mm long, the width is 53.2-54.4 per cent, but on 2 females of 437 and 450 mm it is 63.2 and 61.8 per cent, respectively. One specimen which falls out of line with the above, a male 315 mm long, has a disc width of 58.0 per cent.

Prickles cover the upper surface of disc on all our specimens but the tail thorns are relatively fewer on the smaller sizes, there being 1 to 2 rows on a female of 198 mm in total length and a scattering few on a male of 190 mm. A male of 349 mm is the smallest which shows a few of the peculiar knob-like thorns which, on adult males, are present in a conspicuous patch on each pectoral, in advance of the orbits. The lower surface, on the larger specimens, is covered with prickles, in varying degrees of density, anterior to the scapular arch, over the abdominal region and on the tail, the rest of disc being smooth; on the smaller specimens the prickles are restricted to the rostrum, and sparsely, to the tail.

The teeth of females 198-450 mm long are in 32-40 series, in each jaw, and of males of 242-432 mm in 26-34 series, the number of the latter smallest on two males 390 and 421 mm long and largest on two males of 306 and 425 mm, respectively. The jaws of males less than about 300 mm long are only slightly arched but become increasingly so with growth.

The claspers of males around 300 mm long extend a trifle beyond the tips of the pelvics; at 350 mm they extend beyond a distance equal to about that from tip of snout to mouth, and are pliable; at 390 mm they are starting to harden, and on those of 395 mm and larger they are stiff and reach beyond pelvics a distance equal to about that from tip of snout to spiracles, or a little more.

The disc of some specimens is marked above with many obscure to rather prominent darkish brown blotches ranging in size from a little less than to a little more than that of the orbit, and the tail has a number of dark bars or blotches, up to from 6 to 10, with pale interspaces. The caudal fin in all cases is blackish.

Two of our specimens deserve special mention, a female 250 mm long and a male of 349 mm taken, respectively, in Lat. 01° 45'N, Long. 46°46'W, in 275 fathoms, "Oregon" station 2084, and Lat. 01°49'N, Long. 46°48'W, in 225 fathoms, "Oregon" station 2083. Each of these has one small dorsal fin (Fig. 13E), originating from tip of tail a distance equal to about 18-20 per cent of the total length of the specimen, the length of the base of the fin being almost one-fifth this distance and the height about one-third the base. A similar abnormality has been recorded, for the type specimen of *Raja garmani* (Garman 1881 and Garman 1913, pl. 18, fig. 2, as *Raja ornata*) has 3 dorsal fins instead of the usual 2 and other instances of accessory dorsal fins on rajids are described by Schnakenbeck (1942).

Known from the Atlantic coast of Nicaragua to the offing of the Amazon River in 135-350 fathoms.

PSEUDORAJA FISCHERI Bigelow and Schroeder 1954

One specimen, a female 270 mm in total length, is included in an "Oregon" and "Silver Bay" collection of elasmobranchs taken in otter trawl hauls made chiefly within and near the Straits of Florida in depths of 185-305 fathoms, but lacks a station number. Known previously from 4 specimens taken at "Oregon" station 726 from the southern part of the Gulf of Mexico, near Campeche Bank, in 225 fathoms.

The present specimen differs somewhat in coloration from the specimens previously seen, brown above on disc with many dark spots of a size about ¼ to nearly as large as orbits, and lacking whitish spots; the tail has 8 dark cross-bars, narrow to wide, and the upper and lower caudal fin is partly dusky.

Family ANACANTHOBATIDAE

Two new species of anacanthobatids, collected by the "Oregon," necessitate a revision of our recently published account (Bigelow and Schroeder 1953, pp. 327-331), as follows:

Characters of the family. Rajoidea with snout expanded terminally or not, its tip with a filament. No dorsal fins. Tail slender, rounded or squarish, with or without a narrow thickened lateral fold, or with a crease, low down on each side and with a small upper and lower caudal fin. Pelvics so deeply notched outwardly that the anterior subdivision is leglike, of three segments, resembling the pelvics of *Cruriraja* among rajids and of *Typhlonarke* among electric rays; inner margin of posterior lobes of pelvics attached to sides of tail nearly or quite to their tips; outer margin of pelvics attached along part of its length to inner margin of pectoral on females and immature males but entirely free from pectorals on mature males so far as known. Skin smooth everywhere except for alar thorns on disc of mature males. Outer corners of pelvis with a well developed prepelvic spur.

The type genus of this family, *Anacanthobatis* von Bonde and Swart 1924, is placed in the suborder Myliobatoidea (family Dasyatidae) by Fowler (1941, p. 397) and by Smith (1949, p. 71). But the nature of its pelvics (see above) and the presence of a rostral projection from the cranium actually locates it in the Rajoidea.

Genera. Two genera are known, *Anacanthobatis,* von Bonde and Swart, 1924, Natal Coast, South Africa, Central America to British Guiana, probably the Gulf of Mexico also (p. 224); and *Springeria* Bigelow and Schroeder 1951, Gulf of Mexico.

Key to Genera

1. Snout not expanded terminally . . . . *Anacanthobatis*
2. Snout expanded terminally in leaf-like form . . . *Springeria*

Three species of *Anacanthobatis* are now known.

Key to Species of *Anacanthobatis*

1. Pelvics completely fused along their whole length with root of tail . . . *marmoratus* von Bonde and Swart 1924 off Durban, Natal.
   Pelvics not completely fused along their whole length with root of tail . 2
2. Length of snout about 4 to 5 times as long as diameter of eye . . . . *americanus* n. sp., p. 217
   Length of snout about 9 times as long as diameter of eye . . . . *longirostris* n. sp., p. 223

ANACANTHOBATIS AMERICANUS sp. nov.

Figures 14-16

Study material. Female, 337 mm in total length to base of terminal filament, holotype, U. S. Nat. Mus. No. 196445, from Lat. 11°35'N, Long. 62°41'W, in 212-250 fathoms, "Oregon" station 2353, and two mature males, and a female, 326-328 mm, paratypes, M. C. Z. Nos. 40364, 40365, 40366 from same station, between Grenada and Venezuela; a female of 350 mm and two males 310-330 mm from the same region, "Oregon" stations 2771, 2779; also 7 males and 6 females, 95 to 349 mm, from 4 stations 2009, 2010, 2011, 2012) off British Guiana in 150-400 fathoms and 1 station (1890) about midway between Jamaica and Honduras in 100 fathoms.

Distinctive characters. Evident differences between *americanus* and *marmoratus* are that on *americanus* the rostral filament is brownish, the upper surface of disc is plain grayish brown, the caudal fin obvious though small, and the skin is without papillae, whereas on *marmoratus* the rostral filament is dark red, the disc mottled with very small white spots and faintly brown ocelli, the caudal fin so small as to be hardly noticeable and that dark red, soft, papilla-like projections, about 1 to 3 mm long, are sparsely scattered over the upper surface of disc and pelvics. It differs from *longirostris* in its shorter snout and longer tail (see p. 224).

von Bonde and Swart (1924, p. 19) have described, as *dubius*,

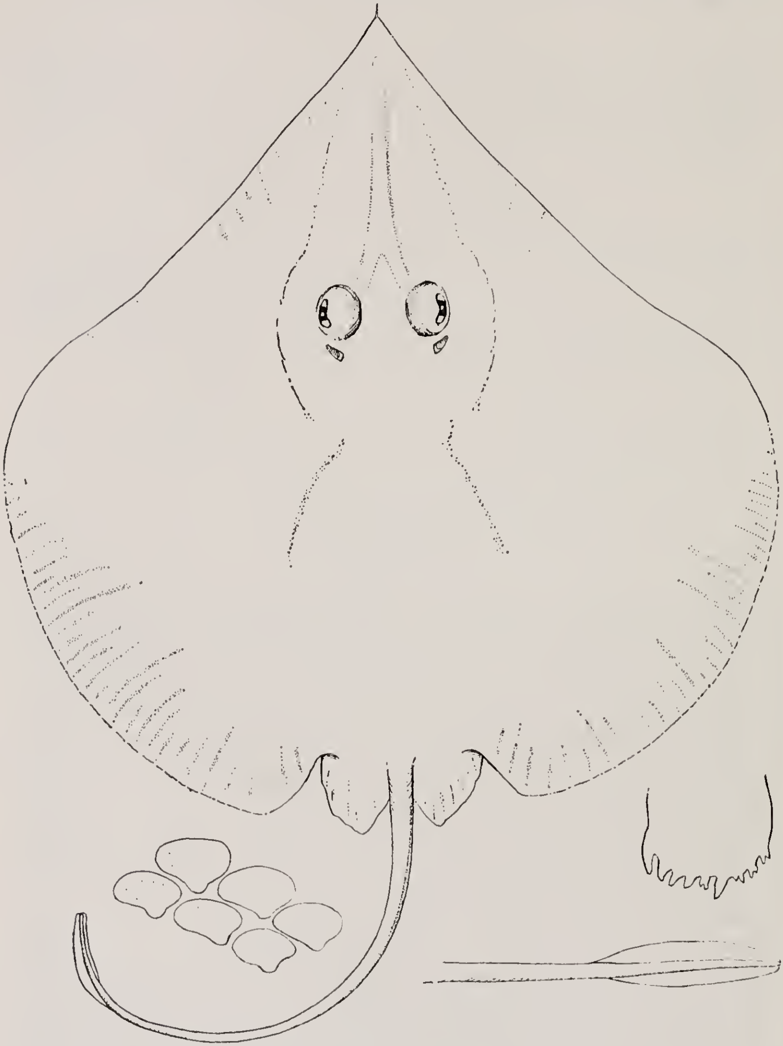

Figure 14. *Anacanthobatis americanus*, dorsal view of type, female 337 mm long; teeth from upper jaw, about x10; caudal fin about x1, left section of nasal curtain to show fringes, about x4.

a male differing from *marmoratus* in that its pelvics are fused with its pectorals along about one-half their length as they are in female *marmoratus*. Our series of *americanus* shows, however, that immature males have the pectorals fused as they are in *dubius*, but that this fusion disappears on mature males so that the pectorals and pelvics are completely separated (p. 222) as they are on mature males of *marmoratus*. Hence it is probable that *dubius* is an immature *marmoratus*.

Description. Proportional dimensions in per cent of total length. Female, 337 mm long, holotype, and mature male, 327 mm long, paratype.

Disc. — Extreme breadth 58.5, 58.6; length 57.0, 55.7.

Snout length. — In front of orbits 19.3, 17.4; in front of mouth 22.2, 20.5.

Orbits. — Horizontal diameter 4.0, 4.0; distance between 3.0, 2.2.

Spiracles. — Length 1.2, 1.4; distance between 6.4, 6.0.

Mouth. — Breadth 4.5, 5.8.

Exposed nostrils. — Distance between inner ends 3.6, 4.0.

Gill openings. — Length, 1st 0.8, 0.6; 3rd 0.8, 0.6; 5th 0.6, 0.5: distance between inner ends, 1st 11.6, 10.7; 5th 6.1, 5.1.

Caudal fin. — Length of base, upper 6.8, 7.6; lower 5.6, 6.7.

Pelvics. — Length of anterior limb 13.1, 14.4; distanee, origin anterior limb to tip of posterior lobe 16.4, 17.1.

Distance. — From tip of snout (from base of filament) to center of cloaca 46.6, 46.0; from center of cloaca to tip of tail 53.4, 54.0.

Disc 1.03 times as broad as long; maximum angle in front of spiracles 88° on the female, 80° on the male; end of snout with a very short slender filament. Anterior margins of disc nearly straight on female but sinuous on male being slightly convex in front of orbits and concave between orbits and outer angles; outer and posterior margins broadly rounded; axis of greatest breadth about 62 per cent of distance back from tip of snout (exclusive of filament) to axils of pectorals, on female, about 70 per cent on male. Tail exceedingly slender, without lateral folds but with a crease low down along each side more or less in evidence from near axils of pelvics to origin of caudal fin, tail mostly roundish in cross section but flattened below posteriorly, its length from center of cloaca 1.15 times distance from center of cloaca to tip of snout on female, 1.17 times on male.

Skin completely naked everywhere, without armature of any sort except for alar thorns on male. Upper surface with mucous pores aside the rostral process and extending rearward along the median zone from nuchal to pelvic region.

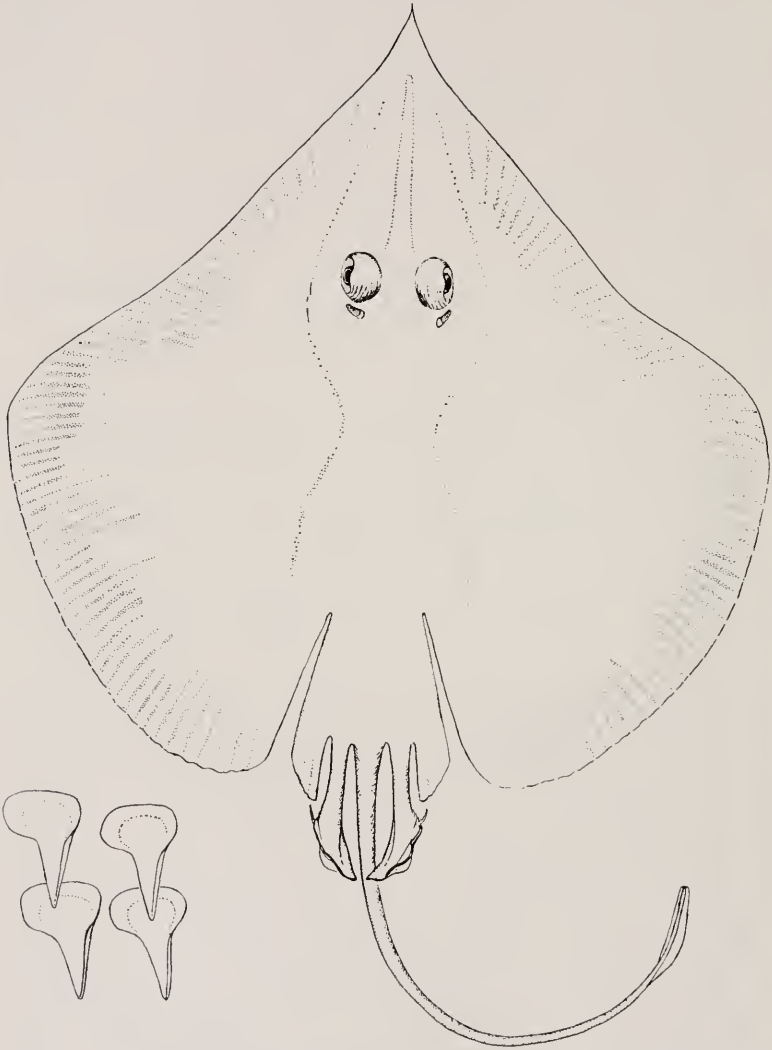

Figure 15. *Anacanthobatis americanus*, dorsal view of mature male 327 mm long, M. C. Z. No. 40364; teeth from upper jaw, about x10.

Snout in front of orbits 8.0 times as long, to base of rostral filament, as distance between orbits on female, 8.7 times on male; its length in front of mouth 6.2 and 5.1 times as great, respectively, as distance between exposed nostrils. Orbits 1.7-1.8 times

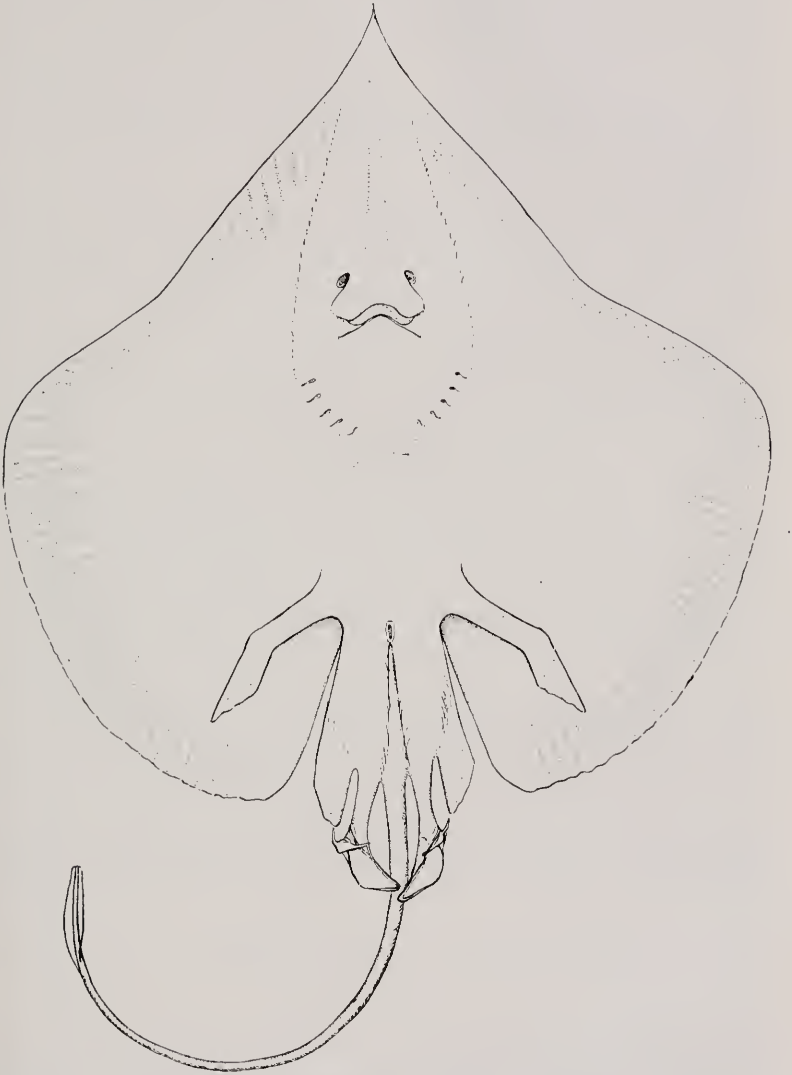

Figure 16. *Anacanthobatis americanus,* ventral view, same specimen as Figure 15.

as long as distance between orbits and 3.3 times as long as spiracles which are noticeably small. Nasal curtain with fine fringe; outer margin of nostrils only slightly expanded, with irregular edge; exposed nostrils very small. Mouth slightly arched on female, strongly so on male, teeth $\frac{25}{24}$ on female, $\frac{24}{21}$ on male, with ovate base, arranged in quincunx at and near center of mouth, in slightly oblique rows toward outer corners of mouth, with a low triangular cusp on female but on the mature male with a sharp slender cusp directed obliquely outward except for a few series near corners of mouth where the cusps are triangular.

Gill openings minute, the first about ⅙-⅒th as long as breadth of mouth, the fifth ¾-⅚ths as long as first; distance between inner ends of first pair about 3.2 times as long as distance between exposed nostrils, between fifth pair 1.7 times, on female, 2.7 and 1.3 times, respectively, on male.

Anterior rays of pectorals extending forward to tip of snout; rostral cartilage firm, very narrow throughout its length, extending nearly to base of terminal filament. A long membranous translucent area on each side of rostrum.

No dorsal fins. Upper caudal fin with base about twice as long as distance between exposed nostrils, of shape shown in Figure 14, its maximum width about ⅒th as great as length of its base; lower caudal somewhat fleshy, about half as wide as upper, its origin a little posterior to origin of upper, the two discontinuous at tip of tail. Pelvics with anterior leglike subdivision slightly shorter than distance from its own origin to rear tip of pelvic, fleshy, broader than thick, inner edge of terminal segment scalloped, corresponding to tips of the three radial cartilages; posterior lobe of pelvics with rounded tip, reaching rearward slightly beyond rear limit of disc; outer margin of pelvics adnate to pectorals for more than half their length on female but entirely free from pectorals on male; inner margin joined about 7⁄10ths its length to side of tail in both sexes. Alar thorns of the male in 4-5 rows, the length of patch of thorns equal to about 60 per cent of the distance from tip of snout to orbits, the width about 25 per cent the length, the 2 anterior thorns on each side somewhat apart from the rest of the patch. The claspers of the male extend beyond the tips of the pelvics by a distance about equal to the internarial space, the tips with 2 sharp hooks exposed (Fig. 16).

Color. Upper surface grayish brown, terminal filament slightly darker. Lower surface pale grayish white in advance of axis through nostrils and around mouth, becoming mottled with dark brown from a little posterior to mouth to scapular arch; remaining disc and pelvics dark brown except for broken white and brown markings along anterior part of limb-like section of pelvics; cloacal opening edged with white. Tail brownish above and below except at and near tip which is conspicuously white with a few brownish mottlings.

Males and females revealed no wide differences in proportional dimensions except as follows. On 3 females 325-349 mm, 2 mature males of 325-327 mm, and 2 immature males of 257-269 mm, in percentages of total length: distance from snout to mouth 22.2-22.8; 19.7-20.5; 18.6-18.6, respectively; axis of disc across anterior margin of orbits 31.0-34.8; 24.6-27.8; 28.2-31.1; length of disc to axils of pectorals 52.3-53.3; 44.3-44.5; 48.4-49.3. The axis of disc at greatest breadth is 55-62 per cent of distance back from tip of snout to axils of pectorals on females and immature males, about 70 per cent on mature males in which the pelvics have separated from the pectorals. Our smallest mature male is 325 mm in total length while the largest male with the pelvics still connected to the pectorals is 266 mm.

Variations. The breadth of the mouth differs considerably between two males of about the same size, being 10.5 mm wide or 4 per cent of total length on a 258 mm specimen and 15.5 mm wide or 5.8 per cent on one of 266 mm in total length. Tooth counts of several males and females, ranged from 21 to 26 series in upper jaw, 20 to 26 in lower jaw, in various combinations, irrespective of sex or age.

The smallest specimen, a new born male 95 mm long with a disc 54 mm wide, is brownish above and below with most all of the tail whitish. The very small tentacle at tip of snout is present.

Thus far known from off the Atlantic coasts of Central and South America between Lats. 16°35' and 07°34'N, in depths of 100-400 fathoms.

ANACANTHOBATIS LONGIROSTRIS sp. nov.

Figures 17, 18

Study material. A female, 507 mm in total length to base of terminal filament, holotype, U. S. Nat. Mus. No. 196446, probably from the northern part of the Gulf of Mexico off the Mississippi Delta, Lat. 29°09'N, Long. 87°53'W, in 500-575 fathoms, "Oregon" station 2823;[1] and a very young male 135 mm long from Santaren Channel, Lat. 23°59'N, Long. 79°43'W, in 350 fathoms, "Combat" station 450.

Distinctive characters. Its extraordinarily long snout sets *longirostris* apart from its closest relatives *A. americanus*, described herein, and also from *A. marmoratus*. The snout length from the base of the small terminal filament to the orbits is 9.3 times the diameter of orbit whereas this distance is 3.9-4.8 times the orbit on *americanus* (5 specimens) and only about 3 times as long on the type of *marmoratus*. The tail of *longirostris*, also, is relatively much shorter being little more than two-fifths the total length of the specimen, measured from center of cloaca, while on the other two species it is at least half the total length.

Description of holotype. Proportional dimensions in per cent of total length.

Disc. — Extreme breadth 56.8; length 66.4.

Snout length. — In front of orbits 29.8; in front of mouth 32.8.

Orbits. — Horizontal diameter 3.2; distance between 3.3.

Spiracles. — Length 1.4; distance between 5.3.

Mouth. — Breadth 4.9.

Exposed nostrils. — Distance between inner ends 4.8.

Gill openings. — Length, 1st 1.1; 3rd 1.1; 5th 0.9; distance between inner ends, 1st 10.1; 5th 7.1.

Caudal fin. — Length of base, upper 3.6; lower 2.0.

Pelvics. — Length of anterior limb 13.6; distance, origin of anterior limb to tip of posterior lobe 14.0.

Distance. — From tip of snout (from base of filament) to center of cloaca 57.4; from center of cloaca to tip of tail 42.6.

Disc 0.86 times as broad as long; maximum angle in front of spiracles 72°; end of snout with a very short slender filament. Anterior margins of disc sinuous; outer and posterior margins broadly rounded; axis of greatest breadth about 65 per cent of distance back from tip of snout (exclusive of filament) to axils of pectorals. Tail exceedingly slender, squarish in cross section (Fig. 18), its four sides very slightly rounded, with a thickened fold beginning beyond tips of pelvics a distance equal to that between the spiracles, low down on each side, continuing to origin of upper caudal fin, the greatest width (posteriorly) of fold about 1 mm or about half the width of tail approaching the

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[1] This specimen lacked a station number or locality data when received but Harvey R. Bullis, Jr. informs us that it probably was taken at "Oregon" station 2823.

caudal fin. Length of tail from center of cloaca 0.74 times distance from center of cloaca to tip of snout.

Skin completely naked everywhere, without armature of any sort. Upper surface with an irregular longitudinal row of 9 or

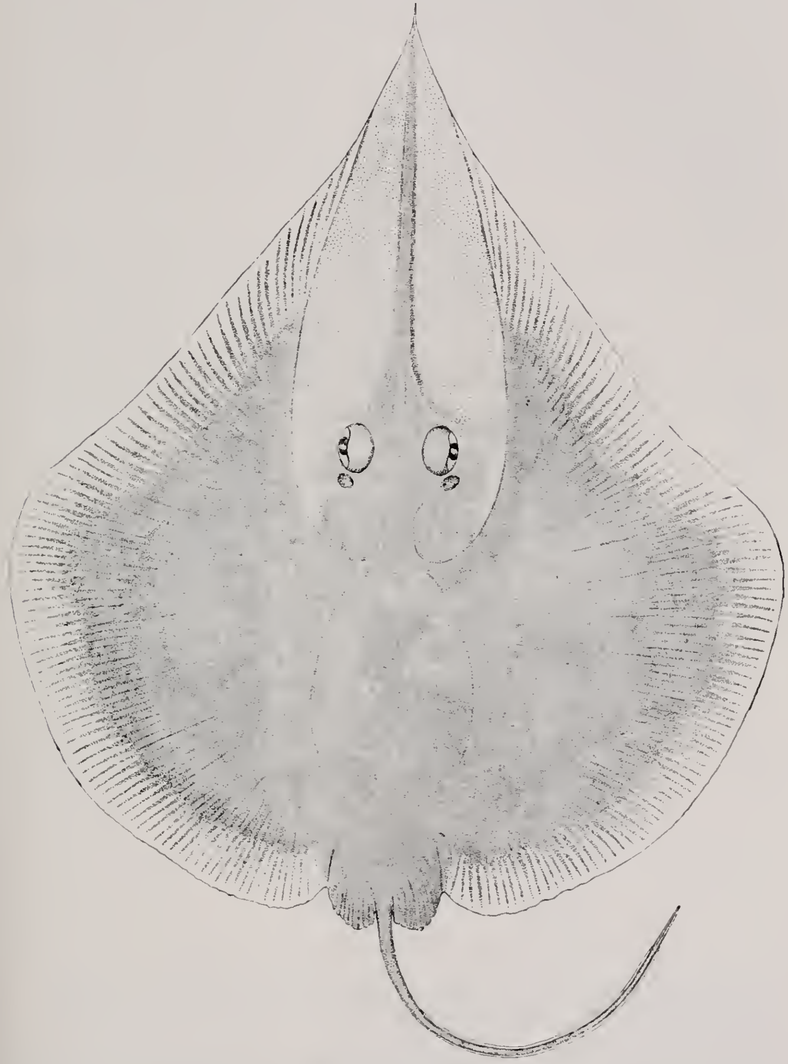

Figure 17. *Anacanthobatis longirostris,* dorsal view of type, female 507 mm long.

10 pale-edged mucous pores extending from nuchal to scapular region, and close to the midline of disc on each side.

Snout in front of orbits 9.0 times as long, to base of rostral filament, as distance between orbits; its length in front of mouth 6.8 times as great as distance between exposed nostrils. Orbits 0.97 times as long as distance between orbits and 2.3 times as long as spiracles which are noticeably small. Nasal curtain with fine fringe; expanded outer margin of nostrils smooth but fringed on anterior margin. Mouth slightly arched. Teeth $\frac{28}{27}$, with ovate base, arranged in quincunx, with a nearly flat crown but a small triangular cusp on posterior edge directed toward throat.

Gill openings very small, the first about $\frac{1}{5}$th as long as breadth of mouth, the fifth about $\frac{4}{5}$ths as long as first; distance between inner ends of first pair 2.1 times as long as distance between exposed nostrils, between the fifth pair 1.5 times.

Pectoral rays prominent, the anterior ones extending forward to near end of snout; rostral cartilage firm, very narrow throughout its length, extending nearly to base of terminal filament. A

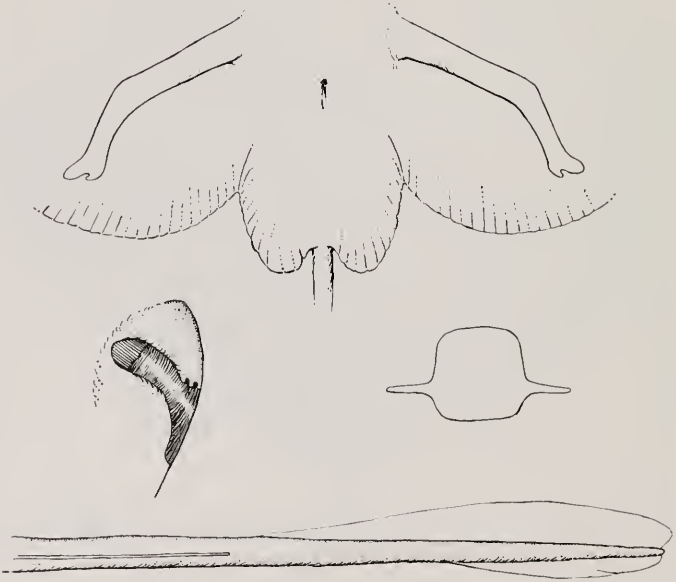

Figure 18. *Anacanthobatis longirostris,* pelvic fins, about x0.5; cross section of tail about x6; nostril, to show knobs on anterior part of flap, about x4; caudal fin, about x3.

large and long membranous translucent area each side of the rostrum.

No dorsal fins. Upper caudal fin with base about ¾ths as long as distance between exposed nostrils, of shape shown in Figure 18, its maximum width about ⅑th as great as length of its base; lower caudal barely discernible, its base about ⅔rds that of upper caudal, its height less than one-half, the two discontinuous at tip of tail. Pelvics with anterior leglike subdivision about equal in length to distance from its own origin to rear tip of pelvic, fleshy, broader than thick, its distal margin notched; posterior lobe of pelvics with rounded tip, reaching rearward slightly beyond rear limit of disc; outer margin of pelvics adnate to pectorals for about ⅔rds their length; inner margin joined about ⅚ths its length to side of tail.

Color above light purplish, the terminal filament black. Lower surface a lighter shade of that above; end of snout dusky. Preservation may have changed its color.

The young male has a relatively shorter snout, narrower disc and longer tail than the much larger type. Thus the distance from tip of snout (less filament) to mouth is 24.1 per cent, width of disc 49.6 per cent and distance from cloaca to tip of tail 54.8 per cent, respectively, in the total length, these proportions being 32.8, 56.8 and 42.6 per cent on the large female. It is usual among the Rajoidea for new born and juveniles to differ considerably in proportional dimensions from half-grown and larger individuals. Particularly is this so in the lengths of snout and tail. The teeth of the male are similar to those of the female, in 28 series in the upper jaw, with flat crown and a small triangular cusp pointing inward. In color the male is pale brown above and below, including the terminal filament.

Known only from the localities and depths given in the study material.

Suborder MYLIOBATOIDEA

Family DASYATIDAE

Dasyatis geijskesi Boeseman 1948

This species has been known in literature from only a single specimen, an immature male 1060 mm in total length, with a disc about 340 mm wide, taken off the coast of Surinam. However, it appears to be not rare in this region for, according to Dr. D. C. Geijskes who collected the holotype, it is known locally by the vernacular name of "sesée spari" (Boeseman 1948, p. 42). Two specimens are included in our collection, a male and a female, both with the tail complete.

Study material. Immature male 1000 mm in total length with a disc 235 mm wide, and a female 890 mm long, disc width 227 mm, M. C. Z. No. 40425, from the offing of Ilha de Maracá, Brazil, Lat. 02°34'N, Long. 49°18'W, in 10 fathoms, "Oregon" station 2055.

Distinctive characters. This species differs noticeably from all other known dasyatid rays of the Atlantic in shape of disc with narrowly projecting snout, and in pelvic fins with long anterior margins and narrowly pointed and somewhat falcate outer corners.

Description. Proportional dimensions in per cent of disc width of a male and a female 235 mm and 227 mm wide, respectively.

Disc. — Vertical length 107, 105; width across anterior edge of orbits 90.3, 91.4.

Snout length. — In front of orbits 42.5, 40.0; in front of mouth 43.5, 41.8.

Orbits. — Horizontal diameter 3.6, 3.5; distance between 11.5, 11.5.

Visible eye. — Horizontal diameter 2.1, 2.6.

Spiracles. — Length 5.1, 5.7.

Mouth. — Breadth 9.0, 8.6.

Exposed nostrils. — Distance between inner ends 12.8, 11.7.

Gill openings. — Length 1st 2.8, 2.4; 3rd 2.8, 2.4; 5th 2.1, 1.8; distance between inner ends 1st 16.8, 17.0; 5th 12.8, 13.2.

Distance. — From tip of snout to center of cloaca 92.5, 92.7; from center of cloaca to origin of tail spine 42.5, 43.5.

Disc 0.89-0.95 times as broad as long; anterior margins deeply concave, the snout projecting conspicuously, slightly blunted at tip; outer margin broadly rounded, outer posterior margins moderately and evenly convex, but posterior corners well rounded; inner margins weakly convex and somewhat excavate at axils. Axis of greatest breadth about 57-58 per cent of distance rearward from tip of snout to axils of pectorals and 50 per cent to rear limit of disc.

Tail from center of cloaca about 3.6 times as long as distance from center of cloaca to tip of snout on the male, 3.3 times on the female, slender, whip-like, flattened dorsoventrally in advance of tail spine but rounded posteriorly; a very narrow and short cutaneous fold below beginning opposite origin of tail spine, its length about twice the distance between the 5th pair of gill openings; no fold above. One tail spine, its length about equal to the distance between the orbits, its origin from center of cloaca about equal to the distance from tip of snout to mouth.

Disc above, on the male, with a mid dow of 5 flattened thorns from nuchal to scapular region, the 3 rear thorns the largest, followed by about 16 tiny thorns ending in advance of axils of pectorals, between which and the tips of pelvics there are 4 unevenly spaced flattened thorns and another large one between pelvics and tail spine; pelvics and rest of disc smooth. Upper surface of tail encrusted with prickles throughout its length, with prickles sparsely distributed along sides and below on anterior half. Lower surface of disc smooth. The disc and tail of our female lack armature but it is apparent that, on the disc at least, thorns will appear on older individuals.

Snout in front of orbits about 11 times as long as orbit or 3.5-3.7 times as long as distance between orbits, its length in front of mouth 3.4-3.6 times as great as distance between exposed nostrils and 2.5-2.6 times as great as that between inner ends of first gill openings. Distance between orbits 3.2 times as great as length of orbit. Orbit about ⅔ as long as spiracle. Nasal curtain with posterior margin somewhat arched forward on the male, nearly straight on the female, its free edge finely fringed, with a small median notch. Jaws moderately arched, nearly straight on central sector.

Teeth $\frac{47}{58}$ on male, $\frac{52}{56}$ on female, oval or rhomboid, in quincunx, with a flat roughened crown.

Distance between inner ends of first gill openings 1.3-1.4 times as long as distance between exposed nostrils; between fifth gill openings about 0.8 times as long as that between first pair.

Pelvic fins with a straight anterior margin which is about 1.7 times as long as distance from origin of pelvic to its rear limit, this proportionately the longest yet reported for any dasyatid.

Color. Plain brown above on disc, pelvics, and anterior half of tail, the posterior part of which is faintly colored. Disc below whitish, the anterior margins narrowly edged with grayish, the posterior margins with a wider band of gray; rear margins of pelvics vaguely gray; tail faintly mottled on anterior half, white posteriorly.

Known from off the coast of Surinam and off Brazil at Lat. 02°34′N, Long. 49°18′W, in a depth of about 10 fathoms.

DASYATIS VIOLACEA (Bonaparte) 1832

Figure 19

During the course of exploratory long-line fishing, the U. S. Fish and Wildlife vessel 'Delaware'' took a large specimen of this little known pelagic stingray south southeast of Nantucket Island; Lat. 38°35'N, Long. 68°14'W, on a hook fished somewhere between 25 and 50 fathoms, over a total depth of about 2200 fathoms. We wish to express our gratitude to Ernest D. McRae, Jr., Field Party Chief on the ''Delaware'' and to Frank J. Mather III of the Woods Hole Oceanographic Institution for preserving the specimen for us. A second specimen, also, was taken by the ''Delaware'' in the offing of Chesapeake Bay, Lat. 36°46'N, Long. 70°00'W, about 300 miles out from the coast. Unfortunately this specimen was lost overboard.

Study material. Female 1635 mm in total length with a disc 800 mm wide and 603 mm long, from the offing of Nantucket Island, Lat. 38°35'N, Long. 68°14'W, M. C. Z. No. 40233; a Mediterranean specimen (male) from the collection of C. L. Bonaparte, 175 mm wide and 164 mm long to origin of spine (remainder of tail missing), Acad. Nat. Sci., Phila., No. 385, evidently newly born; an embryo 157 mm wide from the Pacific Ocean; and a female 556 mm wide from the east-equatorial Pacific, M. C. Z. No. 39977.

Distinctive characters. D. violacea is set sharply apart from all other known members of the family Dasyatidae in that the entire lower surface as well as its upper is of a very dark purplish violet or chocolate plum color. In shape of disc it most nearly resembles *Himantura schmardae* (Werner) 1904 among western Atlantic species, but differs conspicuously from *schmardae* in the relative distance from cloaca to base of tail spine, this being 30-35 per cent of width of disc in our Atlantic and Mediterranean specimens of *violacea* as against 78-80 per cent in the two specimens of *schmardae* that we have measured (Bigelow and Schroeder 1953, p. 390).

Proportional dimensions in per cent of width of disc of the above three specimens with disc widths of 800 mm, 175 mm, and 556 mm, respectively.

Disc. — Vertical length 75.5, 69.7, 77.7.

Snout length. — In front of orbits 8.3, 11.1, 11.2; in front of mouth 14.0, 14.3, 14.4.

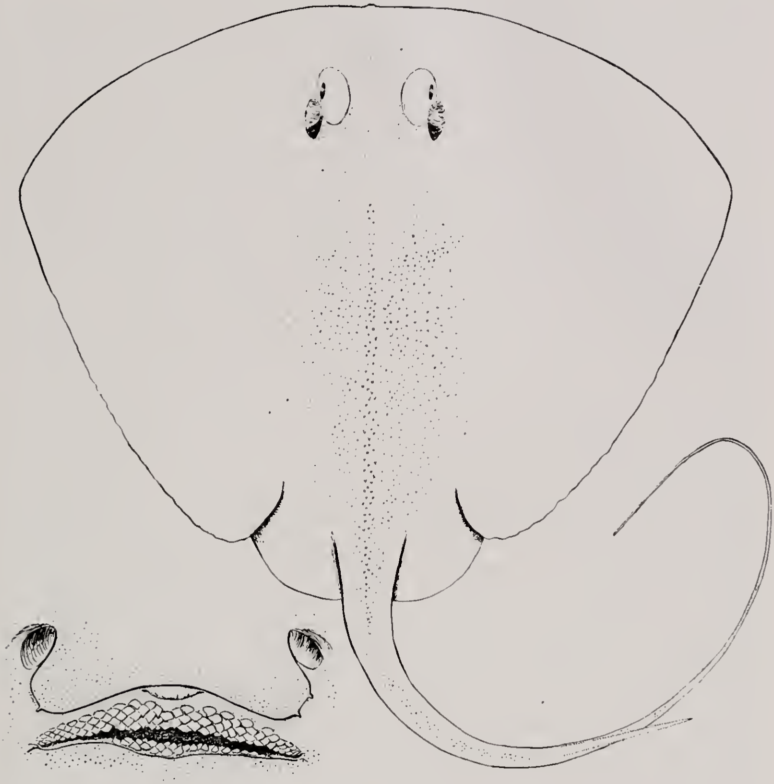

Figure 19. *Dasyatis violacea*, female 800 mm in disc width, from offing of Nantucket, Massachusetts, M. C. Z. No. 40233; jaws, nostrils and nasal curtain of same, about x0.5.

Orbits. — Horizontal diameter 6.7, 9.4, 5.1; distance between 7.5, 9.2, 8.7.

Visible eye. — Horizontal diameter 2.5, 3.6, 3.4.

Spiracles — Length 5.0, 5.7, 6.0; distance between 15.6, 18.3, 17.3.

Mouth. — Breadth 10.2, 9.2, 10.4.

Exposed nostrils. — Distance between inner ends 8.4, 9.2, 9.5.

Gill openings. — Length 1st 3.2, 2.5, 3.1; 3rd 3.3, 2.5, 3.2; 5th 1.9, 2.0, 2.0; distance between inner ends 1st 16.0, 19.4, 19.8; 5th 13.4, 12.6, 13.7.

Distance. — From tip of snout to center of cloaca 70.0, 62.7, 73.8; from center of cloaca to origin of tail spine 35.1, 35.0, 29.7.

Description of western Atlantic specimen. Disc 1.33 times as broad as long; anterior margin in the form of a broad arc, with a very small projection at its center; outer corners abruptly rounded; posterior margins nearly straight anteriorly but becoming weakly convex posteriorly; posterior corners abruptly rounded; inner margins weakly convex. Axis of greatest breadth 48 per cent of distance rearward from tip of snout to axils of pectorals and 42 per cent to rear limit of disc. Thickest part of body, at scapular region, 19 per cent of width of disc.

Tail from center of cloaca about twice as long as distance from center of cloaca to tip of snout, robust at origin where its width is about equal to width of mouth, narrowing rapidly approaching origin of spine where it is only about one-fourth as wide and at tip of spine one-tenth as wide, thence becoming progressively narrower, exceedingly so approaching tip, nearly circular in cross section throughout its length except flattened above under spine; a short, low, cutaneous fold below, beginning a little posterior to origin of spine and extending to a little beyond its tip, or a distance about equal to that from tip of snout to first gill openings. One tail spine, length of exposed part slightly greater than distance between first gill openings; distance from origin of spine to center of cloaca half the distance from center of cloaca to tip of snout.

Disc above with an area of very small, erect, sharp spines, with stellate base beginning a little in front of and between orbits, scattered on interorbital, becoming progressively more sparse toward scapular region where they are somewhat larger, more irregularly spaced and cover a broader band, present over most of back above abdominal region and extending on to tail. Tail with small, sharp, close set prickles along most of its length; also a very narrow median band of slightly larger spines, some of them bluntish, in haphazard arrangement, extends from the scapular region on to tail, more or less losing their identity, approaching origin of spine. Tail spine 153 mm long, 10 mm wide at base, lateral teeth about 100 on each side. Pectorals and pelvics smooth. Lower surface smooth.

Snout in front of orbits 1.2 times as long as orbit, its length in front of mouth 1.7 times as great as distance between exposed nostrils. Distance between orbits 1.1 times as great as length of orbit. Orbit 1.3 times as long as spiracle. Nasal curtain not reaching upper tooth band, its free posterior margin smooth edged, and arcuate, following contour of upper jaw, without a median notch. Nostrils separated by a septum which at narrowest part is about ¼ the width of mouth. Roof of mouth with a cutaneous curtain with about 13 notches or fringes on each side of its midline; floor of mouth with a transverse row of about 10 fleshy papillae. Upper and lower jaws nearly straight.

Teeth $\frac{34}{38}$, arranged in quincunx, with ovate base, most of them with a single short bluntish cusp, probably worn, for some teeth have a sharp cusp, some of the cusps slanting toward corners of mouth; teeth in center of upper jaw somewhat smaller than those on outer sectors, those in center of lower jaw notably larger than on outer sectors.

Distance between inner ends of first gill openings 1.9 times as long as distance between exposed nostrils; between fifth gill openings 0.8 times as long as that between first pair.

Pelvics sub-quadrangular, but with broadly rounded corners, extending well beyond posterior margin of disc.

Color. Chocolate plum, somewhat paler below than above, without markings of any sort.

Remarks. Bonaparte's (1832) specimens are described as being violet purple below as well as above, when freshly taken, but the one we have seen (see Study material), after long preservation, is pale reddish brown both above and below. Also, its nasal curtain is fringed and has a median notch, as is usual among the Myliobatoidea (except the Mobulidae) but there are exceptions within a species where some individuals may have the nasal curtain smooth edged and without a median notch, for example the Butterfly Ray *Gymnura altavela* (see Bigelow and Schroeder 1953, fig. 95B and p. 403). The newborn Mediterranean ray[1] has only $\frac{15}{17}$ teeth, of various sizes, pavement-like, without cusps, while a full term embryo with a disc width of 157 mm, from the Pacific Ocean,[2] has a tooth count of $\frac{16}{18}$. It is to be noted that among most species of rays there is a wide disparity in the number of teeth as between very young and old individuals.

In 1955 Ishiyama and Okada[3] described, from Japanese waters and from the Marianas Islands east of the Philippines, a pelagic stingray which they named *Dasyatis atratus*, closely resembling *violacea* of the Atlantic. Thanks to the kindness of Dr. C. L.

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[1] We thank Dr. James E. Böhlke for the loan of this specimen.

[2] Dr. C. L. Hubbs presented this specimen to the M. C. Z. collection.

[3] Jour. Shimonoseki Coll. Fisher, *4* (2), p. 211.

Hubbs, we have received an excellent specimen that was taken in the equatorial Pacific eastward from the Marquesas Islands, 5°5′N, 110°28′W, that is clearly identical with *atratus*. The proportional dimensions of this specimen (p. 230) agree closely throughout with the ranges covered by our Mediterranean and Atlantic specimens, as does the shape of its disc and of its pelvics. In short, we see no basis for separating *atratus* from *violacea*.

Habits. This ray is pelagic in habit and both of the western Atlantic specimens were hooked about 25-50 fathoms below the surface, over very deep water. No information in this respect is available for the several specimens that have been taken in the Mediterranean at one time or another.[1]

The stomach of the Atlantic specimen pictured here (Fig. 19) contained 1 small sea horse (*Hippocampus*), 2 small shrimps, fragments of 2 small squids, the herring (*Clupea harengus*) with which the hook was baited, and a small amount of unidentifiable material.

Size. The largest specimen yet recorded (see Study material) is 800 mm broad and 1635 mm long to tip of tail.

Range. In the Atlantic (including tributary seas) *violacea* is known only from the Mediterranean and from the western Atlantic between latitudes 36°46′ and 38°35′N, over deep water, well out from the coast. In the Pacific it has been reported in print only from Japanese waters and from the Marianas Islands to the east of the Philippines, but Dr. C. L. Hubbs has informed us (letter of June 13, 1959) that the collection of the Scripps Institution of Oceanography contains specimens of *violacea* from the Pacific, northwest of the Galapagos, off Lower California, north and south of Hawaii, off the Marshall Islands, and off Japan, all taken on long-lines near the surface where the total depth was about 2000 fathoms, except for one found in the stomach of a shark.

It seems probable too that *Dasyatis purpurea* (Müller and Henle 1841) recently reported from southern Africa by Smith (1949, p. 71), like *atratus* Ishiyama and Okada, is a synonym of *violacea*. If this identification be correct *violacea* can justly be characterized as cosmopolitan in all the great oceans in temperate and tropical latitudes for which it doubtless has its pelagic habit to thank.

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[1] For a list of these, see Tortonese, 1956 : 273.

Family UROLOPHIDAE

UROTRYGON MICROPTHALMUM Delsman 1941

Figures 20-23

Thanks to the material listed below, we now are able to give a more detailed description of this species than we could in Fishes of the Western North Atlantic. Part 2 (Bigelow and Schroeder 1953, p. 428) when we had no specimens at hand.

Study material. Eleven specimens from off the mouth of the Amazon River, vicinity of Lat. 02°N, Long. 49°W, "Oregon" stations 2055, 2057, and 4 specimens from off the east coast of Venezuela, Lat. 09°39′N, Long. 60°49′, and vicinity, stations 2210, 2211, and 2215, males and females, 117-234 mm in total length, from depths of 9-15 fathoms.

Distinctive characters. The only known western Atlantic rays with which *Urotrygon micropthalmum* might be confused are *Urotrygon venezuelae* Schultz 1949 and *Urolophus jamaicensis* (Cuvier) 1817. A relatively smaller orbit (diameter about ⅕ of interorbital width) and a nearly smooth disc set *micropthalmum* apart from *venezuelae* in which the orbit diameter is about ⅖ the interorbital width and the disc and tail are roughened with small prickles, and by an irregular row of blunt somewhat larger prickles from nuchal region to tail spine. It differs from *Urolophus jamaicensis* in that the tip of its snout is pointed, its orbits are much smaller (they are about equal to the interorbital in *jamaicensis*), its caudal fin is narrower relatively, and its tail from center of cloaca to tip is longer than the distance from center of cloaca to tip of snout (shorter than distance from cloaca to snout in *jamaicensis*).

Description. Proportional dimensions in per cent of total length. Male 221 mm long and female of 234 mm from off the mouth of the Amazon River, M. C. Z. No. 40237.

Disc. — Extreme breadth 46.6, 46.7; length 50.0, 46.2.

Snout length. — In front of orbits 17.2, 14.1; in front of mouth 15.8, 14.1.

Orbits. — Horizontal diameter 1.3, 1.2; distance between 7.0, 6.0.

Spiracles. — Length 2.2, 1.9; distance between 7.7, 6.8.

Mouth. — Breadth 5.9, 5.4.

Exposed nostrils. — Distance between inner ends 6.8, 4.7.

Gill openings. — Length 1st 0.9, 1.1; 3rd 1.2, 1.1; 5th 0.8, 0.9; distance between inner ends 1st 12.2, 11.6; 5th 7.2, 6.9.

Pelvics. — Length of outer margin 9.7, 8.1; rear margin 8.1, 11.5.

Distance. — From tip of snout to center of cloaca, 44.8, 44.1; from center of cloaca to origin of tail spine 21.7, 23.9; to tip of tail 55.2, 55.9.

Disc 0.93-1.01 times as broad as long (0.98-1.06 on 4 other specimens); margins of disc rounded, the inner margin being very short. Some of our specimens have a nearly circular disc while on others the disc is slightly convex anteriorly and strongly so posteriorly. The anterior margin on Delsman's (1941, fig. 8)

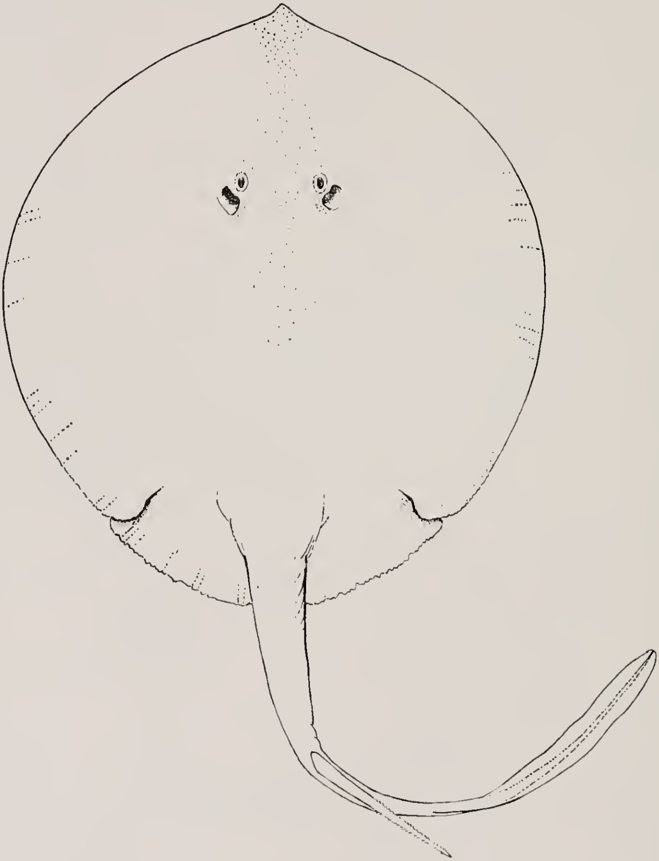

Figure 20. *Urotrygon micropthalmum,* dorsal view of female 234 mm long, M. C. Z. No. 40237.

illustration is angular but in his description he states "margins of disc circular." Axis of greatest breadth about 50 per cent of distance back from tip of snout to rear limits of disc. A lateral ridge extends from opposite axils of pelvics to about opposite origin of tail spine. Tail strongly depressed dorso-ventrally from origin (where its width about equals interorbital space) to origin of spine, posterior to which it becomes much more slender and laterally compressed, ending in a point; its length from center of cloaca 1.23-1.27 times distance from tip of snout to center of cloaca.

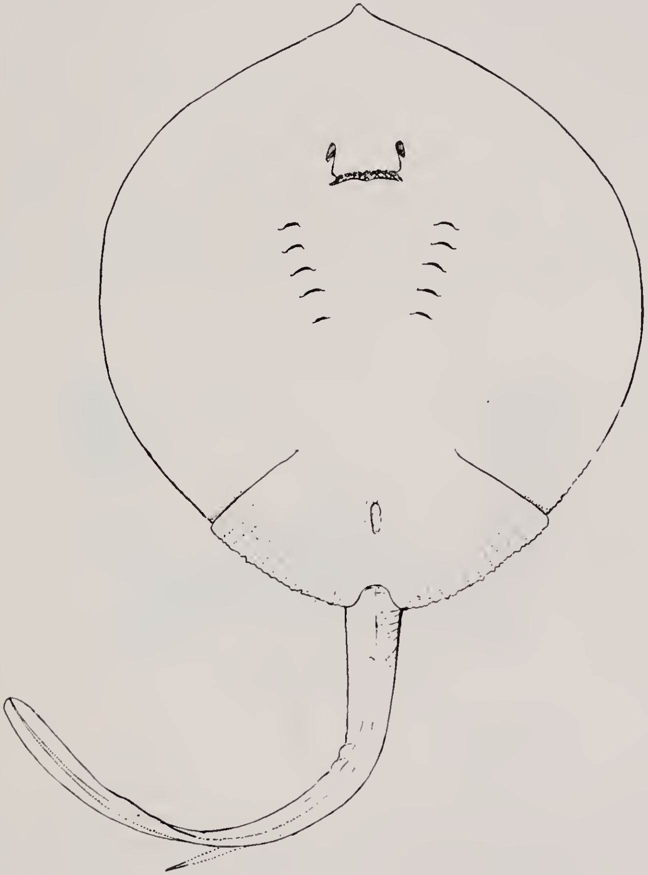

Figure 21. *Urotrygon micropthalmum*, ventral view of specimen shown in Fig. 20.

Upper surface of male smooth except for a few minute prickles on tip of snout, 1-2 rows along inner margin of spiracles and an occasional prickle elsewhere on disc and tail; female with a patch of minute prickles from tip of snout, where densest, to scapular region, including area close in advance of orbits, those along margin of spiracles more numerous than on male; a few prickles scattered elsewhere on disc and on tail nearly to its extremity. Small females have few or no prickles. Lower surface smooth on male but the female has a few prickles on extreme tip of snout and a single row along edge of disc in advance of nostrils.

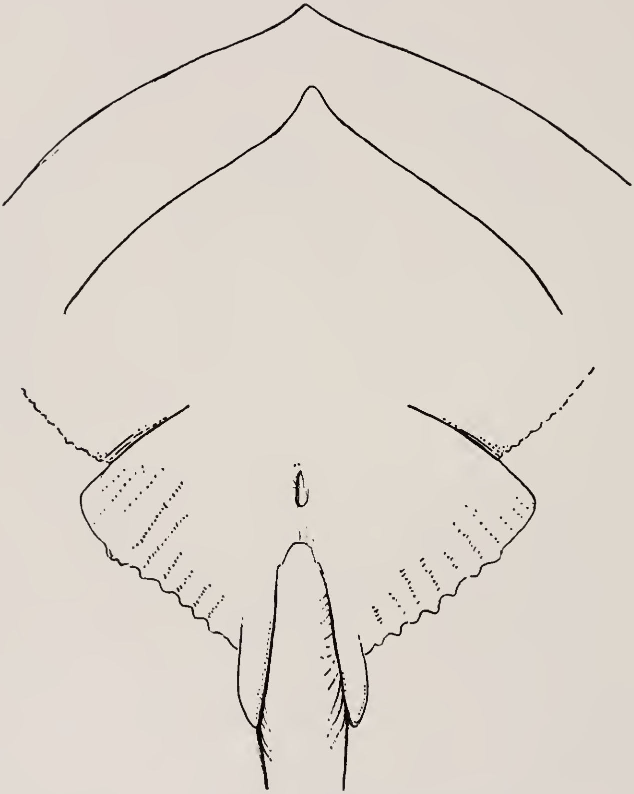

Figure 22. *Urotrygon micropthalmum,* anterior contour of disc to show variation in tip and in width of snout of two males, each about 200 mm long, about x0.6; pelvic fins of a male 206 mm long, about x0.9.

One tail spine, the distance of its origin from center of cloaca about equal to distance from snout to first pair of gill openings, its length a little greater than distance from snout to mouth; very narrow, with a sharp point.

Snout in front of orbits 11.8-13.5 times as long as orbit, its length in front of mouth 2.3-3.0 times as great as distance between exposed nostrils, its tip slightly produced in a sharp point (see Fig. 22 for variations). Distance between orbits 5.0-5.5 times as great as length of orbit. Orbit 0.6 times as long as spiracle which is immediately aside and behind and notably larger. Nasal curtain fringed; outer fold of opening of nostril deep-set, with somewhat rough edge. Jaws slightly bowed, the lower with a shallow median indentation, the upper curved to correspond to the lower. Teeth with oval base, arranged more or less in quincunx, those of male in $\frac{31}{30}$ series, with a canine-like cusp directed inward, those of female in $\frac{36}{34}$ series, with a low triangular cusp. The teeth of a very young male, only 117 mm long, already have rather prominent cusps, triangular in shape. The cusps on a female of 170 mm are barely discernible while one mature female of 232 mm has teeth with a very low, broad cusp.

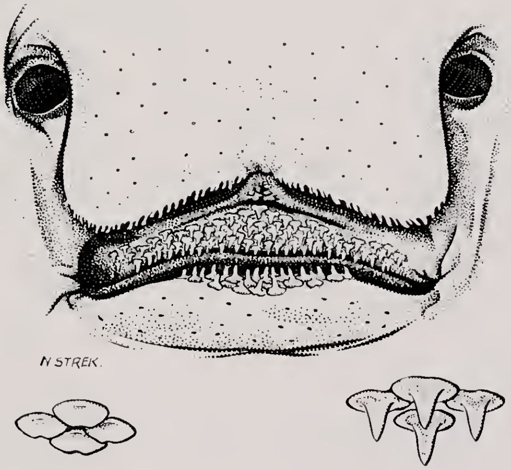

Figure 23. *Urotrygon micropthalmum*, nostrils, nasal curtain and mouth of a male 222 mm long, about x3.5; lower right, teeth from upper jaw about x14; lower left, teeth from upper jaw of female 234 mm long, about x14. Drawing by N. W. Strekalovsky.

Distance between first gill openings, 1.8 times as great as space between exposed nostrils in male, 2.4 times in female whose internarial space is notably shorter; distance between fifth gill openings 1.1 and 1.4 times; first and fifth gill openings on male and fifth on female slightly shorter than the others, the longest a little shorter than diameter of orbits. On two other males, 199-206 mm long the distance between first gill openings is 1.6-1.7 times as great as between exposed nostrils, while on three females, 169-238 mm, it is 1.9-2.0 times as great. Caudal fin originates as an upper and lower fleshy fold; its dorsal origin under rear part of tail spine just beyond which it widens and is supported by rays to extremity of tail; its ventral origin a little in advance of origin of dorsal fold, its first rays appearing about midway between its origin and tip of tail; upper and lower fins of about same width, the maximum about equal to width of fifth gill opening, the fins extending to extreme tip of tail, but not confluent there (barely confluent on 1 of our 15 specimens). Pelvics of male squarish, the rear margin 8.1 per cent of total length of specimen, extending beyond disc by a distance equal to about half that between the spiracles; pelvics of female wing-shaped, with straight to slightly convex anterior and convex posterior margins, the latter 11.5 per cent of total length, extending beyond disc a distance about equal to that between the spiracles (Fig. 20); rear margins faintly scalloped in both sexes. Apparently the shape and width of the posterior margin of the female pelvics undergo a change with age for those on a newborn specimen 85 mm in total length, and on one of 161 mm, closely resemble the squarish form of males of all sizes, but we have one female of 197 mm, containing a full term embryo, with pelvics intermediate in shape between that of the male and the female shown in Figures 21, 22.

Color. Plain grayish brown or chocolate brown above on disc, pelvics and tail. Lower surface marked with a wide irregular band of grayish along outer parts of disc and pelvics, with one or more blotches in between, otherwise pale. Caudal dark brown above and below.

Size. Our longest specimen, a female of 234 mm, has a disc 109 mm broad, the longest male, 221 mm, a disc 103 mm broad, immature to judge from the development of its claspers. The type specimen, a juvenile male, is 220 mm in total length, according to Delsman (1941, p. 66).[1]

Remarks. A specimen 232 mm long contains a full term embryo which was protruding from the cloaca head first, with tail bent forward over the back so that its tip reached the snout. Its pectorals are tightly folded under the body and the total length of the "capsule," in situ, is 42 mm, its width 17 mm. If stretched out, the embryo would be about 85 mm in total length. Its coloration above and below is essentially the same as that of the adult. Two other specimens, 187 and 197 mm long, respectively, each had an embryo with nearly all of the tail protruding; evidently these would have been born tail first.

Known from off the mouth of the Amazon River and the east coast of Venezuela, from depths of 9-30 fathoms, in localities given under Study Material. The type locality, off the Amazon, is Lat. 1°06'N, Long. 47°53'W.

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[1] Erroneously described by Bigelow and Schroeder 1953, p. 429, as 220 mm broad.

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Plate I. *Diplobatis pictus.* Photograph of a freckeled and a non-freckled color variety.

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 128, No. 5

BIRDS OF TIKAL, GUATEMALA

By

Frank B. Smithe and Raymond A. Paynter, Jr.

With One Plate

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
January 14, 1963

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No. 5 — *Birds of Tikal, Guatemala*

By

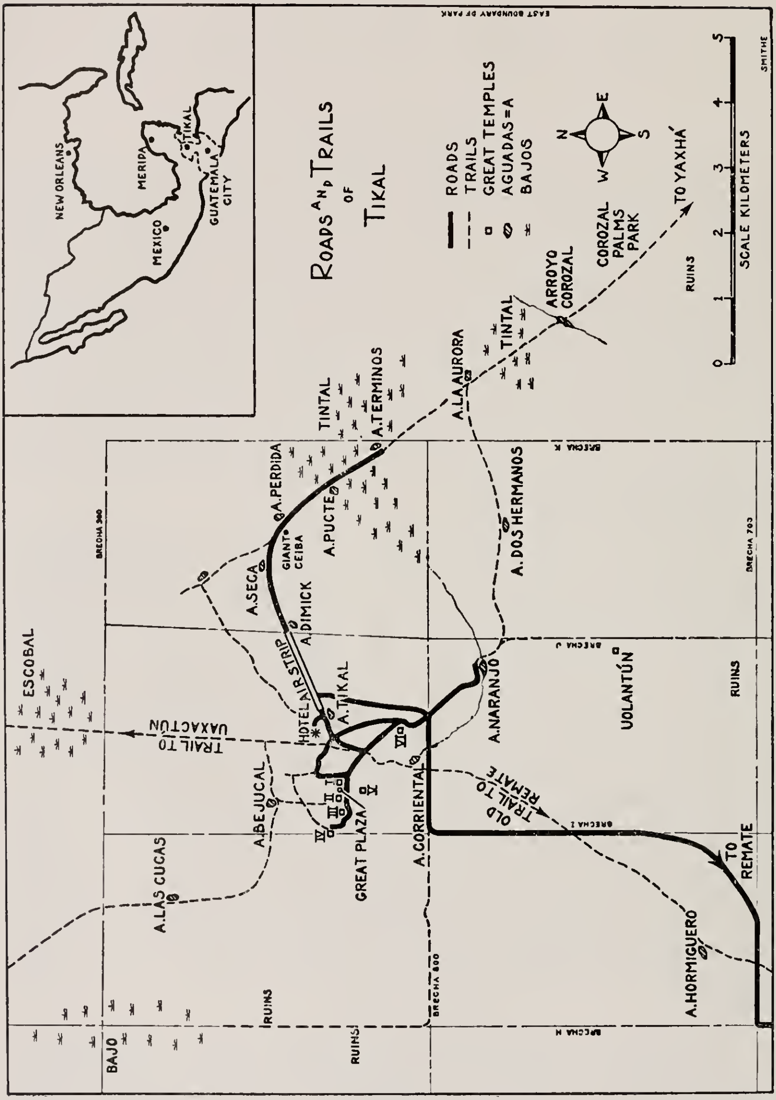
Frank B. Smithe and Raymond A. Paynter, Jr.

INTRODUCTION

At the base of the Yucatán Peninsula, in the Department of Petén, Guatemala, is Tikal, the largest of the ancient Maya centers. Tikal seems to have been populated first about 1,500 B.C. and to have reached its pre-eminence during the Maya Classic Period (200-900 A.D.) when it may have served as many as 100,000 people and was, for that time, one of the most densely inhabited places on earth. Then, suddenly it was abandoned and lay undisturbed for a millennium. The remains of this great city, occupying 16 square kilometers, are now covered for the most part by dense vegetation. Its massive buildings, some over 60 meters high, are barely distinguishable from the surrounding uninhabited lowland forest.

In 1956 The University Museum of the University of Pennsylvania began a ten-year project to study the archaeology of Tikal and to preserve many of its buildings. The Government of Guatemala designated the site, and 576 square kilometers around it, a National Park, the first such park in Central America. Both agencies have encouraged biological research, recognizing that a thorough knowledge of the environment may be of use in understanding why a great Maya center should have arisen at Tikal (physiographically a rather inhospitable locality), how it could have reached such vast proportions and why, after about 2,000 years of occupancy, it was abruptly deserted. Also, it is appropriate that the fauna and flora should be surveyed while the new park is still relatively undisturbed by modern man. This report is, therefore, a contribution to the natural history of the area and possibly a small step toward an eventual understanding of some of the intriguing riddles left by the ancient Maya.

The study is roughly limited to the birds which occur within a five-kilometer radius of Aguada Tikal (Map). Although a restricted area, it may be considered as representative of most of the northern Petén — a forested region with few physiographic discontinuities. Discrepancies between the avifauna of Tikal and that found at the nearby village of Uaxactun (Van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Tyne, 1935), and thirty kilometers to the south at Lake Petén Itzá (Taibel, 1955), will be considered.

Field work at Tikal was begun by Smithe in 1956, during a visit extending from 28 March to 4 April. In 1957 he remained from 8 March to 9 April, and was accompanied by Paynter for half that time. The following year field studies were conducted from 5 February to 12 March; Jorge Ibarra worked with Smithe during most of February and returned to Tikal for ten days in late November and December. In 1959 Smithe remained at Tikal from 22 April to 14 August. Paynter paid a five-day visit in late March, 1960. José Maria Marquéz, an employee of the archaeological project and a resident of Tikal, assisted Smithe in 1957 and 1959, and collected for him sporadically at other times. Unfortunately, few observations were made in the autumn and early winter. This probably has resulted in a failure to record several transient species, but they are of little significance in this study.

Approximately twelve hundred specimens were made into skins or skeletons or are preserved in alcohol. All are deposited in the Museum of Comparative Zoology.

All weights are of adult birds, unless indicated differently, and the means are accompanied by their standard errors (σ_m). The wings were measured flattened, and the bills from the base of the culmen.

ACKNOWLEDGEMENTS

We are grateful for the whole-hearted cooperation of the Government of Guatemala; we owe especial thanks to Jorge Ibarra, Director of the Museo Nacional de Historia Natural, whose enthusiasm and interest were with us throughout the study. Carlos Castaneda and Cloyd Smith of Guatemala City have been very helpful in matters pertaining to transportation and supplies.

Of course, it was at the invitation of The University Museum that we made this survey. We have been in constant debt to their "Proyecto Tikal" field party for facilities and assistance and are particularly obligated to Edwin M. Shook, Aubrey S. Trik, William R. Coe, and Robert F. Carr.

The senior author has been assisted frequently by Dean Amadon and Charles O'Brien of the American Museum of Natural History.

PHYSIOGRAPHY

What is known as the physical geography of the northern Petén has been well described by Wadell (1938). The characteristics of the Tikal region were considered by Stuart (1958). In brief, the region is one of low rolling hills, typical of mature Karst topography, and similar to most of the southern portion of the Yucatán Peninsula. The limestone is, however, of Oligocene age (Sapper, 1937) and therefore more mature and worn than that found farther north on the Peninsula. There are, for example, no *cenotes* (deep sinkholes) which are a characteristic feature of young Karst areas such as Yucatán. None of the hills is high. The altitude of the park ranges only from about 200 to 300 meters above sea level. The calcareous soil is thin and the bedrock is frequently exposed.

There are no permanent surface streams, but numerous depressions are filled in the rainy season and retain water during the early part of the dry season. The small basins are known locally as *aguadas.* Larger low-lying areas, called *bajos,* some covering several square kilometers, also become flooded in the wet months. They shrink considerably in the winter but may hold some water from one year to the next. The ancient Maya constructed reservoirs to catch the runoff from great plazas, causeways, and buildings. At the archaeologists' camp there is one of these, covering an acre or so, which has been excavated and repaired, creating a permanent pond. Aguada Tikal, as it is known, has proved to be highly attractive to birds and is undoubtedly responsible for the presence of some species which otherwise would be absent from the park. Underground streams or pools, which are often found in Karst regions, have not been discovered in spite of drilling several wells as deep as 150 meters.

CLIMATE

The climate of the Petén is tropical and relatively dry, although it is wetter than most of the Yucatán Peninsula. The annual rainfall varies considerably from year to year. For example, at El Paso Caballo, about 50 kilometers west of Tikal, a nine-year record shows an annual range from 990 to 2369 mm. (Lundell, 1937). As expected, the same variability seems true at Tikal, although as yet there are few data from here. Through the courtesy of Edwin M. Shook (*in litt.*), we have available the weather records obtained at Tikal from 1 June 1959 to 30

November 1960. For the year June 1959 through May 1960 the total precipitation was 1267 mm., but when the year is calculated from December 1959 through November 1960, thus including the 1960 rainy season, the total rises to 1623 mm.

There is a dry period from November or December through April, during which there is usually considerably less than 100 mm. of precipitation per month. Much of this occurs as heavy fog at night. The rains usually begin in May, reaching peaks in June or July and in September or October.

The mean temperature varies little throughout the year. At El Paso Caballo the averages for ten years showed January to be the coldest month with a mean of 23.9° C., and April and May to be the warmest months with a mean of 30° C. (Page, 1938). At Tikal similar ranges and patterns seem to prevail (Shook, *in litt.*).

VEGETATION

Except where disturbed by man, all of the National Park is thickly covered by semideciduous forest which attains a maximum height of 50 meters. According to Holdridge's broad classification (1956; 1957), this is a "Tropical Dry Forest"—the type of climax forest which occurs in tropical lowland where the annual rainfall is between 1,000 and 2,000 mm. and where there is a prolonged dry season. Lundell (1937) would define this as "quasi-rainforest" which, to the layman, is probably a more meaningful term than "Tropical Dry Forest."

Two main types of forest, viz "high forest" and "low forest," are readily distinguishable and are of significance in the distribution of the avifauna. The high forest is located in the better drained areas. Here the trees are sometimes as tall as 50 meters, there are numerous lianas, the forest floor is dark, and the vegetation of the understory is relatively thin. There are local differences in the composition of the high forest; in some sections there is a preponderance of *zapote* (*Achras zapota*), in other areas mahogany (*Swietenia* sp.), *ramon* (*Brosimum alicastrum*), or Spanish cedar (*Cedrela mexicana*).

A considerably smaller part of Tikal is occupied by low forest. This forest type occurs in poorly drained *bajos*. The trees rarely exceed 20 meters in height and usually are much lower, considerable light reaches the ground, and the understory is choked with thorny shrubs and vines. There are two principal types of low forest at Tikal, the *escobal* forest and the *tintal* forest.

In the former the escoba palm (*Chysosophila argentea*) and the *botan* palm (*Sabal* sp.) are common. In the *tintal*, which is the more extensive type of the low forest at Tikal, the logwood tree (*Haematoxylum campechianum*) is predominant. The birds *Amazilia yucatanensis, Cissilopha sanblasiana,* and *Granatellus sallaci* were found only in the *tintal. Vireo griseus semiflavus* was particularly common here, but also occurred in sunny, low growth near the airfield.

Around the archaeologists' camp, the airfield, and some ruins, the forest has been cleared and its place taken by grasses and shrubs in various densities and heights. This type of vegetation rarely occurred naturally prior to the current archaeological project. Many changes in the avifauna are being brought about by the creation of large tracts of this habitat.

ANNOTATED LIST

TINAMIDAE

Tinamus major percautus Van Tyne

Great Tinamou

Appears to be most abundant in the drier areas within the high forest.

Breeding activity has been noted from April to July. Small chicks were collected on July 13.

Six males ranged in weight from 916.5 to 1106.0 grams, with a mean of 1020.2 ± 28.2; three females 822.0, 1089.0 and 1135.2 grams.

Crypturellus boucardi boucardi (P. L. Sclater)

Slaty-breasted Tinamou

Prefers the more open regions surrounding the camp and the cleared ruins; common.

Reproductively active birds were found from late March to late July. Two of the specimens exhibiting enlarged gonads were in immature plumage. Van Tyne (1935) made similar observations.

The mean weight of seven males was 426.6 ± 14.3 grams, with a range from 368.5 to 467.0; two females were 463.4 and 474.1 grams.

Neither *C. soui* nor *C. cinnamomeus* has been found at Tikal, although both occur elsewhere in the Petén, the latter only 12 miles away at Uaxactun (Van Tyne, 1935). Presumably this is because there is not yet sufficient sunny, brushy cover, the preferred habitat of these species.

PODICIPEDIDAE

PODICEPS DOMINICUS BRACHYPTERUS (Chapman)

Least Grebe

In regions with pronounced seasonal variation in rainfall the Least Grebe is highly mobile, taking advantage of temporary pools and departing for more favorable areas as the dry season progresses. Its extended and irregular breeding period (*vide* Gross, 1949; Paynter, 1955) and extraordinarily high reproductive potential, resulting in the production of as many as 24 fledged offspring in a year (Gross, *ibid.*), are undoubtedly adaptations which allow the species to successfully utilize transient and irregularly available habitats.

Least Grebes appear to be occasional residents at Tikal, but now that some aguadas are being made into year-round reservoirs the species should become permanently established. There is no previous record for the Petén.

A pair, with two chicks, was observed in mid-February 1958 at Aguada Tikal. The young were caught by children, and died; the adults disappeared. In the winter of 1959 a pair was again present. Two birds collected in early August 1959, at a more distant water hole, showed indications of gonadal activity. The male weighed 137.3, and the female 133.6 grams.

PODILYMBUS PODICEPS subsp.

Pied-billed Grebe

A single Pied-billed Grebe was observed by Aubrey Trik, on 8 November 1959, at Aguada Tikal. This is the first report from the Petén.

PHALACROCORACIDAE

PHALACROCORAX BRASILIANUS subsp.

Olivaceous Cormorant

For two weeks, from late October to early November 1959, a lone cormorant was present at Aguada Tikal (Trik, *in litt.*). The species was again reported in the spring and summer of 1960 (Carr, *in litt.*). A. E. Greer (*in litt.*) saw seven or eight in July 1961.

Anhinga anhinga subsp.
Anhinga

A female Anhinga came to the reservoir by the camp at the same time as the cormorant in 1959; it also disappeared about two weeks later (Trik, *in litt.*).

ARDEIDAE

Tigrisoma mexicana mexicana Swainson
Bare-throated Tiger-Heron

When the archaeological project at Tikal was begun in 1956 the Tiger-Heron was found at the aguada near the camp. Since the removal of the vegetation it has not been seen there, although it is fairly common at pools within the undisturbed forest.

A female weighed 1149.0 grams; an unsexed specimen, 1106.0 grams.

Nycticorax violaceus violaceus (Linnaeus)
Yellow-crowned Night-Heron

Yellow-crowned Night-Herons are becoming increasingly common at Tikal now that the camp aguada has been made into a reservoir. In November 1959 as many as six or eight pairs were present. This heron was not seen at Tikal, or recorded from the Petén, prior to July 1959.

A male weighed 663.1 grams.

Neither author has yet seen *N. nycticorax* at Tikal, but two visitors reported the species in March 1960 and July 1961. There is no prior record from the Petén, although the similarly patterned Boat-billed Heron (*C. cochlearius*) is known from Lake Flores. We are, therefore, hesitant to include the Black-crowned Night-Heron in this list.

Ardeola ibis ibis (Linnaeus)
Cattle Egret

A male, displaying no evidence of breeding, was collected on 25 April 1959. This appears to be the first record from the Petén of this rapidly spreading species. The Cattle Egret was first found in Guatemala in November 1958, in Alta Vera Paz (Smithe and Land, 1960).

It weighed 318.3 grams.

BUTORIDES VIRESCENS VIRESCENS (Linnaeus)
Green Heron

A fairly common species. The single specimen in the collection was taken in mid-February. It is a male with a relatively long wing (175 mm.) and with a purple gloss on the sides of the neck. It seems referable to the nominate form and is probably a winter visitor. The breeding race of the Petén is presumably *B. v. maculatus* since Van Tyne (1935) identified a bird collected in June at Pacomón as that form and Taibel (1955) took breeding birds at Flores, which he also placed in that race.

The bird weighed 183.0 grams.

HYDRANASSA CAERULEA (Linnaeus)
Little Blue Heron

The most abundant heron at Tikal. There is no evidence that the species breeds here, although birds are found throughout the year with the largest numbers, of course, in the winter.

A female in nearly fully adult plumage weighed 291.9 grams.

HYDRANASSA RUFESCENS subsp.
Reddish Egret

Three Reddish Egrets appeared at Aguada Tikal on 12 March 1958. They remained for a day and have not been observed again.

EGRETTA THULA subsp.
Snowy Egret

A pair was noted at the Aguada Tikal on 14 May 1959. This is a new record for the Petén.

EGRETTA ALBUS subsp.
Common Egret

From 5 February to 4 March 1958 a lone egret was present at Aguada Tikal.

CICONIIDAE

MYCTERIA AMERICANA Linnaeus
Wood Ibis

Aubrey Trik (*in litt.*) identified a single Wood Ibis at the aguada by the camp on 24 November 1959. The species had not been recorded before from the Petén.

CATHARTIDAE

Sarcoramphus papa (Linnaeus)
King Vulture

Observed fairly regularly but never more than one individual at a time.

Coragyps atratus (Bechstein)
Black Vulture

The most abundant of the vultures. There has been a gradual increase in numbers since observations were begun. Presumably this is correlated with the cutting of the forest and the growth of the village of workers associated with the Tikal Project.

Cathartes aura subsp.
Turkey Vulture

Noted regularly but only about one tenth as abundant as *Coragyps atratus*.

ACCIPITRIDAE

Elanoides forficatus subsp.
Swallow-tailed Kite

During the spring visits of Smithe in 1956, 1957, and 1958 this kite was seen only once (6 March 1958). In 1959, however, when observations extended to mid-August, birds were seen with fair regularity in June, July, and August. They usually appeared singly but occasionally as many as three were sighted at once. Paynter observed single birds on 23 and 28 March 1960.

The Swallow-tailed Kite is known to breed in the Petén (Van Tyne, 1935), but the birds observed at Tikal would seem to be migrants because of the lack of a suitable habitat.

Chondrohierax uncinatus subsp.
Hook-billed Kite

A pair of Hook-billed Kites was seen near a water hole on 27 June 1957. An adult female, weighing 251.5 grams and having a slightly enlarged gonad, was taken. This is the only record from Tikal.

The characters differentiating *C. u. uncinatus* from *C. u. aquilonis* are present only in the males, rendering identification of this specimen impossible. *C. u. aquilonis* may be the local race in view of its presence in Quintana Roo (Paynter, 1955).

HARPAGUS BIDENTATUS FASCIATUS Lawrence
Double-toothed Kite

Three specimens of this rare hawk represent the first records from the Petén. A female was in breeding condition on 3 April 1957. An adult female weighed 189.5 grams and an immature male 174.7 grams.

ACCIPITER BICOLOR BICOLOR (Vieillot)
Bicolored Hawk

On 20 March 1957 a gravid female was collected. An immature male weighed 232.7 grams.

BUTEO PLATYPTERUS PLATYPTERUS (Vieillot)
Broad-winged Hawk

An immature female was collected by Jorge Ibarra on 4 December 1958. This is the first observation of the Broad-winged Hawk in the Petén or anywhere on the Yucatán Peninsula.

BUTEO MAGNIROSTRIS DIREPTOR (Peters and Griscom)
Roadside Hawk

The most common hawk at Tikal; probably it will increase as the forest is further cleared.

Of seven skins, three approach *B. m. conspectus;* two have the rufous tail markings reduced, and one, with the tail well washed with rufous, is generally pale and close to birds from Yucatán. Such variation is expected in view of Paynter's findings (1955) in nearby Quintana Roo.

Breeding birds were noted on 11 February and 17 March. The former date seems especially early. Late March is the earliest record from farther north on the Yucatán Peninsula (Paynter, 1955).

A juvenile female weighed 303.0 grams; an adult female 307.3 grams.

BUTEO NITIDUS subsp.
Gray Hawk

Smithe twice observed this hawk in late March and early April 1956. There was no certain observation again until A. E. Greer, Jr. reported (*in litt.*) seeing a single bird on 20 and 21 July 1961.

LEUCOPTERNIS ALBICOLLIS GHIESBRECHTI (Du Bus)
White Hawk

Observed fairly frequently.

Two males collected on 22 March and 7 April had enlarged gonads.

SPIZAETUS ORNATUS VICARIUS Friedman
Ornate Eagle-Hawk

This large, trusting, hawk is uncommon, but not rare.

A specimen marked as a male, but whose large size would seem to indicate it is a female, weighed 1607.5 grams.

GERANOSPIZA CAERULESCENS NIGRA (Du Bus)
Blackish Crane-Hawk

Four specimens were collected, constituting the first records of the species from the Petén. This is usually considered to be rare in Mexico and Central America, but at Tikal it is not uncommon and is seen more frequently than *Leucopternis albicollis*.

A juvenile male weighed 358.0 grams.

Specimens were taken in March and June but no indication of breeding, other than slight gonadal enlargement, was noted.

FALCONIDAE

HERPETOTHERES CACHINNANS CACHINNANS (Linnaeus)
Laughing Falcon

Frequently seen and even more often heard.

A male weighed 408.0 grams.

MICRASTUR SEMITORQUATUS NASO (Lesson)
Collared Forest-Falcon

Two birds collected on 6 August 1959 are the only records from the Petén.

An immature male weighed 641.7 grams; an adult male 547.7 grams.

MICRASTUR RUFICOLLIS GUERILLA Cassin
Barred Forest-Falcon

This small Forest-Falcon was collected on four occasions. The three specimens preserved as skins show a wide variation in the amount of barring on the ventrum, a phenomenon noted frequently (e.g. Paynter, 1955).

Two males weighed 163.7 and 169.0 grams; a female 200.0 grams.

A male with enlarged testes was taken on 17 June.

FALCO DEIROLEUCUS Temminck
Orange-breasted Falcon

The Orange-breasted Falcon was first noted at Tikal by E. P. Edwards (*in litt.*) in June 1958, when a bird was seen in the vicinity of the Great Plaza. It had not been found in the Petén previously. In early May 1959 a specimen was obtained by Smithe from the top of one of the temples. It was a female, with a slightly enlarged ovary, weighing 653.7 grams. In June and July a pair was present in the Great Plaza, usually in a tree on top of one of the tallest buildings. They may have nested.

FALCO RUFIGULARIS PETOENSIS Chubb
Bat Falcon

Fairly common in open areas. A female was gravid on 25 March.

FALCO SPARVERIUS subsp.
American Sparrow Hawk

No specimens have been collected at Tikal although the species is usually present during the winter months. It is undoubtedly a migrant and winter visitant in the Petén.

CRACIDAE

Crax rubra rubra Linnaeus
Great Curassow

Common, but retreating to the undisturbed forests as the archaeological work progresses.

Birds in breeding condition have been collected in March, April, and May. A chick with its wings and tail partly feathered was taken in early May and a bird about one-quarter grown, weighing 773.1 grams, on 9 August.

Penelope purpurascens purpurascens Wagler
Crested Guan

Abundant in undisturbed regions.

Birds were collected in March, April, June, and July but the only indication of breeding was a third-grown male, weighing 824.9 grams, collected on 16 June.

An adult female weighed 2405.8 grams.

Ortalis vetula intermedia Peters
Plain Chachalaca

Chachalacas are abundant in the scrub bordering the airport and near the camp.

Breeding birds were taken in February, March, and May, and a quarter-grown juvenile on 15 June.

Three adult females weighed 399.2, 459.0 (gravid), and 525.2 grams. The last is unusually heavy.

PHASIANIDAE

Odontophorus guttatus (Gould)
Spotted Wood-Quail

Abundant and easily observed in heavy forest with open understory.

Individuals which were in breeding condition were collected from late March to the second week in June.

Four males weighed 297.6, 309.1, 317.4 and 318.0 grams; a female 284.2 grams.

Dactylortyx thoracicus sharpei Nelson
Singing Quail

A series of ten skins and two skeletons represents the first record of the species in Petén. It is not a rare bird but is excessively shy; much skill is required to collect it.

The Tikal population is clearly referable to *D. t. sharpei* and shows no approach to *D. t. paynteri* from Quintana Roo.

Breeding was noted from late April through July.

Five males weighed 195.4, 197.9, 205.5, 206.7, and 224.0 grams; five females 162.2, 177.4, 184.8, 193.8, and 195.6 grams. Sexual dimorphism is suggested by these data.

MELEAGRIDIDAE

Meleagris ocellata Cuvier
Ocellated Turkey

Turkeys are fairly common in the area about the airstrip, sometimes coming onto the field in the evening to feed.

On 30 May 1959 Smithe found a nest with eight eggs within moderately dense forest.

Basing his opinion on morphological evidence, Paynter (1955) believed it unwarranted to maintain *ocellata* in the monotypic genus *Agriocharis*. Genetic support for this can be found in successful attempts to cross-breed the two species. Leopold (1959) reports hybrids produced by poultry breeders and in 1960 Paynter saw several domestic turkey × ocellated turkey crosses which had been raised by D. B. Legters in Yucatán. While such crosses do not prove the two species congeneric, it would appear more logical to consider these as intrageneric, rather than intergeneric, crosses.

RALLIDAE

Aramides cajanea albiventris Lawrence
Rufous-necked Wood-Rail

During the first years of work at Tikal the Wood-Rail was frequently noted at the aguada by the camp. Later the surrounding vegetation was cleared and the birds have not been seen there since 1959.

A male taken in mid-June showed no indications of breeding but one taken on 31 July had very enlarged gonads. The latter weighed 515.4 grams.

Porzana carolina Linnaeus
Sora

Soras have not been reported from the Petén previously. Smithe observed the species at Aguada Tikal from 28 March to 4 April 1956, from 8 to 23 March 1957, and from 23 February to 12 March 1958. In 1959 he spent from 22 April to 14 August at Tikal but saw no Soras. This may have been because the birds had migrated north by late April or it could be because the aguada, which had been cleared of vegetation in late 1958, was no longer suitable. Paynter saw no Soras during his visit from 23 to 28 March 1960.

Laterallus ruber (Sclater and Salvin)
Ruddy Crake

Prior to the clearing of the vegetation from Aguada Tikal these little rails were common. None had been seen since 1958. The Ruddy Crake requires sunny ponds, bordered by thick vegetation. There are few habitats suitable at Tikal but the raw ditches bordering the airfield may one day develop into ideal sites.

A female collected on 20 March 1957 had an enlarged ovary. A male and a female taken on 5 and 6 April of the same year exhibited no gonadal activity.

Two females and a male weighed 44.6, 48.2, and 44.5 grams, respectively.

Porphyrula martinica (Linnaeus)
Purple Gallinule

A single Purple Gallinule was seen at Aguada Tikal from 28 March to 4 April 1956.

HELIORNITHIDAE

Heliornis fulica (Boddaert)
Sungrebe

A female collected at Aguada Tikal on 27 July 1959 is the only record of the Sungrebe from the Petén. Its gonad contained small ova.

The bird weighed 131.9 grams.

JACANIDAE

Jacana spinosa subsp.

American Jacana

Three Jacanas were present at Aguada Tikal from 28 March at least until Smithe's departure on 4 April 1956. The species has not been seen again, presumably because the pond has been cleared of floating vegetation.

CHARADRIIDAE

Charadrius vociferus vociferus Linnaeus

Killdeer

A common wintering bird, found primarily on the airstrip. As many as 28 individuals have been seen at once. The species appears to have been overlooked by earlier collectors in the Petén.

A female weighed 86.5 grams.

SCOLOPACIDAE

Tringa solitaria solitaria Wilson

Solitary Sandpiper

One or two of these sandpipers are usually at the camp reservoir during the winter and spring.

A female, collected 15 May 1959, weighed 47.5 grams.

Actitis macularia (Linnaeus)

Spotted Sandpiper

A few Spotted Sandpipers are found through most of the year. The species has been recorded as late as 15 May and as early as 23 July.

Calidris melanotos (Vieillot)

Pectoral Sandpiper

A single Pectoral Sandpiper collected on 28 February 1958 is the only record from the Petén. The specimen, a male, weighed 59.5 grams.

COLUMBIDAE

Columba speciosa Gmelin
Scaled Pigeon

The Scaled Pigeon is probably fairly common but it is seldom seen because of its habit of sitting quietly in the dense crowns of tall trees.

Birds with enlarged gonads were collected in February, June, and August, implying a prolonged breeding season.

Two males weighed 258.7 and 292.0 grams and two females 247.6 and 278.7 grams.

Columba nigrirostris Sclater
Short-billed Pigeon

Probably the most numerous of the larger pigeons, but because it frequents high trees it is difficult to observe. When Short-billed Pigeons feed in fruiting trees they may be found at more moderate heights and are rather fearless.

Breeding specimens were collected in February, April, and June.

Six females, all gravid to some degree, ranged in weight from 136.7 to 170.4 grams, with a mean of 156.9 ± 5.6. Two males weighed 168.8 and 173.0 grams.

Columbina talpacoti rufipennis (Bonaparte)
Ruddy Ground-Dove

We are following Goodwin (1959) in merging *Columbigallina* with *Columbina.*

Common about the camp and other cleared areas. Records of breeding were obtained in March, although the season is undoubtedly prolonged, if not continuous through the year.

Three males weighed 42.8, 43.2, and 44.6 grams; two females 45.0 and 60.0 grams.

Claravis pretiosa (Ferrari-Pérez)
Blue Ground-Dove

The Blue Ground-dove is abundant in shady, cleared areas. It was noted breeding from mid-February to early June.

The weight of five males was 58.3, 68.4, 70.0, 72.5, and 72.6 grams; that of three females 65.3, 72.4, and 73.0 grams.

LEPTOTILA PLUMBEICEPS PLUMBEICEPS Sclater and Salvin
Gray-headed Dove

L. plumbeiceps is relatively abundant but difficult to find in the forest.

Fledglings were taken on 25 February and 30 April; adults with enlarged gonads in February, April and May.

Three adult males weighed 135.7, 158.7 and 171.2 grams and an adult female 170.0 grams.

It is surprising that *L. verreauxi* has not yet been found at Tikal. It has been recorded elsewhere in the Petén by Van Tyne (1935) and Taibel (1955).

GEOTRYGON MONTANA MONTANA (Linnaeus)
Ruddy Quail-Dove

Found on the floor of dark forest. Fairly common, but not so abundant as *Leptotila plumbeiceps.*

Breeding was noted in April, June, and July; recently fledged birds were collected in June and August.

Three males and three females weighed 135.6, 141.1, 149.8, and 121.6, 136.1, 152.4 grams respectively.

PSITTACIDAE

ARATINGA ASTEC ASTEC (Souancé)
Olive-throated Parakeet

The parakeet occurs in the vicinity of the airstrip where the forest has been replaced by second growth.

A male and female weighed 80.0 and 85.2 grams, respectively. The female, collected on 18 May, was gravid.

PIONOPSITTA HAEMATOTIS HAEMATOTIS (Sclater and Salvin)
Brown-hooded Parrot

A shy, quiet species which is difficult to see in the high forest, its preferred habitat. It is relatively common, but appears not to have been recorded previously from the Petén.

Males with enlarged gonads were collected in May and July.

The weights of a male and a female were, respectively, 150.0 and 153.3 grams.

Pionus senilis senilis (Spix)

White-crowned Parrot

These are probably the most abundant of the parrots at Tikal. They often frequent the tall trees in the camp, as well as heavy forest.

Birds were seen going in a hole in a dead tree near Aguada Tikal in the last week of March 1960. They seemed to be preparing to nest. Two males collected at the same season three years earlier had slightly enlarged gonads.

Amazona albifrons nana Miller

White-fronted Parrot

A male with slightly enlarged testes, taken on 17 March 1959, is our only record. Probably it is not so uncommon as this implies since Van Tyne (1935) and Taibel (1955) also record the species from the Petén.

Amazona autumnalis autumnalis (Linnaeus)

Red-lored Parrot

The Red-lored Parrot, a forest bird, is moderately common. Specimens collected from March through early June exhibited gonadal activity; no specimens were taken in other months.

Three males weighed 304.6, 419.2, and 437.2 grams. Similar wide variations have been recorded before (Paynter, 1955).

Amazona farinosa guatemalae (Sclater)

Mealy Parrot

Next to *Pionus senilis,* this appears to be the most abundant parrot at Tikal. A male with enlarged gonads taken in mid-May is our only indication of the time of breeding.

The respective weights of two males and a female were 629.2, 703.1 and 649.0 grams.

CUCULIDAE

Piaya cayana thermophila Sclater

Squirrel Cuckoo

Fairly common on the edges of the heavy forest.

Evidence of gonadal activity was noted in late March and mid-May.

Two males and a female weighed, respectively, 103.2, 108.0, and 96.7 grams.

CROTOPHAGA SULCIROSTRIS SULCIROSTRIS Swainson
Groove-billed Ani

Groove-billed Anis occur only in the vicinity of the airstrip, where there is brush. It is rather an uncommon species at Tikal, although it will doubtless greatly increase as the population expands to occupy the recently created brushy habitat.

In early April a bird had enlarged testes.

A male and a female weighed 81.2 and 70.6 grams, respectively.

DROMOCOCCYX PHASIANELLUS RUFIGULARIS (Lawrence)
Pheasant Cuckoo

Two females, with slightly enlarged ovaries, were collected in thickets on 25 and 27 May 1959. These are the only individuals of the Pheasant Cuckoo which have been observed at Tikal. Their weights were 86.8 and 92.7 grams.

STRIGIDAE

OTUS GUATEMALAE GUATEMALAE (Sharpe)
Vermiculated Screech-Owl

Screech-Owls quite often are heard at Tikal. The single specimen collected, a female, is clearly referable to the nominate form rather than to *O. g. thompsoni*, or an intermediate, which might have been expected.

It weighed 105.2 grams.

CICCABA VIRGATA CENTRALIS Griscom
Mottled Wood-Owl

The Mottled Wood-Owl is the most common owl, or at least the most conspicuous one, at Tikal. Its call, a low grunty hoot, followed by one to four (usually three) loud hoots, is frequently heard from shortly before dusk until dawn.

Three males and a female weighed 234.5, 236.6, 253.0, and 316.8 grams, respectively.

A bird collected on 2 April contained an egg.

CICCABA NIGROLINEATA Sclater
Black-and-White Owl

A single specimen, collected 21 March 1957, is the only record of the species from the Petén.

CAPRIMULGIDAE

Nyctidromus albicollis yucatanensis Nelson

Pauraque

Abundant about the airfield and other open areas.

Two males weighed 66.9 and 75.1 grams; five females 59.4, 67.0, 67.6, 71.6, and 77.5 grams.

A bird taken on 15 March contained an egg.

Otophanes yucatanicus (Hartert)

Yucatán Poorwill

The Poorwill is heard fairly frequently. Four specimens were taken at Tikal. One bird was found at mid-day resting on a beam under the thatch of an open-sided storehouse; two were collected on the floor of the forest during the day; one was taken on the airfield at night in company with *Nyctidromus albicollis.* They seem often to roost in trees and bushes, where they are difficult to collect.

An almost fully plumaged fledgling was collected on 7 June. An adult taken on 16 May fluttered on the ground as if a nest was nearby, but none was found.

A male and a female weighed 21.8 and 28.2 grams, respectively; the fledgling, which could not be sexed, 26.6 grams; an unsexed adult 27.5 grams.

APODIDAE

Chaetura vauxi subsp.

Vaux Swift

Swifts are present in considerable numbers but no specimen was secured. Van Tyne (1935) records *C. v. richmondi* as the form breeding at Uaxactun.

Panyptila cayennensis subsp.

Lesser Swallow-tailed Swift

Edwards (1959) reported a pair of this rare swift nesting on a tree in the Great Plaza on 9 June 1958. In March 1960 Paynter found an abandoned nest inside the chamber on top of Temple IV, but no birds were seen.

TROCHILIDAE

PHAETHORNIS SUPERCILIOSUS LONGIROSTRIS (DeLattre)
Long-tailed Hermit

Quite often observed drinking at pools in the forest or at Aguada Tikal; conspicuous but not abundant.

A bird collected in July had very large gonads while several taken in May were only approaching breeding activity. Two males and a female weighed 5.2, 5.7, and 5.6 grams, respectively.

PHAETHORNIS LONGUEMAREUS ADOLPHI Gould
Little Hermit

Prefers heavy rain forest, usually close to the ground. One bird was collected as it sang on a twig projecting from fallen leaves.

Birds taken on 4 April and 31 July had enlarged gonads.

Three males weighed 2.2, 2.5, and 2.5 grams.

PHAEOCHROA CUVIERII ROBERTI (Salvin)
Scaly-breasted Hummingbird

The species is new for the Petén. It seems to frequent flowering trees 40 feet or more above the ground, making detection difficult. One specimen was secured in February and four in July. Breeding was noted in both of these months.

The respective weights of four males and a female were 8.1, 8.1, 8.7, 9.0, and 8.0 grams.

CAMPYLOPTERUS CURVIPENNIS PAMPA (Lesson)
Wedge-tailed Sabrewing

This is a numerous and conspicuous hummingbird.

Males with enlarged testes were collected in mid-February and in mid-June; peculiarly, three males collected in mid-May had only slightly enlarged gonads.

Males with enlarged testes weighed 6.2, 6.4, 6.5, and 6.6 grams; those with slight gonadal development 6.7, 6.7, and 7.1 grams. A non-breeding female weighed 5.0 grams.

FLORISUGA MELLIVORA MELLIVORA (Linnaeus)
White-necked Jacobin

One of the least common of the hummingbirds at Tikal. A male weighed 6.8 grams.

CHLOROSTILBON CANIVETII CANIVETII (Lesson)
Fork-tailed Emerald

The Fork-tailed Emerald is primarily a bird of low scrub and deciduous forests. It is, as to be expected, rare at Tikal. Only two have been seen here; both were caught in a bird net placed near Laguna Dimick, a waterhole at the end of the airstrip.

A male, with very enlarged testes on 5 August, weighed 2.5 grams.

AMAZILIA CANDIDA CANDIDA (Bourcier and Mulsant)
White-bellied Emerald

A common species, feeding at the tops of the trees within the forest and at lower elevations outside the forest.

Birds in breeding condition were collected in mid-February and early August. Four taken in March, peculiarly, had only slightly developed gonads.

Four males weighed 3.6, 3.7, 3.9, and 4.2 grams; two females 3.2 and 3.3 grams.

AMAZILIA YUCATANENSIS YUCATANENSIS (Cabot)
Fawn-breasted Hummingbird

This hummingbird reaches its southern limit in British Honduras and the Petén. A male was collected at Tikal, on 20 July, in the low *tintal* forest. The specimen had enlarged testes and weighed 4.0 grams. We have no other records from Tikal and only one from elsewhere in the Petén (Santa Ana; Salvin and Godman, 1892).

AMAZILIA TZACATL TZACATL (de la Llave)
Rufous-tailed Hummingbird

An abundant and pugnacious species which occurs in most of the habitats available at Tikal.

Six specimens were collected for study skins; all proved to be males. The weights of five were 4.4, 4.4, 4.5, 5.3, and 5.7 grams.

Slightly enlarged gonads were recorded in March, May, and July.

HELIOTHRYX BARROTI (Bourcier)
Purple-crowned Fairy

The species, and genus, reaches its northern limit in the Petén. It is moderately common at Tikal.

Birds in breeding condition were collected in early April and a nest was found on 28 March.

Four males weighed 4.7, 4.8, 4.8, 5.5 grams; a female 5.5 grams.

TROGONIDAE

TROGON MASSENA MASSENA Gould
Slaty-tailed Trogon

A common species in the forest. Two males with enlarged testes were collected in mid-March and mid-June. Three other males and two females taken about the same time in March showed only slightly enlarged gonads.

Weights of five males were recorded as 142.0, 146.0, 146.2, 151.8, and 160.7 grams; two females 141.3 and 155.6 grams.

TROGON CITREOLUS MELANOCEPHALA Gould
Citreoline Trogon

Another very abundant trogon; more prevalent in thin forest and edges than *T. massena.*

The only record from Tikal of a breeding bird is a female collected in mid-March. A newly-fledged trogon was taken on 24 July.

There is considerable individual variation in weight. Eight males weighed between 65.7 and 95.2 grams, with a mean of 74.1 ± 4.0; six females ranged from 73.8 to 81.8 grams with a mean of 76.3 ± 1.3.

TROGON COLLARIS PUELLA Gould
Bar-tailed Trogon

The species has not been reported from the Petén before; it is rather uncommon at Tikal.

Paynter (1957a) suggested that the population from the outer portion of the Yucatán Peninsula may be smaller in body mass, although indistinguishable in linear measurements, than birds from elsewhere within the range of *T. c. puella.* He records the weights of two Yucatán males as 47.6 and 53.5, and two females as 41.1 and 53.9 grams; two males and a female from Chiapas weighed 63.7, 64.5 and 63.4 grams, respectively. At Tikal two males weighed 53.3 and 62.8 grams; two females 66.5 and 66.7 grams. While these new data support the hypothesis, additional documentation is required, particularly from the outer reaches of the Peninsula. Especially strong evidence is needed in view of the unusually wide variation in weight noted, above, in *T. citreolus*.

Breeding individuals were collected in mid-May and late June.

TROGON VIOLACEUS BRACCATUS (Cabanis and Heine)
Violaceous Trogon

T. collaris and this species are about equally abundant.

A male taken on 22 February had one enlarged testis and one small; a female collected in early June was reproductively active.

Two males weighed 54.4 and 70.6 grams, once again illustrating the wide variation in weight found in trogons; two females were 58.5 and 58.8 grams.

ALCEDINIDAE

CERYLE TORQUATA TORQUATA (Linnaeus)
Ringed Kingfisher

A male, weighing 279.2 grams, taken in 1959, and single birds seen in 1957 and 1960 are the only records from Tikal. It may become more common as the reservoirs are enlarged and made permanent.

CHLOROCERYLE AMAZONA MEXICANA Brodkorb
Amazon Kingfisher

A female, weighing 128.6 grams, with a slightly enlarged ovary was collected on 7 March 1958. It was the only one seen at Tikal. Taibel's single record (1955) from Flores was the first from the Petén.

CHLOROCERYLE AENEA STICTOPTERA (Ridgway)
Pygmy Kingfisher

More common than the larger kingfishers but does not yet seem to be a permanent inhabitant, although it appears to have bred here.

A male with enlarged testes, collected 10 August, weighed 17.5 grams; a non-breeding female 18.2 grams.

MOMOTIDAE

Hylomanes momotula momotula Lichtenstein
Tody Motmot

Paynter (1957a) suggested that birds from the Laguna Ocotal region of northeastern Chiapas were possibly heavier than those from the Petén. Two males and a female from Laguna Ocotal weighed 32.5, 32.7, and 29.7 grams, respectively, while five males from the Petén area were found by Van Tyne (1935) to range from 27.0 to 28.5 grams and two females to weigh 26.5 and 27.5 grams. This suggestion is given additional support by the series taken at Tikal, five males of which weighed 26.5, 26.7, 27.5, 27.9, and 29.2 grams, and two females 26.6 and 26.8 grams. The wing measurements, but not those of the tail, also suggest that the birds from northeastern Chiapas are larger, but there is some overlap. More material from Chiapas is needed.

Birds taken in May and June were in breeding condition. A fledgling was collected on 21 June.

Common, but quiet and easily overlooked in the heavy forest.

Momotus momota lessonii Lesson
Blue-crowned Motmot

Abundant. Breeding birds have been taken on 30 April and 24 May.

The weights of two males were 120.1 and 121.2 grams; three females 105.1, 113.8, and 116.8 grams.

GALBULIDAE

Galbula ruficauda melanogenia Sclater
Rufous-tailed Jacamar

An inhabitant of heavy forest; common.

Specimens collected in April and May were breeding.

Six males weighed from 27.1 to 30.2, with a mean of 28.5 ± .4 grams; a female 28.3 grams.

BUCCONIDAE

Notharcus macrorhynchos hyperrhynchus (Sclater)
White-necked Puffbird

Only one specimen of this puffbird was seen and collected at Tikal. The species had not been reported previously from the Petén.

A male, with slightly enlarged gonads, was taken on 23 February. It weighed 97.5 grams. When dissected it was found to contain a lizard about ten centimeters long, weighing 8.8 grams.

MALACOPTILA PANAMENSIS INORNATA (DuBus)

White-whiskered Puffbird

Rather uncommon but definitely not rare.

Newly fledged young were taken on 13 and 18 June.

Two adult females and a male weighed 38.0, 39.8, and 33.7 grams, respectively.

RAMPHASTIDAE

AULACORHYNCHUS PRASINUS VIRESCENS Ridgway

Emerald Toucanet

Common but not so abundant as the other two species of toucans.

A male and female, collected in mid-May, weighed 130.0 and 115.8 grams, respectively. The female had an enlarged ovary.

PTEROGLOSSUS TORQUATUS ERYTHROZONUS Ridgway

Collared Araçari

Abundant. Breeding birds were collected in March.

A gravid female weighed 161.1 grams and a male 172.7 grams.

RAMPHASTOS SULFURATUS SULFURATUS Lesson

Keel-billed Toucan

One of the most conspicuous and common birds of the heavy forest and its edges.

A three-quarter grown fledgling was collected on 21 June. A female taken on 13 February and a male on 9 August had enlarged gonads while four other birds collected in March and late June showed only slight or no gonadal development.

Two females weighed 382.6 and 454.2 grams; a male 384.3 grams.

PICIDAE

PICULUS RUBIGINOSUS YUCATANENSIS (Cabot)

Golden-olive Woodpecker

An uncommon species of the forest. Two females and a male weighed, respectively, 73.9, 75.8, and 78.8 grams. Indications of breeding were noted in late May and in June.

CELEUS CASTANEUS (Wagler)
Chestnut-colored Woodpecker

This woodpecker is usually considered to be rare to uncommon throughout its range from central Mexico to Panama. At Tikal it occurs in heavy forest where it is, for a woodpecker, fairly common.

Breeding birds were recorded in April and May.

Three males weighed 88.1, 89.3, and 90.4 grams; two females 93.3 and 96.7 grams.

DRYOCOPUS LINEATUS SIMILIS (Lesson)
Lineated Woodpecker

Uncommon.

Two females and a male weighed 143.4, 157.9, and 167.4 grams, respectively.

A bird taken in mid-March had an enlarged ovary.

CENTURUS AURIFRONS DUBIUS (Cabot)
Golden-fronted Woodpecker

Specimens from the Petén are generally darker ventrally than typical *C. a. dubius* from Yucatán, but they are much closer to this race than to *C. a. veraecrucis*.

Prefers forest edges and the more open areas. Uncommon, but doubtless will increase as the Tikal forest is cut.

A bird taken on 6 March had a slightly enlarged ovary; a male had fully developed testes on 10 August.

A female weighed 78.6 grams; two males 76.3 and 89.6 grams.

CENTURUS PUCHERANI PERILEUCUS (Todd)
Black-cheeked Woodpecker

A conspicuous and unwary woodpecker of the light forest and edges which, while uncommon, definitely is not rare, as is implied by the single prior record from the Petén (Van Tyne, 1935).

An occupied nest-hole was found in July and breeding birds were collected in May.

Four males weighed 48.1, 48.9, 52.4, and 54.8 grams; a female 42.0 grams.

VENILIORNIS FUMIGATUS SANGUINOLENTUS (Sclater)

Smoky-brown Woodpecker

The species is common in areas where the trees are low and the undergrowth thick.

A bird with an enlarged ovary was collected on 22 March.

Two males weighed 32.8 and 37.4 grams; five females 29.0, 30.8, 31.6, 31.6 and 32.0 grams.

PHLOEOCEASTES GUATEMALENSIS GUATEMALENSIS (Hartlaub)

Pale-billed Woodpecker

A fairly common, noisy woodpecker found in the forest.

In July a pair was found nesting in a dead palm with a pair of *Centurus pucherani* occupying a hole about three feet lower on the same trunk. A male with very large testes was collected in mid-February. The species may breed throughout the year, as suggested by Paynter (1955).

The weight of a male and female were 221.6 and 241.8 grams, respectively.

DENDROCOLAPTIDAE

DENDROCINCLA ANABATINA ANABATINA Sclater

Tawny-winged Woodcreeper

An abundant species of the heavy forest.

A male collected on 19 March, which had enlarged gonads, is the only definite breeding record.

The weights of four males were 36.5, 36.5, 36.9, and 37.5 grams; two females 28.3 and 35.6 grams.

DENDROCINCLA HOMOCHROA HOMOCHROA (Sclater)

Ruddy Woodcreeper

This species and *D. anabatina* seem to be equally common and to prefer the same habitat.

Birds collected in May and June were breeding.

Five males weighed 34.5, 37.9, 38.0, 38.4, and 38.5 grams; two females 34.3 and 39.0 grams.

SITTASOMUS GRISEICAPILLUS GRACILEUS Bangs and Peters

Olivaceous Woodcreeper

Very numerous at Tikal. All the specimens in a large series from Tikal are clearly referable to *S. g. gracileus*. Van Tyne

(1935) had only two specimens from the Petén, which he called *S. g. sylvioides*. Restudy, with the abundant comparative material now available, would undoubtedly indicate that these birds are *S. g. graciteus*.

Paynter (1957a) demonstrated that *S. g. graciteus* is markedly lighter in weight than *S. g. sylvioides*. These additional data from Tikal confirm that observation. Eight males weighed 11.1 ± .4 grams, with a range of 9.5 to 12.6; three females 10.0, 10.3, and 10.3 grams.

Breeding specimens were collected in May.

XIPHOCOLAPTES PROMEROPIRHYNCHUS EMIGRANS Sclater and Salvin

Strong-billed Woodcreeper

The species was observed twice at Tikal; once on 11 March 1957 and once on 1 August 1959. The bird was collected each time. The presence of this large woodcreeper in the tropical forest is unexpected since it is considered to be a subtropical or a temperate zone inhabitant, usually in pine forests. There is one previous record from the Petén, a bird collected at Poctún, a locality on the pine ridges along the British Honduras border (Salvin and Godman, 1891).

The bird taken in August had slightly enlarged testes. The other bird could not be sexed.

The male weighed 135.4 grams.

DENDROCOLAPTES CERTHIA SANCTITHOMAE (Lafresnaye)

Barred Woodcreeper

One of the less common woodcreepers but not rare, as the absence of previous Petén records would seem to indicate.

Specimens were taken in March, July, and August. The July and August birds were breeding.

The weights of three males were 56.8, 63.8, and 65.7 grams; of two females 59.4 and 62.4 grams.

XIPHORHYNCHUS FLAVIGASTER EBURNEIROSTRIS (Des Murs)

Ivory-billed Woodcreeper

There is a tendency toward *X. f. yucatanensis* in the series of fourteen skins collected at Tikal.

The species ranges widely through the forests, perhaps occurring most frequently in the thin, sunny forest. It is abundant.

Paynter (1955) suggested that *X. f. eburneirostris* might be heavier than *X. f. yucatanensis*. Data obtained at Tikal would seem to disprove this. However, it should be borne in mind that this series is not "typical" of *X. f. eburneirostris* and that many of the specimens weighed by Paynter (*ibid.*) on the Yucatán Peninsula were not "typical" of *X. f. yucatanensis*. Eight Tikal males weighed between 40.0 and 53.5 grams, with a mean of 47.2 ± 1.6; eight females between 36.7 and 43.3 grams, with a mean of 40.6 ± .8.

Breeding birds were collected first in early April and continued to be found until mid-July. No specimens are available from later in the year.

FURNARIIDAE

AUTOMOLUS OCHROLAEMUS CERVINIGULARIS (Sclater)
Buff-throated Foliage-gleaner

This species of the heavy forest was seen only twice.

A male with enlarged testes, collected on 21 April, weighed 43.2 grams. Another male, collected 18 June, had very small gonads and weighed 45.9 grams.

XENOPS MINUTUS MEXICANUS Sclater
Plain Xenops

An abundant forest species, recorded breeding in mid-February and early June. Van Tyne (1935) found nestlings in April and May.

The weight of two males was 11.0 and 11.5 grams; that of three females 9.8, 10.6, and 10.8 grams.

SCLERURUS GUATEMALENSIS GUATEMALENSIS (Hartlaub)
Scaly-throated Leafscraper

This bird, a form of the heavy forest, is infrequently seen.

A specimen with very enlarged testes was collected on 1 May.

Four males and a female weighed 32.3, 33.0, 34.1, and 35.8 grams, respectively.

FORMICARIIDAE

THAMNOPHILUS DOLIATUS YUCATANENSIS Ridgway
Barred Antshrike

Found principally in the thickets bordering the airfield, where it is rather uncommon.

Breeding specimens were collected in the fourth week of March and in mid-May.

There is a possibility that *T. d. yucatanensis* averages somewhat less heavy than *T. d. intermedius,* the contiguous race. Four males from Tikal weighed 22.4, 25.2, 25.5, and 26.2 grams. Paynter (1955) recorded the weight of eight males of *T. d. yucatanensis,* of the Yucatán Peninsula, as ranging from 21.4 to 27.8 grams, with a mean of 24.9 ± 0.7 grams. Two males of *T. d. intermedius* from Chiapas weighed 28.4 and 28.8 grams (Paynter, 1957a); these weights are outside the known range for *T. d. yucatanensis.* Data for females are less abundant. Three females of *T. d. yucatanensis* weighed 22.8, 26.3, and 27.0 grams (Paynter, 1955). One female of *T. d. intermedius* was found to weigh 30.0 grams (Paynter, 1957a).

THAMNISTES ANABATINUS ANABATINUS Sclater and Salvin
Russet Antshrike

A pair of this rare species was collected in heavy forest on 5 July 1959, and constitutes the first record from the Petén.

The male weighed 19.5 and the female 19.2 grams; both had enlarged gonads.

DYSITHAMNUS MENTALIS SEPTENTRIONALIS Ridgway
Plain Antvireo

The species has been considered rare in northern Middle America but it may merely be localized. Prior to 1954 the bird was known in Mexico from two specimens from southern Campeche (Traylor, 1941). However, in 1954 six were collected in Chiapas, where the species was reported to be common (Paynter, 1957a). Van Tyne (1935) collected four Plain Antvireos at Uaxactun, and considered this noteworthy, but at Tikal they are abundant in the low growth which borders the roads and trails.

Breeding individuals were taken in March, May, and June.

A series of nine males ranged from 10.9 to 13.8 grams, with a mean of 12.5 ± .1.

Four females weighed 12.2, 12.5, 12.6, and 13.2 grams.

MICRORHOPIAS QUIXENSIS BOUCARDI (Sclater)
Dot-winged Antwren

Moderately common in brushy areas within the high forest.

Most of the specimens collected in June exhibited enlarged gonads.

The weights of two males were 8.6 and 9.0 grams; four females 7.9, 7.9, 8.6, and 9.7 grams.

Cercomacra tyrannina crepera Bangs
Dusky Antbird

Occurs in essentially the same habitat as *Microrhopias quixensis* but seems somewhat less common.

Specimens were taken in March, April, July, and August. Fully developed gonads were found in July and August.

Five males weighed 15.3, 16.1, 16.7, 16.7, and 17.2 grams; two females 13.7 and 14.9 grams.

Formicarius analis intermedius Ridgway
Black-faced Antthrush

Common but quiet and shy; most easily collected during the dry season when it can be heard among the dry forest litter.

A series of six skins from Tikal is clearly referable to *F. a. intermedius* although slight tendencies toward *F. a. pallidus,* such as ventral pallidness or reduced dorsal rufescence, are evident in some specimens.

A male collected on 1 May and one on 10 July were the only individuals reproductively active. Other specimens were taken in March and exhibited no, or only slight, gonadal activity.

The weights of four males were 58.7, 63.6, 64.8, and 65.0 grams; that of three females 57.2, 59.1, and 67.0 grams.

COTINGIDAE

Attila spadiceus flammulatus Lafresnaye
Bright-rumped Attila

A moderately common inhabitant of the forest.

Breeding birds were taken in May and June.

Three males weighed 42.5, 44.8, and 44.9 grams; three females 38.2, 39.0, and 41.7 grams.

Rhytipterna holerythra holerythra (Sclater and Salvin)
Rufous Mourner

The Rufous Mourner is fairly common at Tikal although it had not been found previously in the Petén.

Evidence of breeding was noted in March and April.

Weights of four males were recorded as 33.2, 35.4, 36.0, and 38.0 grams; that of two females 32.3 and 34.2 grams.

LIPAUGUS UNIRUFUS UNIRUFUS Sclater
Rufous Piha

There is no prior record of *L. unirufus* in the Petén. It is less common than *Rhytipterna holerythra* at Tikal, but not rare.

A female, collected on 19 February, had an enlarged ovary and weighed 87.2 grams. A breeding male, taken on 19 June, weighed 79.2 grams and a non-breeding male, collected on 14 July, weighed 84.4 grams.

PACHYRAMPHUS CINNAMOMEUS FULVIDIOR Griscom
Cinnamon Becard

An occupied nest of this common becard was found by Paynter on 27 March in a small tree in an area where the forest had been thinned to allow restoration of some ruins. Smithe observed a nest from 23 April until the birds departed about 10 May. It was built near the end of a branch hanging close to the water at Aguada Tikal.

Three males weighed 19.9, 20.3, and 20.7 grams; a female 19.3 grams.

PACHYRAMPHUS MAJOR AUSTRALIS Miller and Griscom
Gray-collared Becard

This is a species of lower, drier forest and rather unexpected at Tikal; there was no prior record from the Petén. It is uncommon, but as the rain forest is cut and second growth assumes more importance the population certainly will increase.

The respective weights of a male and female were 21.3 and 22.8 grams.

PACHYRAMPHUS AGLAIAE HYPOPHAEUS (Ridgway)
Rose-throated Becard

Platypsaris and *Pachyramphus* are much too similar to be considered separate genera. Hellmayr (1929) long ago pointed out that they were barely separable and recently Bond (1959) made the same observation.

P. aglaiae is another species for which no specific record in the Petén existed. At Tikal it is uncommon but, like *P. major,* may increase when the forest is further thinned.

Of a series of six skins, two are of adult males. There is no rose on their throats. A male which is approaching full adult plumage has a trace of rose. The females are richly colored. There is no doubt that the series is *P. a. hypophaeus.* There are three specimens from British Honduras in the Museum of Comparative Zoology which also are clearly *P. a. hypophaeus.* Paynter (1957a) recorded a single male from Laguna Ocotal, Chiapas as *P. a. sumichrasti,* but this dark bird lacks any rose on its throat and must be *P. a. hypophaeus,* as is also a male from nearby Ocosingo, Chiapas. The range of the race is, therefore, considerably farther north than had been known. The suddenness with which *P. a. sumichrasti* is replaced by *P. a. hypophaeus* is notable. Specimens of *P. a. sumichrasti,* which even display a tendency toward *P. a. yucatanensis,* have been found a mere 100 miles north of Tikal (Paynter, 1955).

A nest with young nearly ready to fledge was found on 24 June. Breeding specimens were collected in late May and early June. One of these is a male in partial juvenile plumage.

Two adult males weighed 27.7 and 29.2 grams; two adult females 31.1 and 33.8 grams; two immature males 26.5 and 29.0 grams.

TITYRA SEMIFASCIATA PERSONATA Jardine and Selby
Masked Tityra

Common in the crowns of high trees, particularly in those which are dead.

A breeding specimen was collected on 24 May. The gonads of birds taken on 18 June and 29 July were only slightly developed.

Three females and a male weighed 84.6, 86.7, 88.1, and 87.0 grams, respectively.

TITYRA INQUISITOR FRASERII (Kaup)
Black-crowned Tityra

An uncommon bird at Tikal.

Breeding birds were collected in mid-May; there are no data for other times of year.

Three females weighed 46.4, 48.0, and 50.3 grams.

PIPRIDAE

PIPRA MENTALIS MENTALIS Sclater
Red-capped Manakin

One of the most abundant birds along the brushy trails in the forest.

Breeding birds have been collected from mid-March to mid-July. Several of these were in juvenile plumage.

Four males in adult plumage weighed 13.8, 14.4, 14.4, and 14.5 grams; seven males in juvenal plumage ranged from 12.8 to 17.5 grams, with a mean of 15.1 ± .6; five females 14.5, 16.0, 17.0, 17.2, and 17.8 grams.

MANACUS CANDEI (Parzudaki)
White-collared Manakin

The White-collared Manakin is the least common of the family at Tikal.

A male with enlarged gonads on 24 July is the only breeding evidence at Tikal but Van Tyne (1935) found an incubating bird on 6 April at nearby Uaxactun.

The weights of two males were 20.6 and 21.2 grams; two females 18.0 and 19.8 grams.

SCHIFFORNIS TURDINUS VERAEPACIS (Sclater and Salvin)
Thrush-like Manakin

This shy manakin is fairly numerous at Tikal.

Its breeding season is notably prolonged. The earliest evidence of breeding was 23 February and the latest 15 July. Paynter (1955) recorded the season, farther north, from early February to early June. Smithe found a nest on 28 March in the hollow end of a palm stump about six feet above the ground. It contained two eggs.

Six males weighed between 30.0 and 32.5 grams, with a mean of 30.7 ± .3; two females weighed 33.8 and 36.2 grams.

TYRANNIDAE

TYRANNUS TYRANNUS (Linnaeus)
Eastern Kingbird

Observed at Tikal in 1959 first on 23 April and for the last time on 8 May. It had not been reported before from the Petén, but year-round observations doubtless would show it to be a common spring and autumn transient.

TYRANNUS MELANCHOLICUS CHLORONOTUS Berlepsch
Tropical Kingbird

Ubiquitous in the vicinity of the airfield and clearings about the camp.

A fledgling was collected on 30 June. Birds with active gonads were taken in May and June.

Three females and a male weighed 40.9, 42.8, 44.7, and 44.1 grams, respectively.

LEGATUS LEUCOPHAIUS VARIEGATUS (Sclater)
Piratic Flycatcher

A gravid female weighing 29.3 grams, collected on 7 April 1957, is the only record from the Petén.

MYIODYNASTES LUTEIVENTRIS LUTEIVENTRIS Sclater
Sulphur-bellied Flycatcher

A common spring and summer bird found high in the trees on the forest edges and in those scattered through the camp.

Our observations have not been continuous. Therefore, it has not been possible to record the precise date of arrival and departure of this species. Our dates fall well within the period of 18 April to 5 August given by Van Tyne (1935) for the Petén. We recorded breeding birds on 8 and 30 June.

The weights of four males were 44.7, 46.2, 46.3, and 47.0 grams; that of two females 44.2 and 49.2 grams.

MYIODYNASTES MACULATUS INSOLENS Ridgway
Streaked Flycatcher

M. maculatus and *M. luteiventris* seem about equally abundant. They also appear to occupy the same habitat. We have specimens from 3 May until 30 July, but the species is certainly present both earlier and later in the season.

Birds taken in May and June were breeding.

Four males and a female weighed 41.5, 45.2, 45.3, 47.8, and 49.2 grams, respectively.

MEGARHYNCHUS PITANGUA MEXICANUS (Lafresnaye)
Boat-billed Flycatcher

We have but one record from Tikal, a breeding male caught on 16 June in a trammel net placed along a trail. Doubtless it is uncommon because of the nature of the country about Tikal, but also it is probably overlooked owing to its similarity to *Pitangus sulphuratus.*

The bird weighed 65.9 grams.

MYIOZETETES SIMILIS TEXENSIS (Girard)
Vermilion-crowned Flycatcher

One of the most abundant of the tyrannids found at Tikal. Particularly numerous at the aguada at the camp.

Two males weighed 32.1 and 33.5 grams.

PITANGUS SULPHURATUS GUATIMALENSIS (Lafresnaye)
Great Kiskadee

There exists no prior record of this bird in the Petén. Several pairs are found at Tikal in the vicinity of the camp aguada. It has been seen nowhere else but as the forest is removed its range certainly will expand.

Nesting activities have been noted from early March through May. A female weighed 57.8 grams.

MYIARCHUS TYRANNULUS COOPERI Baird
Brown-crested Flycatcher

A relatively common species in areas where the forest has been thinned; particularly abundant about the camp.

Birds with enlarged gonads were collected in May and June.

Three males weighed 38.5, 39.3, and 40.5 grams.

M. cinerascens has been found elsewhere in the Petén (Van Tyne, 1935) and is to be expected as a visitor at Tikal.

MYIARCHUS YUCATANENSIS Lawrence
Yucatán Flycatcher

This small flycatcher had not been found previously in the Petén. It is represented in our collection by the skins of two unsexed birds taken on 23 and 30 July 1959 and by an unsexed skeleton collected also on 23 July 1959. The last was identified in the museum by the few feathers left on the wings and tail of the roughed-out field specimen. The skins are of young birds with wide rufous margins to the wings and to the upper tail coverts.

PLATE I

The *Myiarchus* Flycatchers of the Petén

Yucatán Flycatcher
(*M. yucatanensis*)

Dusky-capped Flycatcher
(*M. tuberculifer*)[1]

Ash-throated Flycatcher
(*M. cinerascens*)

Brown-crested Flycatcher
(*M. tyrannulus*)

Reduced about one-half

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[1] The race depicted is *M. t. connectens*, characterized by rufous edges on the ventral side of the rectrices, rather than *M. t. platyrhynchus*, the form at Tikal, which lacks the rufous margins.


W.C. Dilger

Unfortunately, nothing is known of the relative abundance of this species. It is easily confused with *M. tuberculifer* and probably is frequently overlooked (Plate I).

MYIARCHUS TUBERCULIFER PLATYRHYNCHUS Ridgway
Dusky-capped Flycatcher

About as abundant as *M. tyrannulus* and seems to prefer the same habitat.

A series of five skins is quite dark, thereby approaching *M. t. connectens,* but all the specimens are small and all lack rufous markings on the underside of the rectrices.

Breeding birds were found on 27 March, 4 and 22 June, and 1 July.

Four males and a female weighed 17.1, 17.9, 18.4, 19.1, and 17.7 grams, respectively.

CONTOPUS VIRENS (Linnaeus)
Eastern Wood-Pewee

A very abundant transient. Our earliest spring record is 17 March and the latest, an unusually late date, is 30 May. No field work has been done in the autumn.

Three males weighed 13.2, 14.7, and 15.9 grams; two females 15.3 and 15.9 grams.

CONTOPUS CINEREUS BRACHYTARSUS (Sclater)
Tropical Pewee

Most of the field work at Tikal has been done during the migration period of *C. virens,* at which time *C. cinereus* cannot be differentiated. We are, therefore, uncertain of the status of *C. cinereus.* Our two specimens were collected on 29 June and 5 August.

The June bird had a slightly enlarged ovary; the other is a young bird which could not be sexed. The latter weighed 11.2 grams.

EMPIDONAX FLAVIVENTRIS (Baird and Baird)
Yellow-bellied Flycatcher

Three specimens were collected in February 1958. These are the first records from the Petén. Wintering and transient species have not been studied intensively at Tikal. Therefore, our lack of records of this bird in other months and years is not significant.

Two males weighed 8.6 and 10.3 grams.

EMPIDONAX MINIMUS (Baird and Baird)
Least Flycatcher

A common winter visitor.

TERENOTRICCUS ERYTHRURUS FULVIGULARIS (Salvin and Godman)
Ruddy-tailed Flycatcher

Van Tyne (1935) cites two records of this species in the Petén. A single specimen was taken at Tikal. The species is at the limit of its northern range in this region and probably is rare.

The bird, a male, weighed 7.4 grams.

MYIOBIUS BARBATUS SULPHUREIPYGIUS (Sclater)
Sulphur-rumped Flycatcher

Common and conspicuous, occurring in the lower growth within the high forest.

Birds with fully developed gonads were collected on 29 April and 26 May.

Seven males weighed between 11.0 and 12.4 grams, with a mean of 11.7 ± .2; three females 10.0, 10.4, and 11.6 grams.

ONYCHORHYNCHUS CORONATUS MEXICANUS (Sclater)
Royal Flycatcher

A fairly abundant forest bird.

Breeding individuals were collected from 7 April to 19 July.

Three males weighed 20.2, 20.3, and 20.6; three females 17.0, 17.0, and 18.2 grams.

PLATYRINCHUS MYSTACEUS TIMOTHEI Paynter
White-throated Spadebill

A common bird in the undergrowth bordering the trails in the high forest.

Eight males weighed from 7.8 to 11.7 grams, with a mean of 9.9 ± .4; three females 7.8, 9.0, and 9.6. Paynter (1955) recorded three males of this race from Quintana Roo as weighing

8.0, 8.3, and 9.8 grams, and two females as 7.5 and 10.7 grams. Van Tyne's males from Uaxactan ranged from 9.4 to 10.4 grams and females from 7.8 to 8.0 grams. These data seem to indicate that *P. m. timothei* is somewhat lighter in weight than *P. m. cancrominus*, five males of which from Chiapas were found (Paynter, 1957a) to range from 10.0 to 12.0 grams, with a mean of 11.2 ± .3 and four females of which weighed 8.7, 9.7, 9.9, and 10.2 grams.

Breeding birds were collected on 9 June and 27 July. A fledgling was taken 19 July.

TOLMOMYIAS SULPHURESCENS CINEREICEPS (Sclater)

Yellow-olive Flycatcher

Moderately numerous in the high forest. Generally found in the thin growth of shrubs and trees which occurs under a thick canopy.

A male which had enlarged testes on 1 July is the only breeding record, although specimens collected as early as 24 April exhibited slight gonadal activity.

Three males weighed 13.4, 14.3, and 14.5 grams; two females 14.8 grams each.

RHYNCHOCYCLUS BREVIROSTRIS BREVIROSTRIS (Cabanis)

Eye-ringed Flatbill

The species had been recorded only once from the Petén (Van Tyne, 1935) but at Tikal it is a rather common resident of the heavy rain forest.

Breeding birds were noted from early June to mid-July.

A series of eight males weighed 21.8 ± .3 grams and ranged from 20.7 to 22.9 grams; five females weighed 20.3, 20.7, 21.2, 22.6, and 25.5 grams; the latter bird had a very enlarged ovary.

ONCOSTOMA CINEREIGULARE CINEREIGULARE (Sclater)

Northern Bentbill

Fairly common in the low growth along trail edges, although not previously recorded in the Petén.

Breeding specimens were taken in May and July.

Three males weighed 6.4, 6.7, and 7.5 grams.

ELAENIA VIRIDICATA PLACENS Sclater
Greenish Elaenia

The species was not noted at Tikal until the 1959 field season, suggesting that it may have immigrated to the region about that time or become more numerous. It is another open-country bird which may be expected to increase at Tikal.

Five males weighed 12.6, 12.7, 12.7, 12.8, and 12.8 grams.

Breeding males were collected from 14 May to 29 June.

ORNITHION SEMIFLAVUM SEMIFLAVUM (Sclater and Salvin)
Yellow-bellied Tyrannulet

This small flycatcher had not been found before in the Petén. It seems very local at Tikal, preferring the sunny borders of the forest near the camp. It is, however, rather common where it does occur.

Males with greatly enlarged gonads were collected 21 February and 11 May.

Four males weighed 7.0, 7.2, 7.4, and 7.6 grams.

LEPTOPOGON AMAUROCEPHALUS PILEATUS Cabanis
Sepia-capped Flycatcher

This is another example of a species which elsewhere is considered to be rare but which occurs in good numbers in the forest at Tikal.

Breeding birds were collected between 19 March and 29 May.

Five males and a female weighed, respectively, 9.9, 11.3, 11.3, 11.7, 11.7, and 10.8 grams.

PIPROMORPHA OLEAGINEA ASSIMILIS (Sclater)
Ochre-bellied Flycatcher

Within the heavy forest this is an abundant species.

A bird with a slightly enlarged ovary on 24 March is the earliest indication of the approaching breeding season. Breeding males were collected on 10 May and 2 July.

Four males weighed 12.2, 12.6, 13.6, and 14.4 grams; two females 11.5 and 12.4 grams.

HIRUNDINIDAE

PROGNE SUBIS subsp.
Purple Martin

A single male Purple Martin was observed by Paynter on 24 March 1960. The bird was first seen early in the morning while sunning itself in the top of a dead tree in the camp area. It remained in the vicinity until mid-morning. The observer was aware of the paucity of records of this bird from Central America and is certain the bird seen was not *P. chalybea*.

PROGNE CHALYBEA CHALYBEA (Gmelin)
Gray-breasted Martin

Seen about the airfield with moderate frequency and in flocks not exceeding six birds.

A male collected 19 April had enlarged testes and weighed 40.8 grams. It was one of several apparently nesting in holes in the trunks of palms.

STELGIDOPTERYX RUFICOLLIS STUARTI Brodkorb
Rough-winged Swallow

The species is fairly common at Tikal. Nesting takes place in the ruins during April and May.

Five birds were collected, two of which were breeding. All are referable to *S. r. stuarti* rather than to *ridgwayi*, the race which might have been expected because of the proximity of Tikal to the breeding range of *ridgwayi* on the Yucatán Peninsula. The first suggestion that *stuarti* did not breed exclusively in the mountains was to be found in the discovery of *stuarti* in the Cayo District, British Honduras, on 23 April (Paynter, 1957b). With this additional evidence from the Petén it would seem that the breeding range of *stuarti* extends to the wet lowlands of the Caribbean slope. *S. r. ridgwayi* is probably confined to the outer, drier, portion of the Yucatán Peninsula.

Four males and a female weighed 15.6, 16.0, 16.1, 16.2, and 15.1 grams, respectively.

CORVIDAE

CISSILOPHA SANBLASIANA YUCATANICA (Dubois)
Black-and-blue Jay

This jay is found in the *tintal* forest. It is uncommon.

Birds with active gonads were collected in mid-May, early June, and mid-July.

Two males and a female, all in adult plumage, weighed 126.9, 133.9, and 130.9 grams, respectively.

CYANOCORAX YNCAS CENTRALIS (van Rossem)
Green Jay

Only one Green Jay has been seen during the field work at Tikal. This bird, a male weighing 74.0 grams, is not typical of *C. y. centralis.* Its wing is quite small, indicating an approach toward *C. y. maya.*

PSILORHINUS MORIO CYANOGENYS Sharpe
Brown Jay

One of the most common and conspicuous birds at Tikal.

Breeding specimens were collected on 19 March and 7 April.

A male weighed 241.7 grams.

TROGLODYTIDAE

THRYOTHORUS MACULIPECTUS CANOBRUNNEUS Ridgway
Spot-breasted Wren

As might be expected, Tikal specimens of this wren show an approach toward *T. m. umbrinus* in coloration. Paynter (1957a) indicated that *T. m. canobrunneus* might be lighter in weight than *umbrinus.* The weights of birds from Tikal, again as expected, fall between *canobrunneus* and *umbrinus.* Four males weighed 14.5, 15.3, 16.0, and 16.6 grams; two females 13.4 and 14.6 grams.

An active, conspicuous bird which occurs in forest undergrowth. For a wren, its altitudinal range is notable. It is usually found in low shrubs but at times ranges in vines in trees 30 feet above the ground.

Breeding specimens were collected in May and early July.

Thryothorus ludovicianus albinucha (Cabot)
Carolina Wren

This large wren is found only in the low vegetation bordering the airstrip. It is uncommon.

A male with fully enlarged testes was collected 5 August.

Two males weighed 15.8 and 16.2 grams.

Uropsila leucogastra brachyura (Lawrence)
White-bellied Wren

This is the least common of the forest-inhabiting wrens at Tikal.

Two mature males and a female weighed 9.4, 10.2, and 8.7 grams, respectively; an immature male 10.4 grams.

Six specimens were collected in February, March, May and July, but none was breeding.

Henicorhina leucosticta prostheleuca (Sclater)
White-breasted Wood-wren

Very common in the underbrush within the forest.

Birds with fully enlarged gonads have been taken from 19 March to 31 July.

A series of eight males weighed between 14.3 and 15.9 grams, with a mean of 15.0 ± .2; four females 13.3, 13.5, 13.7, and 16.2 grams.

MIMIDAE

Dumetella carolinensis (Linnaeus)
Catbird

An abundant winter visitant found as late as 2 May. A specimen collected on this date had a slightly enlarged ovary and weighed 49.6 grams; another female weighed 35.9 grams.

TURDIDAE

Turdus albicollis leucauchen Sclater
White-throated Robin

Fairly abundant in light forest and on the borders of clearings.

Van Tyne (1935) referred his Petén specimens to *T. a. parcolor*, a race described from British Honduras, but we are uncertain that this is a recognizable form.

Breeding specimens were collected in May.

Three males weighed 53.3, 63.4 and 73.0 grams; two females 61.5 and 63.1 grams.

TURDUS NUDIGENIS TAMAULIPENSIS (Nelson)
Sooty Robin

Not seen at Tikal prior to 1959 but during the field work in 1959 and 1960 it was fairly common. Alterations in the habitat almost certainly account for the increase in the population.

A male collected 8 May had slightly enlarged testes and weighed 74.0 grams; another male weighed 74.8 grams.

HYLOCICHLA MUSTELINA (Gmelin)
Wood Thrush

A winter visitant occurring in moderate numbers. Our latest spring record is 23 April.

POLIOPTILA PLUMBEA SUPERCILIARIS Lawrence
Tropical Gnatcatcher

A male, with fully enlarged gonads and weighing 6.3 grams, was collected on 7 July. It is the only record from Tikal. A specimen taken at Chuntuqui (Van Tyne, 1935) was the first record from the Petén.

RAMPHOCAENUS RUFIVENTRIS ARDELEO Van Tyne and Trautman
Long-billed Gnatwren

Five specimens of the gnatwren were taken at Tikal. All show a strong approach toward the nominate race. The species occurs in moderate abundance in dense undergrowth.

A breeding specimen was collected in late May.

The weights of two males were 8.9 and 9.7 grams; that of three females 8.1, 11.0, and 11.1 grams.

BOMBYCILLIDAE

BOMBYCILLA CEDRORUM Vieillot
Cedar Waxwing

Cedar Waxwings were observed, in flocks containing as many as 28 birds, on 16 and 28 February 1958 and on 8 May 1959. They seem not to have been found before in the Petén.

VIREONIDAE

SMARAGDOLANIUS PULCHELLUS PULCHELLUS (Sclater and Salvin)
Green Shrike-Vireo

A single, non-breeding, male collected on 23 February 1958 represents the first record of the species from the Petén. Probably it is more common than the dearth of records would seem to indicate. It occurs in the crowns of the tallest trees where it is seldom noticed.

The specimen weighed 24.4 grams.

VIREO GRISEUS GRISEUS (Boddaert)
White-eyed Vireo

The specimen of the White-eyed Vireo was taken on 14 February 1958. Van Tyne (1935) lists a bird, collected at La Libertad, which apparently was the first of the race collected in the Petén. It would seem, as Griscom (1932) indicated, that the subspecies is a rare visitant to the Petén, although just one hundred miles to the north, in Campeche and Quintana Roo, it is common (Paynter, 1955). The lack of brushy second growth must greatly restrict the range of the species in the Petén, but there must be other causes, possibly genetic, limiting *V. g. griseus* because the resident race (*V. g. semiflavus*) is abundant where the habitat is satisfactory.

VIREO GRISEUS SEMIFLAVUS Salvin

Bond (1954) suggests that the *semiflavus* group of vireos is nearer to *V. ochraceus* than to *V. griseus* and he places that group within the former. The *ochraceus* and *semiflavus* groups are without doubt closely allied, but the *griseus* group is certainly close also, although perhaps not so near as *ochraceus* is to *semiflavus*. All the forms of *ochraceus, semiflavus,* and *griseus* are allopatric; it would seem prudent to treat the three groups as conspecific uniting them under the name of *V. griseus,* as was done by Hellmayr (1935).

The bird is common at Tikal in deforested areas and in the *tintal.*

Breeding was noted from 26 May to 6 August.

Three males weighed 9.9, 10.5, and 10.7 grams.

VIREO OLIVACEUS OLIVACEUS (Linnaeus)
Red-eyed Vireo

A specimen was collected on 7 August 1959, an unusually early date for the species to be in Central America. Field work during the spring and fall migrations will doubtless show this to be a common transient.

VIREO OLIVACEUS FLAVOVIRIDIS (Cassin)

A rather common bird of light forest and edges, particularly about the camp. Van Tyne (1935) records the species from 5 April to 30 September.

Breeding birds were taken from 16 May to 3 July.

Three males and a female weighed 16.9, 17.8, 19.3, and 20.9 grams, respectively.

HYLOPHILUS OCHRACEICEPS OCHRACEICEPS Sclater
Tawny-crowned Greenlet

Abundant in the lower levels of the forest.

Graber and Graber (1959) recently reviewed the northern population of the species and resurrected the race *pallidipectus*, a pallid subspecies named from Costa Rica, which was synonomized with the nominate form by Todd (1929) and Hellmayr (1935). We have examined a large series of the species, mainly from Costa Rica, Guatemala, and Mexico, and agree that *pallidipectus* is a distinct form worth nomenclatural recognition. Graber and Graber (1959) limit the nominate race to Mexico, but our material shows that the Petén and British Honduras must also be included in its range.

Breeding birds were collected from 17 March to 14 June.

Four males weighed 9.9, 10.9, 11.0, and 11.0 grams; four females 10.9, 11.2, 11.8, and 13.6 grams.

HYLOPHILUS DECURTATUS DECURTATUS (Bonaparte)
Gray-headed Greenlet

Ubiquitous in the thickets in, or bordering, the forest.

Enlarged gonads were noted in specimens taken in mid-May. A fledgling was collected on 6 July.

Males weighed 8.6, 8.8, 9.0, 9.4, and 9.5 grams; two females 9.1 and 9.7 grams.

PARULIDAE

MNIOTILTA VARIA (Linnaeus)
Black-and-white Warbler

A common winterer.

Two females and a male weighed, respectively, 9.5, 9.5, and 8.2 grams.

HELMITHEROS VERMIVORUS (Gmelin)
Worm-eating Warbler

A male Worm-eating Warbler, collected on 20 March 1957, represents the first record of the species in the Petén. It weighed 13.8 grams.

VERMIVORA PEREGRINA (Wilson)
Tennessee Warbler

The Tennessee Warbler is an uncommon winterer, and had not been reported before from the Petén.

A male and female weighed 8.6, and 9.0 grams, respectively.

DENDROICA PETECHIA subsp.
Yellow Warbler

Smithe observed what he believed to be this species on 19 February and on 20 June 1959. The February observation seems reasonable but the other record is very questionable because of its extremely late date. Van Tyne (1935) recorded *D. p. rubiginosa* from Flores. Doubtless it is a casual visitor.

DENDROICA MAGNOLIA (Wilson)
Magnolia Warbler

Magnolia Warblers are common winter visitors. A female was collected on 8 May 1958, a notably late date. The bird, which exhibited some ovarian enlargement, weighed 9.0 grams.

DENDROICA CORONATA CORONATA (Linnaeus)
Myrtle Warbler

It is remarkable that the Myrtle Warbler, which is a fairly abundant bird at Tikal in the winter, had not been reported before from the Petén. It is particularly conspicuous in March when migrating flocks feed on the lawns about the camp buildings.

Four spring females weighed 10.1, 10.7, 11.4, and 11.5 grams.

DENDROICA VIRENS VIRENS (Gmelin)
Black-throated Green Warbler

The Black-throated Green Warbler is another species not previously recorded from the Petén but which is a common winter resident.

A male weighed 7.5 grams.

DENDROICA FUSCA (Muller)
Blackburnian Warbler

Smithe saw a male on 30 March 1956. This is the only time the species, which is a transient in northern Central America, has been seen in the Petén.

DENDROICA PENSYLVANICA (Linnaeus)
Chestnut-sided Warbler

We have two specimens collected on 6 and 14 February 1958. These are of interest not only because they are the first evidence of occurrence of the species in the Petén, but because the bird had not been known to winter farther north than Nicaragua.

A female weighed 9.2 grams; a bird presumed to be a male 8.2 grams.

SEIURUS AUROCAPILLUS (Linnaeus)
Ovenbird

A moderately numerous winterer.

A female weighed 21.7 grams.

SEIURUS MOTACILLA (Vieillot)
Louisiana Waterthrush

Seems much less common than the Northern Waterthrush. Both are usually found in the vicinity of Aguada Tikal. The species is present until roughly the first week in May. The earliest fall record from the Tikal is 1 August.

A male and female weighed 20.8 and 17.6 grams respectively.

SEIURUS NOVEBORACENSIS NOTABILIS Ridgway
Northern Waterthrush

A fairly common species. At least one or two birds are present at Aguada Tikal most of the year. Our latest spring date is 8 May and the earliest autumn date is 10 August.

Four males weighed 16.4, 18.4, 18.9, and 19.0 grams.

OPORORNIS FORMOSUS (Wilson)

Kentucky Warbler

Kentucky Warblers are among the most abundant of the wintering Parulidae.

Three males weighed 11.6, 11.9, and 15.9.

OPORORNIS PHILADELPHIA (Wilson)

Mourning Warbler

A Mourning Warbler, which is a transient in northern Central America, was collected on 11 May. It was a male, weighing 11.4 grams. Van Tyne (1935) took a single bird at Uaxactun. These are the only Petén records.

GEOTHLYPIS TRICHAS BRACHIDACTYLA (Swainson)

Common Yellowthroat

Yellowthroats are rather common near the aguadas and in weedy areas in the vicinity of the camp. A bird collected on 18 May is notably late.

Two females and a male weighed 9.5, 11.5, and 9.5 grams, respectively.

ICTERIA VIRENS VIRENS (Linnaeus)

Yellow-breasted Chat

An uncommon visitor. In late March and early April the chat seems to be more common. Transients from the south probably augment the wintering population.

A female weighed 28.4 grams.

GRANATELLUS SALLAEI BOUCARDI Ridgway

Gray-throated Chat

This small chat had not been found previously in the Petén. At Tikal it is confined to the *tintal bajo,* the low forest which completely loses its leaves during the dry season. This type of forest occurs about two miles east of the airstrip and covers a comparatively small area. The species is common here. Paynter (1955) noted a similar localization of the species farther out on the Yucatán Peninsula.

A series of six skins is clearly referable to *G. s. boucardi.*

Five mature males weighed 10.1, 10.5, 11.0, 11.4 and 11.5 grams; an immature male 9.6 grams; a female 11.1 grams. These data continue to support the suggestion (Paynter, 1957a) that *G. s. sallaei* is the heavier subspecies.

Breeding specimens were collected 3 May, 9 June, and 29 June. A male in immature plumage was breeding.

WILSONIA CITRINA (Boddaert)
Hooded Warbler

A ubiquitous visitor. Probably the most common of the warblers.

Five males and a female weighed, respectively 9.2, 9.6, 9.8, 9.9, 10.2, and 9.3 grams.

WILSONIA PUSILLA subsp.
Wilson's Warbler

We have single sight records for 10 March 1957, 7 February 1958, and 28 March 1960. The bird has not been reported before from the Petén. It is probably a rare winterer in this region, as one would expect with the knowledge that it has not been reported from the Yucatán Peninsula.

SETOPHAGA RUTICILLA (Linnaeus)
American Redstart

A very common species during the winter. It has been seen as late as 7 May.

A female weighed 7.4 grams.

BASILEUTERUS CULICIVORUS CULICIVORUS (Deppe)
Golden-crowned Warbler

One of the most abundant birds of the wooded areas.

Reproductively active specimens were taken in May and June.

Eight males ranged in weight from 8.9 to 11.5 grams, with a mean of 9.7 ± .2; three females 8.2, 8.7, and 9.1 grams.

ICTERIDAE

GYMNOSTINOPS MONTEZUMA (Lesson)
Montezuma Oropendola

A common and conspicuous species.

On 4 May a male was collected which had enlarged gonads. It is surprising that we have not yet found oropendolas nesting in Tikal.

A male and female weighed 509.5 and 211.8 grams, respectively.

CASSIDIX MEXICANUS subsp.
Boat-tailed Grackle

A single, female Boat-tailed Grackle was seen regularly at the camp aguada during Paynter's visit in March 1960. The population undoubtedly will increase greatly if the pond is maintained in its present condition.

DIVES DIVES DIVES (Deppe)
Melodious Blackbird

This is another species which is profiting by the cutting of the forest and the establishment of a village. It is one of the most conspicuous birds near the camp.

Females weighed 87.0 and 97.7 grams.

ICTERUS GALBULA (Linnaeus)
Baltimore Oriole

Apparently the Baltimore Oriole is of rare occurrence in the Petén. A young male, weighing 35.9 grams, was collected 12 February 1958 and is the first record from the region. An immature male or a female was tentatively identified by Paynter on 24 March 1960.

ICTERUS SPURIUS (Linnaeus)
Orchard Oriole

Van Tyne (1935) did not record the Orchard Oriole at Uaxactun but at Tikal it is a very abundant winterer in the vicinity of the camp and airfield. Sometimes in March and April it occurs in flocks of more than 100 individuals. The species has been seen as late as 3 May, but the majority of birds leave in late April.

A female weighed 19.3 grams; two immature males 18.2 and 22.6 grams.

ICTERUS PROSTHEMELAS PROSTHEMELAS (Strickland)
Black-cowled Oriole

The most common of the breeding icterids, preferring the thinly wooded area and forest edges about the camp.

Birds with fully enlarged gonads were collected on 3 April and 8 July. A fledgling was taken 1 August.

A male weighed 30.1 grams; three immature females 25.8, 26.2, and 27.3 grams; two mature females 28.3 and 29.9 grams.

ICTERUS MESOMELAS MESOMELAS (Wagler)

Yellow-tailed Oriole

A male with enlarged gonads, collected on 30 June, is the only Tikal record. This is a species which may increase as the settlement at Tikal grows.

The bird weighed 43.6 grams.

THRAUPIDAE

TANAGRA LAUTA LAUTA Bangs and Penard

Yellow-throated Euphonia

The species is abundant, particularly in the vicinity of the camp.

Breeding birds were collected from April to June.

Seven males weighed from 11.7 to 14.7 grams, with a mean of 12.8 ± .4; a female 15.9 grams.

TANAGRA GOULDI GOULDI (Sclater)

Olive-backed Euphonia

This euphonia is more of a forest species than *T. lauta* and, therefore, not so conspicuous. Our records are limited to the months of June and July, suggesting that the bird may be absent earlier, or more likely, that it becomes more noticeable during the breeding season. The only previous record from the Petén (Van Tyne 1935) was also of a summer (August) bird.

Nearly all of the birds collected were breeding.

Five females weighed 10.8, 12.4, 12.5, 12.9, and 13.2 grams; three females 13.1, 13.2, and 14.0 grams.

TANGARA NIGROCINCTA LARVATA (DuBus)

Masked Tanager

Moderately abundant. Often found in company with honeycreepers fairly high in flowering trees.

A male with fully enlarged gonads was collected on 2 April. Specimens taken in June were also breeding.

Three males weighed 16.7, 17.9, and 19.5 grams.

THRAUPIS ABBAS (Deppe)
Yellow-winged Tanager

Another species which is found primarily in trees within the camp area, and which probably will increase in numbers.

Breeding specimens were taken from 28 March to early August. A newly fledged bird was collected on 7 June.

Three adult males and a female weighed 41.4, 44.8, 50.6, and 47.6 grams, respectively. The fledgling, a male, weighed 39.8 grams.

PIRANGA RUBRA RUBRA (Linnaeus)
Summer Tanager

There is no previous record from the Petén of this winterer, but it is fairly common, especially in shade trees about the camp.

A male weighed 27.2 grams and a female 29.6 grams.

PIRANGA ROSEOGULARIS TINCTA Paynter
Rose-throated Tanager

This weakly characterized race of a species endemic to the Yucatán Peninsula, including the Petén, was uncommon. Three birds were taken, all of which were in low forest or edges.

A male in immature plumage was breeding in mid-May. An adult male had enlarged gonads on 30 June.

An adult male and a female weighed 22.2 and 24.5 grams; the immature male 22.8 grams.

PIRANGA LEUCOPTERA LEUCOPTERA (Trudeau)
White-winged Tanager

There exists no prior record of the species from the Petén. This tanager was noted for the first time at Tikal in 1959 when a small series was taken between April and August. The birds were found on the edges of wide trails through moderately heavy forest.

Breeding specimens were collected on 10 June and 1 August.

Three males and a female weighed 15.3, 15.6, 16.3, and 16.0 grams, respectively.

HABIA RUBICA NELSONI (Ridgway)

Red-crowned Ant-Tanager

Surprisingly, a series of eleven skins is clearly referable to *H. r. nelsoni*, the form of the Yucatán Peninsula, rather than to *H. r. rubicoides.*

Red-crowned Ant-Tanagers are abundant within the forest and have been noted breeding from mid-March to early July.

A series of ten males weighed a mean of 33.5 ± .3 grams, with a range of 26.8 to 38.2 grams; three females 30.5, 30.8, and 33.2 grams.

HABIA GUTTURALIS PENINSULARIS (Ridgway)

Red-throated Ant-Tanager

Seems to occur about the camp and along the edges of trails with greater frequency than *H. rubica.*

The weight of eight males ranged from 36.4 to 44.4 grams, with a mean of 39.4 ± 1.0 grams; five females were 30.1, 30.8, 31.9, 33.4, and 34.8 grams.

Breeding birds were taken in May, June, and July. A fledgling barely able to fly was collected on 17 July.

LANIO AURANTIUS AURANTIUS Lafresnaye

Great Shrike-Tanager

An abundant species in the forest.

Breeding birds were collected from 7 April to 3 July.

Eleven males weighed from 32.5 to 38.5 grams, with a mean of 36.1 ± .6 grams; eight females from 33.5 to 41.6 grams, with a mean of 36.7 ± .3 grams.

EUCOMETIS PENICILLATA PALLIDA Berlepsch

Gray-headed Tanager

Wherever army ants are swarming the Gray-headed Tanagers are to be found.

It is a fairly common bird at Tikal, usually occurring in bushy areas bordering the trails.

A male taken on 24 May had fully developed gonads.

Two males weighed 24.2 and 27.2 grams; six females ranged from 24.7 to 31.5 grams, with a mean of 27.0 ± 1.0.

Cyanerpes cyaneus carneipes (Sclater)
Red-legged Honeycreeper

The honeycreeper is common in the crowns of flowering trees, or in those with flowering epiphytes.

Breeding specimens were collected from 23 April to 4 June.

The weights of a series of six males were 11.1 to 13.9 grams, with a mean of 12.3 ± .4; those of five females 10.0, 13.0, 13.1, 14.4, and 15.3 grams.

FRINGILLIDAE

Saltator atriceps atriceps (Lesson)
Black-headed Saltator

This saltator is liimted to brushy trailsides and to the vicinity of the camp and airfield, where there is much second growth.

Breeding males were taken on 6 May and 6 June.

Two males weighed 76.6 grams, each; a female 83.8 grams.

Caryothraustes poliogaster poliogaster (DuBus)
Black-faced Grosbeak

A moderately common species which occurs in flocks within the forest.

Birds collected from 28 May to 7 July were breeding.

The weights of a series of five males were 39.4, 39.9, 41.7, 42.2, and 44.8 grams; of two females 39.9 and 44.8 grams.

Richmondena cardinalis flammigera (Peters)
Cardinal

A few cardinals have been seen at Tikal in the scrub at the eastern edge of the airfield. A male, in breeding condition, was collected on 28 June and is the second specimen of the species from Guatemala, the first having been taken at Flores, Petén (Taibel, 1955).

Taibel (*ibid.*) described *R. c. petenensis* on the basis of his one specimen and without reference to *flammigera* or *yucatanica*, two races of obvious importance. We have not examined the type of *R. c. petenensis* but expect it will be found to agree with *R. c. flammigera*, the race to which our Tikal specimen is clearly referable.

The bird weighed 32.9 grams.

GUIRACA CAERULEA subsp.
Blue Grosbeak

Has been seen on a few occasions, particularly in the spring.

CYANOCOMPSA PARELLINA PARELLINA (Bonaparte)
Blue Bunting

We are unable to appreciate the characters said to distinguish *C. p. dearborni* from the nominate form and, contrary to Van Tyne (1935), place our Petén specimens in *C. p. parellina.*

Blue Buntings are abundant in the weeds and scrubs bordering the airstrip and camp.

Eight males weighed between 13.2 and 17.7 grams, with a mean of 15.5 ± .5 grams; three females were 13.8, 14.1, and 16.3 grams.

CYANOCOMPSA CYANOIDES CONCRETA (DuBus)
Blue-black Grosbeak

Fairly common in the heaviest forest.

Breeding specimens were found on 28 May and 10 August.

Two males and a female weighed 30.5, 32.8, and 29.5 grams, respectively.

PASSERINA CYANEA (Linnaeus)
Indigo Bunting

Indigo Buntings are found throughout the winter in the weeds bordering the airstrip.

Two immature males weighed 13.6 and 13.7 grams.

PASSERINA CIRIS CIRIS (Linnaeus)
Painted Bunting

This is another winter visitor which is common in the vicinity of large clearings.

A mature male weighed 16.9 grams; two immature males 15.4 and 16.7 grams; three females 16.2, 19.4, and 21.7 grams.

SPIZA AMERICANA (Gmelin)
Dickcissel

Dickcissels have been seen at Tikal only in April and very early May when large migrating flocks pass through.

Three males weighed 26.9, 27.3, and 27.4 grams.

SPOROPHILA TORQUEOLA MORELLETI (Bonaparte)

White-collared Seedeater

The White-collared Seedeater is confined to weedy growth at the airfield and camp.

Breeding specimens were collected in June and early July and a nest with young was found on 8 July. The season is undoubtedly much more prolonged than indicated by our few records.

An immature male weighed 8.7 grams; three mature males 7.3, 8.0, and 8.2 grams; a female 7.8 grams.

ORYZOBORUS FUNEREUS Sclater

Thick-billed Seed-Finch

This is the least common of the seed finches occurring at Tikal, and like *Sporophila torqueola* and *Volatinia jacarina* is found only in the vicinity of the airfield and camp.

A bird collected in mid-May had fully enlarged gonads.

Three males weighed 12.0, 12.5, and 13.2 grams.

VOLATINIA JACARINA SPLENDENS (Vieillot)

Blue-black Grassquit

Like *Sporophila torqueola*, found at Tikal only near human habitation and the airstrip.

Two immature males weighed 8.7 and 9.2 grams; an adult male 8.6 grams and two females 9.0 and 9.2 grams.

ARREMONOPS CONIROSTRIS CHLORONOTUS (Salvin)

Green-backed Sparrow

A very common species in the underbrush bordering trails within the forest.

Breeding was noted in April, May and June.

The weights of a series of nine males ranged from 23.2 to 28.9 grams, with a mean of 26.8 ± .6; a female weighed 25.6 grams.

The sibling species, *A. rufivirgatus*, has not yet been found at Tikal but may be expected to appear now that a considerable area has been cleared of heavy forest. There seems to be no published record of *A. rufivirgatus* from anywhere in Guatemala. However, Jorge Ibarra collected a single, unsexed, specimen at La Libertad, Petén, on 27 April 1956. The bird was sent to Paynter who identified it as *A. r. verticalis*, the subspecies known before only from Yucatán, Campeche, and Quintana Roo.

DISCUSSION

Two hundred and thirty-one species of birds, with an aggregate of 233 species and races, have been found at Tikal. Eight of these forms are transients during the spring or fall: *Calidris melanotus; Tyrannus tyrannus; Contopus virens; Progne subis; Vireo o. olivaceus; Dendroica fusca; Oporornis philadelphia; Spiza americana.* Future field work may treble the number of species recorded in this category.

Seventeen per cent (37 forms) of the avifauna consists of visitants (Table I), all of which are common Central American

Table I

WINTER VISITORS

Butorides v. virescens (?)
Hydranassa rufescens
Buteo platypterus
Falco sparverius
Porzana carolina
Charadrius v. vociferus
Tringa s. solitaria
Actitis macularia
Empidonax flaviventris
Empidonax minimus
Dumetella carolinensis
Hylocichla mustelina
Bombycilla cedrorum
Vireo g. griseus
Mniotilta varia
Helmitheros vermivorus
Vermivora peregrina
Dendroica petechia subsp.
Dendroica magnolia
Dendroica c. coronata
Dendroica v. virens
Dendroica pensylvanica
Seiurus aurocapillus
Seiurus motacilla
Seiurus noveboracensis notabilis
Oporornis formosus
Geothlypis trichas brachidactyla
Icteria v. virens
Wilsonia citrina
Wilsonia pusilla
Setophaga ruticilla
Icterus galbula
Icterus spurius
Piranga r. rubra
Guiraca caerulea subsp.
Passerina cyanea
Passerina c. ciris

winterers. In addition, in the winter some northern birds, chiefly herons, probably augment the local populations, but without banding records it is impossible to be certain which species are involved.

A total of 173 forms are known to breed at Tikal or, because of their sedentary nature, are assumed to breed there. *Butorides virescens* might be added to this total, but to date our only specimen seems to be a wintering bird. Furthermore, 15 species (Table II) which breed in northern Guatemala (except possibly *Podilymbus podiceps* and *Ardeola ibis*) have been recorded at Tikal but probably have not yet bred there. These birds are dependent on water and doubtless have been attracted to Tikal by the newly-made reservoirs; eventually most may become permanent residents.

Table II

LOCAL SPECIES NOT KNOWN TO BREED AT TIKAL

Podilymbus podiceps (winterer?)
Phalacrocorax brasilianus
Anhinga anhinga
Nycticorax violaceus
Ardeola ibis (wanderer?)
Hydranassa caerulea
Egretta thula
Egretta albus
Mycteria americana
Elanoides forficatus
Chondrohierax uncinatus
Porphyrula martinica
Ceryle torquata
Chloroceryle aenea
Cassidix mexicanus

From the work of Van Tyne (1935) and Taibel (1955) we have a good knowledge of the avifauna of the northern part of the Petén. When the records of these two workers are compared with the results of the survey at Tikal, it is seen that 46 species which breed in the Petén have not as yet been found at Tikal (Table III). Some of these birds are uncommon in northern Central America, as for example *Lepidocolaptes souleyetii* or *Todirostrum sylvia*, but in time they may be discovered at Tikal, just as some rare forms found at Tikal were not previously known from the Petén. In both instances continued observations undoubtedly will reveal their presence. However, the vast majority of the species listed in Table III require habitats differing from those now present in the National Park, or at least

Table III

BREEDING SPECIES RECORDED FROM PETÉN BUT NOT AT TIKAL

Crypturellus soui
Crypturellus cinnamomeus
Cochlearius cochlearius
Ictinia plumbea
Rosthramus sociabilis
Hypomorphnus urubitinga
Busarellus nigricollis
Colinus nigrogularis
Aramus guarauna
Columba cayennensis
Columbina minuta
Leptotila verreauxi
Ara macao
Tyto alba
Pulsatrix perspicillata
Nyctibius griseus
Anthracothorax prevosti
Chloroceryle americana
Melanerpes formicivorus
Lepidocolaptes souleyetii
Gymnocichla nudiceps
Pyrocephalus rubinus
Muscivora tyrannus
Empidonax albigularis
Todirostrum cinereum
Todirostrum sylvia
Elaenia flavogaster
Camptostoma imberbe
Tachycineta albilinea
Campylorhynchus zonatus
Troglodytes aedon
Henicorhina leucophrys
Dumetella glabrirostris
Chamaethlypis poliocephala
Coereba mexicana
Amblycercus holosericeus
Psomocolax oryzivorus
Tangavius aeneus
Agelaius phoeniceus
Sturnella magna
Tanagra affinis
Thraupis episcopus
Piranga bidentata
Saltator coerulescens
Tiaris olivacea
Arremon aurantiirostris

some of the existing biotopes must be more extensive if they are to support these birds. Certain of the species need ponds and marshes but most require large cleared areas with open fields or low second growth — the type of habitat ocurring around towns and villages. Thus, as the human population increases at Tikal we should see a corresponding increase in the avifauna. It will be of great interest to learn how long it will take some of the more sedentary birds to discover this island of low vegetation lying within a vast quasi-rainforest.

Tables II and III also illustrate that there are relatively few water-dependent species recorded from the Petén which have not already been found at Tikal, even though the reservoirs are small and were built only a few years ago. The birds requiring water which still are not known at Tikal are mostly those that inhabit larger bodies of water or streams. Thus, it may be seen that water-dependent species are quick to discover a newly created habitat, even though it may be well isolated from similar habitats. The fact that these birds frequently wander after the breeding season undoubedly explains this phenomenon.

Lying well south of the driest part of the Yucatán Peninsula, and a moderate distance north of the wet foothills of Alta Vera Paz, one would expect the avifauna of Tikal to be transitional between that found in each of the two contrasting regions, with a pronounced tendency toward the latter type.

Confining our discussion to the breeding species, and eliminating aquatic birds and the wide-ranging vultures *Coragyps atratus* and *Cathartes aura*, we are left with a total of 164 forms. Employing the lists presented by Paynter (1955: 300-303), who divided the land birds of the Yucatán Peninsula into two broadly generalized, and admittedly subjective, groups based on whether they were characteristic of more humid areas or of drier regions, we find that at Tikal 86 of the 164 birds are typical of more humid regions, 55 are typical of drier areas, and 23 have not been found on the peninsula north of the Mexican border and thus do not appear on Paynter's lists. These 23 species (Table IV) are all characteristic of moderately wet to very wet areas; therefore, about two-thirds (109 forms) of the Tikal avifauna is composed of forms typical of more humid regions, confirming what was expected on geographical considerations alone.

For the entire peninsula of Yucatán north of the Mexican border the general habitat preferences of the 217 land birds are divided almost evenly, with 112 forms (51.6 per cent) characteristic of drier regions and 105 species (48.4 per cent) typical of more humid areas. It is not possible, of course, to compare the relative figures for the entire Yucatán Peninsula with those for the limited area of Tikal, although they are useful in intraregional analyses.

The mainland of the Yucatán Peninsula, from the wet forest of the Guatemala-Mexico border north to the arid scrub at the tip, possesses 70 endemic, or nearly endemic, species and races. Sixty-eight of these are land birds of which 50 (73.6 per cent),

TABLE IV

SPECIES BREEDING AT TIKAL WHICH ARE NOT KNOWN FROM MEXICAN PORTION OF YUCATÁN PENINSULA

Leucopternis albicollis
Falco deiroleucus
Panyptila cayennensis
Phaethornis superciliosus
Phaeochroa cuvierii
Florisuga mellivora
Heliothryx barroti
Malacoptila panamensis
Centurus pucherani
Xiphocolaptes promeropirhynchus
Automolus ochrolaemus
Thamnistes anabatinus
Rhytipterna holerythra
Lipaugus unirufus
Pachyramphus cinnamomeus
Terenotriccus erythrarus
Ornithion semiflavum
Leptopogon amaurocephalus
Tangara nigrocincta
Piranga leucoptera
Turdus albicollis
Smaragdolanius pulchellus
Oryzoborus funereus

including seven full species, are characteristic of drier areas and 18 (26.4 per cent) prefer more humid regions. As has been pointed out by Paynter (1955), the drier region of the peninsula is isolated from similar areas in Middle America by the quasi-rainforest at the base of the peninsula and the much greater proportion of endemism occurring in the dry area avifauna is to be expected.

At Tikal there is a sharp reduction in the peninsular elements in the avifauna. North of the Mexican border peninsular endemics make up 31.3 per cent (68 forms) of the land bird fauna; at Tikal they comprise only 14 per cent (23 forms) of that fauna (Table V). Concomitant with this reduction there is, as to be expected, a marked difference in the proportion of humid region to dry region endemic elements within the fauna. North of the Mexican border 44.6 per cent of the birds typical of drier regions are endemic, and 17.1 per cent of the species of more humid regions are endemic; at Tikal only 7.2 per cent of the birds characteristic of drier areas are peninsular endemics while the 27.2 per cent of the humid region element is endemic to the Yucatán Peninsula.

TABLE V

YUCATÁN PENINSULA ELEMENT AT TIKAL

Buteo magnirostris direptor
Ortalis vetula intermedia
Dactylortyx thoracicus sharpei
Meleagris ocellata
Otophanes yucatanicus
Campylopterus curvipennis pampa
Amazilia yucatanensis yucatanensis
Pteroglossus torquatus erythrozonus
Sittasomus griseicapillus gracileus
Thamnophilus doliatus yucatanensis
Myiarchus yucatanensis
Myiarchus tuberculifer platyrhynchus
Playtrinchus mystaceus timothei
Cissilopha sanblasiana yucatanica
Thryothorus maculipectus canobrunneus
Thryothorus ludovicianus albinucha
Uropsila leucogastra brachyura
Ramphocaenus rufiventris ardeleo
Granatellus sallaei boucardi
Piranga roseogularis tincta
Habia rubica nelsoni
Habia gutturalis peninsularis
Richmondena cardinalis flammigera

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MISCELLANEOUS NAUTILID TYPE SPECIES OF ALPHEUS HYATT

By Bernhard Kummel

With Thirty Plates

CAMBRIDGE, MASS., U.S.A.
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No. 6 — *Miscellaneous Nautilid Type Species of Alpheus Hyatt*

By Bernhard Kummel

The impact of Alpheus Hyatt on the study of fossil nautilids is keenly felt by all students of this group of animals. Preparation of the section covering the order Nautilida for the forthcoming volume on the nautilid cephalopods as Part K of the Treatise on Invertebrate Paleontology has necessitated re-examination of many genera and species introduced by Hyatt. Many of these genera and species have been little recognized or used since their introduction because in many cases the original descriptions left much to be desired, and there were no illustrations. Fortunately, many of Hyatt's nautilids are preserved in the Museum of Comparative Zoology. In this paper are presented descriptions and illustrations of 32 species, of which 17 are holotype specimens, including 9 which are types of genera introduced by Hyatt. There are in addition 14 plesiotypes of specimens Hyatt discussed in his "Phylogeny of an Aquired Characteristic." All of these specimens are illustrated by photographs for the first time.

The objective of this paper is the illustration and brief description of these little-known Hyatt types. Discussion of the broader relationship of the various taxa is being presented in another contribution and in the forthcoming Treatise volume.

The species described and illustrated are as follows:

Anomaloceras anomalum (Barrande) Hyatt, 1894, pp. 494-495, pl. 8, figs. 16-20.
Millkoninckioceras konincki (Miller and Kemp) = *Koninckioceras* (*Nautilus*) *ingens*, Hyatt, 1884, p. 295; 1893, pp. 439-440.
Planetoceras retardatum Hyatt, 1893, pp. 421-422.
Tainoceras duttoni Hyatt, 1893, pp. 401-402, text-figs. 3, 4.
Metacoceras wolcotti Hyatt, 1891, pp. 337-339, figs. 36, 37; 1893, pp. 394-396, fig. 2.
Diodoceras avonensis (Dawson), Hyatt, 1894, p. 536, pl. 8, figs. 36-39.
Lispoceras trivolve Hyatt, 1893, p. 428.
Lispoceras rotundum Hyatt, 1893, pp. 428-429.
Leuroceras aplanatum Hyatt, 1893, pp. 437-438.

Stroboceras anglicum Hyatt, 1893, pp. 410-411.
Subclymenia occulta Hyatt, 1893, pp. 414-416.
Subclymenia gibbosa Hyatt, 1893, pp. 414-416.
Thrincoceras depressum Hyatt, 1893, pp. 430-432, figs. 9-10.
Thrincoceras kentuckiense Hyatt, 1893, pp. 432-434, figs. 11-15.
Vestinautilus cariniformis Hyatt, 1893, p. 420.
Vestinautilus koninckii (d'Orbigny) Hyatt, 1872, p. 91, pl. 4, figs. 7-9; 1894, pp. 540-541, 602, pl. 9, figs. 5-13.
Oncodoceras fusiforme Hyatt, 1893, pp. 455-456.
Liroceras globatum (deKoninck), Hyatt, 1894, pp. 541-543, pl. 10, figs. 1-14.
Coelogasteroceras coxi, Hyatt, 1894, pp. 498-499, pl. 10, fig. 33.
Peripetoceras freieslebeni (Geinitz), Hyatt, 1894, pp. 545-546, pl. 11, figs. 1-3.
Potoceras dubium Hyatt, 1894, pp. 537-539, pl. 10, figs. 15-22.
Ephippioceras ferratum (Cox), Hyatt, 1894, p. 539, pl. 10, figs. 23-26.
Eutrephoceras faxoense Hyatt, 1894, p. 558, pl. 13, figs. 9-12.
Eutrephoceras imperialis (Sowerby), Hyatt, 1894, pp. 559, 605, pl. 13, figs. 13-16.
Cenoceras intermedium (Sowerby), Hyatt, 1894, pp. 550, 604, pl. 11, figs. 15-16.
Cenoceras granulosum (d'Orbigny), Hyatt, 1894, p. 553, pl. 11, figs. 36-39, pl. 31.
Cenoceras clausum (d'Orbigny), Hyatt, 1894, p. 552, pl. 12, figs. 12-15.
Cenoceras aratum (Quenstedt), Hyatt, 1894, pp. 551-552, pl. 11, figs. 32-35.
Cenoceras lineatum (Sowerby), Hyatt, 1894, p. 551, pl. 11, figs. 22-27.
Cenoceras sp. Hyatt, 1894, p. 549, pl. 11, figs. 19-21.
Cymatoceras deslongchampsianum (d'Orbigny), Hyatt, 1894, p. 554, pl. 12, figs. 22-27.
Cymatoceras radiatum (Sowerby), Hyatt, 1894, pp. 554-555, pl. 12, figs. 29, 30; pl. 13, figs. 1, 2.
Cymatoceras sp. indet. Hyatt, 1894, pp. 553-554, pl. 12, figs. 16-21.
Remeleceras impressum Hyatt, 1894, pp. 525-526, pl. 8, figs. 1-8.

SYSTEMATIC DESCRIPTIONS

Order NAUTILIDA Agassiz, 1847

Superfamily TAINOCERATACEAE Hyatt, 1883

Family RUTOCERATIDAE Hyatt, 1884

Genus ANOMALOCERAS Hyatt, 1884

(=*Hyatticeras* Cossman, 1900; *Alpheiceras* Cossman, 1900 [obj.])

Type species. Nautilus anomalus Barrande, 1865a

ANOMALOCERAS ANOMALUM (Barrande)

Plate 13, figures 5-7

Anomaloceras anomalum (Barrande) Hyatt, 1894, pp. 494-495, pl. 8, figs. 16-20.

Hyatt's several illustrations of this species are of a specimen he had sawed in two and polished; the figures represent various stages during his grinding operation. The specimen is quite typical for the species but not well preserved insofar as the external features of the conch are concerned. Hyatt's figure 20 on plate 8 represents accurately the state of the inner whorls as shown on the polished section.

Locality. Bohemia.

Repository. MCZ 8810.

Family KONINCKIOCERATIDAE Hyatt, 1900

Although it is argued below that the type species of *Koninckioceras, K. ingens,* is unrecognizable and that the generic name should not be used, I consider that the family-group name based on it should continue to be used in the interests of stability.

MILLKONINCKIOCERAS n. gen.

Type species. Koninckioceras konincki Miller and Kemp, 1947 (=*Nautilus ingens* deKoninck, *non Conchyliolithes* (*Nautilites*) *ingens* Martin, 1809, type of *Koninckioceras* Hyatt, 1884, *nom. dubium;* = *Koninckoceras* Hyatt, 1900, *nom. null.*).

When Hyatt established the genus *Koninckioceras* in 1883 he stated: "Type, *Kon.* (*Naut.*) *ingens* sp. DeKon. Calc. Carbon. pl. 23, Mus. Comp. Zool. Camb." This specimen deKoninck described and illustrated as *Nautilus ingens* Martin (1809). It is in the collections of the Museum of Comparative Zoology. Most authors have accepted the specimen in the Museum of Comparative Zoology as the type. After thorough correspondence on this question with Dr. Curt Teichert, it seems inescapable that Hyatt's genus *Koninckioceras* must have for its type species *Conchyliolithus* (*Nautilites*) *ingens* Martin (1809, pl. 41, fig. 5).

Martin's description of his species reads as follows: "CONCHYLIOLITHUS N. Ammonites (*ingens*) anfractibus subextrinsecis teretibus laevibus, ambitu integro, dissepimentis integris. S. p.

"A fossil shell. The original a *Nautilus;* spiral, depressed. (Syst. G. 6. Fam. Ammonitae.) Volutions three, nearly external, even, round, and gradually tapering to the centre, which is hollow or sunk beneath the level of the outward whirl. Ambit entire. Dissepiment entire, oblique, slightly waved. The structure of the siphuncle unknown. Found near Ashford. Limestone. This is the largest of the Ammonitae yet discovered in Derbyshire. The specimen represented is about twice the size of the figure."

The above description, needless to say, leaves much to be desired. The illustration is that of a large evolute nautiloid, probably with a more or less oval whorl section. As drawn, the specimen is an internal cast with prominent striations, which was probably not the intent of the author.

M'Coy (*in* Sedgwick and M'Coy, 1855, p. 559) assigned a number of specimens to *Nautilus ingens* (Martin) which he described as follows:

"Discoid, gibbous, of about four whorls (rarely more than one half preserved), about one half of each whorl of the spire concealed by the involutions; umbilicus wide, usually with sloping sides, and then defined by an obtuse angulation from the sides of the shell, or (in other specimens, or other parts of same specimen) moderately convex and undefined; volutions thick, sides either very convex or slightly flattened, periphery either broadly rounded or obtusely carinate along the middle; edge of the mouth with a rounded, angular sinus in the middle; septa simple, moderately convex; siphon nearly central, a little nearer the inner than the outer margin. Dimensions of small specimen, diameter five inches, proportional diameter of last whorl $\frac{48}{100}$, diameter of umbilicus $\frac{55}{100}$, width of last whorl $\frac{50}{100}$. Shell having the surface marked with fine, obsolete, transverse lines of growth. Last few septa, with a diameter of one inch and a half, four lines apart; with a diameter of four inches, one inch apart. Adult diameter about nine inches.''

There is no indication that M'Coy had available for study Martin's type specimen. In his discussion of *Nautilus ingens,* M'Coy made the following comments: ''The examination of a great number of large specimens induces me to propose the union of *Nautilus pentagonus* (Sow.) with this species, because out of a great number of specimens with rounded periphery, some have the inner whorls convex on the sides, and the outer ones flattened, and there are all gradations between the broadly rounded periphery of the true *N. ingens,* and the keeled exterior of the *N. pentagonus;* but it curiously happens that the two widest extremes which I have seen are at the two ends of one large fragment from Closeburn, which in itself would set the question completely at rest; further this latter specimen so strongly keeled in its unseptate portion, shows the impression of simply rounded whorls of the spire on its inner margin.''

Sowerby's illustration of *Nautilus pentagonus* (his plate 249) is a composite figure, embodying BMNH 43865b (Pl. 25, figs. 1, 2, of this report) for the general shape and the two patches of matrix, and BMNH 43865a (Pl. 24, figs. 1-3, of this report) for the septal surface and siphuncle at the aperture (M. K. Howarth, personal communication). Foord (1891) discussed *Nautilus pentagonus* and Sowerby's types but placed them in the genus *Solenochilus.* In the synonymy of his *Solenochilus pentagonus* he placed with question *Conchyliolithus* (*Nautilites*) *ingens* Martin and specifically excluded *Nautilus ingens* deKoninck (1851, p. 710, and 1878, p. 105) and Hyatt (1884, p. 295). Foord (1891, p. 177) was in agreement with M'Coy's opinion that *N. pentagonus* Sowerby should be united with *N. ingens* Martin. At the same time, however, even though he recognized that Martin's name *ingens* should have precedence over *pentagonus,* he concluded that ''there is so much uncertainty about the former species that I have thought it best, after carefully examining the specimens at the Jermyn-Street Museum, as well as those of the British Museum, to allow Sowerby's name to supersede Martin's.'' In 1893 Hyatt selected *N. pentagonus* Sowerby as the type of his new genus *Lophoceras.*

It appears inescapable that the generic name *Koninckioceras* has for its type the species *ingens* of Martin and that this is an unrecognizable species. Hence the generic name *Koninckioceras* should not be used for specimens other than the type. I reject M'Coy's conclusion that *ingens* and *pentagonus* are synonyms.

Miller and Kemp (1947) accepted Foord's (1891, pp. 176-178) conclusion that *N. ingens* deKoninck was not conspecific with *Conchyliolithus* (*Nautilites*) *ingens* Martin and introduced the specific name *konincki* for Hyatt's specimen of *Koninckioceras*. Since the generic name *Koninckioceras* cannot be utilized, the new name *Millkoninckioceras* is proposed for the species *konincki* which is described on the following pages.

As now interpreted, the family Koninckioceratidae includes the following genera: *Edaphoceras* Hyatt, 1884, *Endolobus* Meek and Worthen, 1865, *Foordiceras* Hyatt, 1893, *Millkoninckioceras* n. gen., *Knightoceras* Miller and Owen, 1934, *Koninckioceras* Hyatt, 1883 (unrecognizable), *Lophoceras* Hyatt, 1893, *Planetoceras* Hyatt, 1893, *Subvestinautilus* Turner 1954b, *Temnocheilus* M'Coy, 1844, *Tylodiscoceras* Miller and Collinson, 1950, and *Valhallites* Shimanskii, 1959. The family ranges through the Mississippian and Permian.

MILLKONINCKIOCERAS KONINCKI (Miller and Kemp)

Plate 5, figure 1; Plate 6, figure 2

Nautilus ingens deKoninck, 1851, p. 710, pl. 60, fig. 1; 1878, p. 105, pl. 23, fig. 4.

Koninckioceras (*Nautilus*) *ingens*, Hyatt, 1884, p. 295.

Nautilus ingens, Foord, 1891, pp. 176-178.

Koninckioceras ingens Hyatt, 1893, pp. 439-440; Miller and Owen, 1934, p. 245.

Koninckioceras konincki Miller and Kemp, 1947, p. 353, pl. 51, figs. 1, 2; Miller and Youngquist, 1949, pp. 34-36, pl. 9, fig. 1, text-fig. 3.

Interpretation of this genus until now has been based on Hyatt's brief original diagnosis, the original figures by deKoninck (1878), and supplementary remarks made by Hyatt in 1893 in which he clearly states that deKoninck's figures represent a restoration and are in error in many details. The holotype is illustrated here for the first time.

The specimen is an incomplete phragmocone of 135 mm. in diameter, consisting of two volutions; the innermost volutions are not preserved.

The whorl section is depressed and elliptical in outline, measuring 42 mm. in height and 59 mm. in width on the most adoral camarae. The venter is broadly arched merging onto broadly convex umbilical shoulders and lateral areas. The umbilical shoulder is more distinctly rounded, the umbilical wall very broad and flattened, sloping to the umbilical seam at approximately 45 degree angle. The whorl section of the preserved inner volutions maintain the same shape and proportional dimensions as the outer volutions. The impressed zone is broad and shallow, enclosing only the venter of the preceding whorls. The umbilicus measures approximately 60 mm. in diameter.

The sutures are essentially straight over the venter, lateral areas, and umbilical wall but have a shallow dorsal lobe. The siphuncle is small, presumably tubular, and subcentral in position, that is, closer to the venter than to the dorsum. No shell is preserved on any part of the specimen.

Locality and horizon. Lower Carboniferous, Halloy, Belgium.

Repository. Holotype — MCZ 5205.

Remarks. The genus *Koninckioceras* has been thoroughly reviewed by Miller and Youngquist (1949) who also reproduced deKoninck's original figures.

Genus PLANETOCERAS Hyatt, 1893

Type species. Planetoceras retardatum Hyatt, 1893, pp. 421-422.

PLANETOCERAS RETARDATUM Hyatt

Plate 7, figures 1-3

The type specimen of this genus and species is a small individual, only moderately well preserved. The specimen measures 29.7 mm. in diameter, 16.6 mm. for the width of the last whorl, 9.5 mm. for the height of the last whorl; the umbilicus measures 13 mm. in diameter. The conch is evolute, tarphyceraconic, and the most adoral quarter whorl is not in contact with the preceding whorl. The whorl section of the outer volution is depressed with a broad, slightly convex venter, broadly rounded ventral shoulders which grade imperceptibly onto a slightly convex lateral area. The umbilical shoulder is marked by a conspicuous angular ridge; the umbilical shoulder is broad, slightly convex and slopes inward at a steep angle. The nature of the inner volutions is not known. As well as one can tell, the suture is essentially straight or at most has extremely shallow broad ventral and lateral lobes. The siphuncle is small, tubular, and slightly ventral of the center.

No surface markings, except faint growth lines, are visible on the test. The aperture has a large tongue-shaped hyponomic sinus marked by a raised border.

Locality and horizon. Belgium, Visé.

Repository. Holotype — MCZ 2392.

Remarks. Hyatt included in his new genus, *Planetoceras,* *Coelonautilus globatus* (Sowerby) described by Foord (1891, pp. 127-130) from the Carboniferous Limestone of Cork, Kildare. Hyatt had two poorly preserved topotypes of this species for study which are in the collections of the Museum of Comparative Zoology. In addition, Hyatt (1893, p. 422) considered the possibility that *Nautilus atlantoideus* deKoninck and *Nautilus neglectus* deKoninck of the Tournaisian of Belgium and *Nautilus distensus* deKoninck of the Viséan of Belgium belonged also to his genus *Planetoceras.*

After its introduction into the literature, the genus *Planetoceras* was all but forgotten until Miller, Dunbar, and Condra (1933) discussed it and presented a diagnosis. The fact that Hyatt did not supply an illustration of his species and that his description left much to be desired has made interpretation of the genus difficult. The diagnosis of the genus presented by Miller, et al. (1933, p. 138) is remarkably accurate in view of the data available to them. These authors assigned two new species to *Planetoceras, P. bellilineatum* and *P. tiltoni,* both of which I believe are valid species of this genus. The former species differs from *P. retardatum* in that the whorls are in contact throughout the specimen. However, as these authors pointed out, the specimen is small and most probably an immature form. In nearly every other aspect there is good agreement between these species. *Planetoceras tiltoni* is based on a large specimen (225 mm.) that has the general morphological architecture of *Planetoceras.* It is unique, however, in that the adoral half volution has a median concave zone on the venter.

Hyatt (1893) originally placed his new genus in the family Triboloceratidae, and he maintained this viewpoint in the 1900 edition of Zittel-Eastman, Text-Book of Palaeontology. This procedure was followed by Miller, et al. (1933) and Schmidt (1951). *Planetoceras* was placed in the family Koninckioceratidae by Kummel (in Flower and Kummel, 1950), and this procedure was followed with question by Shimanskii (1957). The general character of the conch allies it with members of the Koninckioceratidae much more closely than with the Triboloceratidae. However, too few specimens of this genus have been studied to date, and more data are needed.

Family TAINOCERATIDAE Hyatt, 1883

Genus TAINOCERAS Hyatt, 1883

Type species. Nautilus quadrangulus McChesney, 1860, pl. 3, fig. 5

TAINOCERAS DUTTONI Hyatt

Plate 3, figure 1; Plate 4, figure 1; Plate 6, figure 1

Tainoceras duttoni Hyatt, 1893, pp. 401-402, text-figs. 3, 4; Miller, Dunbar, and Condra, 1933, p. 146; Miller and Unklesbay, 1942, pp. 720, 728-729 (not pl. 115, figs. 1, 2); Miller and Youngquist, 1949, pp. 85-88, text-figs. 27, 28.

Tainoceras unklesbayi Miller and Youngquist, 1949, p. 91, pl. 33, figs. 1, 2.

The original description and illustrations of this species by Hyatt (reproduced in full by Miller and Youngquist, 1949) are more satisfactory than most for this author. Hyatt summarized the distinctness of his species by the following opening statement of his description: "This interesting form is easily distinguished from all others of its genus, so far described, by reason of the great transverse breadth of the whorls through the umbilical shoulders, the consequent breadth of the smooth umbilical zones of the whorls and the unusual prominence and size of projecting ridges which form the shoulders." On the other hand, Miller and Youngquist (1949, p. 88) felt that "the most distinctive character of *T. duttoni* seems to be the fact that its conch bears longitudinally elongate dorsolateral and ventrolateral nodes but rounded ventral nodes." These authors had only Hyatt's description and illustrations to go by, which are wanting in several details. The ventral nodes are illustrated on a portion of the inner whorls (Hyatt's fig. 3; here Pl. 4, fig. 1) where they appear rounded in Hyatt's stippled drawing but are in fact obliquely elongate, becoming more markedly so on the living chamber where the nodes are so much larger (Pl. 6, fig. 1).

Miller and Unklesbay (1942) recognized a specimen of this species from the Toroweap formation, near Coconino Point in Grand Canyon, Coconino County, Arizona. Later, Miller and Youngquist (1949, p. 91) introduced a new name for this specimen (*T. unklesbayi*) on the basis that the ventral nodes in *T. duttoni* "are moderately small and are rounded whereas in *T. unklesbayi* they are large and are obliquely elongate." This statement as to the differences is due to Hyatt's faulty drawing, as the specimen has nodes quite comparable to those of the specimen from Arizona. *Tainoceras unklesbayi* is clearly a synonym of *T. duttoni.* Another species which appears to be very similar to *T. duttoni* is *T. shellbachi* Miller and Unklesbay (1942) which the authors differentiated on the basis of the whorls being more slender and the nodes rounded rather than elongate. It is quite conceivable that *T. shellbachi* falls within the limits of variation of *T. duttoni.* Unfortunately, all of these species are known from only one or two specimens.

Hyatt's holotype of *T. duttoni* has a diameter of 162 mm., measures 62.5 mm. for the height of the last whorl and approximately 108 mm. for the width of the last whorl. The umbilicus is 45 mm. in diameter.

Locality and horizon. Upper Valley of Zuni Plateau, 12 to 15 miles S.W. of Grants, a station on N.M.A. and P.R.R., collected by Capt. Dutton, U.S.A. Miller and Youngquist (1949, p. 88) suggest that the horizon is the Chupadera formation.

Repository. Holotype — MCZ 8804.

Genus METACOCERAS Hyatt, 1883

Type species. Nautilus (*Discus*) *sangemonesis* Meek and Worthen, 1861, p. 470; 1866, pp. 386-388, pl. 29, figs. 3-3b; also Kummel 1953b, pl. 1, figs. 3-5.

METACOCERAS WALCOTTI Hyatt

Plate 11, figure 5

Metacoceras walcotti Hyatt, 1891, pp. 337-339, figs. 36, 37; Hyatt, 1893, pp. 394-396, fig. 2.

It is uncertain whether the single specimen of this species in the Museum of Comparative Zoology is any of those illustrated by Hyatt. No data accompanies this specimen except a note by Hyatt which reads "side view of 3 internal whorls showing striae." This specimen could possibly be the holotype figured by Hyatt (1891, fig. 37), but this cannot be established with any certainty.

The specimen at hand is approximately 192 mm. in diameter, and crushed with only one side of the conch preserved. Hyatt's illustrations of this species are reconstructions, and whether they are based on single specimens or are composite drawings cannot be determined. The present illustration is at least of a specimen studied by Hyatt.

Horizon and locality. No horizon or locality data accompanies this specimen but in 1891 and in 1893 Hyatt indicated that his material came from Bend, San Saba County, Texas.

Repository. MCZ 8823.

Superfamily TRIGONOCERATACEAE Hyatt, 1884

Family TRIGONOCERATIDAE Hyatt, 1884

Genus DIODOCERAS Hyatt, 1900

Type species. Nautilus avonense Dawson, 1868, p. 311, fig. 124

DIODOCERAS AVONENSIS (Dawson)

Plate 1, figures 3, 4

Nautilus avonensis Dawson, 1868, p. 311, fig. 124.
Endolobus avonensis, Hyatt, 1894, p. 536, pl. 8, figs. 36-39.
Diodoceras avonensis, Hyatt, 1900, p. 526; Miller, Dunbar, and Condra, 1933, p. 195.

This is one of the many genera that Hyatt established in the 1900 edition of the Zittel-Eastman, Text-Book of Palaeontology. At that time no diagnosis was given, except listing *Nautilus avonensis* (Dawson) as the type, and placement of the genus in the family Estonioceratidae. The genus has been pretty well neglected, except for a brief mention by Miller, et al. (1933). Dawson's type specimen is in the Museum of Comparative Zoology.

The type specimen is an internal cast consisting of the first half volution, the latter half of the second volution, and slightly less than a half volution of the living chamber, and one camera. The fragmentary specimen is embedded in matrix, and only a portion of the venter and one side of the volutions are preserved.

The conch is evolute with a wide, deep umbilicus. Each volution is impressed by the preceding volution only to a very slight degree. The whorls are broad, elliptical, and depressed. The venter is convex, sloping directly to a more acutely rounded umbilical shoulder. The venter, ventral shoulders, and lateral areas are not distinguishable. The umbilical shoulder is broad, convex, and slopes steeply toward the umbilicus. The first half volution consists of a rapidly expanding, slightly curved cone, the whorl section at the most adoral part being oval. The adoral half of the second volution has a whorl section much like that of the living chamber.

The suture is straight except for a shallow, broad V-shaped dorsal lobe. The siphuncle is subcentral in position, that is, slightly ventral of the center of the whorl. On the earlier volutions the siphuncle is closer to the venter than on the outer volution.

Only small remnants of shell are preserved, and these show no surface markings of any kind.

Locality and horizon. Windsor formation, approximately six miles (?) north of Minudie, Nova Scotia.

Repository. Holotype — MCZ 2830.

Remarks. Hyatt (1894, pp. 536-537) commented extensively on this specimen in his classic paper on the Phylogeny of an Acquired Characteristic. He interpreted the presence of a cicatrix at the tip of the tiny first half whorl, an observation in which I am not in agreement. The preservation, being that of an internal cast, is not nearly good enough; and the so-called cicatrix is merely an imperfection in preservation, as the extreme tip of this volution is absent.

Diodoceras has been placed in the family Trigonoceratidae (= Triboloceratidae) by Flower and Kummel, 1950, and Shimanskii, 1957. Aside from the type species no other species of this genus have been reported.

Genus LISPOCERAS Hyatt, 1893

Type species. Lispoceras trivolve Hyatt, 1893, pp. 426-427

LISPOCERAS TRIVOLVE Hyatt

Plate 9, figures 1-4; Plate 10, figure 4; Plate 12, figures 1-3

Lispoceras trivolve Hyatt, 1893, p. 428; Schmidt, 1951, p. 24; Miller and Garner, 1953, p. 116.

Lispoceras trivolve var. *simplum* Hyatt, 1893, p. 428.

The three specimens on which Hyatt established this species and his variety *simplum* are preserved in the Museum of Comparative Zoology. The holotype (Pl. 12, figs. 1-3) measures 46 mm. in diameter and is moderately well preserved. The conch is widely umbilicate with a narrow, shallow impressed zone. The outer whorls have a depressed, lenticular outline with no distinct lateral areas. The venter is broadly arched, merging with a narrowly rounded umbilical shoulder which lies about mid-way between the venter and the dorsum. The umbilical wall is only slightly convex, but very broad. Only the outer volution and one quarter are preserved, the remainder of the inner whorls not being present. The earliest quarter of the preserved volutions are more rounded in cross-section than the more adoral portions.

The depressed lenticular aspect of the whorl section becomes more pronounced adorally.

The conch bears fine longitudinal lines, equally developed over the whole whorl section and on the preserved volutions. Fine growth lines describe a fairly deep, rounded hyponomic sinus. Only fragments of the suture are visible, and it is not possible to develop its pattern. The siphuncle lies roughly mid-way between the center of the whorl and the venter.

The "imperfect living chamber" described by Hyatt (1893, p. 428) is illustrated on Plate 9, figures 1, 2. This specimen is nearly a quarter of a volution in length. The whorl section is lenticular in cross-section, the posterior part measuring 16.3 mm. in height and 28 mm. in width. The anterior part of this living chamber measures 17.3 mm. in height and 24.5 mm. in width; there is a pronounced lenticularity of the living chamber adorally. The portions of the shell which are preserved are smooth except for sinuous growth lines. The dorsal area of the conch has no impresesd zone.

The specimen Hyatt designated var. *simplum* is illustrated on Plate 9, figures 3, 4 and Plate 10, figure 4. This is a fragmentary, distorted specimen consisting of slightly more than one volution, mainly phragmocone, with a small amount of living chamber preserved; the inner volutions are missing. As the specimen is distorted, any measurements would not be significant; this factor may also account for the fact that the whorl section tends to be more oval in cross-section than the holotype. In spite of the faulty preservation, I am inclined to agree with Hyatt that this specimen is conspecific with the holotype. As pointed out by Hyatt, the longitudinal ornament is greatly reduced on this specimen and disappears completely on the most adoral part of the phragmocone. The suture is essentially straight with the shallowest sort of ventral and lateral lobes and an obtuse but prominent dorsal lobe which perhaps is actually an annular lobe. There is no dorsal impressed zone.

Locality and horizon. Lower Carboniferous, Visé, Belgium.

Repository. Holotype — MCZ 5206; paratypes — MCZ 5147, 5148.

LISPOCERAS ROTUNDUM Hyatt

Plate 12, figures 4, 5

Lispoceras rotundum Hyatt, 1893, pp. 428-429.

"The form of the whorl is quite distinct in this fossil, the abdomino-dorsal diameter being but little shorter than the transverse on the last whorl. The whorl is rounder or more nearly approaching a quadrate form, the abdomen less depressed than in trivolve. In other words, the whorl begins when much younger than in *L. trivolve* to show a tendency to form lateral zones, and differentiate the abdomen and dorsum. The sutures are not distinctly different from those of trivolve. The longitudinal ridges are well marked on this cast, occupying the entire surface, but are finer in the older stages than in the young. The transverse lines of growth are also present but much fainter, and these differed only slightly from that of trivolve. The aperture has a blunt V-shaped hyponomic sinus and very broad, low crests on either side, rising to the highest point at the abdominal angles (or where these would be if present), very faint sinuses near the umbilici rising into a saddle on the dorsal face.

''This fossil shows plainly that the saddles of the sutures across the dorsum were continuous in the metanepionic sub-stage, and that the subsequent introduction of annular lobes when the whorls came into contact split this saddle in the center of the dorsum, as in other species of the same family.

''Siphuncle is above the center in all stages observed, but is somewhat more above this point in the adult, about one-third of the distance towards the venter.

''A fragment of the young in paranepionic sub-stage shows the whorl to have been at this time elliptical, the ventro-dorsal diameter longer than the transverse, with very slight ventral and dorsal saddles and lateral lobes in the sutures; the siphuncle is just above the center. In the ananeanic sub-stage the transverse diameters become the longest. There is a distinct depression of the rounded abdomen and a tendency to form lateral zones with abdominal angles and umbilical shoulders, the venter being somewhat narrower than the dorsum. The sutures in correlation with these changes have hardly perceptible ventral and lateral lobes and an equally faint dorsal or annular lobe. This last is in the center of a broad dorsal saddle which occupies the umbilical zones as in *L. trivolve.*

''There is also a faint trace or nascent zone of involution on this part which may indicate contact with the next younger whorl. This ananeanic whorl is decidedly broader and more depressed than the next to be described. The siphuncle is somewhat farther removed from the center than in the nepionic stage.

''The latest stage preserved consisted of the cast of a complete living chamber with the septal floor exposed. In this whorl, which probably represents some part of the paraneanic sub-stage, the transverse diameters continue to be a little longer than the ventro-dorsal. It has more rounded umbilical shoulders and more depressed abdominal angles; the lateral zones are narrower and more convergent outwardly than in younger whorls. The umbilical zones and zone of impression are not distinctly differentiated, the presence of this last zone being indicated on the cast more by the faint lobe in the dorsal than by the form of that side of the whorl. The shell would perhaps have shown traces of contact, but this was not present. In other words, the whorl approximates more to the diagonal type at this time than it has previous to this in the early part of the ananeanic sub-stage.

"The sutures differ from those of the ananeanic sub-stage only in the larger size and better definition of annular lobe, which was barely indicated and only seen after very careful inspection in the early ananeanic sub-stage, about one-half of a whorl younger. The siphuncle is small and its position the same as in the preceding sub-stage.

"The dorso-ventral diameter of the aperture was 13 mm., and the transverse about the same length; the same diameters at the base of the living chamber were respectively 10 mm. and 8.5 mm. The diameter of the whole shell when restored was reckoned at 35 mm."

Locality and horizon. Carboniferous, Kildare, Ireland.

Repository. Holotype — MCZ 5146.

Genus LEUROCERAS Hyatt, 1893

Type species. L. aplanatum Hyatt, 1893, pp. 437-438

LEUROCERAS APLANATUM Hyatt

Plate 1, figures 1, 2

Leuroceras aplanatum Hyatt, 1893, pp. 437-438; Miller and Garner, 1953, p. 116.

The specimen upon which Hyatt based his genus and species is in the Museum of Comparative Zoology, and is another of the genotypes established by Hyatt but never illustrated. The specimen is involute, compressed, broadly lenticular in cross-section. The diameter of the conch is 78 mm., the width of the most adoral whorl is estimated to be 29 mm., and the height 35 mm. The umbilicus measures 18 mm. in diameter. The whorl section is compressed with broad, convex, lateral areas and narrowly rounded venter. The greatest width of the whorl is approximately at the center of the whorl. The umbilical shoulders are broadly convex, and the umbilical shoulder slopes to the umbilical seam at a steep angle.

The suture forms a narrow rounded ventral saddle, a broad shallow lateral lobe extending across the whole whorl-side, with the beginning of a saddle on the umbilical whorl. Presumably, there is a shallow dorsal lobe; but on this I cannot be certain; nor does there appear to be a small annular lobe as suggested by Hyatt (1894, p. 437). The lateral areas of the penultimate whorl bear three fine longitudinal lines located on and adjoining the umbilical shoulder. The outer volution is completely smooth. Whether or not these lines are present on the innermost whorls cannot be told because of poor preservation of this portion of the conch.

The siphuncle lies slightly ventral of the center of the whorl, The living chamber on the holotype occupies the outer quarter volution.

Remarks: Hyatt placed his new genus in his family Rineceratidae and believed *Nautilus perplomatum* Portlock (1843, p. 403, pl. 29A, fig. 11) from the Lower Carboniferous of Ireland, *Coelonautilus derbiensis* Foord (1891, pp. 131-132; = *N. chesterensis* deKoninck, 1878, p. 97, pl. 31, figs. 4a-c; Tzwetaev, 1888, p. 54, pl. 5, figs. 19-22) and *Coelonautilus globularis* Foord (1891, pp. 132-133) as being congeneric. With this conclusion I have serious misgivings. Portlock's species is so poorly described and illustrated that direct comparisons are at best tenuous. The remaining species are much more inflated forms of quite different aspect.

Assignment of *Leuroceras* to the Trigonoceratidae is based largely on the presence of longitudinal lines on the inner whorls; the general features of the conch suggest that it may be a compressed member of the Liroceratidae. However, since the genus is known only from a single specimen, whose preservation leaves much to be desired, it is probably best to leave it in the Trigonoceratidae for the time being with question.

Locality and horizon. Lower Carboniferous, Visé, Belgium.

Repository. Holotype — MCZ 3387.

Genus STROBOCERAS Hyatt, 1884

Type species. Gyroceras hartii Dawson, 1868, p. 311, fig. 124.

STROBOCERAS ANGLICUM Hyatt

Plate 14, figures 1-4

Stroboceras anglicum Hyatt, 1893, pp. 410-411.

Hyatt did not illustrate the two specimens he assigned to this species, but his description is as follows: "*Stroboceras anglicum,* n.s., is a more compressed phylogerontic form, also in the collection of the Museum of Comparative Zoology, from Settle, in Yorkshire. The shell has the elevated, sulcated central ventral zone and fluted lateral zones and fluted faces inside of these on the lateral aspects, and internally gibbous lateral faces with longitudinal ridges dividing them into facets at a much earlier stage. In fact all the characteristic elements of the mature whorl of *Stroboceras* as they appear in the early stage of *edwardsianum* are so rapidly developed that the whorl in the paranepionic substage is equivalent to that of the early ephebic stage in *edwardsianum* and very similar to that figured by De Koninck in his figure 10, referred to above, but the lateral faces are narrower and have broad lateral flutes without ridges and lateral gibbous zones with three ridges. In these characteristics the shell approximates to the *Nautilus sulcatus,* equal here to *S. belgicum,* as figured by De Koninck in "Calcaire Carbonifere," pl. 27, fig. 2, but it is much smaller, 14.5 mm. in diameter instead of nearly 25 mm. in diameter, as in that figure.

"It is, in other words, a fine example of the action of Tachogenesis (accelerated or abbreviated development), and this extends to the earlier appearance of the first quarter of the second whorl of the gerontic form and characteristics of an aged whorl. The abdomen becomes smooth, very narrow and concave, the sides smooth, the lateral fluted facets disappear, and the sole distinction between the lateral ventral zones and the gibbous lateral faces lies in the difference of the curves. The whorl becomes as purely senile as is the old whorl of *S. sulcifer* as shown in De Koninck's figure. This species is consequently more specialized and accelerated in development than *edwardsianum,* and *edwardsianum* is more specialized and has therefore more accelerated development than *S. sulcifer* and some other species in which the whorls are stouter, not so much compressed and the young still more like the adults of *Coelonautilus stygialis.* The progressive stages are also more prolonged in these last named and less specialized forms, and the gerontic stage begins later in the life of the individual."

The holotype is the specimen illustrated on Plate 14, figures 1 and 2. This specimen measures 29 mm. in diameter, 12.3 mm. for the height of the last whorl, and 9.5 mm. for the width of the last whorl; the umbilicus is 11 mm. in diameter. The paratype consists of slightly more than one half of an early volution (Pl. 14, figs. 3, 4). This specimen is 15 mm. in diameter.

Locality and horizon. Carboniferous, Settle, Yorkshire, England.

Repository. Holotype — MCZ 3392a, Paratype — MCZ 3392b.

Genus SUBCLYMENIA d'Orbigny, 1850

Type species. Goniatites evolutus Phillips, 1836, p. 237, pl. 20, figs. 65-68.

SUBCLYMENIA OCCULTA Hyatt

Plate 2, figures 1, 2

Subclymenia occulta Hyatt, 1893, pp. 414-416.

There are two specimens in the Museum of Comparative Zoology, illustrated here on Plate 2, that are in a tray with a label in deKoninck's handwriting reading, "*Nautilus* n. sp. Carb., Visé" and another label written by Hyatt reading, "*Subclymenia gibbosa*, Hyatt Geol. Surv. Tex." In his discussion of the genus *Subclymenia* in 1894, Hyatt clearly states that he had specimens from Yorkshire and Visé; but he also stated that he had only one specimen of *Subclymenia gibbosa* and one of *S. occulta.* To the best of my knowledge no specimens of this genus from Yorkshire are in the Museum at the present time.

Careful study of the two specimens in the collection and Hyatt's descriptions of them clearly indicates that one of the specimens (Pl. 2, figs. 1, 2) is his type of *Subclymenia occulta.* The other specimen (Pl. 2, figs. 3, 4) is probably the one Hyatt assigned to *S. gibbosa.* However, as will be more fully developed in the discussion of that species, there are some discrepancies between Hyatt's description and the specimen. This I believe can be explained as a result of Hyatt's not clearly distinguishing which specimen he was referring to in his discussion of the ornamentation and internal whorls. He stated that he had laid bare the conical apex of the conch in his two species, *S. occulta* and *S. gibbosa,* then proceeded into a long detailed description which agrees well with the features of *S. occulta* but are not shown, for the most part (due to preservation) in the other specimen. It is possible that the initial volutions of the latter specimen may have been destroyed since Hyatt's study; there are, however, no indications on the specimen to show this. It is more readily apparent that the specimen illustrated here on Plate 2, figures 1, 2 is the type of *S. occulta.* On this specimen Hyatt mentions filing away the venter to expose the suture; these marks are present on the specimen.

The type specimen of *S. occulta* is a moderately well preserved evolute, slightly distorted conch measuring 61.6 mm. in diameter. Approximately the last half volution is living chamber; the rest of the shell is phragmocone. The whorl section of the outer volution is subrectangular. The whorl section of the adoral part of the living chamber measures 22 mm. in width and 20.3 mm. in height. The venter of the outer volution is only slightly concave, the ventral shoulders angular. The lateral areas are broadly convex merging onto broadly rounded umbilical shoulders which in turn grade onto a steeply sloping, convex umbilical wall.

The initial portion of the conch is a slender, slightly curved, slowly expanding cone which bears fine radial growth lines and on the lateral area longitudinal lines. The intersection of the growth lines and longitudinal lines gives a beaded appearace. Beginning approximately at the end of the first half volution, the growth lines project adapically across the umbilical wall; on the ventral half of the lateral areas they curve adorally, a pattern which continues through the remainder of the conch. Beginning at the adoral end of the first volution, the longitudinal lines become confined to the central half of the lateral areas and continue in this fashion to the aperture. The better preserved areas of the venter on the outer whorl show four fine longitudinal lines closely spaced next to the angular ventral shoulder. The venter inside these longitudinal lines is smooth except for the deep tongue-shaped pattern of the very fine growth lines inscribing a hyponomic sinus.

The only portion of the suture that is exposed is the deep V-shaped ventral lobe which Hyatt mentioned.

Locality and horizon. Lower Carboniferous, Visé, Belgium.

Repository. Holotype — MCZ 8824.

SUBCLYMENIA GIBBOSA Hyatt

Plate 2, figures 3, 4

Subclymenia gibbosa Hyatt, 1893, pp. 414-416.

Hyatt introduced this species name for the specimen which deKoninck (1880, pp. 83-84, pl. 45, figs. 5, 6) assigned to Phillips' (1836, p. 237, pl. 20, figs. 65-68) species, *S. evoluta,* the genotype of *Subclymenia.* He concluded that the Belgian specimens differed from the British species in that they were "broader on the abdomen at all stages of growth, the English form being narrower on the abdomen, with lateral zones decidedly convergent, smaller whorls, and the ventro-dorsal diameter also longer proportionately than in the Belgian form."

As mentioned in the discussion of *S. occulta,* there are only two specimens in the collections of the Museum of Comparative Zoology, both from the Lower Carboniferous of Visé, Belgium. The label in the tray with these two specimens, written by Hyatt, reads *Subclymenia gibbosa.* However, one of the specimens is clearly the type of *S. occulta.* The other specimen, illustrated here on Plate 2, figures 3, 4, I believe is the one Hyatt had assigned to *S. gibbosa* in spite of the fact that there are discrepancies between his discussion and the specimen — discrepancies that are a result of Hyatt's long discussion which not always clearly indicated which of the two species he had in mind.

The present specimen is a distorted conch of fair preservation, except for the innermost volutions. The adoral quarter volution is living chamber. The shape of the whorl section is very similar to that of *S. occulta* except that the venter on the living chamber is much more concave.

The ornamentational pattern of sinuous growth lines and longitudinal lines, with a beaded appearance, is present only on the penultimate adoral half volution. The adoral half volution has no ornamentations at all on the lateral areas, which could possibly be due to poor preservation; and there are the faint longitudinal lines on the venter next to the ventral shoulder.

The long, sinuous, V-shaped ventral lobe is well exposed. This is followed by a long, narrow, angular saddle on the acute ventral shoulders, and a broadly, deeply concave lobe that extends from the ventral shoulder to the umbilical seam. The siphuncle was not observed.

Locality and horizon. Lower Carboniferous, Visé, Belgium.

Repository. Holotype — MCZ 8825.

Genus THRINCOCERAS Hyatt, 1893

Type species. Thrincoceras depressum Hyatt, 1893, pp. 430-432, figs. 9-10.

THRINCOCERAS DEPRESSUM Hyatt

Plate 23, figure 1

Thrincoceras depressum Hyatt, 1893, pp. 430-432, figs. 9-10; Schmidt, 1951, p. 24; Miller and Garner, 1953, p. 116.

Hyatt's illustration of the type specimen of this species leaves much to be desired as it is largely a reconstruction and not an accurate drawing of the specimen. The conch is broadly evolute with a wide deep umbilicus. The whorls are depressed, subquadrate with a broad flattened venter, rounded ventral shoulders, narrow convex lateral areas and broadly rounded umbilical shoulders. The umbilical walls are broad and slope into the umbilical seam at a high angle. The conch measures approximately 115 mm. in diameter, 61 mm. for the width of the last whorl, 45 mm. for the height of the last whorl, and 52 mm. for the diameter of the umbilicus.

The conch bears fine longitudinal lines throughout its length which are most conspicuous on the umbilical shoulders and lateral areas and less so on the venter. This, however, is most probably a reflection of preservation.

The specimen bears numerous cracks which cross the whorls at many different angles. Hyatt selected one of the cracks as most probably coinciding with the course of the suture. There does not appear to be any real justification for this observation. The position of the siphuncle is not visible.

Locality and horizon. Bullitt County, Kentucky, presumably from Mississippian strata.

Repository. Holotype — MCZ 8813.

THRINCOCERAS KENTUCKIENSE Hyatt

Plate 20, figure 1; Plate 21, figure 1; Plate 22, figures 1, 2

Thrincoceras kentuckiense Hyatt, 1893, pp. 432-434, figs. 11-15; Foord, 1900, pp. 99-100.

The two specimens on which Hyatt established this species are in the collections of the Museum of Comparative Zoology. The original drawings used to illustrate these specimens do not accurately portray the poor preservation and are inaccurate in many details. The holotype (Pl. 20, fig. 1; Pl. 22, fig. 1) measures

165 mm. in diameter, and is a broadly evolute conch with a very shallow impressed zone. The outer whorl measures approximately 65.5 mm. in width, 62 mm. in height, and the umbilicus is 64 mm. in diameter. The outer whorl is subquadrate in cross section with a broad, slightly arched venter, sharply rounded ventral shoulders, flattened lateral areas, a conspicuous subangular to rounded umbilical shoulder, and a broad umbilical wall that is slightly convex and sloping to the umbilical seam at approximately a 45 degree angle. The inner whorls are more depressed and rounded in cross section. Though a portion of the inner volutions are absent, it seems probable that there is an umbilical perforation of roughly 10 mm. in diameter.

The suture bears a very shallow ventral, lateral, and dorsal lobe with saddles on the ventral and umbilical shoulders. The siphuncle is small, tubular, and located about midway between the center of the whorl and the venter.

Fine longitudinal lines are preserved on the umbilical wall of the penultimate half volution; the remainder of the conch is so eroded and poorly preserved as to show no surface features.

The paratype, illustrated on Plate 21, figure 1 and Plate 22, figure 2, is slightly better preserved than the holotype though more of the innermost volution is missing. Hyatt's original illustration of this specimen shows the longitudinal lines over the whole length of the specimen, but they are actually only vaguely visible on the first volution. This specimen measures 159 mm. in diameter, 60 mm. for the width of the last whorl, 54 mm. for the height of the last whorl; and the umbilicus is 68 mm. in diameter. In whorl shape, degree of evolution, ornamentation, suture, etc., this specimen is nearly identical to the holotype.

Locality and horizon. Franklin County, Kentucky, presumably from Mississippian strata.

Repository. Holotype — MCZ 8811, Paratype — MCZ 8812.

Genus VESTINAUTILUS Ryckholt, 1852

Type species. Nautilus koníncki d'Orbigny, 1847, pl. 95, figs. 1-6.

VESTINAUTILUS CARINIFORMIS Hyatt

Plate 7, figures 4, 5

Vestinautilus cariniformis Hyatt, 1893, p. 420.

When Hyatt established this species, he stated that it "is part of De Koninck's *cariniferous* [*sic*] figured in his 'Calcaire Carbonifère' on plate 30, figure 2, a-b (not figure 1)." The specimen referred to on plate 30 is a juvenile of *Nautilus koninckii,* the type species of *Vestinautilus*. The *cariniferus* of De Koninck (1878) are illustrated on his plate 28, figures 1-5. It is presumed that plate 30 in Hyatt's statement is an error and that he actually meant plate 28. The *cariniferus* of De Koninck's plate 28, figures 1-5 were all placed by Foord in his species *Coelonautilus paucicarinatus* (Foord, 1891, p. 116). The specimen illustrated by Foord (his figure 17) is nearly identical in its features to the specimen of *cariniferus* illustrated by De Koninck (1878, pl. 28, figs. 1a, b). Hyatt established *cariniformis* for forms which acquired a smooth venter early, as illustrated by De Koninck's *cariniferus* (1878, pl. 28, figs. 2a, b).

Hyatt's type of *V. cariniformis* is a slightly deformed specimen of 54 mm. in diameter, and measuring 34 mm. for the width of the most adoral whorl of the conch and 22.7 mm. for the height. Only the adoral one-half volution and the inner whorls on one side of the conch are well preserved. The venter is broad, slightly convex with broadly rounded ventral shoulders that end at a sharp ridge that disappears on the living chamber. Approximately 3 mm. below this ridge there is another ridge which also disappears adorally on the living chamber but not as markedly as the ridge on the ventral shoulder. From the second ridge there extends a broad, slightly convex umbilical wall. The only other surface markings are very faint growth lines which inscribe a deep rounded hyponomic sinus on the venter.

Only a small portion of the suture is visible on the venter. The siphuncle appears to be about central in position.

Locality and horizon. Lower Carboniferous, Visé, Belgium.

Repository. Holotype — MCZ 8827.

VESTINAUTILUS KONINCKII (d'Orbigny)

Plate 14, figures 5-10

Vestinautilus koninckii, Hyatt, 1872, p. 91, pl. 4, figs. 7-9; Hyatt, 1894, pp. 540-541, 602, pl. 9, figs. 5-13.

The specimen of Hyatt's plate 4, figures 9 and 10 (1894) is preserved in the Museum of Comparative Zoology and is illustrated here. This specimen was thought by Hyatt to represent the nepionic stage and ananeanic substage. There is a note with the specimen stating that the apex, which according to Hyatt represented the "ana- and metanepionic with rounded whorl and cyrtoceran form and ornament like *T. puzosianum*," was lost when the specimen was mounted.

Locality and horizon. Carboniferous, Tourney, Belgium.

Repository. MCZ 8828.

Superfamily AIPOCERATACEAE Hyatt, 1883

Family SOLENOCHILIDAE Hyatt, 1893

Genus ONCODOCERAS Hyatt, 1893

Type species. Oncodoceras fusiforme Hyatt, 1893, pp. 455-456.

ONCODOCERAS FUSIFORME Hyatt

Plate 26, figures 1, 2; Plate 27, figures 1, 2; Plate 28, figures 1, 2;
Plate 29, figures 1, 2; Plate 30, figure 6

Oncodoceras fusiforme Hyatt, 1893, pp. 455-456.

Hyatt's description of his new genus and species is as follows: "The young of the species of this genus, until the end of the ananeanic sub-stage, and perhaps throughout the whole of the neanic stage, is similar to the young and full grown shells of *Aipoceras.* The trigonal form is represented, but it is much modified in all the shells of *Oncodoceras fusiforme.* In some of them it is indicated in the slight flattening of the dorsum and slight convergency of the sides, but in others the whorl is rounded.

"The sutures of the ephebic stage are straight or have slight ventral and lateral lobes, with dorsal saddles and annular lobes.

"The siphuncle is ventral and the shell is smooth.

"The living chambers of the full grown shell are depressed, elliptical in section, and the apertures are apt to be contracted, but this last characteristic may be dependent largely upon the age of the specimen.

"There is no impresesd zone in the type, but this may be present in some other species.

"The type is *Oncodoceras fusiforme,* from Kildare, a specimen consisting of a living chamber complete, with first septum and aperture. This species is closely similar to De Koninck's *conspicuus* in the general aspect of the living chamber and whorl. It, however, has no impressed zone, the dorsum being entire and rounded in four specimens, two from Kildare, one from near Cork, and one from Visé. All four have living chambers of about the same size and age as that figured in *Asymptoceras conspicuum*, sp. De Koninck, in his 'Calcaire Carbonifère.' The aperture is, however, much less contracted and has a depressed oval opening in place of the quadrate outline depicted by De Koninck. It has a broad hyponomic sinus, low crests on either side, reaching their extreme extension on the line of what may be called the nascent abdominal angles. There are shallow narrow sinuses on the imperfectly formed, narrow and rounded lateral zones, very low broad crests on the imperfectly formed umbilical shoulders, and an equally dorsal sinus. The increase by growth is extremely rapid, more so than in *A. gibberosum,* and the full size is reached at the end of the first whorl; the living chamber takes up somewhat less than one-half of this volution.

''The form is like that of *A. gibberosum,* and can be easily confused with that species on the second quarter of the whorl, but later the venter becomes more depressed and the ventro-dorsal diameters are shorter than the transverse, especially near the aperture. The sutures of the adult have very shallow ventral lobes and are either straight or have faint lobes on the lateral faces and a very small annular lobe on the dorsum. The septa are not deeply concave and the siphuncle is ventral.''

The holotype (Pl. 26, figs. 1, 2; Pl. 27, fig. 1) consists of body chamber and first septum and a fairly well preserved aperture. At its widest part the body chamber has a width of 60.7 mm. and a height of 49 mm. The body chamber inscribes a broad curvature, the venter is broadly rounded, grading gradually onto arched flanks. On a portion of the body where a small piece of shell is preserved, the umbilical shoulders are abruptly rounded; the dorsum is broadly convex with no impressed zone. From the last septum to the aperture the body chamber flattens appreciably. The last septum measures 44.5 mm. in width and 42 mm. in height. The aperture has a broad, fairly deep ventral sinus, a shallow lateral sinus; and there appears to be a very shallow dorsal sinus. The siphuncle is small and approximately one mm. from the venter.

The paratype of Plate 27, figure 2 and Plate 28, figures 1, 2 is a slightly distorted specimen of 95 mm. in diameter of one-half volution of which approximately one-third is phragmocone. A fair amount of the shell is preserved, and this is completely smooth. There is no impressed zone. The second paratype (Pl. 29, figs. 1, 2 and Pl. 30, fig. 6) consists of slightly more than a half volution of which approximately half is phragmocone. The whorl section is oval with no indication of the umbilical shoulders as in the holotype. The anterior part of the body chamber is slightly contracted, but the aperture is not preserved except for a small area on the venter which indicates a deep ventral sinus.

Hyatt's paratype from Cork, Ireland, is a highly distorted body chamber which appears to be conspecific with the other specimens.

Locality and horizon. Holotype and paratype from Lower Carboniferous, Kildare, Ireland. Another paratype from Lower

Carboniferous, Visé, Belgium. Unfigured paratype from Lower Carboniferous, Cork, Ireland.

Repository. Holotype — MCZ 5143; paratypes — MCZ 5144, 5201, 5202.

Superfamily CLYDONAUTILACEAE Hyatt, 1900

Family LIROCERATIDAE Miller and Youngquist, 1949

Genus LIROCERAS Teichert, 1940

Type species. Coloceras liratum Girty, 1911, p. 144.

LIROCERAS GLOBATUM (de Koninck)

Plate 18, figures 1-9; Plate 19, figures 1-3

Coloceras globatum, Hyatt, 1894, pp. 541-543, plate 10, figures 1-14.

Hyatt in his 1894 paper devoted two and one-half pages of text and fourteen illustrations of five specimens of this species to present the history of the dorsal furrow. It is of special interest to note his conclusions: "the action of tachygenesis upon degenerative characters is thus clearly apparent throughout the neanic and ephebic stages in this interesting species. This fact is entirely in accord with the principles of Bioplastology as explained above with regard to the action of this law upon retrogressive characters." (Hyatt, 1894, p. 543.)

Hyatt's specimen of his plate 10, figures 1, 2, which illustrated the nepionic and neanic volutions is illustrated here on Plate 18, figures 1-3. Hyatt's specimen of his plate 10, figures 10-12 is the specimen illustrated here on Plate 18, figures 4-6. From this same specimen Hyatt illustrated cross sections of the "meta and paranepionic substages" (his figures 3-6) and an enlarged oblique view of the apex showing the ana- and metanepionic substages. Unfortunately, the apex of this specimen has been broken off and is not in the collections.

The specimen of Hyatt's plate 10, figures 8, 9 which he indicates as showing the ananepionic, and a part of the metanepionic substages, and the cicatrix is illustrated here on Plate 18, figures 7-9. None of the features which Hyatt thought indicated a cicatrix and included on his ilustrations (his plate 10, fig. 9 and the apex of fig. 8) are visible on the specimen — the apex is perfectly smooth with no surface markings of any kind.

The fragmentary specimen of Hyatt's plate 10, figure 13, is in the MCZ collections but not illustrated here because of its poor preservation. However, the specimen of Hyatt's plate 10, figure 14, is illustrated here on Plate 19, figures 1-3.

Locality and horizon. Lower Carboniferous, Visé, Belgium.

Repository. MCZ 8818 (Pl. 18, figs. 1-3), MCZ 8819 (Pl. 18, figs. 4-6), MCZ 8820 (Pl. 18, figs. 7-9), MCZ 8830 (Pl. 19, figs. 1-3).

Genus COELOGASTEROCERAS Hyatt, 1893

(= *Solenoceras* Hyatt, 1884 [obj.] *non* Conrad, 1860; *Conradiceras* Cossman, 1900 [obj.])

Type species. Coelogasteroceras coxi Gordon, 1960 (nom. subst. pro *Nautilus canaliculatus* Cox, 1857, pp. 575-576, pl. 10, figs. 3-3a, *non N. canaliculatus* Eichwald, 1857).

COELOGASTEROCERAS COXI Gordon

Plate 11, figures 3, 4

Coelogasteroceras canaliculatum Hyatt, 1894, pp. 498-499, Plate 10, figure 33.

The specimen from which Hyatt developed his illustration of the "meta- and paranepionic volutions" of this species is in the collections of the Museum of Comparative Zoology. It is a phragmocone of fair preservation measuring 36.6 mm. in diameter. Hyatt's illustration (1894, pl. 10, fig. 33) was made from a polished section of the inner volutions. Due to the poor state of preservation of this portion of the specimen, the outlines of the whorls are just barely visible.

The specimen studied by Hyatt is very typical for the species in all respects.

Locality and horizon. Carboniferous, Edmondson County, Kentucky.

Repository. MCZ 8808.

Genus PERIPETOCERAS Hyatt, 1894

(= *Cyclonautilus* Hind, 1911; *Periptoceras* Chao, 1954; *Nannoceras* Hyatt, 1894 [*nom. null.*])

Type species. Nautilus freieslebeni Geinitz, 1843, p. 95, figured in 1841, p. 637, pl. 11, figs. 1a-c.

PERIPETOCERAS FREIESLEBENI (Geinitz)

Plate 10, figures 1-3; Plate 11, figures 1, 2

Peripetoceras freieslebeni, Hyatt, 1894, pp. 545-546, pl. 11, figs. 1-3.

When Hyatt established the genus *Peripetoceras*, he designated *N. freieslebeni* (Geinitz, 1841, p. 637, pl. 11, fig. 1) as type;

however, he was clearly describing and interpreting the genus on two specimens from the Permian of Tunstall Hill, England, which are in the Museum of Comparative Zoology. The original illustrations of *Nautilus freieslebeni* (Geinitz, 1841, plate 11, figures 1a, b, c) are drawings of what appear to be a deformed individual. The specimen is a smooth subglobular nautilicone with whorls that are slightly flattened laterally and ventrally with small umbilici, a deep rounded hyponomic sinus, slightly sinuous sutures, and a small subcentral siphuncle. At a later date Geinitz (1848, pl. 3, figs. 1a, b, c) again described and illustrated the same species. The illustrations of the 1848 paper are superior to those of the 1841 paper, and even though there are differences between the two sets of illustrations, they appear to be of the same specimen. A later illustration of this species by Geinitz (1861, plate 11, figures 7a, b, c) is of a different specimen, much smaller in size, of rounded whorl section, evolute conch — a specimen with the appearance of an evolute *Liroceras* or *Hemiliroceras*. The identity of this specimen with the type of *N. freieslebeni* is not clearly established.

Hyatt had two specimens, one of which (Pl. 10, figs. 1-3) consists of one-third volution of living chamber plus a fragmentary quarter volution of an inner whorl. The other specimen, a paratype (Pl. 11, figs. 1, 2), consists of one-half volution of phragmocone — this is the specimen which Hyatt (1894, Pl. 11, figs. 1-3) illustrated with cross-sectional drawings of the whorl section.

The former specimen consists mainly of living chamber, has a subquadrate, elliptical, depressed whorl section. The venter is broad and flattened, the ventral shoulders broadly rounded. The lateral areas are only slightly convex and converge toward the venter. The umbilical shoulder is more sharply rounded than the ventral shoulder, and the umbilical wall is convex and slopes steeply to the umbilical seam. The umbilicus must have been approximately one-fifth the diameter of the conch and rather deep. The siphuncle is small, circular in outline, and located midway between the center of the whorl section and the dorsum. Only a small remnant of the test is preserved on the umbilical shoulder, and this shows prominent growth lines.

The second specimen is identical to the first in the shape of the whorl section. Portions of the suture are visible, and these show a shallow ventral and lateral lobe. More of the test is preserved, and these inscribe a deep rounded sinus on the venter.

Locality and horizon. Permian, Tunstall Hill, England.

Repository. MCZ 8806, 8807.

Remarks. The inadequate description and illustrations of Hyatt's specimens and the same for the German specimens described by Geinitz readily explain the difficulties encountered in the interpretation of this genus and the fact that it has been recognized and discussed by few subsequent authors. Miller and Youngquist (1949, pp. 119-120) briefly commented on this genus and concluded that no species from the Permian of North America are referable to it. These authors did, however, believe that it should contain *Solenochilus henryvillense* Miller and Gurley of the Lower Mississippian of Indiana, *Cyclonautilus umbilicatus* Hind of the early Upper Carboniferous of England, and possibly *C. dubius* Bisat of the early Upper Carboniferous of Wales. As pointed out by Miller and Youngquist, *C. umbilicatus* is the genotype of *Cyclonautilus* Hind, which should be suppressed as a synonym of *Peripetoceras* which has priority. Recently, Gordon (1960, p. 137) described *P. whitei* from the Coal Measures, Fountain County, Indiana. *Peripetoceras hsuyuchiani* Chao (1954, pp. 44-45, pl. 6, figs. 5-6) from the Permian of Hunan, China, is wrongly placed in *Peripetoceras;* it appears to be a typical representative of *Liroceras. Nautilus wanneri* Haniel (1915, pp. 136-138, pl. 55, fig. 4; pl. 56, fig. 1) is similar to *Peripetoceras freieslebeni* in its flattened ventral and lateral areas; it differs only in its much greater degree of involution. I would consider it a valid species of *Peripetoceras.*

Genus POTOCERAS Hyatt, 1894

Type species. Potoceras dubium Hyatt, 1894, pp. 537-539, pl. 10, figs. 15-22.

POTOCERAS DUBIUM Hyatt

Plate 8, figures 1-4; Plate 19, figures 16-18

Potoceras dubium Hyatt, 1894, pp. 537-539, pl. 10, figs. 15-22.

The interpretation of this genus has been a difficult problem ever since its introduction because Hyatt's description was mainly in context of his thesis on the history of the impressed zone, and his illustrations were nothing more than outline drawings. In addition, the locality and horizon of Hyatt's type specimen is unknown.

The type and only specimen of this species is in the Museum of Comparative Zoology. It consists of a phragmocone 37.5 mm.

in diameter. Hyatt had broken the specimen into a number of distinct segments to facilitate his study of the impressed zone. The conch is moderately involute with depressed, smooth whorls. The most adoral camerae measure 17.7 mm. in height and 25.6 mm. in width. The venter is broadly arched grading imperceptibly onto slightly arched lateral areas. The umbilical shoulders are more clearly marked and the umbilical wall convex but sloping to the umbilical seam at a steep angle. The umbilicus measures 9.5 mm. in diameter. The siphuncle is subcentral in position; that is, it is closer to the venter than to the dorsum. The suture is essentially straight except for the barest indication of a slight lobe on the flanks, a very shallow dorsal lobe and an annular lobe. Hyatt's illustrations of these adoral camerae (1894, pl. 10, figs. 20, 21), which are outline drawings, are duplicated here in the form of photographs of the specimen (Plate 8, figures 1, 2). The front view of the ana-, meta-, and paranepionic substages and the neanic volution (in part Hyatt's, pl. 10, fig. 16, 1894) is shown on Plate 19, figure 18. The initial part of the conch is an asymmetrical cone of 6.5 mm. in length, at which time the first strong curvature of the shell takes place and also the beginning of the impressed zone. This first volution has very faint radial and longitudinal lines. As indicated by Hyatt himself, these lines are much more distinct in his drawings than they are on the specimen. The cicatrix, shown in Hyatt's plate 10, figure 17, is actually a very faint transverse narrow depression, but one can't be sure if it is an original shell feature or due to scratching or impact during the cleaning of the specimen. Hyatt's figures 17 and 18 of his plate 10 of the "ana-, meta-, and paranepionic stages" are correct insofar as the gross outline of the shell is, but the details of the shell surface are not faithfully reproduced.

On this earliest volution the siphuncle is very near the venter; as growth proceeds the position of the siphuncle becomes more central.

Locality and horizon. There is no locality or horizon data with this specimen. Hyatt ventured an opinion that it is Devonian and had verification of his opinion from a brachiopod attached to the conch which Schuchert thought compared closely with species of *Martinia* from the IbergerKalk of the Upper Devonian of Grund, Germany.

I sent the same brachiopod to G. A. Cooper, and he could not make a positive identification but thought that some Mississippian forms from the United States are more similar to it than any

Devonian forms. He also adds that the lithology is suggestive of the Visean.

Repository. Holotype — MCZ 8805.

Family EPHIPPIOCERATIDAE Miller and Youngquist, 1949

Genus EPHIPPIOCERAS Hyatt, 1884

Type species. Nautilus ferratus Cox, 1857, pp. 574-575, pl. 10, figs. 2-2a.

EPHIPPIOCERAS FERRATUM (Cox)

Plate 15, figures 4-7

Ephippioceras ferratum, Hyatt, 1894, p. 539, pl. 10, figs. 23-26.

The specimen studied by Hyatt for his 1894 paper is in the Museum of Comparative Zoology. Unfortunately, the portion of the innermost volutions that Hyatt illustrated and discussed is not in the collections. The mature conch is a fairly well preserved phragmocone of 45.5 mm. in diameter and is illustrated here. The general characters of this genus and species have been recently discussed by Miller and Youngquist (1949, p. 129), and Hyatt's specimen adds nothing new to this interpretation, except that few good illustrations exist in the literature.

Locality and horizon. Carboniferous, Edmondson County, Kentucky.

Repository. MCZ 8816.

Superfamily NAUTILACEAE de Blainville, 1825

Family NAUTILIDAE de Blainville, 1825

Genus EUTREPHOCERAS Hyatt, 1894

Type species. Nautilus dekayi Morton, 1834, p. 33, pl. 8, fig. 4

EUTREPHOCERAS FAXOENSE Hyatt

Plate 15, figures 8, 9

Eutrephoceras faxoense Hyatt, 1894, p. 558, pl. 13, figs. 9-12.

In proposing this species Hyatt commented that it "differs from *Eutrephoceras dekayi* in the extreme subdorsan position and smaller size of the siphuncle in the nepionic stage, has larger umbilical openings and is also apparently a smaller form. Otherwise it is very close in sutures and form to this species." Hyatt's holotype is a phragmocone of one-half volution measuring 35.5 mm. in diameter, preserving the inner volutions in an excellent state of preservation. The conch is smooth, with no shell preserved, involute, with an umbilicus of only a few millimeters in diameter. The most adoral camerae are depressed with broadly arched venter and lateral areas which imperceptibly grade together. The umbilical shoulders are more distinctly rounded and the umbilical wall broadly convex. The adoral camera measures 20.8 mm. in height and 30.8 mm. in width. The suture is essentially straight; and the siphuncle is subcentral, being closer to the dorsum than to the venter.

The whorl section at the end of the first half volution is subtrigonal with a more distinct narrow obtusely rounded venter and more strongly converging whorl sides. The most interesting aspects of these earliest volutions is that the siphuncle rests right on the dorsum, and progressively from this stage the siphuncle migrates away from the dorsum.

Locality and horizon. Danian, Faxoe, Denmark.

Repository. Holotype — MCZ 8815.

EUTREPHOCERAS IMPERIALIS (Sowerby)

Plate 30, figures 1-3

Eutrephoceras imperialis, Hyatt, 1894, pp. 559, 605, pl. 13, figs. 13-16.

Hyatt apparently had several specimens of this species, but only the specimen illustrated by his front view (Hyatt, pl. 13, fig. 13) is in the collections. In addition, there are two fragments of phragmocone and a nearly perfectly preserved juvenile form (Pl. 30, figs. 1, 2 of this report). I agree with Hyatt on the near identity of this species with *E. dekayi.*

Locality and horizon. London clay, Isle of Wight.

Repository. MCZ 8834a, b.

Genus CENOCERAS Hyatt, 1884

Type species. Nautilus intermedius J. Sowerby, 1816, p. 53, pl. 125.

CENOCERAS INTERMEDIUM (J. Sowerby)

Plate 14, figures 11-13

Cenoceras intermedium, Hyatt, 1894, pp. 550, 604, pl. 11, figs. 15-16.

In the description of this species Hyatt figured the specimen illustrated here as illustrative of the paranepionic and ananeanic substage. The specimen consists of one-half volution of phragmocone which on the most adoral camera measures 14.5 mm. in width and 12.3 mm. in height; the adapical camera measures

9.5 mm. in width and 7.3 mm. in height. The whorl section is subtrapezoidal in cross-section with a flattened venter and converging, flattened lateral areas. The suture has shallow ventral and lateral lobes; the dorsal lobe is broad, V-shaped and with an annular lobe. The impressed zone is very slight on the most adapical camerae but increases in width and depth adorally. The siphuncle is slightly dorsal of the center of the whorl. No shell is preserved on any part of the specimen, and the internal cast is smooth.

Locality and horizon. Middle Lias. Balingen.

Repository. MCZ 8829.

CENOCERAS GRANULOSUM (d'Orbigny)

Plate 19, figures 4-12

Cenoceras granulosum, Hyatt, 1894, p. 553, pl. 11, figs. 36-39, pl. 12, fig. 31.

Hyatt had three specimens of this species of which he illustrated and discussed two. His comments were as follows: "In this species, which is well characterized by its compressed form and tubercular ornamentation, the compressed form is present even in the nepionic stage. Figs. 37 and 38 (Pl. 19, figs. 6, 7, 10-12 of this report) show that the umbilical perforation is of medium size. Contact takes place on or near the dorsal edge of the cicatrix on the apex, as shown in Fig. 31, pl. xii (Pl. 19, figs. 4, 5 of this report). The cicatrix is plainly visible in several specimens of this species and it is also obvious that in none of them does the dorsal furrow appear until after the gyroceran bend begins. The dorsum of the metanepionic substage remains rounded and gibbous until the bending begins and then it becomes flattened and immediately hollow, showing the commencement of the dorsal furrow as in Figs. 36 and 37 (Pl. 19, figs. 6, 7 of this report), and this continues to deepen and broaden throughout the paranepionic, as is shown in Figs. 38 and 39 (Pl. 19, figs. 10-12 of this report)."

Locality and horizon. Oxfordian, Chatillon, France.

Repository. MCZ 8831a (Pl. 19, figs. 10-12), 8831b (Pl. 19, figs. 6-7), 8831c (Pl. 19, figs. 4, 5), 8831d (Pl. 19, figs. 8, 9).

CENOCERAS CLAUSUM (d'Orbigny)

Plate 30, figures 4, 5

Cenoceras clausum, Hyatt, 1894, p. 552, pl. 12, figs. 12-15.

Hyatt's comments on this juvenile specimen are as follows: "This species has a small umbilical perforation. The form and general aspect are very similar to those of other compressed shells of this genus, but the shell in the paranepionic substage has peculiarly well-marked and broad growth bands with interrupted longitudinal ridges. The ana- and metanepionic volutions are shown in Figs. 13-15 (Pl. 30, figs. 4, 5 of this report) and have a rounded dorsum, the dorsal furrow appears in the paranepionic at the gyroceran bend and deepens rapidly as the shell grows around the perforation. The amount of involution is probably about the same as in *Cenoceras granulosus*, which it also resembles in general aspect as well as in ornamentation.''

Locality and horizon. Inferior Oolite, St. Vigor, near Bayeux, France.

Repository. MCZ 8832.

Cenoceras aratum (Quenstedt)

Plate 19, figures 13-15

Nautilus aratus, Saemann, 1853, p. 158, pl. 19, fig. 13; Hyatt, 1872, p. 91, pl. 4, figs. 5, 6.

Cenoceras aratum, Hyatt, 1894, pp. 551-552, pl. 11, figs. 32-35.

Hyatt made the following comments on this specimen: ''The specimen shown in Figs. 32-35 (Pl. 19, figs. 13-15 of this report) was figured first in my *Embryology of Fossil Cephalopods*, is one of Saemann's originals and although quite perfect in some respects has no shell.

''It is a cast in iron of the interior and shows the characteristics figured very distinctly. The early beginning of the annular lobe in the third suture and that of the dorsal furrow in the metanepionic between the third and fourth sutures is very interesting in view of the fact that this shell had a comparatively large umbilical perforation and the curvature of the first whorl is so uniform that its early origin cannot reasonably be attributed to that as a cause. The furrow deepens immediately and affects the outline of the fourth suture. A slight dorsal lobe appears in the suture of the third septum at the same time with the annular lobe, and is better given in Fig. 33 than in Fig. 34. The flattening of the dorsum is apparent in the second suture, and, so far as I could see after repeated observations, my former figure in *Embryology of Cephalopods* was erroneous in placing an annular lobe in this suture. This species shows highly accelerated development in all of its characteristics and this acceleration is obviously genetic and independent of the size of the umbilical perforation, which is very large considering the fact that it is a Jurassic species."

Locality and horizon. Middle Lias, Swabia.

Repository. MCZ 8833.

CENOCERAS LINEATUM (Sowerby)

Plate 17, figures 1-9

Cenoceras lineatum, Hyatt, 1894, p. 551, pl. 11, figs. 22-27.

Hyatt's two specimens of this well known and common species are very well preserved. Hyatt only illustrated the inner whorls of the larger specimen; and here the whole specimen and its various parts are illustrated for the first time. The small specimen of Hyatt's plate 11, figures 24-27 is here illustrated on Plate 17, figures 8 and 9. Hyatt's drawing of the apex is highly restored.

Locality and horizon. Inferior Oolite, Bayeux.

Repository. MCZ 8821a, b.

CENOCERAS sp.

Plate 12, figures 6, 7

Digonioceras sp. (?) Hyatt, 1894, p. 549, pl. 11, figs. 19-21.

This fragmentary juvenile specimen, of four camerae, Hyatt originally assigned to his genus *Digonioceras.* This genus, however, is a synonym of *Cenoceras* (Kummel, 1953a); since most Lias nautiloids are best assigned to the highly variable genus *Cenoceras,* Hyatt's specimen seems to belong here also. Hyatt's drawings are slightly inaccurate, even his Figure 21 which is supposed to be a correction of a portion of his Figure 20.

Locality and horizon. Middle Lias, Balingen.

Repository. MCZ 8809.

Family CYMATOCERATIDAE Spath, 1927

Genus CYMATOCERAS Hyatt, 1884

Type species. Nautilus pseudoelegàns d'Orbigny, 1840, p. 70, pl. 8.

CYMATOCERAS DESLONGCHAMPSIANUM (d'Orbigny)

Plate 9, figures 5, 6; Plate 16, figures 1-8

Cymatoceras deslongchampsianum, Hyatt, 1894, p. 554, pl. 12, figs. 22-27.

This specimen of Hyatt's plate 12, figure 24 is illustrated here on Plate 9, figure 6; that of Hyatt's plate 12, figures 22 and 23 are here on Plate 16, figures 6 and 7; that of Hyatt's plate 12, figure 27 is here on Plate 16, figure 8. A mature specimen, which probably yielded one or more of the juvenile volutions studied by Hyatt, is illustrated here on Plate 16, figures 1 and 2.

Locality and horizon. Cretaceous, Rouen, France.

Repository. MCZ 8817 a-f.

CYMATOCERAS RADIATUM (Sowerby)

Plate 15, figures 1-3

Cymatoceras radiatum, Hyatt, 1894, pp. 554-555, pl. 12, figs. 29, 30; pl. 13, figs. 1, 2.

Hyatt's specimen is a well preserved representative of this species and his illustrations reasonably accurate. The specimen consists of slightly less than one-half whorl of phragmocone. The portion of the innermost volutions showing the beginning of the dorsal furrow (Hyatt, 1894, pl. 13, fig. 1) is illustrated here on Plate 15, figure 3.

Locality and horizon. Rouen, Cretaceous.

Repository. MCZ 8814.

CYMATOCERAS sp. indet.

Plate 17, figures 10-11

Cymatoceras sp. indet. Hyatt, 1894, pp. 553, 554, pl. 12, figs. 16-21.

The specimen of Hyatt's plate 12, figure 16 is that illustrated here. There are two additional, polished specimens in the collections which served for Hyatt's figures 17 and 20 of his plate 12. These specimens are typical of the small inner volutions of cymatoceratids which are fairly common in the Cretaceous of Texas. Kummel (1953c) has described and illustrated a number of these specimens.

Locality and horizon. Cretaceous, Texas.

Repository. MCZ 8822.

Genus of Uncertain Position

Genus REMELECERAS Hyatt, 1894

Type species. Remeleceras depressum Hyatt, 1894, pp. 525-526, pl. 8, figs. 1-8.

REMELECERAS DEPRESSUM Hyatt

Plate 13, figures 1-4

This interesting species was better illustrated by Hyatt than most of his specimens; even so, interpretation of the genus has been difficult since there is no locality or horizon data with the specimen. Hyatt's description is as follows: "This extraordinary form is described and figured in this memoir on account of its interesting connection with the history of the impressed zone, notwithstanding the absence of any information with regard to the locality. The side view, Fig. 1, Pl. 8 (Pl. 13, fig. 1 of this report), shows the sutures, which are similar to those of *Estonioceras,* and the impression of what appears to be the annular muscle at the base of the living chamber is very distinct. This may be seen on the dorsal side, Fig. 3 (Pl. 13, fig. 2 of this report), where the lower line has a deeper and broader depression in the cast reaching across the contact furrow. These two lines of depression depart from each other widely on the ventral side, Fig. 2 (Pl. 13, fig. 3 of this report), the outer one forming a broad saddle. They of course correspond to raised ridges on the inner surface of the shell of the living chamber and may have been due to abnormal action in the secretions along the upper and lower borders of the annular muscle.

"The depth of the contact furrow in the full-grown shell near the end of the incomplete living chamber was somewhat greater than is given in Fig. 4 (Pl. 13, fig. 4 of this report), but only a shade deeper, and is also slightly deeper than this beyond the base of this living chamber on the septate part of the volution. In younger stages, shown successively in Figs. 5-7, with their accompanying sections, Figs. 6-8, this furrow diminishes in depth and breadth and almost disappears on the third fragment. This shows that it did not begin to exist in this shell until late in the neanic stage and the younger nepionic stage must have been similar to that of Estonioceras.

"It is also interesting and suggestive to note that the depth and development of the dorsal lobe correlates exactly with the depth and breadth of the contact furrow. The lateral asymmetry in the dorsal lobes of the sutures is another fact to be noted in this specimen.

"The central whorls existed in this specimen, but were completely concealed by the matrix. A section was made of these, but they exhibited no structures.

"The siphuncle was not visible.

"This cast reminds the observer more closely of *Estonioceras* (?) *lamellosum,* as figured by Angelin and Lindstrom, than any other form, but according to Schröder this last is a true estonioceran form with only a slight contact furrow."

Locality and horizon. Unknown.

Repository. Holotype — MCZ 5082.

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PLATES

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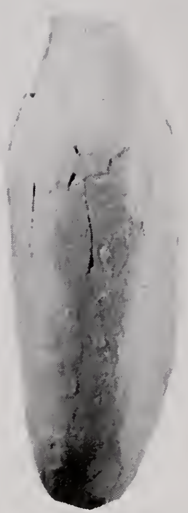
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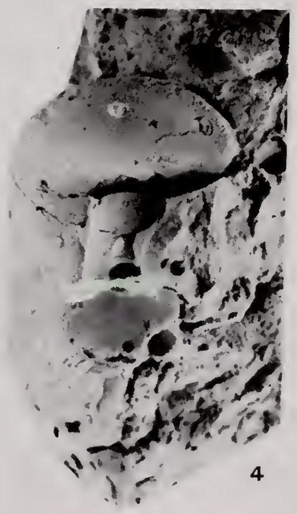
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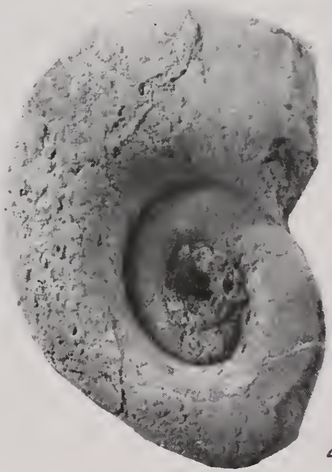

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PLATE 3. TAINOCERAS DUTTONI

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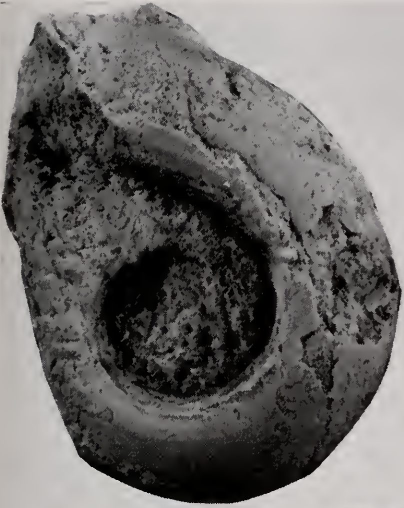

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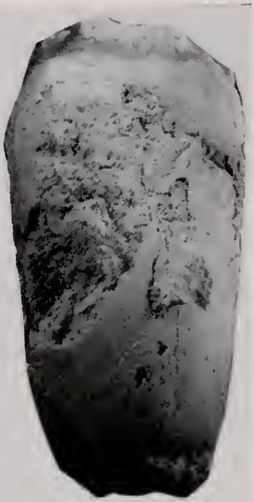

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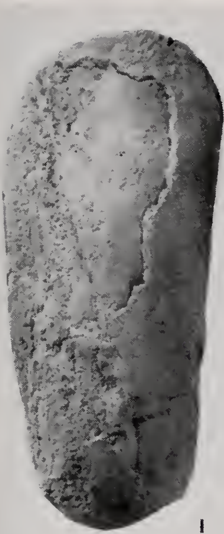

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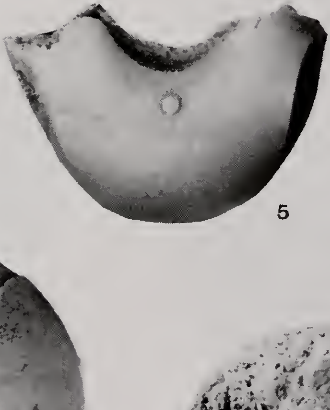

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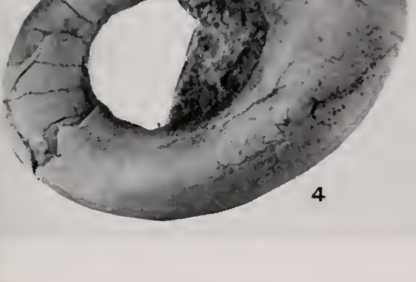

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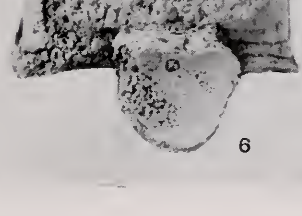

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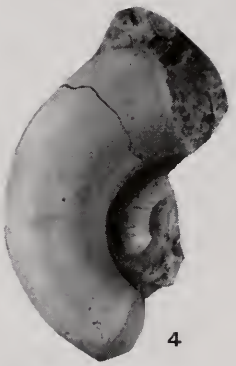

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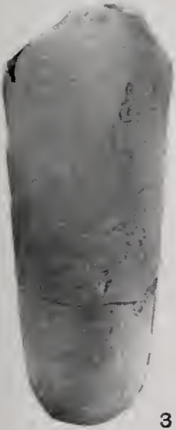

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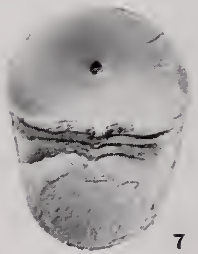

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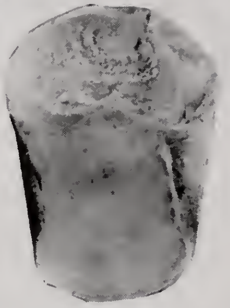
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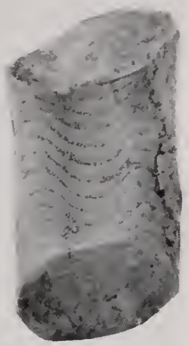
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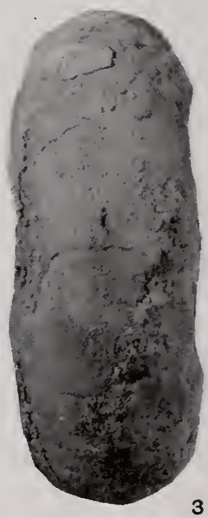
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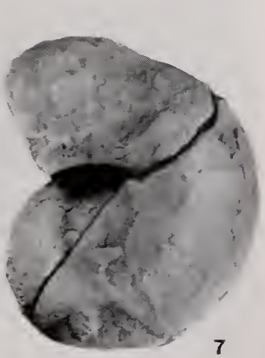
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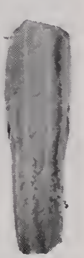

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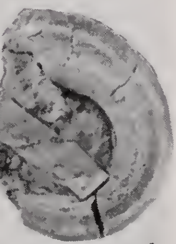

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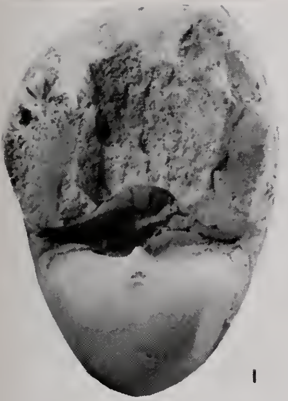
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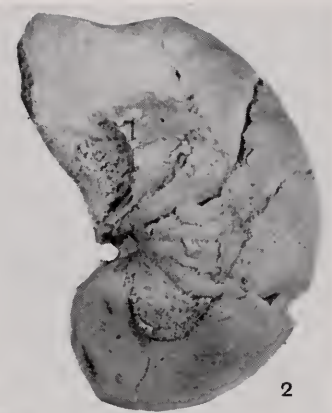
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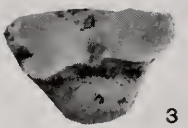
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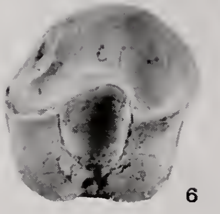
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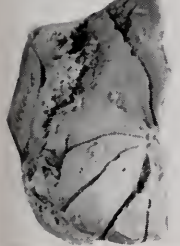
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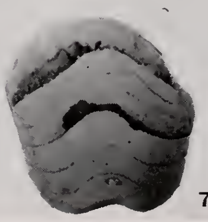
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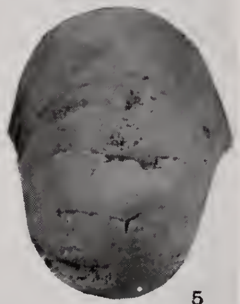

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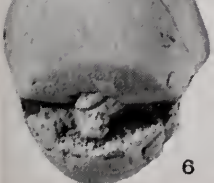

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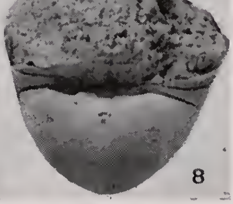

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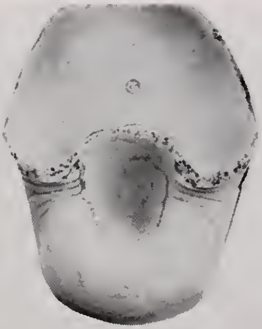
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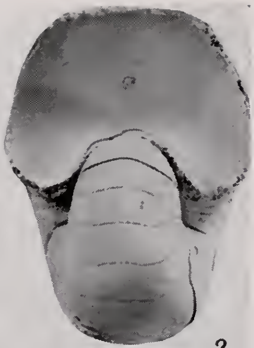
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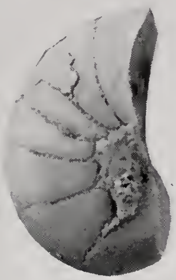
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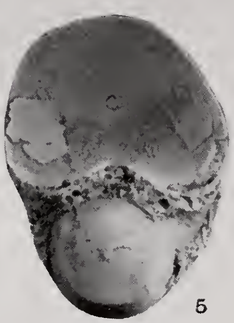
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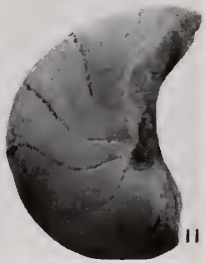
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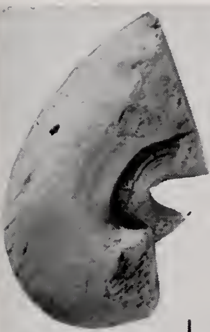

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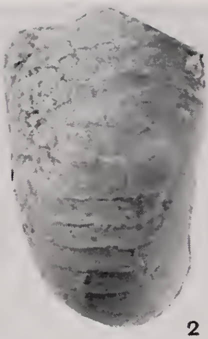

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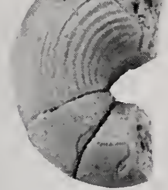

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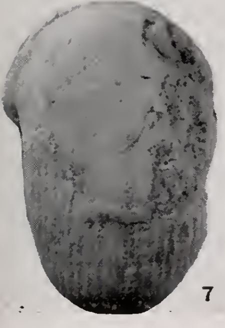

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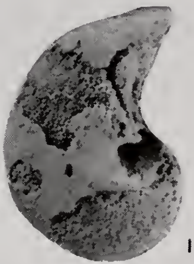
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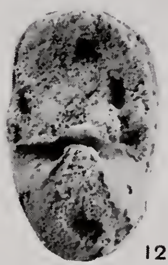
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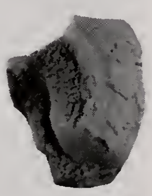
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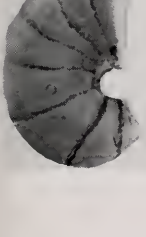
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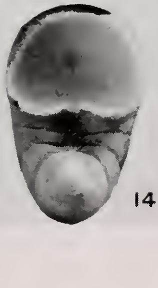
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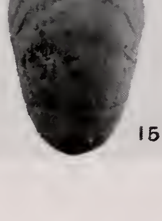
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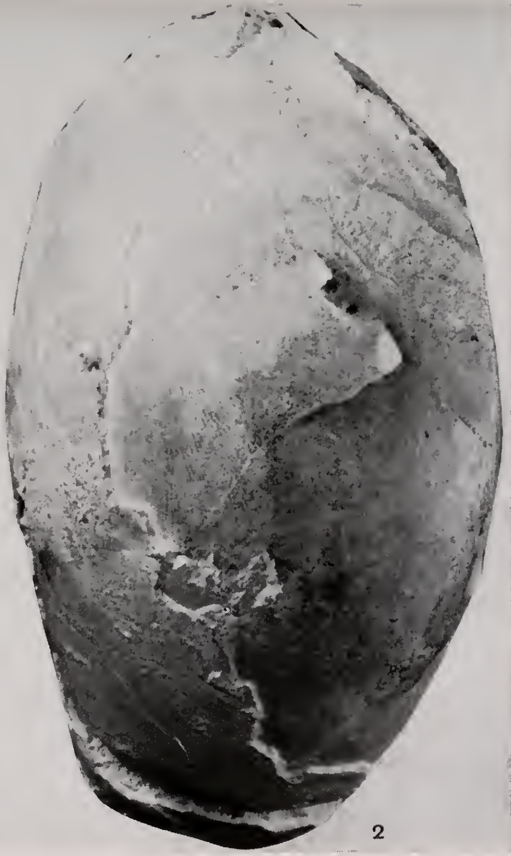

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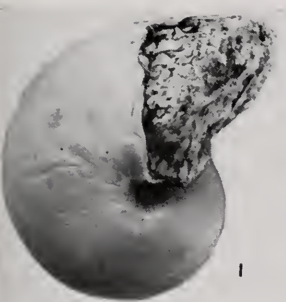

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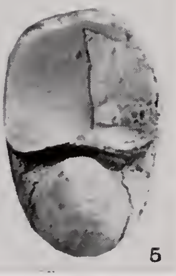

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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
VOL. 128, NO. 7

THE GENUS *STIZOIDES* (HYMENOPTERA: SPHECIDAE: STIZINI) IN NORTH AMERICA, WITH NOTES ON THE OLD WORLD FAUNA

BY JAMES E. GILLASPY
Museum of Comparative Zoology, Cambridge, Mass.

CAMBRIDGE, MASS., U.S.A.
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JANUARY 31, 1963

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BY JAMES E. GILLASPY
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Bull. Mus. Comp. Zool., 128(7): 369-391. January 1963

No. 7 — *The Genus Stizoides (Hymenoptera: Sphecidae: Stizini) in North America, with Notes on the Old World Fauna*

By James E. Gillaspy[1]

INTRODUCTION

The new species described here increases the New World fauna of *Stizoides* to two, both from North America. In the Old World, on the other hand, twenty-five species names have current status, and the genus is widespread there over the warmer regions, with the exception of east Asia. The figure quoted may not accurately reflect the Old World fauna, however, as the taxon has not been comprehensively revised since the time of Handlirsch's monograph in 1892, and some of the species, which have been differentiated largely on the basis of color, will likely prove to be not above subspecific rank. The species of *Stizoides* are predominantly of dark coloration, including the wings, contrasting with the abundant yellows and whites of many other Stizini and related groups. Three species, *niger* (Radoszkowsky), *verhoeffi* Bytinski-Salz, and *foxi* Gillaspy, new species, are almost totally black, and likewise, apparently, occasional specimens of *klugi* (Smith). At least seventeen species are entirely black and red, according to Lohrmann (1943: 205). The remainder have more or less yellow, two African species, *persimilis* (Turner) and *ctenopus* (Arnold), having abdominal bands of this color on tergites after the first or second, increasing in width on the posterior tergites. *Citrinus* (Klug) of Egypt is almost entirely yellow. Carpenter (1920: 294) apparently attributed an apatetic or aposematic significance to red and black coloration of the type prevalent in this genus, terming it "lycoid." A number of structural features of *Stizoides* are of particular interest beyond the confines of the genus, especially with reference to the Bembicini, for example the single apical spur of the middle tibia of some species and characters of the seventh and succeeding abdominal segments of the male. At least two species appear to have the behavioral trait of cleptoparasitism, laying their eggs on prey of other wasps.

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[1] This investigation was in large part accomplished under a National Science Foundation grant (NSF-G17497) for study of the evolution of structure and behavior of nyssonine digger wasps.

In the New World there has long been only a single species known that was assignable to *Stizoides,* the North American form described as *Stizus unicinctus* by Say in 1823. However, W. J. Fox in 1894 listed a "*unicinctus*" from Lower California with the notation: "This is the first specimen of this species seen by me that has the abdomen entirely black." Fox's specimen was presumably destroyed with collections of the California Academy of Sciences in the San Francisco earthquake and fire of 1906, but its lack of abdominal maculation, along with the availability now of additional specimens so characterized, including one from the same area, make plain this was the first recorded example of our second North American species of *Stizoides.* This species, in contrast to the rather widespread *unicinctus*, has a narrow range in the southwestern part of the North American continent, with records at present only from the southern part of the Baja Californian peninsula and from southeastern Arizona.

The limits of the taxon here regarded as constituting a genus, *Stizoides*, appear well defined. Parker (1929: 11) noted the edentate mandibles as unique in the tribe Stizini, and Lohrmann and Beaumont also cite this character, which apparently applies to all *Stizoides.* In addition to this, various partially diagnostic characters are present. Among these are: the strong convergence of the compound eyes toward the clypeus; the presence of an epimeral area; the two sub-parallel free terminal veins at the apex of the hind wing median cell, the latter extending well past the origin of the cubital vein; the flat posterior face of the propodeum; the lateral spiracle-bearing lobes of the seventh tergite of the male; and the pattern of apodemes of the seventh sternite of the male. Within the genus, however, relationships of the species remain in many cases obscure, with principal dependence upon color characters of uncertain value and upon distribution for separation of the species. Vachal and others have contributed a few structural characters of considerable interest, but these have not been broadly applied, and do not provide a conspectus of the species. The generic description presented below has been prepared as a summary of the features in common of the two New World species, and will not apply in some particulars to those of the Old World. Certain relationships of the two faunas are considered in the discussion following the diagnosis.

A number of institutions and individuals have loaned or provided access to specimens used in this study, or have assisted by responding to query concerning presence of *unicinctus* in their collections. In the following list symbols are provided where they will serve to facilitate subsequent reference: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; CAES, Connecticut Agricultural Experiment Station, New Haven; CAS, California Academy of Sciences, San Francisco; CIS, California Insect Survey, Berkeley; CU, Cornell University, Ithaca, N. Y.; FSDA, Florida State Department of Agriculture, Gainesville; INHS, Illinois Natural History Survey, Urbana; ISU, Iowa State University, Ames; IWC, Iowa Wesleyan College, Mt. Pleasant; JEG, James E. Gillaspy; MCZ, Museum of Comparative Zoology, Cambridge, Mass.; NCDA, North Carolina Department of Agriculture, Raleigh; NCSC, North Carolina State College, Raleigh; National Museum, Paris, France; OHSU, Ohio State University, Columbus; RRD, R. R. Dreisbach, Midland, Mich.; TAMC, Agricultural and Mechanical College of Texas, College Station; UARIZ, University of Arizona, Tucson; UARK, University of Arkansas, Fayetteville; UCD, University of California, Davis; UG, University of Georgia, Athens; UIDA, University of Idaho, Moscow; UMICH, University of Michigan, Ann Arbor; UMINN, University of Minnesota, St. Paul; UNEV, University of Nevada, Reno; USNM, U. S. National Museum, Washington, D. C.; and Universitetets Zoologiske Museum, Copenhagen, Denmark.

SYSTEMATIC DESCRIPTION

Genus STIZOIDES Guerin

Stizus: subg. *Stizoides* Guerin, 1844, Iconogr. Regn. Anim. 3 (text): 438 [type: *Larra fasciata* Fabricius, 1798 (designated by Parker, 1929: 10) = *Stizoides assimilis* (Fabricius)].

Larra: Smith, 1856, Cat. Hym. Brit. Mus. 4: 337 (part).

Stizus: Patton, 1879, Bull. U. S. Geol. Surv. 5: 346; Cresson, 1887, Trans. Amer. Ent. Soc., Supp.: 115, 278 (part); Fox 1895, Proc. Acad. Nat. Sci. Phila.: 266 (part); Kohl, 1896, Ann. k. k. Naturhist. Hofmus., Wien 11: 421-424 (part); Dalla Torre, 1897, Cat. Hym. 8: 519-534 (part); Bingham, 1897, Fauna Brit. India Hym. 1: 276-277 (part); Mickel, 1918 (1917): 432-435 (part).

Stizus: (*tridentatus* group) Handlirsch, 1892: 97; Berland, 1925, Faune de France 10: 78; Arnold, 1929: 314; Arnold, 1944: 77; Mochi, 1939: 187.

Stizoides: Ashmead, 1899, Can. Ent. 31: 346; Parker, 1929: 10; Pate, 1937, Mem. Amer. Ent. Soc. No. 9: 61; Lohrmann, 1943, Mitt. Münchn. Ent. Ges. 33: 189, 205; Krombein, 1951: 994; Beaumont, 1954: 313; Bytinski-Salz, 1955: 51-52; Van der Vecht, 1961, Zool. Verhandel. No. 48: 53.

Stizolarra Saussure, 1887, Soc. Entom. 2: 9 (part).

Omphalius Vachal, 1899 (not Philippi, 1847, not Erichson, 1891): 534-535 [type: *Omphalius niger* Vachal (monotypic) = *Stizoides niger* (Radoszkowsky) (new synonymy)]; Pate, 1937, Mem. Amer. Ent. Soc. No. 9: 61.

Scotomphales Vachal, 1900, Bull. Soc. Ent. France: 233 (new name for *Omphalius* Vachal); Pate, 1937, Mem. Amer. Ent. Soc. No. 9: 57; Beaumont, 1954: 313 (new synonymy).

Stizus: subg. *Tachystizus* Minkiewicz, 1934, Polski Pismo Ent. 12: 251 [type: *Crabro tridentatus* Fabricius (designated by Pate, 1937, Mem. Amer. Ent. Soc. No. 9: 63)].

Female. — Size medium, between that of *Bembecinus* and *Stizus,* form slender, appearing cylindrical, head, thorax, and abdomen being of about equal width. *Color* largely black, including wings, latter with bluish or violaceous reflection; distal segments of tarsi, margins of some abdominal segments, and, in *unicinctus*, anterior two-thirds of tergite 2, reddish, this distributed through the integument and thus differing from the yellows and whites of other genera, which underlie the clear, sclerotized integument; wing 1 clear at apex beyond closed cells, or including apex of marginal cell, also clear in costal cell with extension into 1st submarginal cell past end of subcosta, latter appearing completely interrupted before stigma; wing 2 without marginal clear areas. *Vestiture* inconspicuous, largely of simple erect or recumbent black or brownish hairs, specialized silvery-appressed hairs not present. *Sculpture* consisting of punctures and micro-reticulation, punctures coarser than in allied genera, particularly strong on thorax, where they are round, deep, and dense, often separated by less than their own diameter. *Head* one and one-third wider than its length from vertex to anterior margin of clypeus, slightly wider than thorax measured at prothoracic lobes; vertex on level of upper extremity of compound eyes, except between lateral ocelli, where it is distinctly higher; compound eyes in front faintly emarginated before anterior ocellus, distinctly converging toward clypeus; maxillary and labial palpi with 6 and 4 segments, respectively; maxillae short, length beyond base of palpi less than one-third of vertical length of compound eyes; mandibles edentate; labrum slightly wider than long, semicircular in outline; clypeus small, very weakly arched in lateral profile, broadly biconcave in frontal outline through basal emargination along frontoclypeal suture between tentoria, opposed by apical emargination; tentorial pit a foramenlike opening at bottom of tentorial fovea, marking nearest approach of clypeus to subantennal line, from which it is separated by about intersocketal distance; scape about 2 X longer than its greatest width; intersocketal carina present, with low point at middle of antennal sockets dividing sharply carinate upper portion from very broad and rounded lower part; antennae slightly clavate; lateral ocelli with outer side slightly less rounded, circumocellar sulcus on this side with short appendiculate sulcus extending somewhat obliquely inward across vertex; all ocelli with lens modified to some extent by an impressed line or unevenness on surface inward with respect to ocellar triangle; anterior ocellus in shallow depression formed by strongly mounded surface before it, and lower mounds between it and lateral ocelli. *Thorax* with notaulices not evident exteriorly (dissection reveals curved phragmata internally); dorso-lateral metanotal area strongly flangelike posteriorly, forming the dorsolateral metanotal scale which extends caudad over a well-defined prespiracular pit at the base of the propodeum and also overlies and conceals a considerable segment of the narrowly rimlike connecting bridge between the median mesonotum and the metapleuron; propodeum rounded postero-laterally, flattened behind, sides of propodeal triangle in basal area converging at an angle of about 70 degrees toward apex on posterior face of propodeum, apex being between thin vertical carinae extending upward from submarginal sulcus. *Legs* with pecten of tarsus 1 comprised of 11-12 main bristles distributed over segments 1-4, distal lobe of each segment furnished with 2, basitarsus with 3-4 before the lobe; pretarsal structures moderately developed, arolium outwardly extending approximately as far as outer limit of basal third of claws; middle tibiae with two apical spurs, inner one slightly shorter. *Fore wings* with stigma small, not as wide as costal cell; marginal cell slightly receding from anterior wing margin at its outer end, shorter than 1st submarginal but latter less than 1½ X as long; second submarginal cell narrowed above but not petiolate, although 1st and 2nd recurrents may join radial at same place. *Hind wings* without bullae; free abscissa of radius and cubitus extending beyond transverse cubital vein and these almost parallel with each other; cubital vein joining median vein at distance before end of submedian cell greater than width of that cell. *Abdomen* without an area of specialized micropunctation on sternite 2.

Male. — Similar in appearance to female, but size appears to average slightly smaller. Flagellar segments 4-11 excised distally on side inward to curvature of antennae, increasing in degree on more distal segments. Abdominal sternite 2 without carina, process, or specialized punctation; tergite 7 glabrous across entire base, lateral lobes broad, separated medially by less than width of either; sternite 7 extending to apex of tergite 7, median apodeme traversing most of its length; sternite 8 trifurcate, without ventral spine. Genitalic cuspis shorter than digitus.

Discussion. — The North American *unicinctus* and *foxi* appear more closely related to *tridentatus* (Fabricius) than to the other Old World species I have seen and on the basis of information available from descriptions, five other species at least may also belong here, forming a category to which *Tachystizus* Minkiewicz is applicable. The two North American species lack the silvery facial pubescence and distinctly shortened inner calcar of tibia 2 of *tridentatus* and differ from it also in length ratios of the three basal flagellar segments, the pattern of banding of the abdomen, and the male genitalia, but an overall affinity seems apparent. The remaining Old World species I have seen are: *assimilis* (Fabricius) (1 ♀, Deesa, India, USNM; 1 ♂, east India, kindly sent as an exchange from the Universitetets Zoologiske Museum, Copenhagen, Denmark), *fenestratus* (Smith) (2 ♂ 1 ♀, Boma, Congo, 13° 0′ E, 6° 0′ S, 17-19.VI.15; 3 ♀, Thysville, Congo, 15° 0′ E, 5° 30′ S, 21.VI.15, all Lang and Chapin, AMNH), and *niger* (Radoszkowsky) (1 ♂, Olokemeji, Ibadan, Nigeria, USNM; 1 ♂, Faradje, 29° 40′ E, 30° 40′ N, —.IX.12, Lang and Chapin, USNM). These have in common a micropunctate, velutinous area, medially placed at the base of sternite 2 and present in both sexes. This is mentioned by Vachal (1899) as a character of his new genus *Scotomphales*, and it is also apparently present in *cyanipennis* (Saussure) and *poecilopterus* (Handlirsch), as revealed by descriptions. At least five species are thus differentiated from the remainder of *Stizoides*, cleaving the genus into two major subgroups.

Beaumont (1954: 313) advanced the question of the proper disposal of *Scotomphales*. Through the courtesy of the Paris Museum I was able to examine the male specimen upon which this genus was based and find it is the same as the now relatively well known *Stizoides niger* (Radoszkowsky), which was based upon a female specimen. Vachal applied the specific name *niger* to his species and regarded it as likely the same as the *niger* of Radoszkowsky. It is now plain that the species is widespread in equatorial Africa, Vachal's specimen being from Bata, Spanish Guinea, and that of Radoszkowsky from Angola, while, besides the specimens I have seen from Nigeria and the Congo, Turner (1912) and Arnold (1929) list it from Uganda and Angola. The primary character cited by Vachal for *Scotomphales* is the presence of only one apical spur of the middle tibia. This is a tribal character of the closely related Bembicini, but presumably of independent origin in *Stizoides*. Two of the species available to me, *niger* and *fenestratus*, have the inner calcar absent; one, *tridentatus*, has it strongly reduced in size; while three, *assimilis*, *unicinctus*, and *foxi*, have it normal, only slightly shorter than the outer calcar. Another distinction mentioned by Vachal concerns sternite 8, which he described as unispinose. My dissection of the type specimen reveals the central spine to be unusually long but lateral spines to be present although slender, very like the condition in *assimilis* and *fenestratus* and differing, along with them, from the other *Stizoides* I have seen.

Three nominate categories are validated by structural characters and available for the species falling under the genus *Stizoides*. These are treated here as subgenera, with assignment of species as follows where it has been possible to examine specimens, or where descriptions have included the pertinent characters:

No specialized area of sternite 2; tibia 2 with two apical calcaria

Tachystizus
- *crassicornis* (Fabricius)
- *foxi* new species
- *funebris* (Handlirsch)
- *klugi* (Smith)
- *melanopterus* (Dahlbom)
- *tridentatus* (Fabricius)
- *unicinctus* (Say)
- *verhoeffi* Bytinski-Salz

Specialized area of sternite 2 present
  Tibia 2 with two apical calcaria
    Stizoides sensu stricto
      assimilis (Fabricius)
      **cyanipennis* (Saussure)
      **poecilopterus* (Handlirsch)
  Tibia 2 with one apical calcar
    Scotomphales
      fenestratus (Smith)
      niger (Radoszkowsky)

The following species are unassigned, but all or most may belong under *Tachystizus: abdominalis* Dahlbom; *amoenus* (Smith); *blandinus* (Smith); *citrinus* (Klug); *conscriptus* (Nurse); *cornutus* (Smith); *ctenopus* (Arnold); *cyanopterus* (Gussakovskij); *egregius* (Gussakovskij); *erythrogaster* (Turner); *mionii* Guerin; *persimilis* (Turner); *simpsoni* (Turner); and *stenopus* (Arnold).

Key to North American Species of *Stizoides*

1. Antennae 13-segmented, abdomen 7-segmented (males) 2
   Antennae 12-segmented, abdomen 6-segmented (females) 3
2. Abdominal tergite 2 black; sternite 6 transversely swollen at base; last segment of antennae strongly curved and tapering ..... *foxi* n. sp.
   Abdominal tergite 2 reddish in anterior two-thirds; sternite 6 normal; last segment of antennae less strongly curved and the apex truncate .... *unicinctus*
3. Abdominal tergite 2 black; femur 3 stout, less than 4 X longer than greatest width; abdominal punctation strongly developed, particularly evident on sternites .... *foxi* n. sp.
   Abdominal tergite 2 reddish in anterior two-thirds; femur 3 more slender, more than 4 X longer than greatest width; abdominal punctation, particularly of sternites, in large part sparse, weakly defined .... *unicinctus*

STIZOIDES (TACHYSTIZUS) FOXI new species
(Figs. 1, 2, 5, 7, 9, 11)

Stizus unicinctus: Fox 1894: 104.

Holotype.— ♀, ARIZONA: Madera Cyn., Santa Rita Mts., 31.VIII.58 (R. M. Bohart) [MCZ No. 30490].

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*I have not seen specimens of these and the tibial calcaria are not specifically mentioned in species descriptions, but are probably normal (two).

Description of type female. — Length 13 mm. Color black except tarsi more or less reddish, margins of abdominal segments faintly so, and apex of fore wings beyond closed cells (but with slight extension into apex of marginal cell) clear. Sculpturing generally stronger than that of *unicinctus*, punctures deeper, of more sharply defined round shape, more often dense to an extent that space between punctures is less than their diameter, best compared on abdominal tergite 2 laterally, sternite 2, and pygidium. Ratio of least interocular distance at clypeus to greatest facial interocular distance at vertex 1.00:1.71:1.45. Single curved, flangelike median carina traversing upper epimeral area. First three segments of flagellum 62:36:34. POL/OOL = 1.75. Legs stouter than in *unicinctus*, 3rd femur 3.7 X longer than greatest width, which is almost median. Abdomen with sternite 2 most densely and finely punctate medially near base, sparsely punctate along median apical margin, but without sharp gradation in density or size of punctures.

Allotype. — ♂, same data as the holotype [MCZ No. 30490].

Description of allotype male. — Length 15 mm. As in the female, abdominal maculation lacking. Abdominal sternite 6 with a rounded transverse ridge extending the width of the segment at base, and apical margin of sternite 5 shallowly emarginated in accordance with contour of the ridge.

Paratypes. — ARIZONA: Cochise Co., Apache, 1 ♂, 13.VIII.44 (W. W. Jones, CIS); Apache, 3-5 mi. SW, 4300′, on *Baccharis glutinosa*, 1 ♀, 1 ♂, 8.VIII.59 (H. E. Evans, CU); Cochise, fls. *Lepidium*, 1 ♂, 21.VII.61 (J. E. Gillaspy, JEG); Dos Cabezos, ♂, 20.VIII.58 (E. G. Linsley, CIS); Pearce, 3 mi. E, fls. *Lepidium*, 2 ♀, 7 ♂, 21.VII.61 (J. E. Gillaspy, JEG); Willcox, 2.5 mi. S, ♀, 17.VIII.56 (E. Ordway, AMNH). Pima Co., Continental, on fls. *Kallstroemia*, 3 ♀, 2-4.VIII.59 (K. V. Krombein, USNM). Santa Cruz Co., 3 ♀, 2 ♂, same data as types (UCD); Patagonia, 10 mi. SW, on *Croton*, 4 ♂, 13.IX.58 (P. D. Hurd, CIS). BAJA CALIFORNIA: San Pedro, 1 ♂, 7.X.41 (Ross and Bohart, CAS).

Recorded distribution. — BAJA CALIFORNIA: San Jose del Cabo, October (Fox, 1894: 104).

Discussion. — The observed range in length of females is 10-16 mm., of males 13-17 mm. Indistinct red may occur on the pygidium and other abdominal sclerites, and one specimen has narrow preapical bands of this nature on tergites 3-4. There may in some cases be two carinae of the upper epimeral area, rather than one.

STIZOIDES (TACHYSTIZUS) UNICINCTUS (Say)

(Figs. 3, 4, 6, 8, 10, 12)

Stizus renicinctus Say, 1823, West. Quart. Reporter 2: 77 [type: ♂ "Inhabits Arkansa" (presumably destroyed)].

Stizus unicinctus Say, 1824, Amer. Ent. 1: 4, pl. 2, figs. 3-4, ♂ (emend.); Leconte, 1859, Writ. of Th. Say Ent. 1: 4, pl. 2, figs. 33-34; Cresson, 1863, Proc. Ent. Soc. Phila.: 268; Patton, 1879, Bull. U. S. Geol. Surv. 5: 346, 361; Cresson, 1887, Trans. Amer. Ent. Soc., Supp.: 278; Handlirsch, 1892: 103; Fox (not Say), 1894: 104; Fox, 1895, Proc. Acad. Nat. Sci. Phila.: 268; Dalla Torre, 1897, Cat. Hym. 8: 533; Johnson and Rohwer, 1908, Ent. News 19: 374; Smith, 1908, Neb. Univ. Stud. 8: 12; Williams, 1913: 230; Mickel, 1918 (1917): 435; Rau and Rau, 1918: 180-193; Wheeler, 1919: 15, 19, 22; Carter, 1925: 133; Brimley, 1938: 448; Rau, 1938: 543; Nielsen, 1945, Spolia Zool. Mus. Hauniensis 7: 141; Rau, 1946: 2.

Larra unicincta: Cresson, 1865, Proc. Ent. Soc. Phila. 4: 472; Packard, 1867, Proc. Ent. Soc. Phila. 6: 444; Packard, 1870, Guide Study Ins.: 164; Cresson, 1872, Trans. Amer. Ent. Soc. 4: 223.

Stizoides unicinctus: Ashmead, 1899. Can. Ent. 31: 347: Lohrmann, 1943: 206; Krombein, 1951: 994; Krombein, 1958: 195; Arens and Arens, 1953: 191-192; Evans, 1955: 299.

Megastizus unicinctus: Smith, 1915: 10-11.

Description of female. — Color black except clear areas of wings, reddish basal band of tergite 2, and usually more or less reddish on antennae, mandibles, pygidium, and sometimes elsewhere on abdomen. Sculpturing of thorax strongly developed, punctures dense, deep, and round, but abdominal punctures mostly shallow, widely spaced, not round in shape. Inner margins of compound eyes converging more strongly toward clypeus than in *foxi,* ratio of least interocular distance at clypeus to greatest facial interocular distance (this is between antennal sockets and anterior ocellus) and to least interocular distance at vertex 1.00:1.83:1.65. Antennal segments 3:4:5 = 60:38:36. POL/OOL = 1.85. Upper epimeral area traversed medially by two curved, lamellate carinae which diverge anteriorly. Legs slender, 3rd femur 4.0 X longer than greatest width, which is before middle of segment. Abdomen with sternite 2 sparsely punctate, particularly in median basal area, and the punctures uneven in size and shape.

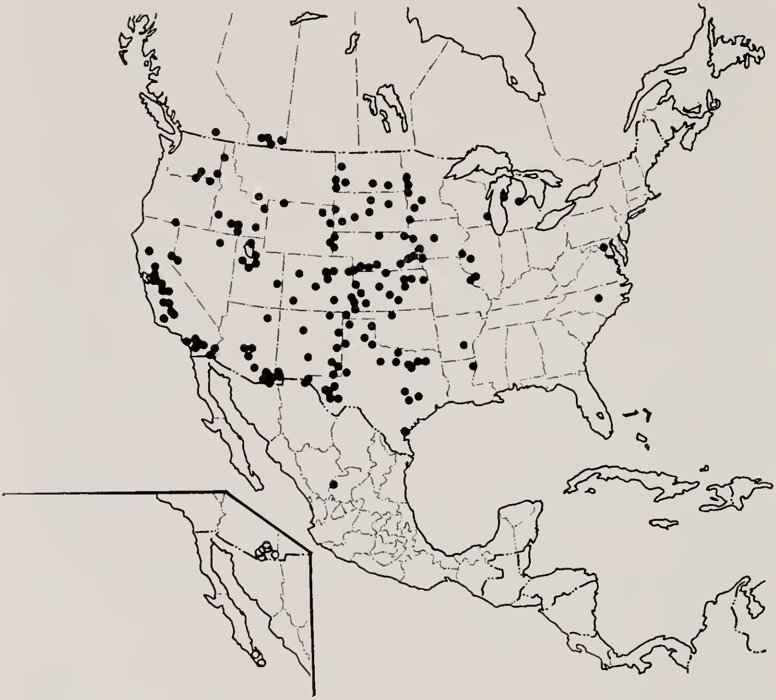
Male. — Similar to female. Abdomen with sternite 6 unmodified.

Discussion. — The ratios above are from a Scott, Kansas, specimen. The range in length of the specimens I have seen is 12-20 mm. for the female and 9-17 mm. for the male. It is possible the specimens from at least some areas in the south are of larger average size, but little important variation otherwise is seen over the rather extensive range. The abdominal maculation is relatively constant in shade, always with considerable reddish element.

Distribution. — The accompanying map summarizes distributional data taken from more than five hundred specimens of *unicinctus* examined in this study and also from published records, as well as in certain cases from persons who have specimens in their keeping or possession. The species is apparently well represented in southern Canada, and in addition to three Alberta localities reported by Carter, I have seen four specimens from Medicine Hat, Alberta, 8-13.VIII.39 (R. H. Strickland, ANSP) and three specimens from Vernon, British Columbia, 5.IX.45 (H. B. Leech, USNM). A female from 15 kilometers east of Sombrerete, Zacatecas, Mexico, collected 28-31.VII.51 (H. E. Evans, MCZ) indicates a considerable southward range, although the only other Mexican record is from the northern border of the country.

In the United States, *unicinctus* is apparently quite uncommon east of the Mississippi River. Along the Mississippi, I have seen specimens from: Carlinville, Illinois, twenty-four specimens (11 ♂ 13 ♀) taken between the years 1887 and 1902 (INHS); and Carman, Illinois, Quiver Lake, one specimen, 3.VII.37 (C. O. Mohr and B. D. Burks, INHS); and the Raus (1918) report the species at St. Louis. I have also seen two females from Tallulah, Louisiana, 24.VII.25 (UMICH, UMINN). Eastward of the Mississippi, the New York and New Jersey catalogs do not record it, and collections surveyed, as listed elsewhere, divulged only the specimens listed below. R. R. Dreisbach of Midland, Michigan, has kindly supplied me with records of a Michigan specimen from each of two localities, Midland Co., 23.VIII.38 and Benzie Co., 29.VII.40, and I have seen one male from "Mich." (USNM). I have seen specimens from Havana, Illinois, year 1894, on *Ceanothus*, at night (INHS); a male from Milwaukee, Wisconsin, 28.VII.04 (S. Graenicher, MCZ); a female from Washington, D. C. (Chittenden, USNM); and a male from "North Carolina"

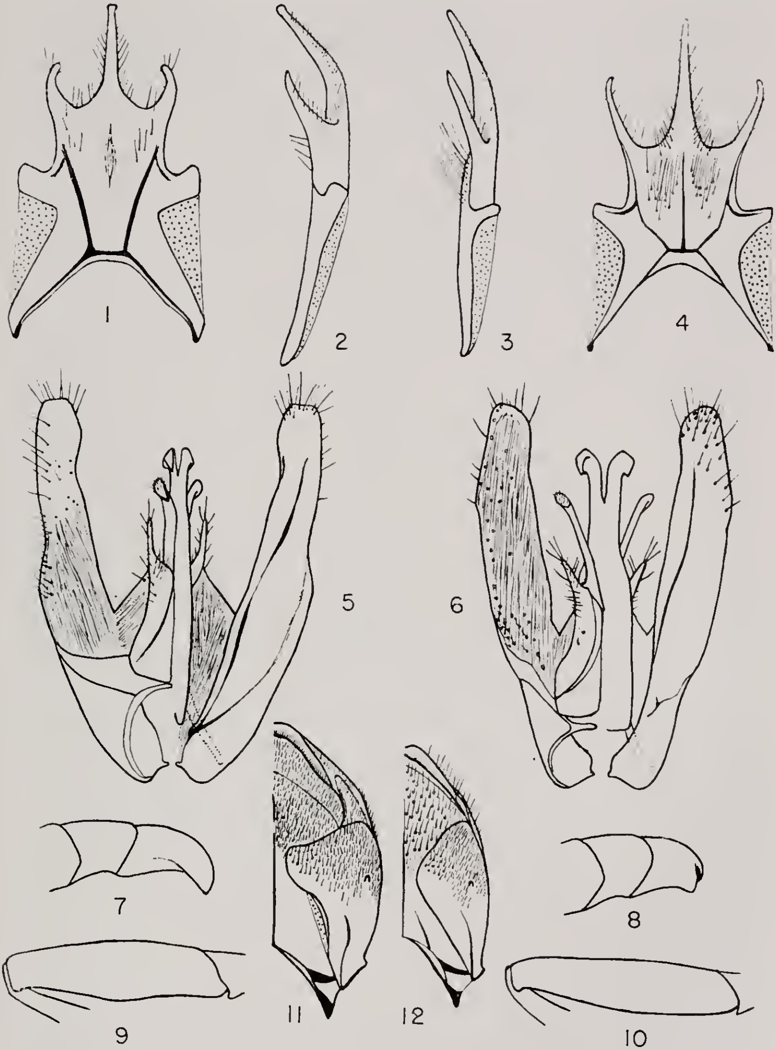
(T. Pergande Collection, USNM). Brimley (1938: 448) recorded the species from Raleigh, North Carolina, and the specimen is reported to be still in existence, having been collected 19.IX.00 (Franklin Sherman, NCDA). Thus, despite the considerable number of collections surveyed, I have seen or have records of only nine specimens from east of the Mississippi, and all except two Michigan records are quite old.



Map showing distributional records of North American *Stizoides*. *Unicinctus* (Say) indicated by solid dots on the larger map, *foxi* n. sp. by hollow circles on the insert map.

BIOLOGY OF *STIZOIDES*

The life history of *Stizoides* was first reported upon by Williams (1913: 230), and his observations on the North American *unicinctus* revealed a mode of life considerably at variance with that of other stizines and bembicines. He found this species in



Stizoides foxi n. sp. Fig. 1, sternite 8, male, ventral; Fig. 2, same, lateral; Fig. 5, male genitalia; Fig. 7, terminal segments of antenna, male; Fig. 9, femur 3, lateral, female; Fig. 11, segment 7, male, ventral. *Stizoides unicinctus* (Say). Fig. 3, sternite 8, male, ventral; Fig. 4, same, lateral; Fig. 6, male genitalia; Fig. 8, terminal segments of antenna, male; Fig. 10, femur 3, lateral, female; Fig. 12, segment 7, male, ventral.

a cleptoparasitic role, laying its egg on the stored grasshopper prey of a sphecine wasp. Cleptoparasitism is known to occur in various aculeates, including *Nysson* and some Pompilidae, but not in groups closer to *Stizoides.* Williams' brief observations encompassed the major points known to now about *Stizoides* life history, although later workers have provided support for his findings and enlarged upon them to some extent. European observers (Arens and Arens, 1953) found the Old World *tridentatus* behaving similarly, and it seems possible this pattern of life occurs throughout the genus, although the observed species represent a rather small segment of the structural diversity present.

Unicinctus is readily distinguished from its near relatives in North America through being almost entirely of an intense black color except for a reddish abdominal band. It is perhaps less abundant in collections than would be expected, being apparently recognized as common and not taken by many "sophisticated" collectors. Its habitus, which may be apatetic or aposematic, is one often found in spider wasps, larrids, and scoliids, but not in other New World stizines or bembicines. In an attempt to gain some concept of the seasonal pattern of occurrence of this wasp the date records from specimens that were examined in this study were tabulated, arbitrarily dividing the range into northern (Kansas-Nevada, northward) and southern (Oklahoma-California, southward) districts and utilizing semi-monthly (1-15, 16-end) time periods. A number of records available from specimens not seen by me agree in general with the data presented. Despite the conceivable biases that could affect a museum sample, including the varying motivations and commitments of the collectors involved, the results appear to warrant a number of conclusions as to population trends. The general concordance of number of collections with number of specimens and the decline in percentage of males serving as an independent index of the progress of the season, encourage confidence that relative abundance is reflected to a fair degree, although a larger sample could be desired, especially in the southern area. It may be noted here that Bytinski-Salz (1955: 51) found period of occurrence one of the few differences setting apart his new species, *S. verhoeffi,* from the very similar, sympatric *S. klugi.*

From the data presented above, the following seem evident: the approximate main periods of flight (mid-June to mid-September in the north and mid-May to mid-October in the south); the peak of abundance in late July in the north and evidence

NORTHERN AREA

Extreme records: ♀, June 6 — ♀, September 16

	MAY		JUNE		JULY		AUG.		SEPT.		OCT.		NOV.	
	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-30	1-15	16-31	1-15	Totals
1			(1)	(11)	(15)	(29)	(15)	(11)	(7)	(5)	(2)			(96)
2			1	12	11	22	9	12	10	4	1			82
3			0	20	22	40	17	11	14	1	1			126
4			1	32	33	62	26	23	24	5	2			208
5			33		95		49		29		2			
6			61%		64%		57%		52%		—			

SOUTHERN AREA

Extreme records: ♂, May 2 — 2 ♀, November 6-8

	MAY		JUNE		JULY		AUG.		SEPT.		OCT.		NOV.	
	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-30	1-15	16-31	1-15	Totals
1	(5)	(9)	(13)	(8)	(5)	(16)	(4)	(7)	(6)	(5)	(8)	(5)	(2)	(93)
2	0	5	4	13	0	7	3	4	5	5	11	7	3	67
3	9	13	12	35	9	26	7	10	3	4	4	0	0	132
4	9	18	16	48	9	33	10	14	8	9	15	7	3	199
5	27		64		42		24		17		22		3	
6	82%		73%		83%		71%		41%		18%		0%	

TOTAL SPECIMENS: 407

1. Number of separate collections in each semi-monthly period.
2. Number of females for each semi-monthly period.
3. Number of males for each semi-monthly period.
4. Total males and females for each semi-monthly period.
5. Monthly total, males and females (semi-monthly totals combined).
6. Percentage of males for each month.

that the peak is probably somewhere between mid-June and the end of July in the south, where the protracted season makes a larger sample particularly desirable; overall accordance with a univoltine annual cycle; protandry; percentagewise and actual reduction of males in August; and longer survival of females at the end of the season, the decline in abundance of males producing a reversal in the ratio of the sexes in September. The peak in late June in the southern area is an effect of large collection size and contra-indicated as a meaningful statistic by the small number of collections, although a June peak of activity in this area remains a possibility.

The observations of Williams, mentioned previously, and others of Smith (1915: 10-11) disclosed *Priononyx atratus* (Lepeletier) serving as the apparent host of *unicinctus*, while the Raus (1918: 180-193) found both this species and *Priononyx thomae* (Fabricius) victimized. All noted *unicinctus* frequenting nesting sites of the host species, and the Raus (1918: 191) concluded that stored grasshoppers were located by two methods: "by inspecting all breaks in the surface of the earth where *Priononyx* nests are likely to occur, in order to locate the nest when closed, and by shadowing the *Priononyx* while she is storing her prey and closing the hole." There was agreement also that *unicinctus* opens the nest of the host, destroys the egg of the latter on the stored grasshopper, and replaces it with her own. Williams and the Raus presented certain limited observations which support this conclusion. Nielsen (1945: 141) regarded the parasitic relationship as unproven although admitting it to the status of a strongly supported supposition. The observers all noted the parasite entering open burrows and opening closed burrows, and Williams encountered one smoothing over an area which proved to have beneath it a "filled-up" burrow. On the stored grasshopper he found an egg which he took to be that of *unicinctus*, since it was shorter and more cephalad in placement than that of *atratus*, with which he was familiar. Apparent vestiges of the *atratus* egg remained in the usual position. at the base of one of the hind femora of the grasshopper. It is perhaps to be gathered that the burrow was more or less normally closed, somewhat in the fashion of *Priononyx*, in this case; in contrast, however, *unicinctus*, according to Smith, ". . . is not particular about refilling the burrow, nor does she attempt to hide the location of it in any manner, as does the *Priononyx*. Oftentimes *Megastizus* [*Stizoides*] *unicinctus* will leave the nest when the burrow is not more than half refilled with soil. Occasionally the *Priononyx* will be driven from her nest by *Megastizus* while in the act of filling up her burrow." The Raus noted only one *unicinctus* in the act of nest closure: "She came out and kicked in all of the loose dirt, then dug up more with her mandibles, kicked it under her body into place, and picked up and placed a few more bits until the hole was once more nicely covered." In possible contrast to this closed burrow, however, the Raus were mystified at finding a considerable number of open burrows, apparently of *Priononyx,* with the stored grasshoppers ruined by ants and dipterous parasites. They speculated on the possibility that this was the work of *unicinctus.* The closed burrow contained a stored grasshopper: "The egg of *thomae* was in its usual position on the right femur, at the base of the abdomen, but lo! it was only an empty sac! Evidently *Stizus* [*Stizoides*] *unicinctus* had mutilated the egg by malaxation, or had sucked the contents for food. We found no *Stizus* egg; but it is probable that, in the difficulty of opening the nest in a harsh cinder bed, it was knocked off by crumbling walls."

No other published information bearing on the relationship of *unicinctus* to its insect hosts is known to me, but Rau (1946: 2) noted it visiting flowers of *Pycnanthemum flexuosum* (Libiatae), the Raus (1918: 190) on white snakeroot, *Eupatorium urticaefolium* (Compositae) and Rau (1938: 543) observed a sleeping aggregation: "Six of these wasps were found July 20, 1919, asleep, close together, on one head of teasel-grass at the edge of a field of wheat stubble." Mickel [1918 (1917): 117] adds *Melilotus alba* (Leguminosae), *Achillea millefolium* (Umbelliferae) and *Asclepias* sp. (Asclepiadaceae) to the list of flowers visited. I have found the following flower records, listed here under their families, on labels of specimens examined in this study: Asclepiadaceae (*Asclepias latifolia, A. subverticillata, A. verticillata*); Capparidaceae (*Wislizenia refracta*); Caprifoliaceae (*Symphoricarpos occidentalis*); Chenopodiaceae (*Salsola kali*); Compositae (*Baccharis salicina, Baileya pleniradiata, Haplopappus hartwegi, Kuhnia oligophylla, Lepidospartum squamatum, Solidago* sp.); Convolvulaceae (*Cuscuta arvensis*); Cruciferae (*Stanleya primata*); Euphorbiaceae (*Croton californica, Euphorbia marginata*); Leguminosae (*Acacia greggii, Lepidium montanum, Medicago sativa, Prosopis juliflora*); Polygonaceae (*Polygonum* sp.); Tamaricaceae (*Tamarix gallica*); Umbelliferae (*Polytaenia nuttallii*); Verbenaceae (*Phyla incisa*).

In southern Idaho in 1955 I observed sleeping aggregations of *unicinctus* on two occasions. In the early morning of August 10, on the floor of a valley-like crater some hundreds of feet long in Jerome County, about nine miles south of Shoshone, an aggregation of *unicinctus* (2 ♀♀, 4 ♂♂) and *Prionyx* (*Priononyx*) *atratus* (Lepeletier) (2) [1 ♂ det. A. Menke] was found on a live tumble mustard (*Sisymbrium altissimum*) plant. The wasps were in a loose gathering with no individuals in physical contact. More specialized, perhaps, are dense, ball-like clusters of *Stictiella pulla* (Handlirsch), *Steniolia elegans* Parker, and *Steniolia scolopacea albicantia* Parker, observed during the same season, and the cluster of *Zyzzyx chilensis* (Eschscholz) pictured by Claude-Joseph (1929: 419). At a locality 10 miles north of Owinza, Lincoln County, on August 15, another such aggregation was observed. In this instance eight *unicinctus* and three *atratus* were atop a plant belonging to the goosefoot family (Chenopodiaceae), at a height of ½ meter, at 1900 hours, in the shade. Nearby, in a sunny area, *Steniolia elegans* females were still actively hunting. Again the aggregation was loosely formed, with no individuals in actual contact in a cluster. This side-by-side sleeping contrasts with behavior in the vicinity of the burrow, where there may be decided aggressive action on the part of the host toward the parasite, with incidence of fierce pursuits and physical tussles. The Raus report this type of behavior, and also the Arens (Arens and Arens, 1953), although in the case of the latter authors the European *Stizoides tridentatus* was involved. Williams, on the other hand, noted a case in which an *atratus* abandoned her prey when she returned and encountered a *unicinctus* occupying her burrow.

In the Old World the Arens (*loc. cit.*) in European Russia (Lake Serebryanka-Udelnaya, Khopersky Reserve, Voronezh region and along the sandy banks of the Khopro River, opposite the Kalinova cordon) found *Stizoides tridentatus* and *Sphex maxillosus* (Fabricius) displaying numerous evidences of a parasite-host relationship, although, as in the case of *unicinctus,* such formal proof as a reared parasite, or other relatively indisputable evidence, was not secured. Four colonies of the *Sphex* were reported, each with female *Stizoides* present. The latter were "for hours" in low searching flight over the *Sphex* colonies. They tended to remain in the vicinity of the burrows and, in the absence of the host, entered them for sometimes extended periods. Upon leaving they spattered the burrow with soil in a superficial "closure," regarded by the Arens as a behavioral vestige from free-living ancestors. Returning *Sphex* unceremoniously ejected *Stizoides* that were in their burrows if the latter did not succeed in darting forth themselves, and *Sphex* were also seen to harass the parasites in the air outside the nests. The observed nectar host of the *tridentatus* in the vicinity was *Eryngium intermedium* (Umbelliferae).

Only one other observation from the Old World is known to me and is of doubtful pertinence, since the wasp concerned was not definitely identified as a *Stizoides*, but would be of unusual interest if confirmed. Carpenter (1920: 293-294), writing about observations made in 1912 on an island in Lake Victoria, British East Africa, mentioned a wasp that appeared in a colony of *Bembix ugandensis* Turner. He described it as "a medium sized fossor of quite a different type, with the black and orange 'lycoid' colouring." It remained for some time in and near the *Bembix* burrows, as noted for *Stizoides* in the *Priononyx* and *Sphex* colonies. A returning *Bembix* abandoned her prey in a manner reminiscent of Williams' *P. atratus* when she encountered the intruder in her nest, but finally entered the nest on a third return trip despite the presence of the other wasp within. No conflict was apparent, the intruder coming out after a few seconds and then re-entering while the *Bembix* was still inside. Victimization of the Diptera-predatory, progressive-provisioning *Bembix* would appear to constitute a considerable behavioral departure for *Stizoides* on the basis of other observations of the genus, since the sphecines prey on Orthoptera and practice mass provisioning. Evans (1955: 299) has noted that cleptoparasites are characteristically associated with forms to which they are closely related, as shown by Wheeler (1919). The closest relatives of *Stizoides* are in the genus *Stizus*, whereas the sphecines are relatively distant phyletically; however, *Stizus* and the sphecines have in common the use of Orthoptera as prey, and Evans says: "Undoubtedly *Stizoides* arose as a cleptoparasite of *Stizus* (judging from many similar cases in the wasps and bees), and *unicinctus*, at least, underwent sufficient modification of its behavior patterns to enable it to attack another, much more common hunter of Orthoptera, *Priononyx*."

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LAND AND FRESHWATER MOLLUSKS OF THE CROOKED ISLAND GROUP, BAHAMAS

By

William J. Clench

With Three Plates

CAMBRIDGE, MASS., U.S.A.
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No. 8 — *Land and Freshwater Mollusks of the Crooked Island Group, Bahamas*

By

WILLIAM J. CLENCH

The Crooked Island group of islands is in the southeastern portion of the Bahama Archipelago. This group consists of three main islands and a few small cays and islets. These are all situated upon a shallow bank and partially enclose a shallow sea, the Bight of Acklins. In addition, there are included a few nearby islands or cays which are separated by deep water from the Crooked Island Bank; Plana or French Cays are 15 to 20 miles east of the northern end of Acklins Island, and Samana or Atwoods Cay is about 25 miles north of Northeast Point, Acklins Island.

HISTORICAL

As mentioned in other reports on various island groups in the Bahamas, the early history of collectors is virtually unknown. An early governor of the Bahamas, Sir Rawson W. Rawson, was a collector of note and sent many mollusks, mainly from Fortune Island, to Thomas Bland of New York. Mr. Rawson was governor of the Bahamas between 1864 and 1869 and during his tenure visited and collected on many of the "Out Islands" and was, in many cases, the first to collect mollusks on most of the more inaccessible islands.

In the summer of 1930, Paul Bartsch of the United States National Museum made an extensive trip covering many island groups in the southern Bahamas. Large collections were made on the major islands of the Crooked Island group as well as on West Plana Cay.

In 1933 the yacht "Utowana" visited Crooked and Fortune Islands and the Plana Cays. Staff members of this museum, Thomas Barbour and James C. Greenway, made excellent collections of land mollusks on these islands. Again, in 1934, the "Utowana" visited Crooked Island, Atwoods (Samana) and the South Cay in the Mira Por Vos group. Mr. Greenway collected the material on Atwoods and on South Cay, Mira Por Vos. I believe this was the first time any naturalist had ever visited these two rather inaccessible islands.

More recently, under the auspices of the Museum of Comparative Zoology and the United States National Museum. Mr.

David W. Robertson, now residing on Great Exuma, his son Robert, a student and colleague of mine, and Robert's companion of former collecting trips, Augustus W. Scott, made an expedition to the Crooked Island group. They left George Town, Great Exuma on August 10, 1958, on the "Sea Queen," a 25-foot native sloop, for the Crooked Island Group, and returned to Great Exuma on September 8th. After returning to Nassau, "Gus" Scott decided to visit these islands again for additional collecting. He arrived on Crooked Island on September 17 and left on September 28. Scott's second trip was to cover a section of Crooked Island not easily accessible on their trip on the "Sea Queen." Extensive collections by both expeditions were made on Fortune, Crooked, Acklins and Castle Islands.

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I am most grateful to many persons for the material made available for this study; to James C. Greenway for his time and effort during the several trips made by the "Utowana" throughout most of the Bahama Islands and to Harald A. Rehder of the United States National Museum for making available to me all of their material from these islands. I am particularly indebted to David and Robert Robertson and Augustus Scott for the extensive coverage of these islands and for a complete day by day report of their adventures in the form of a typed journal. I am also indebted to my colleagues, Merrill Champion and Ruth Turner, for reading the manuscript. I am grateful to Mr. Charles P. Bethel, Manager of the Development Board, Nassau, Bahamas, for data on Governor Rawson W. Rawson.

No attempt has been made to indicate where specific material is presently located, as both the United States National Museum and the Museum of Comparative Zoology have almost equal collections from all of the stations given in this report.

NOTES ON THE LAND AND FRESHWATER MOLLUSKS

The 48 species and subspecies of land and freshwater mollusks occurring on these islands may be grouped as follows:

Bahamas and beyond	Widely distributed in Bahamas	Limited in distribution in Bahamas	Endemic	Total
17	8	3	20	48

The figures given above approximate quantitatively those of other island groups.

In the table below we list all of the islands and island groups so far studied and the number of species of mollusks on each. The figures given, however, must be considered as approximate since there are so many variables existing between the various islands. For example, Great and Little Abaco have only 25 species recorded so far, as opposed to 48 species for the Crooked Island group. In land area the Crooked Island group is only one-third as great as the Abaco Islands. Variables here are important to consider. As most of the Bahama species are the same or closely allied to species in the West Indies, particularly to those of Cuba, chance introductions are greater as the Crooked Islands are much nearer to the Greater Antilles than are the Abaco Islands — 110 miles versus 260 miles. Much of the Abaco Islands were and still are, in many areas, covered with a stand of Bahama Pine, a thin forest growing on lime rock which is ecologically rather uniform. There are no pine forests on the Crooked Islands and they have a far greater number of variable habitats. Far more detailed collecting was done in the Crooked Island group than in the Abaco Islands where only a few localized areas have been searched for land and freshwater mollusks.

NUMBERS OF SPECIES

Islands	Bahamas and beyond	Widely distributed in Bahamas	Limited in distribution in Bahamas	Endemic	Total	Land area in sq. miles
Caicos Ids	9	2	5	4 + 4[1]	24	about 166[2]
Turks Ids.	7	0	7	4 + 2[1]	20	
Ragged Ids.	4	2	3	5	14	22[3]
Cay Sal Bank	1	0	1	1	3	7
Great and Little Inagua	13	3	7	23	46	560
Mariguana Id.	1	3	3	7	14	96
Bimini Ids.	15	8	2	2	27	8
Long Id.	9	7	4	8	28	130
Eleuthera	12	10	10	10	42	166
Great and Little Abaco	4	11	5	5	25	776
Grand Bahama	9	12	5	2	28	430
Cat Island	13	12	4	7	36	160
Crooked Id. Group	17	8	3	20	48	219

[1] Four species are endemic to Caicos and Turks Islands, together.
[2] From data sent by Bernard Lewis, Director, The Institute of Jamaica.
[3] Estimated from the United States Hydrographic Office, Chart No. 26-d.

LIST OF THE SPECIES KNOWN FROM THE CROOKED ISLAND GROUP

HELICINIDAE

Eutrochatella acklinsensis, new species

Plate 3, figure 4

Description. Shell reaching a length of 3.5 mm., turrited, rather thin, imperforate and finely sculptured. Color a grayish white. Whorls 5 and strongly convex. Spire moderately extended. Aperture subcircular. Outer lip simple, parietal area glazed. Columella arched. Suture well indented. Sculpture consisting of numerous spiral, incised lines. Nuclear whorls 1½ to 2 and smooth. Operculum unknown.

Length	Width	
3.5 mm.	3.5 mm.	Holotype
3.2	3.4	Paratype

Types. The holotype is in the United States National Museum, no. 390633, from inland from Cornucopia, Acklins Island, Bahamas. Paratypes from the same locality are in the Museum of Comparative Zoology, no. 225315.

Remarks. E. acklinsensis does not appear closely related to any other species in the Bahama Islands. It shows distant relationships with two or three Cuban species of a similar size but differs from all by having the whorls turrited and strongly convex.

Alcadia (Alcadia) mcleani Clench

Alcadia (*Alcadia*) *mcleani* Clench 1937, Proc. New England Zool. Club **16**:74, pl. 3, fig. 6 (Landrail Point, Crooked Island, Bahamas).

Specimens examined. Crooked Island: Stopper Hill; 1¼ mi. SE of Gordon Bluff; S of Cripple Hill; ½ mi. NE of Fairfield; 1¼ mi. W of Church Grove; 1 mi. NW of Colonel Hill; McKi Hill. Acklins Island: Delectable Bay; ¾ mi. S of Binnacle Hill Settlement; Pinnacle Point; Indian Wells; inland from Cornucopia, 3¾ mi. NE of Salina Point.

Helicina rawsoni Pfeiffer

Helicina rawsoni Pfeiffer 1867, Malakozoologische Blätt. **14**:165 (Inagua Island, Bahamas).

Specimens examined. Fortune Island: Walker Bay. Crooked Island: Major Cay Settlement. Acklins Island: 2 mi. SE of Snug Corner; Delectable Bay; 2½ mi. SE of Pompey Bay Settlement; Pinnacle Point; Indian Wells; inland from Cornucopia; 2 mi. S of Binnacle Hill.

Lucidella (Poeniella) tantilla Pilsbry

Helicina tantilla Pilsbry 1902, Nautilus **16**:53 (Palm Beach, Florida).

Specimens examined. Acklins Island: inland from Cornucopia.

Eutrochatella calida Weinland

Helicina calida Weinland 1862, Malakozoologische Blätt. **9**:91 (Crooked Island, Bahamas).

Specimens examined. Fortune Island: Walker Bay; Windsor Point. Crooked Island: Gordon Bluff; Sea View. Acklins Island: Mason Bay; Snug Corner; Delectable Bay; Pompey Bay; Pinnacle Point; Indian Wells; 2 mi. S. of Binnacle Hill; Jamaica Bay. West Plana Cay.

POMATIASIDAE

Opisthosiphon (Opisthosiphon) Acklinsensis Bartsch

Opisthosiphon (*Opisthosiphon*) *acklinsensis* Bartsch 1946. United States Nat. Mus. Bull. **192**:221, pl. 36, fig. 9 (Spring Point, Acklins Island, Bahamas).

Specimens examined. Crooked Island: Landrail Point; Stopper Hill; Marine Farm Hill; Pitts Town Point; Gordon Bluff; ½ mi. NE of Fairfield; 1¼ mi. W of Church Grove; 1 mi. NW of Colonel Hill; McKi Hill; Caigdale. Acklins Island: 2½ mi. S of Chesters; Snug Corner; Delectable Bay; 2½ mi. SE of Pompey Bay; Pinnacle Point (Spring Point).

Opisthosiphon (Opisthosiphon) lucayanorus, new species

Plate 3, figure 2

Description. Shell reaching 16 mm. in length, light in structure, shining and attenuate. Color a nearly uniform straw-yellow, occasional specimens having the middle whorls a dark mahogany-brown. Small dots of brown in both axial and spiral arrangement are faint or lacking. Whorls 6 to 7, decollated and moderately convex. Spire attenuate. Aperture subcircular. Lip holostomatous and reflected. Suture crenulate, slightly channeled and becoming broadly so just about one-sixth of a whorl behind the lip. Sculpture consists of fine growth lines and the rather strongly developed sutural crenulations. Nuclear whorls smooth and opaque. Operculum paucispiral with fine, arcuate ridges on the outer surface.

Length	Width	
14.8 mm.	7 mm.	Holotype
16.6	7.5	Paratype
14.8	7	Paratype

Types. Holotype, Museum of Comparative Zoology, no. 221179, from 3¾ mi. NE of Salina Point, Acklins Island, Bahamas. Additional paratypes are from the same locality and from Binnacle Hill; 2 mi. S of Binnacle Hill and from Pinnacle Point, Acklins Island. A series of paratypes is in the United States National Museum.

Remarks. This species differs from all other Bahama *Opisthosiphon* by being smooth and not axially costate. It differs from *Opisthosiphon acklinsensis* Bart., the only other *Opisthosiphon* in the Crooked Island group, by being smooth and by having the sutural crenulations somewhat broader.

CHONDROPOMA (CHONDROPOMA) GLABRATUM Reeve

Chondropoma semilabre of authors, not of Lamarck.

Chondropoma glabratum Reeve 1863, Conchologia Iconica **14**: *Chondropoma*, pl. 2, fig. 12 (Bahamas).

Chondropoma (*Chondropoma*) *glabratum fortunatum* Bartsch 1946, United States National Mus. Bull. **192**:210, pl. 35, fig. 6 (near Albert Town, Fortune Island, Bahamas).

Chondropoma (*Chondropoma*) *glabratum acklinsense* Bartsch 1946, United States National Mus. Bull. **192**:210, pl. 35, fig. 5 (Jamaica Bay, Acklins Island, Bahamas).

Specimens examined. FORTUNE ISLAND: Windsor Point; Walker Bay; Douglas Town; Albert Town. CROOKED ISLAND: Landrail Point; Marine Farm Hill; Pittstown Point; Gordon Bluff; Sea View; Cripple Hill; ½ mi. NE of Fairfield; between Browns and True Blue. ACKLINS ISLAND: Chesters; 2½ mi. S of Chesters; Mason Bay; 2 mi. SE of Snug Corner; Delectable Bay; Binnacle Hill; 2 mi. S of Binnacle Hill; Pinnacle Point; Cornucopia; 3¾ mi. NE of Salina Point; Salina Point; Jamaica Bay; W of China Hill.

CHONDROPOMA (CHONDROPOMA) GLABRATUM PLANICOLUM Bartsch

Chondropoma (Chondropoma) planicolum Bartsch 1946, United States National Mus. Bull. **192**:213, pl. 34, fig. 7 (West Plana Cay, Bahamas).

Specimens examined. WEST PLANA CAY.

CHONDROPOMA (CHONDROPS) PLANAENSE Bartsch

Chondropoma (Chondrops) planaense Bartsch 1946, United States National Mus. Bull. **192**:196, pl. 33, fig. 5 (West Plana Cay, Bahamas).

Specimens examined. WEST PLANA CAY.

COLONINA HYDII Weinland

Cyclostomus hydii Weinland 1862, Malakozoologische Blätter **9**:90 (Crooked Island, Bahamas).

Colonina fortunensis Bartsch 1946, United States Nat. Mus. Bull. **192**:245, pl. 38, fig. 11 (near Albert Town, Fortune Island, Bahamas).

Colonina nana Bartsch 1946, United States National Mus. Bull. **192**:246, pl. 38, fig. 12 (West Plana Cay, Bahama Islands).

Specimens examined. FORTUNE ISLAND: Upper Landing; Windsor Point; Douglas Town; Albert Town. CROOKED ISLAND: French Wells; Bullet Hill; between Browns and True Blue. ACKLINS ISLAND: Snug Corner; Mason Bay; Delectable Bay; Binnacle Hill; 3/4 mi. S of Binnacle Hill; Pinnacle Point; Cornucopia; 3 3/4 mi. NE of Salina Point; Jamaica Bay; W of China Hill. CASTLE ISLAND: NE end; N coast. WEST PLANA CAY.

Through an oversight, records for *Colonina hydii* Weinland were not included in my report on the "Land and Freshwater Mollusks of Great and Little Inagua Islands," 1959, Bull. Mus. Comp. Zool. **121**:29-53. These are as follows:

Specimens examined. GREAT INAGUA: near Lantern Head. LITTLE INAGUA: 1 1/2 mi. from Northwest Point; NW side of Little Inagua.

COLONELLA ACKLINSENSIS Bartsch

Colonella acklinsensis Bartsch 1946, United States National Mus. Bull. **192**:251, pl. 38, fig. 8 (Pinnacle Point, Acklins Island, Bahama Islands).

Specimens examined. ACKLINS ISLAND: 3/4 mi. S of Binnacle Hill; 2 mi. S of Binnacle Hill; Pinnacle Point; 3¾ mi. NE of Salina Point.

COLONELLA MARIGUANENSIS PLANAENSIS Bartsch

Colonella mariguanensis planaensis Bartsch 1946, United States National Mus. Bull. **192**:250, pl. 38, fig. 5 (West Plana Cay, Bahamas).

Specimens examined: WEST PLANA CAY.

AMNICOLIDAE

LITTORIDINA TENUIPES Couper

Amnicola tenuipes Couper 1844 [in] S.S. Haldeman, Monograph Limniades of North America, Philadelphia, pt. 7, p. 4 of cover, and pt. 8, p. 23, pl. 1, figs. 14-15 (Hopeton, Georgia).

Specimens examined. CROOKED ISLAND: Major Cay Settlement. ACKLINS ISLAND: between Pleasant Point and Claret Cove; 2 mi. S of Binnacle Hill Settlement.

LYMNAEIDAE

LYMNAEA (GALBA) CUBENSIS Pfeiffer

Lymnaeus cubensis Pfeiffer 1839, Archiv für Naturgeschichte **5**:354 (Cuba).

Specimens examined. ACKLINS ISLAND: Delectable Bay; Pompey Bay.

PLANORBIDAE

DREPANOTREMA LUCIDUM Pfeiffer

Planorbis lucidus Pfeiffer 1839, Archiv für Naturgeschichte **5**:354 (Cuba).

Specimens examined. CROOKED ISLAND: 1½ mi. SE of Gordon Bluff; 1¼ mi. ESE of Colonel Hill. ACKLINS ISLAND: Delectable Bay; between Pleasant Point and Claret Cove; Pinnacle Point.

DREPANOTREMA CIMEX Moricand

Planorbis cimex Moricand 1839, Mem. Soc. Phys. Geneve **8**:143, pl. 3, figs. 8-9 (Bahia, Brazil).

Specimens examined. CROOKED ISLAND: Pitts Town Point. ACKLINS ISLAND: Pompey Bay.

TROPICORBIS ALBICANS Pfeiffer

Planorbis albicans Pfeiffer 1839, Archiv für Naturgeschichte **5**:354 (Cuba).

Specimens examined. FORTUNE ISLAND: Albert Town. ACKLINS ISLAND: 2½ mi. S of Chesters; Pompey Bay; Pinnacle Point.

PHYSIDAE

PHYSA CUBENSIS Pfeiffer

Physa cubensis Pfeiffer 1839, Archiv für Naturgeschichte **5**:354 (Cuba).

Specimens examined. ACKLINS ISLAND: 2½ mi. S of Chesters; Pompey Bay.

SUCCINEIDAE

SUCCINEA BARBADENSIS Guilding

Succinea barbadensis Guilding 1828, Zoological Jour. **3**:532 (Barbados).

Specimens examined. CROOKED ISLAND: Stopper Hill; ½ mi NE of Fairfield. ACKLINS ISLAND: 2½ mi. S of Chesters; Delectable Bay Settlement; Pompey Bay Settlement; Binnacle Hill; Pinnacle Point.

PUPILLIDAE

PUPOIDES NITIDULUS Pfeiffer

Bulimus nitidulus Pfeiffer 1839, Archiv für Naturgeschichte **5**:352 (Cuba).

Specimens examined. FORTUNE ISLAND: Albert Town. CROOKED ISLAND: Marine Farm Hill; McKi Hill; Bullet Hill; between Browns and True Blue. ACKLINS ISLAND: 2½ mi. S of Chesters; Mason Bay; Delectable Bay; Binnacle Hill; 2 mi. S of Binnacle Hill; Pinnacle Point. WEST PLANA CAY.

GASTROCOPTA PELLUCIDA Pfeiffer

Pupa pellucida Pfeiffer 1841, Symbolae ad Historiam Heliceorum **1**:46 (Cuba).

Specimens examined. FORTUNE ISLAND: Windsor Point; Douglas Town; Albert Town. CROOKED ISLAND: S of Cripple Hill; 1 mi. NW of Colonel Hill; McKi Hill; Bullet Hill; between

Browns and True Blue. ACKLINS ISLAND: 2½ mi. S of Chesters; Mason Bay; Delectable Bay; Pompey Bay; Binnacle Hill; Pinnacle Point; 3¾ mi. NE of Salina Point; Indian Wells. WEST PLANA CAY.

GASTROCOPTA RUPICOLA MARGINALBA Pfeiffer

Pupa marginalba Pfeiffer 1840, Archiv für Naturgeschichte **1**:253 (Cuba).

Specimens examined. FORTUNE ISLAND: Upper Landing; Windsor Point; Albert Town. CROOKED ISLAND: Landrail Point; 1 mi. NW of Colonel Hill. ACKLINS ISLAND: 2 mi. S. of Binnacle Hill; Pinnacle Point; Cornucopia; 3¾ mi. NE of Salina Point. CASTLE ISLAND: NE end; SW end. WEST PLANA CAY.

STROBILOPSIDAE

STROBILOPS HUBBARDI VENDRYESIANA Gloyne

Helix vendryesiana Gloyne 1871, Jour. de Conchyliologie **19**: 333 (Bellevue, St. Andrew, Jamaica).

Remarks. This rare species is known elsewhere in the Bahamas from Great Inagua and the Caicos Islands.

Specimens examined. ACKLINS ISLAND: 2 mi. S of Binnacle Hill.

SUBULINIDAE

LAMELLAXIS (ALLOPEAS) GRACILIS Hutton

Bulimus gracilis Hutton 1834, Jour. Asiatic Soc. Bengal **3**:93 (Mirzapur, Ceylon).

Specimens examined. CROOKED ISLAND: Marine Farm Hill; N of Cripple Hill; 1¼ mi. N of Church Grove.

OLEACINIDAE

OLEACINA (LAEVOLEACINA) SOLIDULA Pfeiffer

Polyphemus solidula Pfeiffer 1840, Archiv für Naturgeschichte (Wiegmann) **1**:252 (near Matanzas, Cuba).

Specimens examined. CROOKED ISLAND: Stopper Hill; inland from Pitts Town Point; 1¼ mi. SE of Gordon Bluff; ½ mi. NE of Fairfield; 1¼ mi. W of Church Grove; 1 mi. NW of Colonel Hill; McKi Hill. ACKLINS ISLAND: 2½ mi. S of Chesters; Snug Corner; Delectable Bay; 2½ mi. SE of Pompey Bay; Binnacle

Hill; 2 mi. S of Binnacle Hill; 3¾ mi. NE of Salina Point; Indian Wells.

VARICELLA GRACILLIMA FLORIDANA Pilsbry

Varicella gracillima floridana Pilsbry 1907, Man. of Conch. (2) **19**:57 (Key West, Florida).

Specimens examined. FORTUNE ISLAND: near Upper Landing. CROOKED ISLAND: 1 mi. NW of Colonel Hill. ACKLINS ISLAND: 2 mi. S of Binnacle Hill; Cornucopia; Indian Wells. WEST PLANA CAY.

POLYGYRIDAE

POLYGYRA PLANA Dunker

Helix plana Dunker 1843, Abbildungen neuer Conchylien, Cassel, **1**:51, *Helix,* pl. 3, fig. 11 (? West Indies).

Specimens examined. CROOKED ISLAND: Pitts Town Point; Stopper Hill; 1¼ mi. SE of Gordon Bluff; ½ mi. NE of Fairfield; 1¼ mi. ESE of Colonel Hill; Major Cay Settlement.

SAGDIDAE

HOJEDA INAGUENSIS Weinland

Helix inaguensis Weinland 1880, Jahrb. deut. malak. Gesell. **7**:369, pl. 12, fig. 22 (Little Inagua).

Specimens examined. FORTUNE ISLAND: Upper Landing; Douglas Town; Albert Town. CROOKED ISLAND: ½ mi. NE of Fairfield. ACKLINS ISLAND: 2½ mi. S of Binnacle Hill; Pinnacle Point; Cornucopia; 3¾ mi. NE of Salina Point; Indian Wells. WEST PLANA CAY.

LACTEOLUNA SELENINA Gould

Helix selenina Gould 1848, Proc. Boston Soc. Nat. Hist. **3**:38 (Georgia and Florida).

Specimens examined. CROOKED ISLAND: Landrail Point; 1¼ mi. W of Church Grove. ACKLINS ISLAND: Mason Bay.

BULIMULIDAE

DRYMAEUS BAHAMENSIS GREENWAYI Clench

Drymaeus bahamensis greenwayi Clench 1933, Proc. New England Zool. Club **13**:88, pl. 1, fig. 11 (Landrail Point. Crooked Island, Bahamas).

Specimens examined. CROOKED ISLAND: Landrail Point; Gordon Bluff; 1¼ mi. W of Church Grove. ACKLINS ISLAND: between Pleasant Point and Claret Cove; Delectable Bay; Pompey Bay; Binnacle Hill.

UROCOPTIDAE

MICROCERAMUS SWIFTI Bland

Macroceramus swifti Bland 1875, Ann. Lyceum Nat. Hist. New York **6**:83 (Turks Island, also Inagua).

Specimens examined. FORTUNE ISLAND: Windsor Point; Douglas Town; ½ mi. E of Albert Town. CROOKED ISLAND: Stopper Hill; Gordon Bluff; 1¾ mi. E of Colonel Hill. ACKLINS ISLAND: Delectable Bay Settlement; 2 mi. S of Binnacle Hill; Cornucopia; 3¾ mi. E of Salina Point; W of China Hill. WEST PLANA CAY.

MICROCERAMUS RUSSELLI Clench

Microceramus russelli Clench 1937, Proc. New England Zool. Club **16**:63, pl. 3, figs. 4-5 (Blue Hole Hill, 2 mi. NNE of Orange Creek, Cat Island, Bahamas).

Specimens examined. FORTUNE ISLAND: near Upper Landing. CROOKED ISLAND: NE end.

MICROCERAMUS PROVIDENTIA Pilsbry

Microceramus gossei providentia Pilsbry 1904, Man. of Conch. (2) **16**:161, pl. 26, fig. 16 (Nassau, New Providence [Bahamas]).

Specimens examined. CROOKED ISLAND: Marine Farm Hill; S of Cripple Hill; McKi Hill. ACKLINS ISLAND: 2½ mi. S of Chesters; Snug Corner; Delectable Bay; 2½ mi. SE of Pompey Bay: Binnacle Hill; Cornucopia; Pinnacle Point; Indian Wells. WEST PLANA CAY.

MICROCERAMUS (SPIROCERAMUS) ROBERTSONI, new species

Plate 3, figure 1

Description. Shell reaching 6.7 mm. in length, thin, imperforate, dull and sculptured. Color probably gray, whorls 11 and convex. First 5 to 6 whorls forming the conic portion of the spire. Aperture subcircular. Lip simple. Columella nearly straight. Axis simple and not twisted. Suture indented. Sculpture consisting of numerous fine, oblique axial riblets. These riblets are somewhat stronger on the first 5 to 6 whorls.

Length	Width	
6.7 mm.	1 mm.	Holotype

Type. Holotype, Museum of Comparative Zoology, No. 225313 from Delectable Bay Settlement, Acklins Island, Bahamas. Collected by Robert Robertson and Augustus Scott, Sept. 2, 1958.

Remarks. This species is closely related to *Microceramus greenwayi* Clench from Foxtown, Little Abaco Island, Bahamas. It differs by being a little more coarsely sculptured and having the nuclear whorls a little smaller.

This is the second species known in this subgenus from the Bahamas. The remaining few species occur only in central and eastern Cuba.

Gongylostoma bahamensis Pfeiffer

Cylindrella bahamensis Pfeiffer 1861, Malakozoologische Blätter **7**:214, pl. 2, figs. 8-11 (Nassau, Bahamas).

Specimens examined. Crooked Island: Stopper Hill.

CERIONIDAE

Cerion (Strophiops) regium Benson

Pupa decumana 'Ferussac' Pfeiffer 1848, Monographia Heliceorum Viventium **2**:320 (St. Thomas; Cuba ?). non Gray 1825.

Pupa regia Benson 1849, Ann. Mag. Nat. Hist. (2) **4**:125 (Nanking, China [Castle Island, Bahamas]).

Remarks. This species appeared to be quite abundant on parts of Castle Island and in the vicinity of Salina Point on Acklins Island.

Just how the error of Nanking, China (cited as the type locality) occurred, is, of course, unknown. The first to collect this species again was Governor Rawson at some time between 1864 and 1869. The specimens he obtained were sent to many institutions, and specimens were not again collected until Bartsch visited Castle Island in 1930 and Robertson and Scott in 1958.

This is the largest of all species of *Cerion.* It seems to prefer open and exposed places, attached to the stems of bushes and other scrub growth.

For a complete discussion covering the complex history of names concerned with this species, see Pilsbry 1902, Man. of Conch. (2) **14**:236.

Specimens examined. ACKLINS ISLAND: 2 mi. S of Binnacle Hill; Salina Point; Jamaica Bay; W of China Hill. CASTLE ISLAND: NE end; SW end, E and W sides.

CERION (STROPHIOPS) WEINLANDI v. Martens

Pupa weinlandi v. Martens 1860, Malakozoologische Blätter **6**:207, pl. 2, fig. 1 (Crooked Island, Bahamas).

Specimens examined. ACKLINS ISLAND: Snug Corner; Mason Bay; ¾ mi. S of Binnacle Hill; Cornucopia; Jamaica Wells; 3¾ mi. E of Salina Point; Sugar Bay.

CERION (MULTOSTROPHIA) MARMORATUM Pfeiffer

Pupa marmorata Pfeiffer 1847, Zeitschrift für Malakozoologie **4**:83 (locality unknown [Fortune Island, Crooked Island Group, Bahamas]).

Pupa martensi Weinland 1862, Malakozoologische Blätter **9**: 174 (Crooked Island, Bahamas).

Strophia inflata Maynard 1889, Contributions to Science **1**:126, pl. 7, figs. 21a, 30a-b (Salina Point, Acklins Island, Bahamas).

Cerion multistriatum Pilsbry and Vanatta 1896, Proc. Acad. Nat. Sci., Philadelphia **48**:335, pl. 11, fig. 8 (Crooked Island, Bahamas).

Cerion submarmoratum Pilsbry and Vanatta 1897, Proc. Acad. Nat. Sci., Philadelphia **49**:365, text-figs. 3-4 ([Fortune Island] Bahamas).

Cerion martensi cliffordi Clench 1933, Proc. New England Zool. Club **13**:91, pl. 1, fig. 10 (Landrail Point, Crooked Island, Bahamas).

Specimens examined. FORTUNE ISLAND: North Cay; Windsor Well; Douglas Town; Albert Town; N end. CROOKED ISLAND: Goat Cay; French Wells; ¼ mi. NE of French Wells; Landrail Point; between Browns and True Blue; Richmond; S. of Cripple Hill; ½ mi. NE of Fairfield; 2 mi. W of Church Grove; 1 mi. NW of Colonel Hill; Major Cay Settlement; Caigdale; Cove Settlement. ACKLINS ISLAND: Chesters; Snug Corner; Delectable Bay; 2½ mi. SE of Pompey Bay; Jamaica Cay; Binnacle Hill; 3¾ mi. NE of Salina Point.

CERION (STROPHIOPS) UTOWANA Clench

Cerion (*Strophiops*) *utowana* Clench 1933, Proc. New England Zool. Club **13**:92, pl. 1, figs. 1-2 (East Plana Cay, Bahamas).

Specimens examined. EAST PLANA CAY.

CERION (STROPHIOPS) GREENWAYI Clench

Cerion (*Strophiops*) *greenwayi* Clench 1934, Proc. Boston Soc. Nat. Hist. **40**:206, pl. 2, fig. H (Black Booby Cay, Atwoods or Samana Group, Bahama Islands).

Remarks. Only dead and very old specimens of this species were found on West Plana Cay by Bartsch in 1930. Several quite different forms occurred, from typical costate *greenwayi* to nearly smooth, slender or very stout specimens which approximate *C. utowana* Clench from East Plana Cay. It is impossible to tell whether or not these specimens existed at one time or represent populations which existed at different times.

Specimens examined. ACKLINS ISLAND: W end of Blue Mt. SAMANA CAY. WEST PLANA CAY.

CERION (MAYNARDIA) PERICULOSUM Clench

Cerion (*Strophiops*) *periculosum* Clench 1934, Proc. Boston Soc. Nat. Hist. **40**:215, pl. 2, fig. B (South Cay, Mira Por Vos Group, Bahamas).

Specimens examined. MIRA POR VOS: South Cay.

FRUITICICOLIDAE

HEMITROCHUS VARIANS Menke

Helix varians Menke 1829, Verzeichnis Conchy.—Samml. Malsburg, Pyrmont, p. 5. (Locality not given).

Specimens examined. FORTUNE ISLAND: ½ mi. E of Albert Town; North Cay. CROOKED ISLAND: Pitts Town Point; Landrail Point; Caigdale; Bullet Hill; between Browns and True Blue; French Wells. ACKLINS ISLAND: Indian Wells. WEST PLANA CAY.

HEMITROCHUS GALLOPAVONIS Pfeiffer

Helix gallopavonis 'Valenciennes' Pfeiffer 1842, Symbolae ad Historiam Heliceorum **2**:28 (St. Croix; Turks Islands).

Helix caribaea Weinland 1862, Malakozoologische Blätter **9**:195 (Crooked Island, Bahamas).

Helix gallopavonis major Weinland 1880, Jahrbücher deut. malak. Gesell. **7**:373 (Turks Island [Bahamas]).

Helix gallopavonis elatior Weinland 1880, Jahrbücher deut. malak. Gesell. **7**:374 (Turks Island, Bahamas).

This species does not occur on St. Croix.

Specimens examined. FORTUNE ISLAND: Goat Cay; Douglas Town; Windsor Point; N end of Fortune Island. CROOKED ISLAND: Gordon Bluff; Sea View; Richmond; near Cripple Hill; Fairfield; Colonel Hill; Major Cay Settlement; Cove Settlement. ACKLINS ISLAND: Lovely Bay Settlement; Chesters; Snug Corner; between Pleasant Point and Claret Cove; Delectable Bay Settlement; Pompey Bay Settlement; Jamaica Cay; Cotton Cay.

HEMITROCHUS MILLERI Pfeiffer

Helix milleri Pfeiffer 1867, Malakozoologische Blätter **14**:126 (Long Cay [Fortune Island] Bahama Islands).

Specimens examined. FORTUNE ISLAND: Walker Bay; Windsor Wells. ACKLINS ISLAND: Cornucopia Bay.

HEMITROCHUS GILVUS Férussac

Helix gilvus Férussac 1821 [1822], Tableaux Systematiques des Animaux Mollusques, p. 29 [refers to plate 21-B, fig. 1 in Férussac's Histoire Naturelle des Mollusques. Plate 21-B was published in 1821, though the text did not appear until 1850, **1**:171.] (Locality unknown in 1821 but stated to be Cuba in 1850.)

Helix multifasciatus Weinland and v. Martens 1860, Malakozoologische Blätter **6**:17 (Crooked Island, Bahama Islands).

Helix (*Hemitrochus*) *multifasciatus polytaeniata* Pilsbry 1889, Man. of Conch. (2) **5**:30, pl. 31, fig. 29 (no locality given).

Helix (*Helicogena*) *gilvus* Férussac. Torre 1939, Nautilus **52**:77.

Specimens examined. ACKLINS ISLAND: 2½ mi. SE of Pompey Bay Settlement; Binnacle Hill; ¾ mi. S of Binnacle Hill; 2 mi. S of Binnacle Hill; Cornucopia; 3¾ mi. NE of Salina Point. CASTLE ISLAND: N. coast.

Plagioptycha scotti, new species

Plate 3, figure 3

Description. Shell reaching 16 mm. in greater diameter, light in structure, rather dull, finely sculptured and umbilicate. Color a light straw-yellow with two narrow, spiral bands of pale brown at the periphery. Whorls 4½ and convex. Spire depressed, hardly appearing above the body whorl. Aperture subelliptical. Outer lip simple and slightly reflected along the basal margin to the columellar area. Suture impressed. Sculpture consists of numerous, fine growth lines. Basal tooth well within the aperture, centered, elevated and diagonal to the lip margin.

Greater diameter	Height	
14 mm.	5 mm.	Holotype
15.5	6.5	Paratype
15.2	5.8	Paratype

Types. The holotype is in the Museum of Comparative Zoology, no. 225311, from 2 miles south of Binnacle Hill Settlement, Acklins Island, Bahamas. Collected by Robert Robertson and Augustus Scott, August 30, 1958. Additional paratypes in the Museum of Comparative Zoology and the United States National Museum.

Remarks. This species is related to *P. bahamensis* Pfr. from the Turks Islands and to *P. williamsi* Clench from Mariguana Island. *P. scotti* differs from *P. bahamensis* by being larger, having a larger gular tooth, and by being smooth. It differs from *P. williamsi* by being far more depressed, having a more open umbilicus, and by being smooth. Both *bahamensis* and *williamsi* are strongly and axially ribbed.

SPHAERIDAE

Eupera bahamensis Clench

Byssanodonta bahamensis Clench 1938, Bull. Mus. Comp. Zool. **80**:535, pl. 2, fig. 6 (½ mi. E of Arthurs Town, Cat Island, Bahama Islands).

Specimens examined. Acklins Island: Pompey Bay Settlement.

The genus *Eupera* Bourguignat 1854 was placed in the synonymy of *Byssanodonta* d'Orbigny 1846 by Thiele (1934, Handbuch der Systematischen Weichtierkunde **3**:853). This was unfortunate, as the two genera are very different and do not belong even in the same family. *Byssanodonta* is without hinge teeth and is somewhat angled posteriorly on both the dorsal and ventral margins. *Eupera* has well developed hinge teeth and is rounded posteriorly. In addition, all American species of *Eupera* are mottled with a blackish pigment on the inside of the shells, a character not indicated or mentioned by d'Orbigny for *Byssanodonta*.

The following is a synopsis of the genus *Eupera*.

Eupera Bourguignat 1854, Rev. Mag. Zool. (2) **6**:84 (nomen nudum); *ibid.* p. 663, monotypic, *Pisidium moquinianum* Bourguignat (= *Cyclas modioliformis* Anton); Pilsbry and Bequaert 1927, Bull. Amer. Mus. Nat. Hist. **53**:354.

Limosina Clessin 1872, Malakozoologische Blätter **19**:160 (type species, *Cyclas modioliformis* Anton, subsequent designation, Pilsbry and Bequaert 1927).

Clessinella Waagen 1905, Sitz.-Ber. Akad. Wiss. Wien, Math. Naturw. Kl. **114**:171, monotypic, *Sphaerium* (*Clessinella*) *sturany* Waagen.

Byssanodonta of authors [not of d'Orbigny 1846, Voyage l'Amerique Meridionale **5**:621, pl. 84, figs. 21-23, monotypic, *Byssanodonta paranensis* d'Orbigny].

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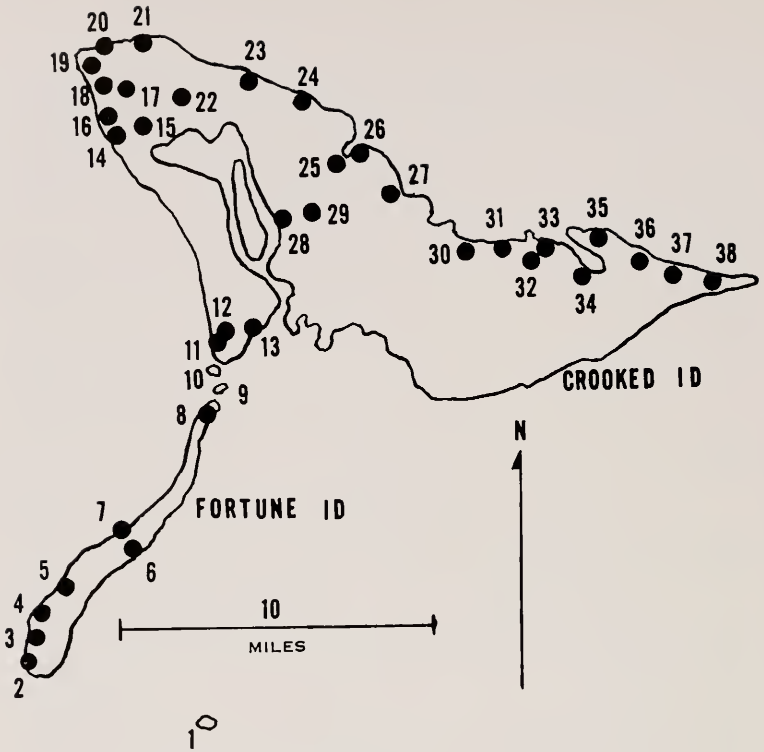


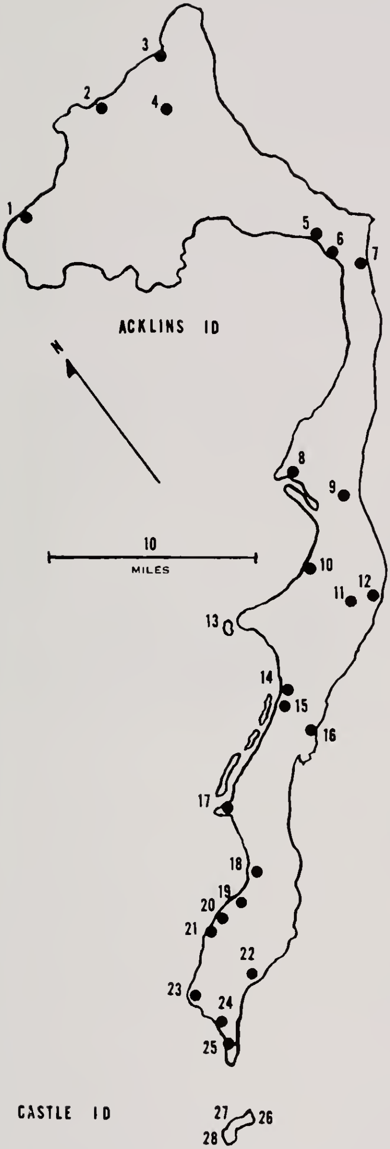
Plate 1.

Localities on Fortune and Crooked Islands

1. North Cay
2. Upper Landing
3. Windsor Wells
4. Windsor Point
5. Walker Bay
6. Douglas Town
7. Albert Town
8. North End
9. Rat Cay
10. Goat Cay
11. French Wells
12. ¼ mi. NE of French Wells
13. ¾ mi. E of French Wells
14. Landrail Point
15. Stopper Hill
16. ¾ mi. N of Landrail Point
17. Marine Farm Hill
18. S from Pitts Town Point
19. Inland from Pitts Town Pt.
20. E of Pitts Town Point
21. Gordon Bluff
22. 1¼ mi. SE of Gordon Bluff
23. Sea View
24. Richmond
25. S of Cripple Hill
26. N of Cripple Hill
27. ½ mi. NE of Fairfield
28. 2 mi. W of Church Grove
29. 1¼ mi. W of Church Grove
30. 1 mi. NW of Colonel Hill
31. Colonel Hill
32. 1¼ mi. ESE of Colonel Hill
33. McKi Hill
34. Major Cay Settlement
35. Caigdale
36. Bullet Hill
37. Between Browns and True Blue
38. Cove Settlement

PLATE 2

Localities on Acklins and Castle Islands



1. Lovely Bay Settlement
2. Chesters
3. Atwoods Harbour
4. 2½ mi. S of Chesters
5. Snug Corner
6. Mason Bay
7. 2 mi. SE of Snug Corner
8. Delectable Bay
9. Between Pleasant Point and Claret Cove
10. Pompey Bay
11. W end of Blue Mts.
12. 2½ mi. SE of Pompey Bay
13. Jamaica Cay
14. Binnacle Hill
15. ¾ mi. S of Binnacle Hill
16. 2 mi. S of Binnacle Hill
17. Pinnacle Point
18. Cornucopia
19. Jamaica Wells
20. 3¾ mi. SE of Salina Point
21. Sugar Bay
22. Salina Point Settlement
23. Salina Point
24. Jamaica Bay
25. W of China Hill
26. NE end
27. N coast
28. SW end

Indian Wells is not positioned on the map as its exact location is unknown to me. It is not given in Bartsch's journal though this is one of his stations. It is, however, in the south of Acklins Island, close to Pinnacle Point.

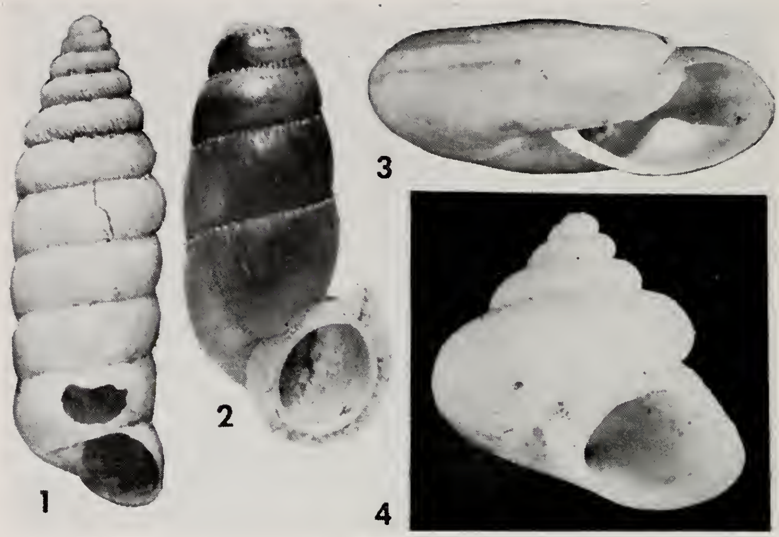


PLATE 3

Fig. 1. *Microceramus (Spiroceramus) robertsoni* Clench. Delectable Bay, Acklins Island, Bahamas. Holotype MCZ No. 225313 (10x).

Fig. 2. *Opisthosiphon lucayanorus* Clench. 3¾ mi. NE of Salina Point, Acklins Island, Bahamas. Holotype MCZ No. 225179 (3.7x).

Fig. 3. *Plagioptycha scotti* Clench. 2 mi. S. of Binnacle Hill Settlement, Acklins Island, Bahamas. Holotype MCZ No. 225311 (4x).

Fig. 4. *Eutrochatella acklinsensis* Clench. Hills inland from Cornucopia, Acklins Island, Bahamas. Holotype USNM No. 390633 (11.4x).

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 128, No. 9

THE LARGER EMBOLOMEROUS AMPHIBIANS OF THE AMERICAN CARBONIFEROUS

By Alfred Sherwood Romer

With Two Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
February 18, 1963

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No. 9 — *The Larger Embolomerous Amphibians of the American Carboniferous*

By

ALFRED SHERWOOD ROMER

I. A LARGE EMBOLOMERE SKULL FROM THE CONEMAUGH SERIES OF OHIO.

Notable in the vertebrate fauna of the Upper Carboniferous of Great Britain is the presence of numerous specimens of large embolomerous amphibians. Remains of this sort, commonly described as *Pteroplax* or *Eogyrinus*, are especially abundant in the coal shales of the Newsham Main Seam near Newcastle-upon-Tyne; the original descriptions were given in a series of papers by Hancock and Atthey, and reviewed by Watson in his important Croonian lecture of 1926 on the Evolution and Origin of the Amphibia.

In North America, however, remains of large Carboniferous embolomeres are rare.[1] In the present paper I shall describe the recently discovered skull of a large embolomere comparable to the familiar British forms, and take the opportunity to review other American remains which may pertain to large Carboniferous embolomeres. For the privilege of describing this skull I am indebted to the authorities of the U. S. National Museum, including Dr. C. Lewis Gazin, Curator of Vertebrate Paleontology, and Associate Curator David H. Dunkle. I am indebted to Dr. Donald Baird for aid and advice, and to the National Science Foundation for aid in the collection and preparation of Carboniferous materials, including partial preparation of the skull under consideration.

A few years ago the Pennsylvania Railroad was engaged in improving its main Pittsburgh-St. Louis line west of Steubenville, Ohio. About ten miles directly west of that city a deep cut was excavated north of the village of Bloomingdale, Wayne Township, Jefferson County, Ohio. In the process of excavation, by bulldozer and drag lines, remains of the skull and jaws of a large amphibian were unearthed near the top of the cut. The locality, in terms of federal land surveys, is SW ¼ SE ¼ SE ¼, Section

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[1] Under the assumption then prevalent that all Carboniferous labyrinthodonts were embolomeres, I assigned, in 1930, a considerable number of specimens from the famous Linton coal mine to this labyrinthodont order: however, Dr. Donald Baird, who has in process a thorough revision of the Linton fauna, finds that a good fraction of these materials are those of temnospondyls rather than embolomeres.

24, Wayne Township. The site is 180 feet northeast of the northeast abutment of an overpass bridge and 20 feet above a spring which drains into the side of the cut. The geology of this area has been described by Lamborn (1930). The shale in which the remains were embedded is 12½ feet above a limestone which is identified as the Ames Limestone, and about 185 feet below the Pittsburgh No. 8 coal. This places it at about the middle of the Conemaugh series of the Pennsylvanian System. It is about 300 feet above the level of the famous Linton amphibian locality (in the northern part of the same county), which is at the Upper Freeport Coal horizon at the summit of the Allegheny series. A modest number of finds of fishes, amphibians, and reptiles have been made from other Conemaugh localities (Romer 1952, p. 105, etc.) but apart from a single centrum mentioned later, no other remains of large embolomeres have been reported. A part of the material was seen and collected, while excavation was in progress, by Dr. Raymond E. Lamborn of the Geological Survey of Ohio; a thorough search made later by Dr. David H. Dunkle of the U.S. National Museum resulted in the discovery of further pieces. The specimen is now catalogued as No. 20636 in the U.S. National Museum collections. From the same horizon were collected several *Platyhystrix*-like amphibian neural spines now being studied by Dr. Peter P. Vaughn; a dozen feet below, at the level of the Ames Limestone, were found several spine fragments of a small *Edaphosaurus*, a small amphibian neural spine, and a few fish teeth including *Cladodus* and a petalodont and part of a cochliodont plate.

Of postcranial remains, there were found only some rib fragments and a few centra and intercentra with diameters of 30 to 35 mm. Presumably the entire skull and jaws were present before excavation; saved from the damage caused by the excavating machinery were broken pieces making up somewhat over half of the skull — mainly the left side — and most of the right jaw ramus. Before the specimen was sent to me for study, it was exhibited as part of a demonstration of the activities of the National Museum before the governing boards of the Smithsonian Institution. For this occasion, the missing parts of the skull and dentition were restored. I am publishing here photographs of the restoration (Pls. 1, 2), despite the fact that various features are open to question, since the illustrations give a much more vivid impression of the skull as it would have appeared in life than the drab factual figures of the parts preserved. It is obvious at once that we are dealing with an animal quite similar to the English embolomeres of the *Pteroplax-Eogyrinus* type; compare, for example, my figures with those of Atthey 1876, plates VIII, IX (*"Anthracosaurus russelli"*) and Atthey 1877, plate XIII.

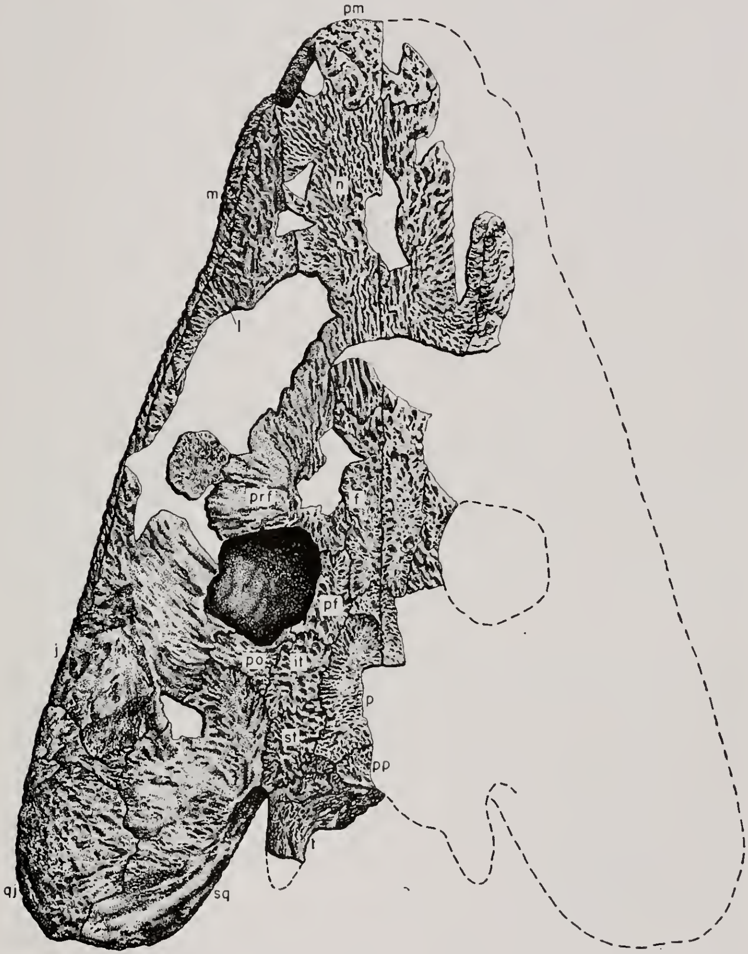

Figure 1. *Neopteroplax conemaughensis.* Skull roof as preserved. x⅓ approximately. Abbreviations: *f*, frontal; *it*, intertemporal; *j*, jugal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *p*, parietal; *pf*, postfrontal; *pm*, premaxilla; *po*, postorbital; *pp*, postparietal; *prf*, prefrontal; *q*, quadrate; *qj*, quadratojugal; *sq*, squamosal; *st*, supratemporal; *t*, tabular.

Skull roof (Figs. 1, 3, 4). Much of the right half of the skull roof was lost beyond recovery during the excavation of the cut. The left side of the skull, however, was nearly completely recovered, as was much of the "snout" region on both sides. On the left, the premaxillary region is slightly imperfect, and a few pieces are missing posteriorly; these are not of great importance except that, unfortunately, areas of the postparietal and parietal close to the midline and including the parietal foramen are absent. The skull had been somewhat crushed dorsoventrally. The length from snout to occiput is 336 mm.; from snout to a line connecting the posterior margins of the quadrates about 395 mm. The *Pteroplax* skull from Newsham described by Atthey in 1876 as "*A. russelli*" is stated to be 13½ inches in length to the occiput, i.e., about 340 mm., very close to the size of the present skull; two figured skull tables from Newsham suggest rather small skulls with lengths of 260-270 mm. The skull proportions are similar to those of *Pteroplax*. There is a moderately long facial region, suggesting piscivorous habits. Crushing has exaggerated the breadth of the cheek region; in life the skull was obviously fairly deep in the quadrate region, the cheeks descending at a considerable angle from the rounded lateral margins of the table. In Figures 3 and 4 the restored skull is seen in dorsal and lateral views, with the effects of crushing eliminated. The width was determined by study of the palatal materials; a latex mold was made of the left half of the roof and fitted over a "form" of modeling clay to find the proper "pitch" of the cheeks.

The sculpture is of a typical labyrinthodont type. It is coarse along the jaw margins, the upper surface of the snout and the table, but relatively smooth over much of the cheek and the region in front of and below the orbit. I find no trace of lateral line canals. Atthey, in the "*A. russelli*" skull, describes a "mucus-groove" along the upper jaws; this appearance, however, may be due (as in the present specimen) to the presence of a marked ridge along the suture between the maxilla and the bones bordering it dorsally.

Determination of sutures is a matter of some difficulty. The animal was obviously mature, and for the most part the sutures between elements are closed. In some instances, as on both sides of the lacrimal anteriorly, the sutures have developed as prominent raised ridges. In nearly every case the approximate boundaries between elements can be defined by study of the radiating pattern of the sculpture of the elements concerned, and the sutures appear to follow low ridges which are not part of the sculpture pattern. In such cases as the contact of jugal and squamosal, where two thin plates of bone are apposed, the breaks due to crushing appear to follow the lines of suture. I have figured a full set of sutures but the reader should be warned that certain of them, at least, are questionable.

The left premaxilla is well preserved, and a fraction of the right element is also present. The bone is thick, forming a rugose rounded terminus to the snout and anteriorly curving downward and somewhat posteriorly to gain the margin of the tooth row. Posterolaterally, it forms half of the margin of the external naris. The maxilla is a very elongate but narrow element. It extends back some 24 cm., tapering in width posteriorly, from the lower margin of the naris to a point below the posterior end of the orbit. Its dorsal contact with the lacrimal is clearly marked off by a raised ridge, and its long suture with the jugal is nearly equally distinct. As in *Pteroplax*, the lacrimal is narrow anteriorly; it enters the posterior margin of the naris for a short distance only. Anteriorly, its suture with the nasal is, like its maxillary contact, a distinct raised ridge. The bone broadens posteriorly, but most of this area of the face is absent in the specimen. With some doubt, I have indicated a short stretch of the supposed jugal contact ventrally and the prefrontal contact dorsally. Obviously in this form, as in *Pteroplax* and *Archeria*, the lacrimal was blocked from entry into the orbital rim by downgrowth of the prefrontal.[1] No evidence of a septomaxilla can be made out in the material.

The left nasal is almost completely preserved, and much of the right is also present. The nasal is a very large element, broad anteriorly where it enters largely into the narial rim, and tapering posteriorly. Anteriorly, there is a distinct, straight, median suture between the two nasals; more posteriorly, the median suture is less certain. The ossification center of the nasal (as indicated by the sculpture pattern) is but about 4.5 cm. back of the front end of the bone, i.e. only about one-third the distance to the frontal suture. In correlation with snout elongation, the posterior portion of the nasal region was a zone of intensive growth, as indicated by the straight longitudinal ridges of the sculpture pattern in this area.

The frontals, almost completely preserved, are of a normal pattern, although somewhat more elongated than in labyrinthodonts with less facial elongation. The fronto-parietal suture is seen on the left side at the expected level.

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[1] Dr. Panchen informs me that this appears to be true of *Palaeogyrinus* as well.

Of the parietals, only a small fragment of the right element is present, but the left is almost complete except that, as noted above, the portion of the median border containing the parietal foramen is unfortunately missing. The lateral border is notably concave in outline along the suture with the supratemporal, and the posterior border is similarly concave along the postparietal suture. There is a broad contact with the tabular. The postparietal, as far as preserved, is of normal pattern.

Of the circumorbital elements, the prefrontal is much expanded, as in *Pteroplax,* extending far forward and downward anterior to the orbit, as noted above, excluding the lacrimal from the orbital region. The more dorsal part of the bone is well sculptured; the preorbital plate is nearly smooth and appears to be thin. Little of the anterior and ventral contacts are preserved, although it appears probable that a break seen in the specimen which runs forward from the lower edge of the orbit was at the jugal-prefrontal contact. The postfrontal differs from that of the Newsham specimen figured as "*A. russelli*" in being less slender anteriorly, but does not differ appreciably from other specimens of *Pteroplax-Eogyrinus.* The postorbital is, as in the English specimens, a rather small element, mainly a flattened vertical plate of bone lying between the orbital margin and the squamosal; above, it broadens somewhat to a contact with the intertemporal. In characteristic embolomere fashion, it has but a small area of contact with the postfrontal along the orbital rim. The bone is little sculptured except at its dorsal margin. Although it is unfortunately far from complete, the jugal is obviously by far the most extensive of all roofing elements, occupying a broad area below the orbit and extending far forward and backward along face and cheek. Ventrally, there is a long distinct suture with the maxilla; more posteriorly, the jugal enters the lower margin of the skull. Part of the suture with the quadratojugal is missing, but most of the line of suture of jugal with postorbital and squamosal is distinct. Anteriorly, much of the area of contact with lacrimal and prefrontal is missing, and the short area of lacrimal contact shown in the figure is doubtful. There is good sculpturing on the more ventral part of the bone, but the upper portions are nearly smooth. In the "*A. russelli*" skull the orbit is essentially triangular in shape, with the jugal margin deeply concave. Here, the jugal margin is more gently curved, so that even if the prefrontal were brought more posteriorly than in Figure 3, the orbit would be much more circular in outline than in the Newsham specimen.

Both intertemporal and supratemporal are well developed, with a good sculpture pattern. The intertemporal extends forward nearly to the orbital margin, almost completely separating postfrontal and postorbital. In contrast to the tendency for reduction of the intertemporal in labyrinthodonts generally, this element is here persistently large — somewhat larger than the supratemporal. Laterally, intertemporal and supratemporal curve smoothly downward from the plane of the skull table. As preserved, the squamosal, slanting outward at about a 45° angle from the skull table, had obviously been disarticulated from the temporal elements, indicating the presence of the zone of weakness usual here in embolomeres. The tabular is well developed, with good contacts dorsally with supratemporal, parietal and postparietal, and a broad occipital contact with the last element. There was a well developed ''horn,'' the distal part of which is missing. There is a typical slit-like otic notch lateral to the tabular.

The squamosal is a broad plate-like element, only lightly sculptured. Nearly straight contacts with the temporal elements above and the postorbital anteriorly are readily seen. Ventrally, there is a line of breakage which appears to follow the position of the sutures with the jugal and most of the quadratojugal. The position of the squamosal-quadratojugal suture near the quadrate is doubtful. As nearly as can be determined, the quadrate extends far upward toward the otic notch at the back margin of the cheek, and there is a long, nearly straight suture between quadrate and squamosal here. The posterior margin of the squamosal is not sculptured. Dorsally, the posterior boundary of the sculptured area is a well-marked and sharp ridge which descends from the anteroventral margin of the otic notch. Posterior to this ridge is a rounded channel which descends along the squamosal nearly to the articular area of the quadrate. The quadratojugal is well preserved, well developed, and well sculptured externally.

Palate (Figs. 2, 5). Most of the palate is preserved on the left side, but the pterygoid is incomplete posteriorly, the ectopterygoid is incomplete, and there are further imperfect areas. On the right, there are merely fragments of premaxilla, maxilla, vomer and palatine anteriorly; nothing remains posteriorly except a tiny pterygoid fragment.

The left premaxilla is preserved nearly completely; its rostral end overhangs the tooth row, internal to which the bone is somewhat excavated for the reception of the anterior dentary teeth.

Most of both vomers are present. The two together form a narrow internarial bar anteriorly, but broaden posteriorly. On the left a vomer-palatine suture is evident. Posteriorly, each vomer

Figure 2. *Neopteroplax conemaughensis.* Palate as preserved. x⅓ approximately. Abbreviations: *ec,* ectopterygoid; *m,* maxilla; *pl,* palatine; *pm,* premaxilla; *ps,* parasphenoid covering basicranial region; *pt,* pterygoid; *q,* quadrate; *qj,* quadratojugal; *v,* vomer.

develops a ridge near its median border; the two ridges diverge toward the back, leaving as preserved a V-shaped groove between them. Posteriorly, the left vomer appears to be complete, with a truncate end in contact with the anterior terminus of the pterygoid. On both sides a shelf of bone is seen rising dorsally from the medial border of the choana toward the skull roof. Presumably this is a dorsal extension of the vomer. At their anterior ends the vomers bear a patch of shagreen teeth, and it is probable that this shagreen extended farther posteriorly in life, to continue along the pterygoid.

Almost the complete outline of the left choana is preserved, as is the medial margin of the right choana. The opening was a long oval, with the medial border somewhat concave, the lateral border convex in contour. The premaxilla entered briefly into its anterior margin, the palatine equally briefly into the posterior margin; the lateral border was formed by the maxilla, the median border by the vomer.

The maxilla, bearing the marginal dentition, has for most of its length only a very narrow exposure on the palate. It is, however, rather broader anteriorly, where it extends to the choanal margin, and appears to have broadened somewhat near the palatine-ectopterygoid suture. Posteriorly, the exact relations of the maxilla with the jugal and ectopterygoid are obscure. Most of the palatine can be seen on both sides. It is a small bone, extending little beyond the boundaries of the large tusk and replacing pit which it carries. Laterally, it is bounded by the maxilla, medially by the pterygoid, anteriorly by the vomer; posteriorly, it is in contact with the ectopterygoid, and some indication of its suture with this bone can be made out. Both palatine and ectopterygoid show some evidence of a sculpture pattern. The ectopterygoid is a long and relatively narrow element, bearing a half dozen tusks or replacing pits. Most of the medial border of the bone, with a long suture with the pterygoid, is preserved on the left side; the lateral margin and posterior end, however, are missing.

The pterygoid is the major element of the palate. Almost the entire palatal ramus is present on the left side. It bears a shagreen of small teeth as well as some indication of sculpture. The medial margin of the palatal ramus is nearly straight, indicating that, in primitive fashion, interpterygoid vacuities were, at the most, narrow slits; it is possible, however, that the vacuities extended forward to the vomerine region and that there was no contact between the two pterygoids anteriorly. The median border of each pterygoid is thin anteriorly; more posteriorly it thickens, with a double ridge facing medially. As the region of the articulation with the basipterygoid process is approached, the bone thickens further and the upper median edge curves dorsally, with the development of an articular process. Unfortunately, the actual basal articular area is missing on the left side;

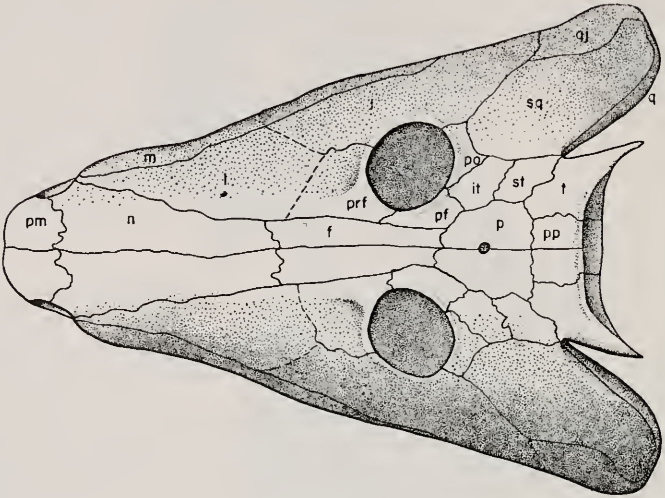

Figure 3. *Neopteroplax conemaughensis.* Dorsal view of restored skull, x¼. Abbreviations as in Figure 1.

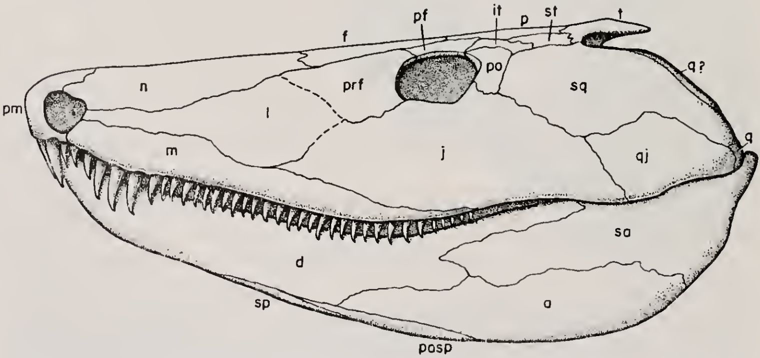

Figure 4. *Neopteroplax conemaughensis.* Restored skull and jaw in side view, x¼. Abbreviations as in Figure 1 and Plate 2.

however, a broken-off mass of the right pterygoid which includes this region is present in position close to the basipterygoid process. Narrow anteriorly, the palatal ramus gradually widens as its lateral margin passes backward along the borders of palatine and ectopterygoid. At the back end of the ectopterygoid region the lateral border, as preserved, swings outward, and then turns posteriorly and slightly medially. There was obviously no development of a pronounced lateral flange. Following a major gap, the distal part of the quadrate ramus is represented by a terminal area applied to the medial surface of the quadrate; from this, two irregular broken pieces extend forward and upward in the direction of the palatal ramus.

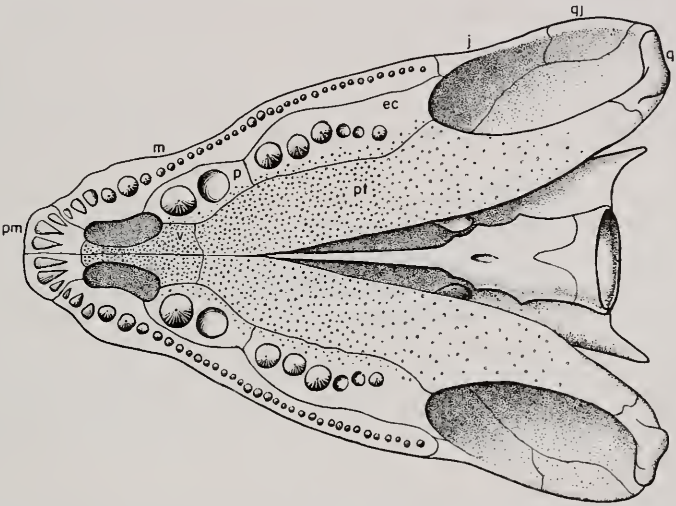

Figure 5. *Neopteroplax conemaughensis.* Restored palatal view, x¼. Abbreviations as in Figures 1 and 2.

There are no visible remains of an epipterygoid. The left quadrate is well preserved and appears to be highly developed. There is a typical articular region of the bone, bounded anteriorly by the quadratojugal and overlapped dorsally by the squamosal and posteromedially by the pterygoid. Extending upward and medially toward the otic notch between the area assigned to squamosal and pterygoid is a strip of bone which, beginning some distance above its base, develops into a long ridge (somewhat imperfect at its summit in the specimen). It is quite possible that I am mistaken as to sutures in this region, and this ridge may belong to either squamosal or pterygoid, but I gain the impression that we are dealing with a very highly developed quadrate.

Braincase. As seen from below (Fig. 2), the region of the skull where remains of the braincase are to be expected, presents a discouraging picture of broken and displaced masses and fragments of bone. In some areas the under side of the roofing bones is visible; for example, there can be seen the thickened and rounded upper margins of both orbits with, parallel to them in a more medial position, longitudinal ridges marking the lateral borders of the area occupied in life by the braincase.

Close to the posterior end is a major mass of bone, the surface of which consists of the parasphenoid expansion beneath the sphenoid region; this mass is tilted toward the left, giving a somewhat asymmetrical appearance. On either side, the broad sheet of parasphenoid curves upward about the braincase margin. The right margin of the parasphenoid is chipped and imperfect here; a concavity on the left side near the back may be likewise an imperfection, but may possibly be part of the lower margin of the fenestra ovalis. The posterior end of the parasphenoid is missing; at the back, as preserved, a median groove represents the beginning of the separation between the two basitemporal processes. The basioccipital and exoccipitals are broken off, so that little can be said of the crushed occipital region, and nothing of the condyle (presumably single). The lateral braincase walls in otic and sphenoid regions are very poorly preserved.[1] The left basipterygoid process is present, although incomplete at its tip; the right is presumably present but concealed by the articular process of the pterygoid. The base of the process is partly defined by a characteristic groove for the carotid artery. Between and slightly to the rear of the basipterygoid processes there is an oat-shaped pit in the mid-line of the parasphenoid; this is bounded on either side by a low ridge. There is no indication of a foramen within this pit; possibly it is a remnant of the embryonic hypophysial pocket.

The parasphenoid rostrum, rounded ventrally, is preserved for 15 mm. forward from the basipterygoid processes. Following a gap, another section of the parasphenoid, some 4 cm. long, is

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[1] I may incidentally note that in the *Eogyrinus* braincase, figured by Watson (1926, fig. 18), the exoccipital appears to be missing and the supposed vagus foramen (X) is presumably the fenestra ovalis (cf. his fig. 12, *Palaeogyrinus*, in which the small exoccipital is present).

present, its ventral surface turned toward the left side of the skull. This section is tipped by thin fragments of shagreen-covered bone. It is tempting to think of this as indicating a shagreen surface on the parasphenoidal rostrum. More probably, however, the association is fortuitous, and this material is presumably a displaced fragment of the right pterygoid. Without apparent break from the parasphenoid there extends upward from the (morphologically) right side of this fragment a sheet of bone, apparently reaching the skull roof, which presumably represents part of the sphenethmoid. More anteriorly, there are no readily interpretable remains of parasphenoid or sphenethmoid.

Lower jaw (Pl. 2; Fig. 6). The right lower jaw is nearly complete. As preserved, its length is 332 mm.; about 1 cm. of the tip is missing, giving a length in life of approximately 342 mm. Except for this missing tip and a chipping-off of the sculptured surface of the dentary over a fraction of the area above the splenial, the outer surface is well preserved. The general jaw shape is that of a typical embolomere, with one notable exception. In such forms as *Pteroplax* and *Archeria*, there is a major unsculptured dorsal expansion of the surangular which rises, with an outward roll, well above the general line of the dorsal margin of the jaw. This expansion is almost totally lacking in the present specimen, the contour of the upper margin of the surangular being only gently convex. In consequence, the jaw lacks the unusual depth in the "angular" region seen in seemingly more typical embolomeres. The nature of the sculptured pattern of the external surface may be seen in Plate 2. Close to the lower margin of the jaw in the splenial region there is a well-marked groove for the lateral line canal; this fades out posteriorly, however, and in contrast to *Archeria* cannot be traced backward and upward over the surface of the angular.

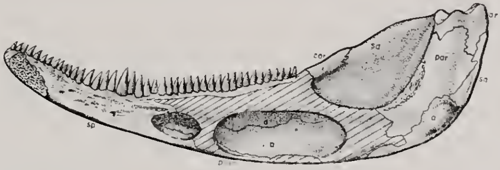

Figure 6. *Neopteroplax conemaughensis.* Jaw in internal view; restored areas hatched. Abbreviations: *a*, angular; *ar*, articular; *cor*, coronoid; *d*, dentary; *par*, prearticular; *posp*, postsplenial; *sa*, surangular; *sp*, splenial, x⅕ approximately.

Except for a diagrammatic representation in Watson's restoration of the "*Eogyrinus*" skeleton (Watson 1926, fig. 28) no attempt has ever been made to trace the sutural pattern of the outer surface of an embolomere jaw, and I find the task here a difficult one. For the most part, the sutures bounding splenial and postsplenial can be fairly readily determined and these elements have a typical labyrinthodont development. As figured, they appear to be much narrower than is actually the case, due to the fact that the outer surface of the jaw ramus curves strongly medially toward its lower margin, and the two elements are hence much fore-shortened in the illustration. Posteriorly, the suture between surangular and angular can be seen running forward from the posterior rim of the jaw somewhat below its half-height and, more dorsally and anteriorly, the suture between surangular and the dentary, which overlaps it externally back of the termination of the tooth row, is readily determined. Farther forward, however, the sutural boundaries of these three elements are far from certain. In most labyrinthodonts the surangular tapers rapidly forward below the dentary; here it appears to extend forward for a considerable distance.

The articular is a massive wedge-shaped element, sheathed medially by the prearticular, and posteriorly and externally by the surangular; anteriorly, it descends into the adductor fossa, but this area is not well seen in the specimen. There is no retroarticular process. The concave articular surface lies essentially in a horizontal plane; it is saddle shaped, concave throughout in anteroposterior section, convex in transverse section, its central portion higher than either extremity. Mediolaterally the articular surface traces an arc of about 45°. Its outer end, which projects well out beyond the plane of the surangular, lies at right angles to the long axis of the jaw, its inner end curves well forward. The articular surface is bounded the length of its posterior margin by a high ridge (somewhat imperfect in the specimen) which is thin and sharp-crested medially, thicker and blunt-tipped laterally. The anterior border is for the most part lower, but there is a prominent ridge for a short distance above the adductor fossa. The articular region is in general quite similar to that of *Pteroplax*.

In internal view the inner surface of the surangular is well exposed posterodorsally. As in other embolomeres, the upper margin of the surangular rolls smoothly outward but, as mentioned above, the high flange developed in this region in *Pteroplax* and *Archeria* is not present here. The posterior end of the coronoid series is seen covering the medial surface of the dorsal edge of the surangular posterior to the tooth row and projecting slightly above the general dorsal contour of the jaw. Farther forward the inner surface of the external sheathing bones of the jaw is sufficiently exposed to show much of the presumed surangular-angular suture and of the dorsal boundaries of postsplenial and splenial.

At the inner end of the articular area a broad sheet of bone descends along the posterior margin of the inner surface of the jaw and forms part of the low inner boundary of the adductor fossa. Most of this bony sheet is formed by the prearticular. Roughly parallel to the curved dorsoanterior margin of this bony sheet is a line of rugosities which not improbably marks the ventral limit of the area of insertion of a medial sheet of adductor musculature. A similar but much more sharply marked area is to be seen in *Archeria* and, apparently, *Pteroplax.* The back edge of the jaw in much of this region is a sharp crest. The surangular here is not confined to the outer surface, but is exposed as well over a narrow strip of the inner surface of the jaw adjacent to the prearticular. The angular is also exposed on the inner surface ventral to the prearticular. It covers a much broader area here than the surangular and bears posteriorly and ventrally a very prominent tuberosity which would appear to be present but less developed in *Pteroplax* and *Archeria.* Presumably this is associated with musculature — possibly a depressor of some type.

The diagnostic feature of the embolomere jaw is the presence on the inner surface of two large meckelian fenestrae. In the present specimen the bars separating these fenestrae from one another and from the adductor fossa have been destroyed, and the surface of much of the coronoid and prearticular regions above the fenestrae is absent. The portions of the inner surface remaining are, however, sufficient to mark out the roots of the bars bounding the fenestrae and thus to indicate the original presence of the embolomere pattern, as restored in Figure 6. A chip of the lower margin of the jaw is missing at the point where there should be present the anterior end of the bar between adductor and posterior meckelian fossa, but the preserved lower edge of the bone (formed by the angular) is thickened in a fashion expected at the base of this bar. Farther forward the lower rim is again imperfect at the posterior end of the splenial, but thickenings here show definitely the anterior and posterior boundaries of the bar between the two meckelian fenestrae. Although most of the coronoid region is gone, a small fraction preserved midway of the tooth row shows a shagreen of small teeth comparable to those which extended most of the length of the coronoid series in *Pteroplax* and which presumably existed here.

From the anterior end of the anterior meckelian fenestra to a point not far back of the symphysis, the inner surface of the jaw is well preserved. Dorsally, there is an essentially horizontal shelf, non-denticulated, extending inward about 1 cm. from the tooth row. At the inner edge of this shelf there is a strong anteroposterior ridge with a smoothly rounded surface. Below this ridge the inner surface descends to the lower margin in an essentially vertical plane, but is somewhat concave in transverse section. This area is similar in pattern in both *Pteroplax-Eogyrinus* and *Archeria.* Presumably, much of the inner surface is occupied by the splenial, and it is probable that the anterior ends of the prearticular and coronoid series enter into the composition of the dorsoposterior part of this area. I have not, however, been able to determine sutures here with certainty.

Dentition. In no instance is a complete tooth present; although there is definite evidence of almost every tooth position, the teeth are generally represented only by broken stumps or alveoli. The tooth bases are all essentially subcircular in outline. Little can be said as to tooth shape — whether, for example, they were recurved at their tips or whether compressed or not (since in general the basal parts of teeth whose shafts are compressed are nevertheless circular in section). Nor are the data sufficient for comment on the nature of tooth replacement. This was presumably of the alternating type common in early tetrapods, but nearly all marginal teeth were present in this specimen at death.

The marginal tooth row in the upper jaw included about 40 teeth. There were three premaxillary teeth, the first two large, with basal diameters close to 10 mm., and slanting somewhat backwardly, the third small. The first maxillary tooth is small; beyond this, however, there develops a "canine" region, as in various other labyrinthodonts. There is no one specific canine or canine-replacement pair but, rather, a series of four or five teeth, all of which are enlarged to a variable degree, with a maximum basal diameter of about 15 mm. Back of this region there follows a row of about 30 teeth of small size, averaging 5.5 to 6 mm. in basal diameter. As seen in Figure 2, the "post-canine" tooth row as preserved does not form a straight linear series, for there is an inward curvature opposite the palatine-ectopterygoid suture; this, however, is due to breaks in the maxilla and consequent displacement. In the lower jaw, as in the upper, about 40 marginal teeth are present. As far as can be determined, the teeth are nearly uniform in size, although there appears to be some slight increase over the mean at a point about one-third the way back along the tooth row.

On the palate, a shagreen of small denticles covers the portions of the vomers on which the surface is well preserved and extends the length of the expanded palatal ramus of the pterygoid. As in other known embolomeres, vomerine tusks are absent. The palatine bears an enormous tusk-pair, with a basal diameter of the fully developed left tooth of about 25 mm.; as is frequently found to be the case, each palatine bore one functional tusk at the time of death, the second being represented by a large replacement alveolus. A row of tusks was present on the ectopterygoid, much as in *Pteroplax.* On the preserved side there are six tusks or alveoli, decreasing in size posteriorly; the first of the series has a basal diameter of about 18 mm., the last 13 mm.

The anterior end of the lower jaw is too imperfect to tell whether or not symphysial teeth were present internal to the marginal row. Posteriorly, a denticulated area of the coronoid series is preserved, but the anterior extent of this denticulation is uncertain and denticles are not present toward the anterior end of the jaw.

Nomenclature. In the present skull we have for the first time clear and positive evidence of the presence in North American Pennsylvanian of large embolomeres of the general *Pteroplax-Eogyrinus* type which were apparently common in the Upper Carboniferous of Great Britain and are best known from the splendid Newsham materials (Hancock and Atthey 1869, 1870, 1871, Atthey 1877, Watson 1926). Prof. Watson distinguished two genera at Newsham, *Pteroplax* and *Eogyrinus,* on the basis of the nature of the tabular "horns."[1] Dr. Panchen informs me that although the features on which Watson originally differentiated the two genera may not be valid, the two may, nevertheless, be distinguished on other grounds. But whether distinct

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[1] The original describers did not designate holotypes. It seems proper, however, that the skull table figured by Hancock and Atthey in plate XV, figure 1, 1868, and by Atthey in plate XII, 1877, be designated as the holotype of *Pteroplax cornuta,* and the skull described and figured by Atthey in 1876 as a specimen of *"Anthracosaurus russelli"* is herewith designated as the type of *Eogyrinus attheyi* (Watson's number D.M.S.W. 27).

or not, the *Pteroplax-Eogyrinus* materials together present a picture of a large, massively built embolomere with a moderately long snout, which was obviously a piscivorous, aquatic inhabitant of the Coal-Measures swamps. The present form was obviously similar in structure, as far as known, to these British amphibians, and was presumably comparable in habits.

But while close to *Pteroplax-Eogyrinus,* the present form is definitely distinct. Certain differences in details of sculpture and sutural pattern might be regarded as individual variations or, at the most, specific in nature, and the apparent contrast in orbital shape is not important. There is, however, a notable difference in the lower jaw, as noted earlier. In all known material from Newsham the jaw is excessively deepened posteriorly, due to a conspicuous outrolled dorsal development of the surangular which is absent in the present specimen. This departure from the typical embolomere jaw structure is definitely a point of at least generic rather than specific distinction. *Pholiderpeton* is a further European type with which comparison might be made. This is inadequately known. In general, there is no clear distinction, as far as the material has been described, between *Pholiderpeton* and members of the *Pteroplax-Eogyrinus* series. Possibly *Pholiderpeton,* like our specimen, lacked the rolled-out surangular. But the condition is unknown in the type specimen, and the jaw material of a second specimen which Watson ascribed to this genus is imperfect in this region.[1]

No name already applied to an American Carboniferous amphibian seems definitely applicable to the present form. In consequence, this skull is herewith made the holotype of a new genus and species of embolomere as *Neopteroplax conemaughensis,* with the combined generic and specific characters being (apart from size) the absence of the expanded dorsal flange of the surangular, the relatively numerous and relatively small marginal teeth, a more circular orbital shape than in *Pteroplax* and the absence of the anterior coronoid tooth development seen in *Eobaphetes.*

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[1] I wish to thank Dr. R. M. C. Eager for examining the part of this second specimen contained in the Manchester Museum collections.

II. OTHER LARGE AMERICAN CARBONIFEROUS EMBOLOMERES

Discovery of new and restudy of old materials is gradually increasing the number of known remains of American Carboniferous embolomeres. In general, they appear to sort out into two size groups, the larger of about the proportions appropriate to the skull just described, the smaller of about the size of typical Texas *Archeria* specimens or the type material of *Cricotus* from Illinois. It is quite possible that certain of the smaller specimens may be growth stages of larger animals. I do not, however, believe that this is generally the case. Growth stages of Paleozoic amphibians, including larval stages, may, of course, be recovered under such favorable conditions as, for example, the famous Linton cannel. But experience with large quantities of Permian labyrinthodont materials strongly suggests that post-larval growth was very rapid until essentially "adult" size was reached, after which further increase in size was very slow indeed. For example, in large amounts of material of *Eryops* and *Trimerorhachis* collected in non-selective fashion, few specimens from any given formation show any marked deviation from the "adult" norm. One may thus reasonably regard the larger and smaller Carboniferous embolomere specimens as representatives of two series with, presumably, differing types of food habits and ecological adaptations. We will here note other known representatives of the series of larger forms, and leave discussion of smaller Carboniferous embolomeres to a later occasion. The finds are here listed in essentially stratigraphic order, beginning with the oldest.

Canso group, Nova Scotia. I have (1958) described, as *Pholiderpeton? bretonense,* the greater part of a lower jaw, seen from the outer surface, from the Point Edward formation, Canso group, of Cape Breton. The sculpture and contours suggest that we are dealing with an embolomere, although, unfortunately, the diagnostic features of the inner surface are not ascertainable.

Figure 7. Sketch of labyrinthodont jaw from the Point Edward formation, from the collections of the Canadian Geological Survey. x½.

Dr. Wann Langston has since discovered in the collections of the Canadian Geological Survey a labyrinthodont jaw (no. P-1503/10015) collected at Point Edward by Dr. W. A. Bell in 1915, which he has kindly forwarded to me for study, and of which a sketch is given in Figure 7. The jaw is nearly complete, lacking only the symphysial region. The surface, however, is imperfect. As can be seen, the specimen is but about two-thirds the size of the *P.? bretonense* type. The contours of the present specimen and the type are identical as far as the latter is preserved,[1] and, as suspected in the case of the type, the outlines are those characteristic of anthracosaurians in general and embolomeres in particular, in the deep angular region and well-expanded dorsal flare of the surangular. As in the type, the teeth are slender and closely spaced. It is unfortunate that the inner surface cannot be seen and hence here, as in the type, it is impossible to say whether or not diagnostic embolomere features were present. This jaw appears to represent a growth stage of *P.? bretonense* or a closely related form.

Dr. Donald Baird has collected further labyrinthodont materials from this formation at Point Edward. In addition to a skull fragment of the loxommid *Spathicephalus,* the materials include (Princeton University no. 17190) a clavicle, a small phalanx, 10 mm. in length, and a single ventral scale, 14 mm. long. The clavicle (Fig. 8) has a long stem extending upward and outward at about a 60° angle. This clavicle is appropriate for an anthracosaurian, rather than a presumably flatter-bodied loxommid. As may be seen from the figure, there is a characteristic triangularly-expanded ventral plate, measuring 8 cm. along its medial border, which is about 5 cm. from the base of the tapering, slender "acromial" process.

The reference of the Point Edward labyrinthodont jaw to *Pholiderpeton* was for convenience only; this English genus appeared to be of approximately the same age. Recently, however, Panchen and Walker (1961) have shown that the ages of various British deposits, including those in which *Pholiderpeton* was reported, are not as great as once thought. On the other hand, "*Pholiderpeton*" *bretonense* may be older than previously stated. The Canso group, to which the Point Edward formation pertains, has been regarded as equivalent to about the middle of the European Namurian and very early Pennsylvanian (Moore *et al.* 1944) or very late Mississippian (Weller *et al.* 1948).

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[1] Superposition suggests that my original estimate of the jaw length of the type was too high, and that this figure may have been but about 30 cm.

Studies now in progress by Mr. Edward S. Belt of Yale University suggest that, in agreement with the work of Bell (1944) and Copeland (1957), the Point Edward beds are at least as early as Namurian A or possibly late Viséan.

Morrow series, Arkansas. Half a century ago Moodie described a fragment of labyrinthodont skull and an embolomere jaw as *Eobaphetes* [*Erpetosuchus*] *kansensis* (Moodie 1911; 1916, pp. 189-192, fig. 42).[1] These specimens came, in all probability, from the Baldwin coal of the Woolsey member of the Bloyd formation of the Morrow series in Washington County, Arkansas,[2] and

Figure 8. A clavicle, perhaps pertaining to *Pholiderpeton? bretonense*, from the Point Edward formation. x½.

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[1] The 1911 figure of the jaw is approximately ×1/3; his 1916 figure, said to be ×1/3 is approximately ×28/100.

[2] The locality and horizon from which this material is derived has long been a source of perplexity to students of early tetrapods. Preserved in slabs of impure coal, they were stated by Moodie to have come from "the Coal Measures of Washington County Kansas," and are so entered in the records of the U.S. National Museum. But the sediments of Washington County Kansas are of Cretaceous and Permian age and contain no "Coal Measures." Through the courtesy of Drs. Nicholas Hotton, III and G. A. Cooper of the U. S. National Museum, the history of the specimens has been traced. It was part of a collection assembled by Prof. Gustave Hambach of St. Louis which was purchased by that Museum in 1909. It mainly consisted of fossil echinoderms, but also included a few other animal and plant fossils which Professor Hambach had picked up in the course of his search for echinoderm materials. As far as known, he never visited Washington County, Kansas, but did work in Washington County, Arkansas and, in fact, described echinoderms of the genus *Pentremites* from the Brentwood limestone in that county (Hambach 1903). Immediately above this limestone is the Baldwin coal. This coal was actively worked at the time at which Hambach's field work was done. It seems certain that this labyrinthodont material was collected during the course of his Arkansas field work, and the substitution of "Kansas" for "Arkansas" is surely due to misreading of the original labels.

hence from a horizon very early in the Pennsylvanian, close to the Namurian-Westphalian boundary of the European classification and equivalent to a low position in the Pottsville series of the eastern interior coalfield of the United States. The jaw is of especial interest as the geologically oldest specimen in which the typical embolomere construction of the inner surface of the jaw is known. Of further interest is the fact that current work by James H. Quinn indicates that the Hale formation underlying the Bloyd without, as far as known, any marked gap, is equivalent in age to the E_2 zone of the European early Namurian. *Eobaphetes* is thus far older than the skull from Swanwick, which Panchen and Walker (1961) cited as the oldest anthracosaurian then known; this English locality is in the Communis zone of late Westphalian A.

The animal represented by the jaw was of large size, although somewhat smaller than *Neopteroplax.* The structure is typically embolomerous, but there are two definite points of difference from *Neopteroplax.* (1) As shown in Moodie's figures, the anterior part of the coronoid region is well supplied with small teeth, whereas this region is bare in *Neopteroplax.* (2) The lower jaw teeth are much stouter than in *Neopteroplax* and, in correlation, fewer in number; on the average, the tooth diameter at the base is about 7 mm., as compared with 5 mm. in *Neopteroplax*, and the total number of dentary teeth may be computed as about 30, as compared with a considerably higher count in *Neopteroplax.* There is no guarantee that the skull fragment (designated by Moodie as the holotype) is part of the same individual as the jaw. From Moodie's figure, one gains the impression that we are dealing with an animal of different character, with smaller and more closely crowded teeth. However, Dr. Nicholas Hotton, III has checked the specimen for me, and reports that Moodie's figure is inaccurate, and that the upper jaw dentition, as regards size and spacing of the teeth, is closely comparable to that of the lower jaw.

The ''ruggedness'' of the dentition, with relatively stout individual teeth and a relatively low tooth count, shows that we are dealing with a form quite distinct from *Neopteroplax* and from various small embolomeres (as *Leptophractus, Archeria*) with numerous slender teeth. The dentition is comparable to that of the form discussed below as *Anthracosaurus lancifer* from Linton, Ohio; but in view of the considerable stratigraphic interval concerned, and the seemingly distinctive nature of the coronoid and symphysial dentitions, *Eobaphetes kansensis* and the Linton form may be regarded as generically distinct. The generic name chosen by Moodie is, of course, unfortunate, since this embolomere has no close relationship to the loxommid *Baphetes*.[1]

Riversdale group, Nova Scotia. Centra of a large embolomere, with a maximum height of 35 mm., were collected by William F. Take of the Nova Scotia Museum of Science, Halifax, on the shore of a cove northeast of Cape Linzee, Inverness Co., Nova Scotia, in 1959. They were found in a sandstone some distance above the Ten Inch Coal Seam of the Port Hood formation of the Riversdale group, equivalent to Westphalian A of Europe, and the lower part of the Pottsville series of the Appalachian region.

Cumberland group, Nova Scotia. Sediments of this group, believed to be essentially equivalent to Westphalian B, are best known from the Joggins cliff exposures of Nova Scotia, famous for the small tetrapods discovered there in erect trees. A few finds from this section may pertain to large embolomeres.

Marsh in 1862 described as *Eosaurus acadianus* two very large disc-shaped objects, presumably central structures of some sort, said to have come from a layer near the top of division 4 of the Logan-Fletcher section of the Joggins exposure, rather high in the Joggins formation of Bell (1914). These discs, with diameters of about 50 mm., do not show any of the distinctive features generally seen in embolomere central elements. But if from the Carboniferous, there is no other group to which they can well be assigned, for we know of no huge sarcopterygian of this age, nor would such a form, if present, be liable to have such well-ossified centra. If belonging to an embolomere, the usual exponential relations between vertebral diameters and linear dimensions would indicate a giant form. Marsh notes the similarity of these centra to those of ichthyosaurs. It may be suggested that there has been confusion as to the pertinence of this specimen, and that these bones are actually centra of a Liassic ichthyosaur.

"*Baphetes*" *minor* was described by Dawson (1870; 1894, p. 268; Moodie 1916, p. 187) from an impression in sandstone of

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[1] Search in the National Museum collections has resulted in the finding of a slab containing additional materials of this specimen. Its development and study will add to our knowledge of the *Eobaphetes* skull and jaw.

an incomplete dentary (Fig. 9) found in the Joggins bluff between Ragged Reef and the Joggins coal mine. The holotype (never before figured) is MCZ 1053. The specimen is about 15 cm. long; it shows impressions of much of the middle and posterior portions of the outer side of a right dentary, and a number of teeth are present as well as impressions of others. For most of the preserved length of the tooth row alternate labyrinthine teeth were present, with intervening alveoli. There is no positive evidence as to what group of labyrinthodonts this jaw pertains. The upward curvature of the jaw margin, posteriorly, is somewhat suggestive of an embolomere rather than a rhachitome, but, on the other hand, the sculpture is stronger than is usual on an embolomere dentary. The contours of the bone suggest an animal rather smaller than *Neopteroplax* — say about three-fourths of the size of the skull described above. This impression is heightened by the fact that the teeth (including alveoli) are spaced about 45 mm. apart, as contrasted with a higher figure in *Neopteroplax*. There is, of course, no evidence as to whether this form has anything to do with the loxommid *Baphetes*. The exact locality of the find is unknown, but it was

Figure 9. The type of "*Baphetes*" *minor,* drawn from a cast of the original impression. x½.

Figure 10. End view of an embolomerous centrum and neural arch from the Joggins, Nova Scotia. x½.

presumably in division 3 of the Logan-Fletcher section (1908), and hence higher in the section than *Eosaurus* and near the top of the Joggins formation.

Finds made at the Joggins by a 1956 expedition from this museum were few in number, but include an embolomere dorsal vertebra, MCZ 3220 (Fig. 10), with a width in the central region of 29 mm. — a size appropriate for such a form as *"Baphetes" minor*. No intercentrum is present; neural arch and centrum are fused, indicating "adult" conditions. This vertebra was collected from the Forty Brine Coal Seam, one mile north of the Joggins pier, and hence in the lower part of Division IV of the classic section.

Stellarton group, Nova Scotia. From the Albion Mine at Stellarton, Nova Scotia, there was collected more than a century ago a pelvis, described by Watson (1926, fig. 27), which is comparable to those of embolomeres. The dimensions are nearly double those of typical *Archeria* pelves and hence appropriate for an embolomere of large size. The pubis is much shorter than in *Archeria*. The embolomere type of pelvis is very probably of a very primitive nature (that of *Ichthyostega* is basically similar) and there is, of course, no absolute guarantee that the animal which owned this pelvis was actually an embolomere. But, on the other hand, there is no positive reason to believe that the pelvis pertains to the loxommid *Baphetes,* the type of which is also from the Albion Mine. The horizon is the basal, Albion member of the upper division (Division II) of the Stellarton Group of Bell's classification (1940), which he regards as lying approximately at the base of Westphalian C. The horizon thus appears to be definitely later than those of the Joggins finds, but equally definitely earlier than that of the famous Linton deposit at the summit of the Allegheny series.

Allegheny series of Linton, Ohio. As noted earlier, I had at one time (1930) assigned to the Embolomeri a considerable amount of material from the famous Linton cannels, under the then prevalent assumption that all Carboniferous labyrinthodonts were embolomeres. In later years, however, it has become apparent that this is far from being the case (Romer 1947, p. 69, etc.), and careful study of the Linton material by Dr. Donald Baird indicates that only a restricted number of specimens from this locality can be reasonably interpreted as embolomeres. Certain of these, including the types of *Leptophractus obsoletus* and *Ichthyacanthus platypus* Cope are animals of small size, and the slender and closely crowded teeth of the *Leptophractus obsoletus* type (as developed by Dr. Baird) suggest that this is not to be regarded as a growth stage of the larger form described below.[1]

Of a large Linton embolomere, the best preserved specimen is American Museum of Natural History specimen 6830, of which obverse and smaller reverse are figured by Cope (1875). The obverse, as seen in his plate XXXVIII, figure 2, shows the left surface of the muzzle of a large amphibian with, below it, the upper margin of much of a lower jaw.[2] The sculpturing of the muzzle is none too well preserved. An oval depression near the left of his figure is obviously the left external naris. A groove below it can be reasonably interpreted as lying along the premaxillary-maxillary suture. Not seen on the figure but apparent on the specimen was a low rugose ridge running backward from a point below the middle of the posterior margin of the naris.

Figure 11. *Anthracosaurus lancifer.* Cast from mold after etching, of specimen figured by Cope (1875), plate XXXVIII, figure 2.

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[1] Cope's figure of the type (1875, pl. XXXIX, fig. 1) is stated to be two-thirds natural size. It is actually natural size.

[2] Cope's figure is said to be four-sevenths natural size. The reduction is actually three-fourths.

The line of this ridge, somewhat arched dorsally, can be traced backward for most of the length of the block; during etching of the block, a sawtooth suture became evident here, and a second suture could be traced a short distance backward from the naris farther dorsally. There, two sutures lie in the position of the maxillo-lacrimal and lacrimo-nasal sutures of *Neopteroplax.*

After etching by Dr. Baird, this slab (Fig. 11) shows the imprint of a comparable region of the right side of the muzzle. The right naris, close to the right edge of the block, is well outlined. A considerable portion of the maxillary, with a lightly pitted sculpture, is present below and back of the naris. Above this area two breaks are present running backward from the narial margin and diverging posteriorly. These breaks lie at the positions at which the maxillo-lacrimal and lacrimo-nasal sutures were seen on the other side, and have obviously occurred along the suture lines.

The etched surface shows clearly the inner margin of the tooth-bearing rim of the left maxilla, and a portion of the left side of the palate, from the anterior portion of the ectopalatine region forward past the tusk-and-pit-bearing palatine element to the region of the left choana; a well-marked anteroposterior ridge represents the external border of this opening. At the left there is seen a detached area of finely denticulated bone, presumably a fragment of pterygoid.

It was not clear from the specimen as figured by Cope whether the lower jaw seen was the right or left. The mold (Fig. 11)

Figure 12. Cast from the mold of a small reverse slab of the specimen shown in Figure 11, illustrated before etching in Cope's 1875 plate XXXVIII, figure 1.

shows that it is the right jaw ramus, of which the upper margin is present for most of the length of the dentary. The external surface of the dentary has a lightly pitted surface. Etching of the reverse specimen (Fig. 12) shows the presence of a highly rugose area anteriorly; this is obviously the symphysial area, indicating that the anterior end of the ramus is essentially complete.

A fairly comprehensive knowledge of the dentition can be obtained from this specimen (Fig. 13). In the upper jaw, the dentition of the right side is not too well preserved, and we merely gain a general picture of a series of marginal teeth toward the front of the mouth which are broad based (an effect partially but not entirely due to crushing), slightly recurved at their tips, and striated for most of their length. The teeth extend about 15-17 mm. beyond the edge of the maxilla, and measure 8-10 mm. in diameter at the outer rim of the maxilla. The left maxillary tooth row is seen to better advantage from the inner side. Here the teeth are visible for their full length. At their bases they are essentially stout cylinders, the tapering which

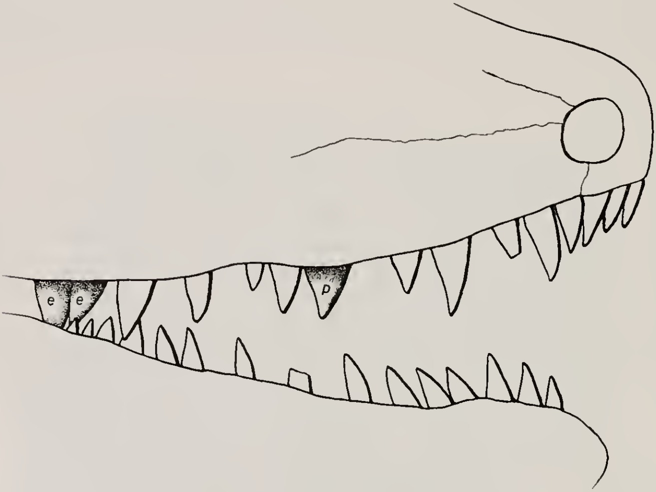

Figure 13. Diagrammatic restoration of the "muzzle" and jaw margins of *Anthracosaurus lancifer*, based on American Museum of Natural History specimen 6830; composite from the two sides of the specimen. Only teeth actually present are indicated. In addition to the marginal tooth row, the palatine (*p*) and anterior ectopterygoidal tusks (*e*) are visible. x½.

gives them a blunt appearance taking place beyond the point where they emerge from the rim of the maxilla. There is some development of a ''canine'' region, tooth length reaching a peak at the fifth maxillary tooth. The tip of this tooth is broken off, but its length in life was on the order of 35 mm. and its basal diameter is 13 mm. Back of this point there is some reduction in tooth size. The posterior maxillary teeth are imperfectly preserved, but those lying opposite the posterior part of the palatine and anterior part of the ectopterygoid would appear to have average lengths of about 25 mm. and basal diameters of 8-10 mm.

Much of the lower jaw dentition is seen in Figures 11 and 12 and Cope's plate XXXVIII (1875). The teeth are more uniform in size than in the upper jaw, and relatively short, none extending more than about 12-13 mm. above the outer rim of the dentary, with (as seen in Figure 12) about 6-8 mm. of their bases concealed within this rim. In Figure 12 are seen three well developed anterior teeth not well shown in Figure 11, and, internally placed, three much smaller teeth. It seems probable that the latter are symphysial dentary teeth, not described, to my knowledge, in other embolomeres, but known in certain other labyrinthodonts. Back of the symphysis the inner surface of the jaw is not preserved, and hence it cannot be told whether or not the anterior part of the coronoid series was denticulate, as in *Eobaphetes kansensis,* described above.

Assuming that the posterior extent of the marginal tooth row was similar to that found in other embolomeres, one can make a close estimate of numbers of marginal teeth. Of maxillary teeth and presumed alveoli, 14 are present to a point opposite the first ectopterygoid fang. Beyond this, to the assumed end of a ''normal'' tooth row, there is room for about 11 additional teeth. Premaxillary teeth are incompletely preserved, but two can be seen on the left side in Cope's figure and a third, not seen in the figures, was present on the front edge of the slab. This gives a total number of upper jaw teeth of about 28 — a figure markedly lower than in such a form as *Neopteroplax,* for example, but a bit higher than that of *Anthracosaurus russelli* as described by Watson (1929). In the lower jaw, 16 teeth or assumed alveoli can be counted in front of the position of the first ectopterygoid tusk. Presumably the tooth row continued, as in the upper jaw, for a further distance to accommodate about 11 additional teeth, giving a total of about 27 dentary teeth — again, a low figure for an embolomere, but close to that present in the Arkansas jaw.

As expected in a presumed embolomere, there is no indication of vomerine tusks, but tusks are well developed on palatine and ectopterygoid. The palatine tusk (accompanied by a pit for its replacing "twin") is a very large tooth, 45 mm. in length and 25 mm. in basal diameter. On the ectopterygoid, following a considerable gap, are two tusks of more modest size, the one completely preserved being about 37 mm. long and 17 mm. in diameter at the base. Presumably there were further ectopterygoid tusks behind the two preserved. Both palatine and ectopterygoid tusks are well striated for most of their lengths, but smooth at the tips.

Rather surely this specimen is an embolomere. This is strongly suggested by the absence of vomerine tusks, and suggested to a lesser degree by the lightness of the sculpture pattern. Still further indication is the fact that, as preserved, the skull was crushed from side to side rather than dorsoventrally as is common in flatter-headed temnospondyls. The size was considerable. We have a reasonably accurate measurement of skull length from snout to anterior ectopterygoid tusks. If the proportions were as in *Neopteroplax*, for example, the skull length to occiput would

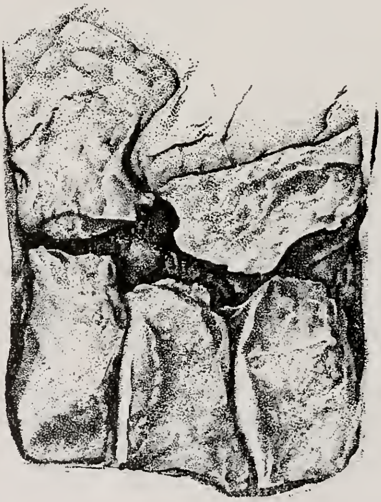

Figure 14. Embolomerous vertebral elements from Linton. From etched reverse of specimen shown in Cope's (1875) plate XXXIX, figure 3. Natural size.

have been approximately 355 mm., i.e., somewhat greater than that of *Neopteroplax*. The jaw length would have been about the same, giving, again, a figure in excess of that of *Neopteroplax* and one rather considerably in excess of the measurements of the Arkansas jaw and the Nova Scotia *"Pholiderpeton."*

Apart from large isolated scales of presumed embolomere type, two further Linton specimens may well pertain to this animal. One is a small block (American Museum of Natural History 6969) the counterpart of which (since lost) Cope figured (1875, pl. XXXIX, fig. 3) as showing vertebral centra. This specimen, as developed by Dr. Baird (Fig. 14), shows two centra and an intervening intercentrum of embolomerous type, together with imperfect remains of two neural arches. The neural spine, as preserved, is low. The central elements have heights of 27-29 mm., i.e., considerably bigger than those of embolomeres of the *Cricotus-Archeria* size range. It is of interest that both intercentrum and pleurocentra are wide anteroposteriorly (about 15 mm.), and that — a most unusual condition — the intercentrum is as stout as the pleurocentra.

A further specimen which may belong here is American Museum of Natural History No. 6939, the mold of which shows remains of a large shoulder girdle (Fig. 15). A nearly complete left clavicle is present, seen from the dorsal surface. Its well

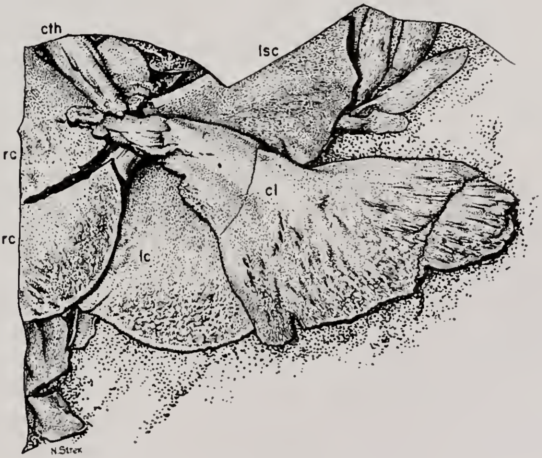

Figure 15. Shoulder girdle material from Linton. x½. Abbreviations: *cl*, left clavicle; *cth*, base of left cleithrum; *lc*, left coracoid plate; *lsc*, left scapular blade; *rc*, right coracoid plate.

developed acromial process lies to the left as the slab is figured; beyond it is the proximal part of the cleithrum. At the left of the slab is seen the inner surface of the right coracoid plate, showing its curved medial margin. Most of the left scapulocoracoid was present, but it is concealed in great part by the clavicle and right coracoid. Above the clavicle is part of the scapular blade: the upper part of the blade appears to have been broken off. Just above the edge of the clavicle there is a break in the thickened posterior rim of the blade, at about the summit of the supraglenoid buttress. Much of the left coracoid plate is visible between clavicle and right coracoid, and just below the stem of the clavicle can be seen part of the curved posterior margin of the subscapular fossa. Toward the upper right are embolomerous scales of appropriately large size.

A specific name for this Linton embolomere appears to be available. Newberry (1873, p. 342. pl. XXXIX, fig. 9) described as *Rhizodus lancifer* a large, incomplete tusk, striated proximally but smooth at the tip, from Linton. (The type specimen is Ohio State University No. 4500.) However, no identifiable crossopterygian remains of any sort have ever been discovered in the very considerable Linton materials. We are quite surely dealing with an amphibian tooth similar to the palatal tusks of the present animal.

Generic assignment presents an interesting problem. Most described embolomeres — including, for example, the Newsham specimens, *Pholiderpeton*, a small embolomere from Linton, and *Archeria* — have slender, closely spaced teeth, and with a high count of 40 or so in each jaw ramus. The only well known exceptions to this, apart from the form here considered, are the *Eobaphetes* jaw and the type of *Anthracosaurus russelli* from Airdrie, Scotland, originally described by Huxley (1863) and refigured by Watson (1929). *Anthracosaurus* and the present form appear to be almost identical in dentition, with powerful marginal teeth and palatal tusks, and with a low tooth count. In past times one hesitated to assign Paleozoic continental vertebrates from North America and Europe to a common genus, because of the supposed vast distance between the two regions. However, due to continually increasing evidence that in the Paleozoic those two areas were part of a common land mass and increasingly strong suspicions that the Atlantic sea barrier was then absent or negligible, I feel no hesitation in assigning this Linton animal to Huxley's genus, as *Anthracosaurus lancifer*

(Newberry). One possible bit of evidence to the contrary is that in the fragment of a large embolomere vertebral column from Linton, described above, the intercentrum is unusually broad, whereas in a series of large vertebrae from Airdrie (Museum of Practical Geology no. 56580-81) the intercentrum is of the more usual slender type. But since there is no certain association of vertebrae with skulls in either case, this need not be considered too seriously.[1]

The discussion of nomenclature above is based on the assumption that the large Linton embolomere is distinct from *Leptophractus obsoletus* from the same locality, the type of which is a much smaller individual with teeth which appear to be of a more slender, recurved and closely crowded nature. Should, however, the *obsoletus* type, on further study, appear to be a growth stage of the larger form, it will be noted that *Anthracosaurus* (Huxley 1863) and *lancifer* (Newberry 1856) have priority over *Leptophractus* and *obsoletus* (Cope 1873).

The Linton cannel is associated with the Upper Freeport Coal at the summit of the Allegheny series, to be correlated in age with the latest Westphalian D. *Anthracosaurus lancifer* is thus somewhat later in time than any of the described British embolomeres, although earlier than *Neopteroplax conemaughensis.*

Conemaugh series, Ohio. Apart from the *Neopteroplax* specimen, the only indication of a large embolomere from the Conemaugh is a single centrum (MCZ 2409) with a width of 36 mm., collected by Dr. and Mrs. Baird northeast of Reeds Mills, Section 36, Cross Creek Township, Jefferson County, Ohio. The horizon is that of the Summerfield limestone of the Conemaugh, equivalent to about the middle of the Stephanian. The size is appropriate for *Neopteroplax,* the type of which comes from a somewhat lower Conemaugh horizon.

Virgil series, Kansas. Williston in 1897 described a large labyrinthine tooth collected near the Vermillion River east of Louisville, Pottawotamie County, Kansas; the horizon is the Waubansee group at the top of the Pennsylvanian. The tooth is surely a palatal tusk of a large labyrinthodont, but it is impossible to say whether embolomere or temnospondyl.

Late Pennsylvanian and earlier Permian of Texas. The typical — and so far the only identified — Permian embolomere is

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[1] Note that in the case of both Airdrie and Linton skulls we cannot be certain that we are actually dealing with true embolomeres, although both are quite surely anthracosaurians of some sort.

Archeria (formerly called "*Cricotus*"). This is (except in late horizons) a small form, with vertebral centra generally averaging little over 20 mm. in diameter. Some years ago, while exploring low horizons in the Permian which are close to the Carboniferous boundary and were formerly considered Carboniferous in age, a party from this museum discovered a "pocket" in southeastern Archer County filled with disarticulated and generally weathered bones and bone fragments. This "Prideaux pocket" lies in the valley of the West Fork of the Trinity River, in Section 1, IRR Co. Survey, Abstract 2237. The local stratigraphy is poorly known, but the locality is probably in the Pueblo formation, close to the base of the Wichita group and not far above the summit of the Pennsylvanian as currently defined in this region. Mingled with elements pertaining to pelycosaurs and the typical rhachitome *Eryops* as well as unidentifiable scraps, are numerous small centra and intercentra, with diameters averaging 22 mm., surely pertaining to *Archeria*. But present as well are a few much larger embolomerous central elements (MCZ No.

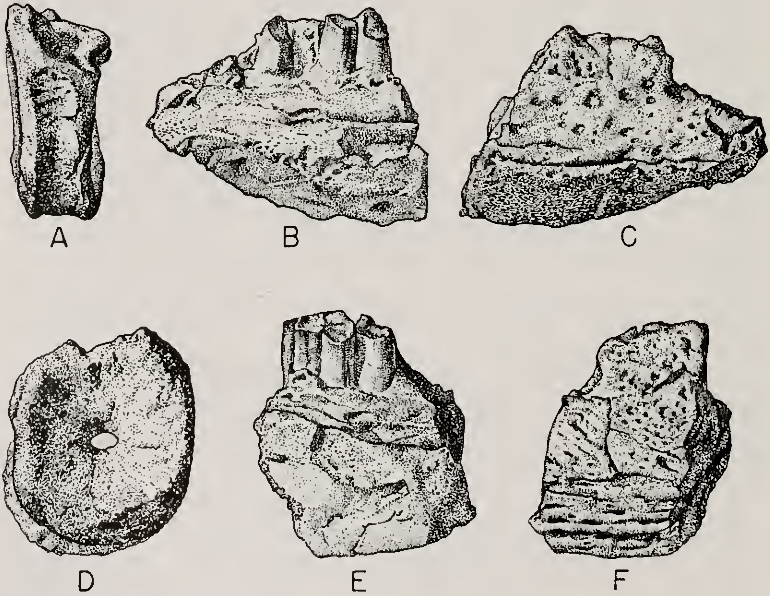

Figure 16. Type materials of *Neopteroplax relictus* sp. nov. *A*, *D*, centrum in lateral and anterior views; *B*, *C*, and *E*, *F*, two jaw fragments in internal and external views. x⅔.

2237) with diameters of approximately 40 mm. We have here, it would seem, the last survivor of the large embolomeres of the Carboniferous.

After the main body of this paper had been completed, some further light was shed on the matter by the discovery, by Mr. Gene Wilson of Ringgold, Texas, of fragmentary remains of a seemingly comparable amphibian at a still lower horizon. The materials (MCZ 2353) include several central elements similar in size to those from the "Prideaux pocket" and two jaw fragments (Fig. 16). The teeth, although broken at the tips, show the close-set pattern seen in *Neopteroplax;* they are transversely oval in section at the level of the outer margin of the dentary, with dimensions of 5½ by 6 to 8 mm. This form can be reasonably interpreted as a surviving member of the genus *Neopteroplax.* Geological and geographical considerations make it unlikely that it is specifically identical with the Ohio Conemaugh form, and despite the fact that no diagnostic features can be named other than the somewhat larger average size of centra and dentary teeth, the new materials are here designated as the holotype of *Neopteroplax relictus,* sp. nov. They were found in shales a few feet below a small outlier of the Blach Ranch Limestone, 2½ miles north and ½ mile east of Graham, Young Co., Texas. The Blach Ranch lies in the Thrifty Formation of the Cisco group; despite the fact that there has been a trend in recent decades for a downward shifting of the Pennsylvanian-Permian boundary in this area of Texas, it is still almost universally agreed that the Thrifty Formation is definitely pre-Permian (and pre-Wolfcamp) in age.[1]

SUMMARY

The skull of a large embolomerous labyrinthodont from the Conemaugh group in Ohio is described as *Neopteroplax conemaughensis,* gen. et sp. nov. Other remains of large American embolomeres are reviewed, including *Pholiderpeton? bretonense* from the Point Edward formation of Nova Scotia; *Eobaphetes kansensis,* which appears to come from the Morrow series in Arkansas rather than Kansas; the problematical *Eosaurus acadianus* and *"Baphetes" minor* from the Joggins exposures in Nova

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[1] I wish to thank Dr. Walter Dalquest of Midwestern University, Wichita Falls, Texas, for bringing Mr. Wilson's find to my attention, and Mrs. Ida Mae Fletcher and Mr. and Mrs. Richard Layfield of Graham for their courtesies during a trip to the site of the discovery.

Scotia; skull and other materials from the Conemaugh of Linton, Ohio, here termed *Anthracosaurus lancifer;* large vertebrae and jaw fragments from the late Pennsylvanian and earliest Permian of Texas named *Neopteroplax relictus* sp. nov.; fragmentary remains from several additional Pennsylvania localities and horizons.

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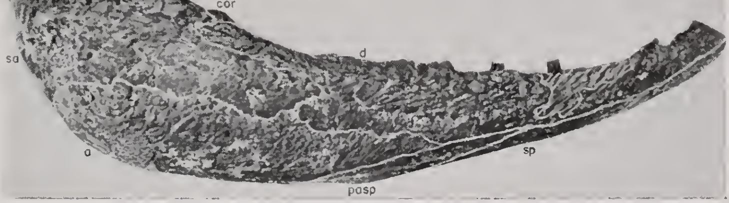
PLATES

Plate 1. The type skull of *Neopteroplax conemaughensis* as restored for exhibition purposes, in dorsal view. x⅓ approximately.

Plate 2. *Above*, the type skull of *Neopteroplax conemaughensis* as restored for exhibition purposes, in ventral view. x⅓ approximately.

Below, right jaw of the *Neopteroplax conemaughensis* type, in external view. The tip of the jaw and small areas of surface indicated by hatching are absent. Probable sutures in white. x¼ approximately. Abbreviations: *a*, angular; *ar*, articular; *cor*, coronoid; *d*, dentary; *posp*, postsplenial; *sa*, surangular; *sp*, splenial.



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AT HARVARD COLLEGE
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THE CAROTID CIRCULATION IN THE RODENTIA

By Daniel A. Guthrie

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
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No. 10 — *The Carotid Circulation in the Rodentia*

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CONTENTS

INTRODUCTION

Tandler's studies of carotid arteries (1899, 1901) indicated that a great deal of variation exists in the cranial trunk arteries of rodents. The present study began as an attempt to discover the extent of this variation. It was hoped that this study might give some indication as to the interrelationships of the various groups of rodents whose phylogeny has not been determined from the fossil record.

The order in which the rodents are discussed in this paper is determined by similarities in arterial pattern, particularly with respect to the internal carotid artery, rather than by the order in which they are commonly placed in current classifications (e.g. Wood 1955). This grouping is one of descriptive convenience and does not necessarily indicate close relationship between groups adjacent in the text.

METHODS AND MATERIALS

The resources of the Mammalogy Department of the Museum of Comparative Zoology were made available to me, and skulls of all rodent genera in this collection were examined. In addition, preserved and fresh specimens of many species were injected with colored latex and dissected. Although a detailed description of the arterial and venous pathways was at first envisioned, this proved to be impractical as work progressed. Dissection of both sides of four latex-injected specimens of *Rattus*, four of *Sciurus*, and four of *Cavia* indicated that while the larger trunk arteries remain constant in their position in each species, the smaller arteries vary considerably in their position, pathways, and branching. Further, the venous system shows on an intraspecific level almost as much variation, even in the larger vessels, as is found between families. The arteries described here are the larger trunk arteries in which intraspecific variation is at a minimum.

The terminology used for familial and higher categories is that of Wood (1955); generic to subfamily names are from Simpson (1945); and specific names are from Ellerman (1940-41). The terminology of Greene (1935) is used for muscles and blood vessels except where noted in the text. The nomenclature used for foramina is essentially that of Hill (1935).

I wish to thank Miss Barbara Lawrence and Dr. Charles Lyman of the Museum of Comparative Zoology for allowing me the use of the collections of the Mammalogy Department, and Dr. Richard Van Gelder of the American Museum of Natural History, Professor Albert E. Wood of Amherst College, and Mr. Richard Thorington, Mr. Charles Mack, and Mr. Neal Todd of Harvard University for their generous donation of specimens for dissection. I am especially grateful to Professors Bryan Patterson and Albert E. Wood for their most helpful criticism of the manuscript of this paper.

SCIURIDAE

Tandler (1899) described the circulation in *Marmota* (*Arctomys* in his terminology) and in three species of *Sciurus*. The following description of carotid circulation is based on the dissection of four latex-injected specimens of *Sciurus carolinensis* (Fig. 1).

The common carotid artery divides into the external carotid and stapedial arteries at the level of the occipital condyle. The internal carotid artery is not found in adult *Sciurus*.[1]

The external carotid artery passes forward dorsal to the hypoglossal nerve, digastric muscle, and hyoid apparatus, and gives rise to the occipital and superior thyroid arteries.[2] At the level of the tympanic bulla the external carotid gives rise to the common trunk of the lingual and external maxillary arteries, and then turns laterally and dorsally across the bulla towards the external auditory meatus. The external carotid gives rise to masseteric arteries and to the anterior and posterior auricular arteries during its course upward across the bulla. The external carotid divides into the superficial temporal and internal maxillary arteries near the auditory meatus.

The internal maxillary artery can be divided into three parts, the mandibular, pterygoid, and orbital portions (corresponding to the first, second, and third, or maxillary, pterygoid, and sphenomaxillary portions in man). The inferior alveolar and middle meningeal arteries branch from the first or mandibular portion of the internal maxillary artery, arising from this artery soon after its origin from the external carotid. The second or pterygoid portion of the internal maxillary artery gives rise to the arteries which accompany the anterior part of the mandibular division of the trigeminal nerve. The latter include the pterygoid, anterior and posterior deep temporal, and buccinator arteries, as well as a number of arteries to the masseter muscles. The third or orbital portion of the internal maxillary artery continues forward passing medially through an opening in the lateral pterygoid ridge and uniting with the medial or inferior portion of the stapedial artery. The orbital portion then continues forward through the alisphenoid canal entering the orbit through the

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[1] Tandler states that the internal carotid exists only as the stem of the stapedial artery.

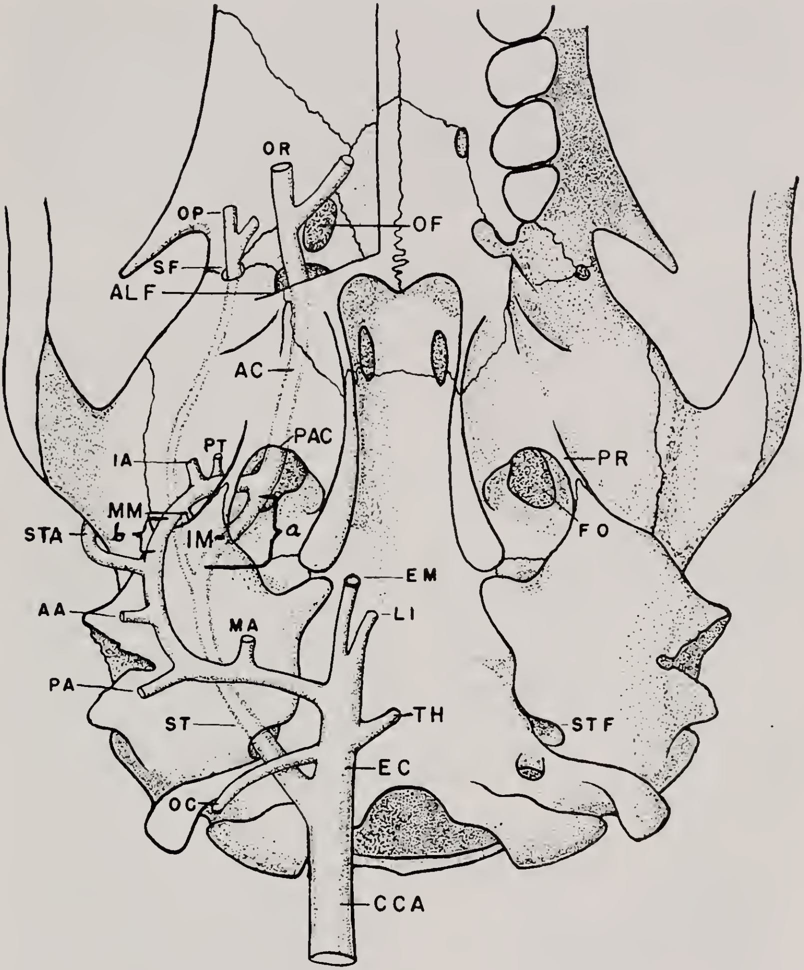
[2] The branches of the trunk arteries mentioned here are not the only branches that occur but rather the more important ones. They serve as markers for identifying and discussing the trunk arteries.

anterior lacerate foramen (sphenoidal fissure of Hill). In the orbit, the orbital portion gives rise to the infraorbital, sphenopalatine, descending palatine, and alveolar arteries.

The stapedial artery enters the tympanic bulla through the stapedial foramen and traverses the bulla enclosed in the stapedial canal which is ossified except in the vicinity of the stapes. While in the bulla this artery divides into two parts which Tandler named the superior and inferior portions. The more medial branch or inferior portion passes out of the bulla between the tympanic bulla and periotic capsule (petro-tympanic fissure), and onto the ventral surface of the skull where it unites with the internal maxillary artery. The more lateral branch or superior portion of the stapedial artery is the ophthalmic artery. It passes out of the bulla through the petro-tympanic fissure, but remains within the skull, passing forward between the squamosal and the dura mater. It enters the orbit through the sphenofrontal foramen, an opening in the suture between the frontal, squamosal, and alisphenoid bones. Tandler noted that in *Sciurus aureogaster* and in *Marmota* there is a rudimentary connection between the posterior communicating artery in the circle of Willis and the ophthalmic artery through the optic foramen.

In *Sciurus,* the main blood supply to the brain is carried by the two vertebral arteries. These arteries unite at the level of the foramen magnum to form the basilar artery. This artery enters

Fig. 1. *Sciurus carolinensis* ×5, AA, anterior auricular artery; AC, alisphenoid canal; ALF, anterior lacerate foramen; CC, carotid canal; CCA, common carotid artery; EC, external carotid artery; EM, external maxillary artery; FO, foramen ovale; IA, inferior alveolar artery; IC, internal carotid artery; IM, internal maxillary artery; LI, lingual artery; MA, masseteric artery; MLF, middle lacerate foramen; MM, middle meningeal artery; OC, occipital artery; OF, optic foramen; OP, ophthalmic artery; OR, branches of the orbital portion of the internal maxillary artery; PA, posterior auricular artery; PAC, posterior opening to the alisphenoid canal; PLF, posterior lacerate foramen; PR, lateral pterygoid ridge; PT, branches of the pterygoid portion of the internal maxillary artery; SF, sphenofrontal foramen; ST, stapedial artery; STA, superficial temporal artery; STF, stapedial foramen; TH, superior thyroid artery. Elimination of the segment of the stapedial artery labelled *a* would result in a carotid pattern similiar to that found in *Eliomys.* Elimination of the segment of the internal maxillary artery labelled *b* and the addition of an internal carotid artery would result in a carotid pattern similar to that found in *Mesocricetus.*



the skull through the foramen magnum passing ventral to the brain. Once in the skull the basilar artery divides into two large posterior communicating arteries. These pass forward on each side of the ventral surface of the brain and give rise to numerous small branches which pass into the brain. Just posterior and ventral to the olfactory lobes, the two posterior communicating arteries reunite. The ring formed by these arteries is the circle of Willis.

Skulls representing nearly every genus included in the family Sciuridae were examined. They all possess stapedial canals and sphenofrontal foramina and lack openings for the internal carotid artery. Although the presence of the connections between the internal maxillary artery and the stapedial artery and between the posterior communicating artery and the ophthalmic artery cannot be ascertained from skeletal material, the pattern described for *Sciurus* seems to be present throughout this family.

Gliridae

Dissection of a latex-injected specimen of *Eliomys quercinus* indicates that this species has a carotid circulation very similar to that found in *Sciurus.* The only difference is the absence of the more medial or inferior portion of the stapedial artery in *Eliomys.* The stapedial artery exists only as the stem for the ophthalmic artery. There is no connection between the stapedial artery and the internal maxillary artery.

An examination of skeletal material indicates that the pattern found in *Eliomys* is present in *Dryomys* and in the subfamily Graphiurinae (*Graphiurus*), the skulls of these forms possessing stapedial canals and sphenofrontal foramina. However, in *Glis, Muscardinus,* and *Glirulus* these structures are not present. In these genera the ophthalmic artery must either arise from the orbital portion of the internal maxillary artery or from the posterior communicating artery in the circle of Willis. These are the only alternatives to a stapedial origin for the ophthalmic artery known to occur in the Mammalia.

Ctenodactylidae

Dissection of a latex-injected specimen of *Pectinator sphenei* shows that the carotid circulation in this form is like that of *Eliomys* except that there is no trace of a stapedial artery. The ophthalmic artery arises from the orbital portion of the internal maxillary artery after the latter artery enters the orbit. The pattern in *Pectinator* is, therefore, possibly the same as that in *Glis.*

Muridae

The cranial arteries of *Rattus* were described by Tandler (1899) and by Greene (1935). The following description is based on these works and on the dissection of four latex-injected specimens of *Rattus norvegicus* (Fig. 2).

The carotid circulation in *Rattus* differs from that found in *Sciurus* in respect to the origin of the orbital portion of the internal maxillary artery, the origin of the ophthalmic artery, and in the presence of an internal carotid artery.

The common carotid artery divides at the level of the thyroid gland into the internal and external carotid arteries. The external carotid artery is similar to that described for *Sciurus*. The

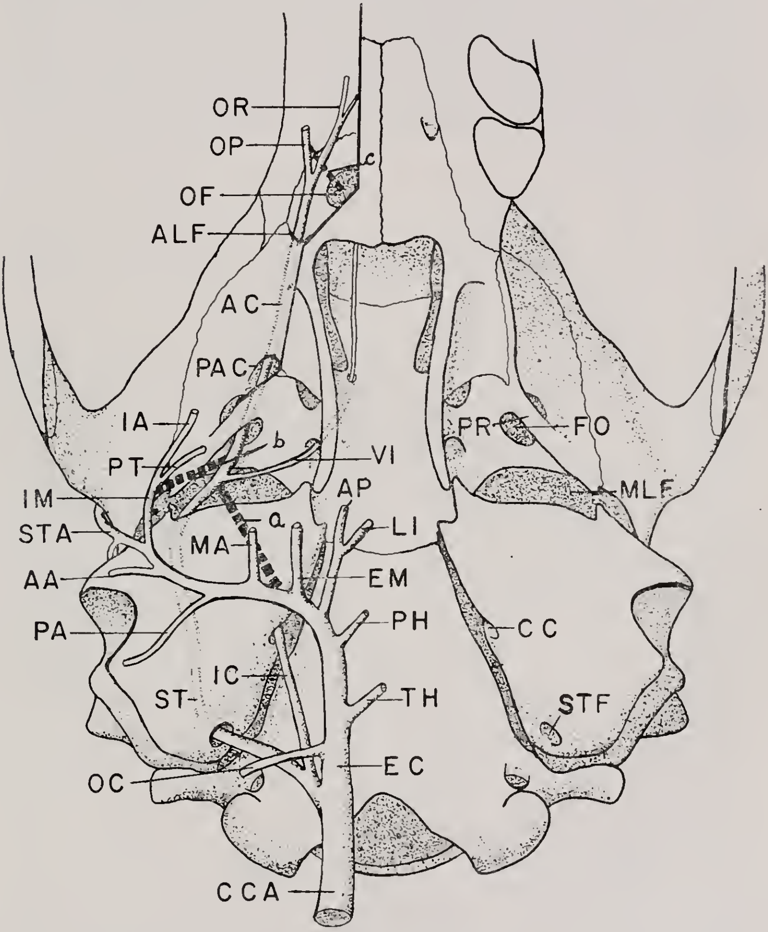


FIG. 2. *Rattus norvegicus* ×5, AP, ascending palatine artery; PH, ascending pharyngeal artery; VI, vidian artery; for other abbreviations see Fig. 1. The dashed lines labelled *a*, *b*, and *c*, designate the courses of arteries found in the embryo of *Rattus* but not in the adult.

internal maxillary artery arises from the external carotid as it does in *Sciurus.* However, the internal maxillary artery gives rise only to branches of its pterygoid and mandibular portions. It has no connection with either the stapedial artery or with an orbital portion as it has in *Sciurus.*

The internal carotid artery gives rise to the stapedial artery (pterygopalatine artery of Greene) shortly after leaving the external carotid and then passes into the skull through a groove (carotid canal) on the medial side of the tympanic bulla joining the posterior communicating artery in the circle of Willis. The small size of this latter artery indicates that the internal carotid arteries, rather than the vertebral arteries, supply most of the blood to the brain.

Except for the connection with the internal carotid artery, the pattern of the circle of Willis is basically the same as that in *Sciurus.* However, because the internal carotid is so much larger than the posterior communicating artery, the former name is used for the artery in the circle of Willis anterior to where the internal carotid enters the circle of Willis.

The stapedial artery enters the tympanic bulla through the stapedial foramen. It traverses the bulla remaining completely enclosed in the stapedial canal which is ossified except in the vicinity of the stapes. This artery emerges on the anterior side of the bulla through the petro-tympanic fissure. Here it sends a small branch to the internal nares (palatine portion of the pterygopalatine artery or Vidian artery of Greene). The rest of the stapedial artery passes laterally through an opening in the lateral pterygoid ridge, passing over the foramen ovale, and enters the alisphenoid canal. It remains in this canal until it reaches the anterior lacerate foramen through which it enters the orbit. Once in the orbit the stapedial artery divides into several branches. These are the ophthalmic artery and the branches of the orbital portion of the internal maxillary artery.

It was determined by dissection that *Mus musculus, Aethomys kaiseri,* and *Dasymys incomitus medius* have the same arterial pattern as that described for *Rattus.* From the presence of canals for the stapedial and internal carotid arteries in other genera it appears that this pattern is present throughout the Muridae. Some variation occurs in this family in the amount of ossification of the alisphenoid and stapedial canals and in the position of the posterior opening of the alisphenoid canal, but these differences do not affect the carotid pattern.

CRICETIDAE

As a great deal of variation occurs within this family, the Cricetidae will be treated by subfamilies.

MICROTINAE and GERBILLINAE

The following description is based on the dissection of a latex-injected specimen of *Microtus pennsylvanicus* (Fig. 3).

The common carotid artery divides at the level of the occipital condyle into the external and internal carotid arteries. The external carotid artery is similar to that described for *Sciurus* except in its relation to the internal maxillary artery. The latter artery, as a branch of the external carotid, is very reduced,

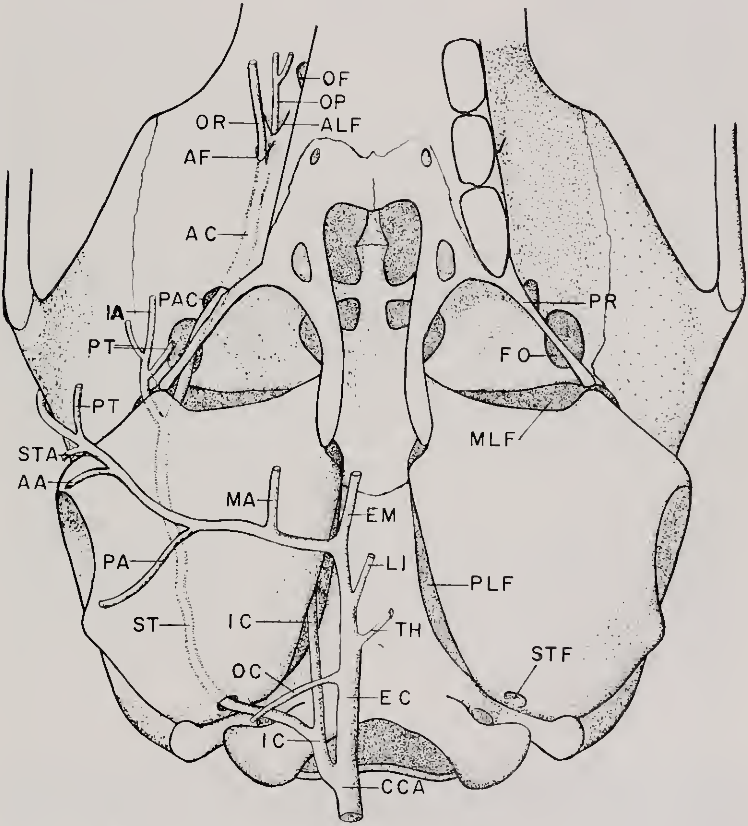


FIG. 3. *Microtus pennsylvanicus* ×6.5, for abbreviations see Fig. 1.

consisting only of a few branches of its pterygoid portion. These arise separately from the external carotid and supply the masseter, buccinator, and temporal muscles.

The internal carotid artery gives rise to the stapedial artery soon after leaving the common carotid and continues into the skull through the posterior lacerate foramen (jugular foramen of Hill) joining the posterior communicating artery in the circle of Willis. The circle of Willis is similar to that found in *Rattus* except that the vertebral arteries are the same size as the internal carotid arteries.

The stapedial artery enters the bulla through the stapedial foramen. While in the bulla this artery sends branches (not shown in Fig. 3) dorsally through the petro-tympanic fissure to the dura mater. A few branches also reach the temporal muscle through openings in the suture between the squamosal and parietal bones. Near the anterior end of the bulla the stapedial artery gives rise to the inferior alveolar artery. This artery passes laterally through the petro-tympanic fissure and the middle lacerate foramen to the mandible. The inferior alveolar artery plus the smaller branches of the stapedial artery in the bulla correspond to the branches of the mandibular portion of the internal maxillary artery.

The stapedial artery passes through the petro-tympanic fissure medial to the lateral pterygoid ridge. Arteries corresponding to part of the pterygoid portion of the internal maxillary artery may arise either here or in common with the inferior alveolar artery as shown in Figure 3. The stapedial artery continues forward through an opening in the lateral pterygoid ridge and enters the skull again through a small foramen. This opening corresponds to the posterior end of the alisphenoid canal in *Sciurus* and *Rattus*. This canal is not ossified in *Microtus*. The stapedial artery emerges into the orbit through its own foramen, termed the alisphenoid foramen by Hill (1935),[3] and branches extensively. The branches correspond to those of the orbital portion of the internal maxillary artery as described in *Sciurus*.

The ophthalmic artery is a branch of the stapedial artery,

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[3] The alisphenoid foramen is actually the lateral part of the anterior lacerate foramen. In *Clethrionomys* the posterior cheek teeth and the maxillary bones surrounding them extend up into this latter opening giving it the shape of an inverted U. In *Microtus* the cheek teeth extend farther upward and the maxillary bone surrounding them has fused with the frontal bone. This divides the anterior lacerate foramen into two parts, the more lateral of which is the alisphenoid foramen.

arising just before the latter artery enters the orbit. The ophthalmic artery enters the orbit through the anterior lacerate foramen or, in some cases, through a sphenofrontal foramen.

Dissection of a latex-injected specimen of *Clethrionomys gapperi* and examination of skulls of the other genera belonging to the subfamilies Microtinae and Gerbillinae indicates that the carotid circulation throughout these groups is basically the same as that described for *Microtus.* Although the sphenofrontal and alisphenoid foramina were not present and the foramen ovale and posterior opening of the alisphenoid canal were confluent in many genera, these differences do not affect arterial pattern.

CRICETINAE

Latex-injected specimens of *Peromyscus leucopus* and *Mesocricetus auratus* were dissected. The arterial pattern found in these genera is basically the same as that described for *Microtus.* Differences do occur, however, in the origin of the ophthalmic artery and in the course of the stapedial artery. An alisphenoid foramen is not found in this group; the stapedial artery enters the orbit through the anterior lacerate foramen, as in *Clethrionomys.* In both *Peromyscus* and *Mesocricetus* the ophthalmic artery branches from the stapedial artery within the tympanic bulla, passing forward into the orbit through the sphenofrontal foramen in the same manner as has been described for *Sciurus.*

Mesocricetus differs from both *Microtus* and *Peromyscus* in that the branches of the stapedial artery corresponding to the mandibular and pterygoid portions of the internal maxillary artery separate from the stapedial artery after it has emerged from the bulla rather than within the bulla.

When the ophthalmic artery originates from the stapedial artery within the bulla, as it does in *Sciurus, Eliomys, Peromyscus,* and *Mesocricetus,* there is usually a groove on the inner surface of the squamosal bone indicating its passage. Most members of the tribe Hesperomyini and all the members of the tribe Cricetini have this groove and stapedial canals. These rodents probably have a carotid circulation similar to that described for *Peromyscus.* However, in the tribe Myospalacini and in some members of the Hesperomyini, notably *Neotoma,* this groove is absent and the stapedial canal is occluded in the adult.[4] In these forms which lack a stapedial artery in the adult the carotid

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[4] The sphenofrontal foramen was not found in any specimen of *Neotoma* examined, although Hill (1935) states that it is present in this genus.

pattern is presumably similar to that described for *Glis* and *Pectinator* with the addition of an internal carotid artery.

In the Platacanthomyini, as in the Hesperomyini, the carotid pattern is variable. *Typhlomys* has a stapedial canal, sphenofrontal foramen, and a groove between these structures indicating a stapedial origin for the ophthalmic artery. *Platacanthomys* lacks these structures. This indicates that *Typhlomys* has a carotid pattern similar to that of *Peromyscus* while the pattern found in *Platacanthomys* is similar to that of *Neotoma* or *Glis*.

NESOMYINAE

The skulls of the members of this group show variation similar to that found in the Platacanthomyini and the Hesperomyini. *Nesomys* has a stapedial canal, sphenofrontal foramen and alisphenoid canal, and probably has a carotid circulation similar to that found in either *Mesocricetus* or *Peromyscus*. *Eliurus, Brachyuromys* and *Brachytarsomys* lack the sphenofrontal foramen and while traces of the stapedial canal are present, the canal is occluded. The latter forms probably have a carotid pattern similar to that described for *Glis* with the addition of an internal carotid artery.

LOPHIOMYINAE

Lophiomys also lacks a functional stapedial canal in the adult and probably has a carotid circulation similar to that found in *Glis* with the addition of an internal carotid artery.

ZAPODIDAE

A latex-injected specimen of *Napeozapus insignis* was dissected and skulls of *Zapus* and *Sicista* were examined. The arterial pattern in this group is basically the same as that found in *Microtus*. Both internal carotid and stapedial arteries are present in *Napeozapus*, the latter giving rise to the ophthalmic artery and to all of the internal maxillary circulation.

Minor differences occur in the course of the stapedial artery because of the shape of the basicranial region. The stapedial artery does not pass onto the ventral surface of the skull after leaving the tympanic bulla, but remains within the skull until reaching the orbit which it enters through the anterior lacerate foramen. Branches corresponding to the mandibular and pterygoid portions of the internal maxillary artery arise from the stapedial artery just anterior to the tympanic bulla and pass ventrally through the middle lacerate foramen. Branches corresponding to the orbital portion of the internal maxillary artery and to the ophthalmic artery arise from the stapedial artery once the latter artery has entered the orbit.[5]

HETEROMYIDAE

Dissection of a latex-injected specimen of *Dipodomys spectabilis* reveals a carotid pattern similar to that of *Napeozapus.* The only difference is the existence of a slender connection between the external carotid artery and the pterygoid portion of the internal maxillary artery, the latter arising from the stapedial artery in *Dipodomys* as it does in *Napeozapus.* This connection branches from the external carotid in the area from which the internal maxillary artery arises in *Rattus* and *Sciurus.*

The foramina in the skulls of *Perognathus* and *Microdipodops* are the same as those found in *Dipodomys. Liomys* and *Heteromys* lack a stapedial foramen and canal, although an alisphenoid canal is present in these forms. The circulation in these genera may be similar to that found in *Geomys* or to that found in *Glis* with the addition of an internal carotid artery.

DIPODIDAE

Examination of the skulls of *Dipus, Jaculus, Scirtopoda, Allactaga, Pygeretmus,* and *Euchoreutes* indicates that the foraminal pattern is uniform throughout this family. An internal carotid canal and a well-ossified stapedial canal are present in these genera. Apparently the stapedial artery does not pass ventrally through the middle lacerate foramen but remains within the skull until reaching the orbit which it enters through the anterior lacerate foramen. The condition of the inferior alveolar artery and the ophthalmic artery cannot be determined from skeletal material. However, the configuration of the foramina and the shape of the skull suggests a carotid pattern similar to that of the Zapodidae.

CASTORIDAE

The carotid circulation described below is based on the dissection of a latex-injected specimen of *Castor canadensis* (Fig. 4).

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[5] The sphenofrontal foramen was not found in any members of the genus *Zapus* examined, although Hill (1935) states that it is present in *Z. princeps.*

The common carotid artery divides into internal and external carotid arteries at the level of the occipital condyle. The external carotid artery is similar in condition to that found in *Sciurus* and *Rattus* except in its relation to the internal maxillary artery.

Although the internal maxillary artery is a branch of the external carotid, it is not one of the terminal branches of this artery as it is in *Sciurus*. Rather, it leaves the external carotid soon after the latter gives rise to the external maxillary artery, and before the external carotid gives rise to the posterior auricular artery. The internal maxillary artery passes ventrally and anteriorly to the area anterior to the bulla passing just anterior to the internal pterygoid muscle. Once near the ventral surface of the skull it gives rise to a well developed mandibular portion which includes both inferior alveolar and middle meningeal arteries, the latter entering the skull through the middle lacerate foramen. The pterygoid portion of the internal maxillary, except for the buccinator and masseteric arteries, also arises here. The buccinator and masseteric arteries arise farther forward and pass laterally

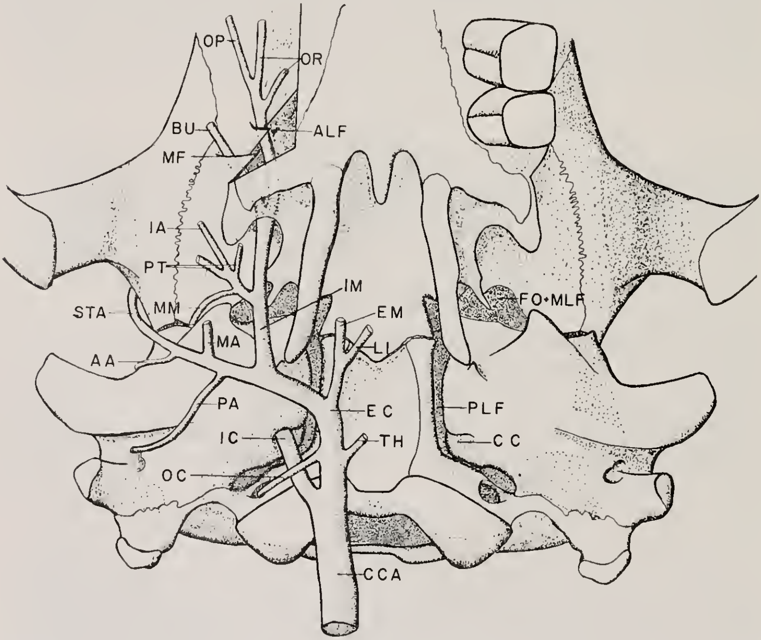

Fig. 4. *Castor canadensis* ×1.4, BU, buccinator and masseteric arteries; MF, masticatory foramen; for other abbreviations see Fig. 1.

through the masticatory foramen in company with the anterior portion of the mandibular trunk of the trigeminal nerve.[6] The orbital portion of the internal maxillary artery continues through the alisphenoid canal into the orbit. The ophthalmic artery arises from the orbital portion of the internal maxillary artery within the orbit.

The internal carotid enters the skull through a groove (carotid canal) on the medial side of the bulla and joins the posterior communicating artery in the circle of Willis. The size of the internal carotid arteries indicates that they, rather than the vertebral arteries, supply most of the blood to the brain. The circle of Willis in *Castor* is similar to that described for *Rattus.*

Caviomorpha

Tandler described the carotid circulation of *Cavia porcella* (1899) and *Lagostomus maximus* (1901). Reference to these descriptions, dissection of latex-injected specimens of *Cavia, Myoprocta,* and *Plagiodontia,* and examination of skulls of nearly all the living genera in this group indicates that the same carotid pattern is present throughout the Caviomorpha. For this reason this suborder is treated as one unit.

The common carotid artery continues forward as the external carotid artery. The stapedial artery is not present in adults although a trace of the stapedial canal is often found, indicating the presence of this artery in the embryo. Similarly, although the internal carotid artery is absent in adult members of this suborder, Tandler (1899) noted its presence in the embryo of *Cavia.*

The external carotid artery in the Caviomorpha resembles that described for *Castor,* although in some cases the lingual, external maxillary, and internal maxillary arteries were observed to arise in common from the external carotid artery. The mandibular and pterygoid portions of the internal maxillary artery differ in the Caviomorpha somewhat from the condition found in *Castor* in that they arise separately from the internal maxillary artery instead of from a common trunk as in *Castor.*

In the forms dissected, the ophthalmic artery is formed by the union of a branch from the orbital portion of the internal maxillary artery and a branch from the posterior communicating artery, the latter entering the orbit through the optic foramen.

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[6] The masticatory foramen is often confluent with the anterior lacerate foramen.

The circle of Willis in the Caviomorpha is similar to that described for *Sciurus.*

HYSTRICIDAE

The carotid pattern in this family appears, from Tandler's (1901) description of *Hystrix cristata,* to be the same as that found in the Caviomorpha. The only difference is the presence in adult *Hystrix* of a rudimentary internal carotid artery. This artery is apparently vestigial in nature, reaching the carotid canal but not remaining open as far as the posterior communicating artery in the circle of Willis. A strand of tissue marks its connection with the latter structure.

GEOMYIDAE

A latex-injected specimen of *Geomys bursarius* was dissected and skulls of the other members of this family were examined. The following description is of the carotid pattern found in *Geomys.*

The common carotid artery continues anteriorly as the external carotid artery. The internal carotid and stapedial arteries are not present. The external carotid artery in *Geomys* is similar to that described for *Sciurus* except in its relation to the internal maxillary artery.

The pterygoid and mandibular portions of the internal maxillary artery, the mandibular portion consisting chiefly of the inferior alveolar artery, arise from the end of the external carotid artery as they do in *Rattus* and *Sciurus.* The orbital portion of the internal maxillary artery arises in common with the common trunk of the lingual and external maxillary arteries. This is the position from which the whole internal maxillary originates in the Caviomorpha and in *Castor* and *Hystrix.* The orbital portion courses forward turning dorsally towards the basicranial region in front of the internal pterygoid muscle. Just before the orbital portion enters the alisphenoid canal it receives a small branch from the pterygoid portion of the internal maxillary artery. The orbital portion enters the orbit through the anterior lacerate foramen and gives rise to the ophthalmic artery within the orbit. The circle of Willis in *Geomys* is similar to that described for *Sciurus.*

Many skulls of *Geomys* and of the other genera in this family have a small indentation on the tympanic bulla in the position of a stapedial foramen, and in most of the geomyids the stapedial canal, although occluded, is still present indicating the presence of the stapedial artery in the embryo.

BATHYERGIDAE

Latex-injected specimens of *Bathyergus* and *Cryptomys* were dissected, and skulls of the other genera included in this family were examined. The following description is of the carotid circulation found in *Bathyergus* (Fig. 5).

The common carotid artery continues anteriorly as the external carotid artery; the internal carotid and stapedial arteries are absent.

The external carotid artery gives rise to the occipital, lingual, and external maxillary arteries as well as to several minor arteries to the throat. It also gives rise to an artery which follows the usual path taken by the external carotid in the other rodents described, but this artery is only the posterior auricular artery.

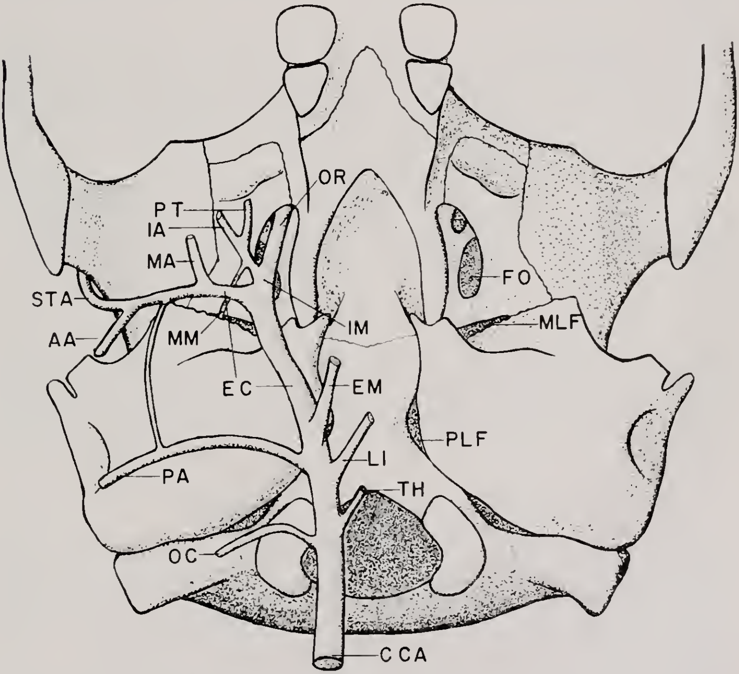

FIG. 5. *Bathyergus suillus* ×3, for abbreviations see Fig. 1.

The external carotid continues forward along the course taken by the internal maxillary artery in *Castor* and the Caviomorpha, passing dorsally anterior to the internal pterygoid muscle. Just anterior to the bulla the external carotid gives rise to the internal maxillary artery. The external carotid continues laterally and dorsally to the mandible reaching the dorsal surface of the skull behind the glenoid fossa. During its upward course the external carotid anastomoses with a slender branch from the posterior auricular artery and gives rise to masseteric, anterior auricular, temporal, and superficial temporal arteries.

The internal maxillary artery divides into two portions soon after separating from the external carotid. The more lateral of these gives rise to the branches of the pterygoid and mandibular portions, the latter consisting of the inferior alveolar artery and a middle meningeal artery which enters the skull through the middle lacerate foramen. The more medial branch is the orbital portion of the internal maxillary. It enters the short alisphenoid canal emerging into the orbit through the anterior lacerate foramen.

The ophthalmic artery has a dual origin from the orbital portion of the internal maxillary artery and from the posterior auricular artery in the circle of Willis connecting with the latter through the optic foramen. The circle of Willis in this genus is similar to that described for *Sciurus*.

Cryptomys differs from *Bathyergus* only in that it lacks the connection between the posterior auricular artery and the anterior part of the external carotid artery.

PEDETIDAE

The carotid arteries of *Pedetes caffer* were described by Tandler (1899). The description here presented is based on Tandler's work and on the dissection of an uninjected late fetus of this species.

The common carotid artery divides at the level of the larynx into the external and internal carotid arteries. The external carotid artery is similar to that described for *Sciurus* except that it does not give rise to any part of the internal maxillary artery.

The internal carotid artery passes through the carotid canal into the skull to join the posterior communicating artery in the circle of Willis. There is no stapedial artery in *Pedetes*.

The internal maxillary artery arises from the internal carotid artery after this artery has entered the circle of Willis. It divides within the skull into two portions, the posterior part leaving the cranial cavity in company with the mandibular portion of the trigeminal nerve through the foramen ovale. This portion corresponds to the mandibular and pterygoid divisions of the internal maxillary. The more anterior portion enters the orbit through the anterior lacerate foramen and corresponds to the orbital portion of the internal maxillary artery.

The ophthalmic artery arises separately from the internal carotid artery in the circle of Willis and enters the orbit through the optic foramen. The circle of Willis itself is similar in form to that found in *Rattus*.

OTHER FAMILIES

It was not possible to obtain preserved members of the families Rhizomyidae, Spalacidae, Anomaluridae, Petromuridae, Thryonomyidae, and Aplodontidae. However, some indication of the carotid circulation in these forms was obtained from skeletal material. The skulls of *Aplodontia, Petromus,* and *Thryonomys* lack stapedial canals and openings for the internal carotid arteries. Although the carotid pattern in these genera could be similar to that described for *Glis* or *Bathyergus,* the relationships suggested in current classifications (e.g. Wood 1955, Simpson 1945) for these genera would favor their possessing a carotid pattern similar to that found in *Castor, Hystrix,* and the Caviomorpha.

The skulls of members of the families Anomaluridae, Spalacidae, and Rhizomyidae possess openings for an internal carotid artery but lack stapedial canals. The basic carotid circulatory pattern in these forms could be like that of *Glis, Castor,* or *Pedetes.* On the basis of current classifications it is suspected that the Anomaluridae possess a carotid circulation similar to that of *Pedetes,* and that the Rhizomyidae and Spalacidae possess a pattern similar to that of either *Neotoma* or *Glis.*

FOSSIL FORMS

None of the fossil rodent skulls examined or figured in the literature possesses well preserved or carefully cleaned basicranial regions. Wood (1962) identifies a sphenofrontal foramen in *Paramys delicatus* indicating the presence of a stapedial artery in this form. *Reithroparamys* lacks a stapedial foramen and appears not to have had a stapedial artery. All the paramyids possess alisphenoid and internal carotid canals.

Sciuravus (Dawson 1961) lacks a stapedial foramen but appears to have a large opening for the internal carotid artery. *Ischyromys* also lacks a stapedial canal.

EMBRYOLOGY

Tandler (1902) described the development of the carotid circulation in *Rattus*. This is the only rodent on which such a study has been made. In the embryo of *Rattus* Tandler found a number of arteries not present in the adult. One of these arteries (*a* in Fig. 2) follows the course taken by the internal maxillary artery in *Castor* connecting the stapedial artery with the external carotid artery. Another embryonic artery follows the course taken by the internal maxillary artery found in *Pedetes* connecting the stapedial artery with the internal carotid artery through the foramen ovale. A third embryonic connection (*b* in Fig. 2) is found between the stapedial artery and the pterygoid portion of the internal maxillary (a branch of the external carotid in *Rattus*). Finally, there is a connection between the ophthalmic artery and the internal carotid artery in the circle of Willis in embryos of *Rattus* (*c* in Fig. 2). Almost all the carotid circulatory patterns found in the Rodentia can be formed from the arterial pattern present in the embryo of *Rattus* by using certain arteries and eliminating others.[7]

Whether or not all the arteries present in the embryo of *Rattus* are present in the embryos of other rodents is not known. However, as noted in the text, traces of a stapedial canal and internal carotid arteries are found in genera not possessing these arteries in the adult.

There are only a few cases where dual origins for arteries are retained in the adult animals, and in these instances one artery is usually smaller than the other. Thus, in the forms which retain dual origins for the ophthalmic artery, one of the two arteries usually carries most of the blood, while the other is reduced in size. Similarly, the connections between the pterygoid portion of the internal maxillary and the stapedial artery in *Sciurus* and the posterior communicating artery in *Rattus* are small vessels carrying little blood.[8]

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[7] The only artery not found in the embryo of *Rattus* is one corresponding to the stapedial origin of the ophthalmic artery as found in *Sciurus*, *Eliomys*, etc.

[8] Injection of latex under pressure swells the arteries abnormally and may make these connections appear larger than they really are.

DISCUSSION

The possibility of variation in carotid circulatory pattern and of the parallel development of similar patterns in isolated groups of rodents is great and makes the value of differences in carotid patterns in determining relationship very indefinite. A knowledge of the genetic control of variation of carotid pattern and of the embryological development of the different patterns would be necessary in order to use differences in pattern confidently as an indicator of phylogenetic relationship. Nevertheless, the variation observed in carotid patterns leads to speculation as to the relationship between the various groups of rodents.[9]

The path followed by the external carotid artery is the same in all rodents examined with the exception of the Bathyergidae. The failure of the external carotid artery to pass laterally over the tympanic bulla in this family may be due to a difference in the shape of the skull. However, the fact that the posterior auricular artery and the thin connection between this artery and the external carotid artery (Fig. 5) take the course normally followed by the external carotid artery suggests that the difference in the course of the external carotid artery in the Bathyergidae is not due just to a simple shift in the position of the artery. The path that the external carotid artery takes in the Bathyergidae is initially the same as that which the internal maxillary artery follows in *Castor*. This suggests that the external carotid in adult Bathyergidae may be derived from other embryonic arteries. A study of the embryonic development of the cranial arteries in the Bathyergidae will be necessary to determine this.

The origins and pathways of four of the other arteries mentioned in this paper vary considerably within the Rodentia. The internal carotid artery varies in its presence in the Rodentia. When present this artery carries the main supply of blood to the brain. When the internal carotid is absent, the vertebral arteries supply the brain with blood. The stapedial artery varies in its presence and in which vessels it supplies. When present the stapedial artery supplies blood to all or part of the internal maxillary artery or to the ophthalmic artery or to both of these arteries. The ophthalmic artery varies in its origin in the

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[9] It should be noted that the variation in carotid pattern is most readily explainable in terms of Wood's classification of the Rodentia (1955). The groupings used in Schaub's (1958), Simpson's (1945), and earlier classifications of the rodents do not coincide with groupings made on the basis of carotid circulation. For this reason Wood's classification is used throughout this discussion.

Rodentia. It may originate from the internal carotid artery or posterior communicating artery in the circle of Willis as in *Pedetes* or *Hystrix,* or from the orbital portion of the internal maxillary artery or from vessels corresponding to this artery as in *Rattus* or *Pectinator.*[10] The ophthalmic artery may also arise from the stapedial artery within the tympanic bulla as it does in *Sciurus.* If the latter origin occurs, the ophthalmic artery usually enters the orbit through a sphenofrontal foramen. In many cases the ophthalmic artery has a dual origin.

The internal maxillary artery varies in its origin and consequently in its pathway. This artery may arise wholly or in part from four different positions. The internal maxillary artery may arise from the stapedial artery as in *Microtus,* from the internal carotid artery as in *Pedetes,* from the anterior end of the external carotid artery as in *Pectinator,* or from a more posterior position on the external carotid artery as in *Castor.* The internal maxillary artery often arises from a combination of two of these positions. The variation of these arteries is summarized in Table 1.

TABLE 1

	internal carotid artery	origin of the ophthalmic artery	origin of the internal maxillary artery
Sciuridae	—	ST ± CW	ST + ECA
Ctenodactylidae	—	OR	ECA
Bathyergidae	—	OR + CW	ECP
Hystricidae	—	OR + CW	ECP
Thryonomyidae	—	OR + CW?	ECP?
Petromuridae	—	OR + CW?	ECP?
Caviomorpha	—	OR + CW	ECP
Castoridae	+	OR	ECP
Aplodontidae	—?	OR + CW?	ECP?
Geomyidae	—	OR	ECP + ECA
Heteromyidae	+	OR	ST or ECA
Dipodidae	+	OR	ST
Zapodidae	+	OR	ST
Spalacidae	+?	OR?	ECA?
Rhizomyidae	+?	OR?	ECA?
Muridae	+	OR	ECA and ST
Cricetidae	+	OR or ST	ECA and/or ST
Gliridae	—	OR or ST	ECA
Pedetidae	+	CW	CW
Anomaluridae	+?	CW?	CW?

Abreviations: CW, circle of Willis (see footnote 10); ECA, external carotid artery, anterior end; ECP, external carotid artery, posterior position; OR, orbital portion of the internal maxillary artery (see footnote 10); ST, stapedial artery.

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[10] The origin of the ophthalmic artery in *Hystrix* is the same as in *Pedetes.* The name of the trunk artery differs as discussed in relation to *Rattus.* Similarly, the origin of the ophthalmic artery is the orbital portion of the internal maxillary artery in both *Rattus* and *Pectinator.* However, the orbital portion is supplied by different trunk arteries in these two genera.

There seem to be three basic carotid patterns present in the Rodentia. The distinction between these patterns is most evident in the differences in origin of the internal maxillary artery. One pattern is that found in *Pedetes* where the internal maxillary artery originates from the internal carotid artery. This pattern is found in no other rodent group with the possible exception of the Anomaluridae. The great difference between this pattern and the patterns found in other rodents may indicate that the Pedetidae are a very ancient group. On the other hand, the great inflation of the bulla in *Pedetes* may prevent the development of the arterial patterns found in other rodents and necessitate the use of the internal carotid artery in carrying blood to the anterior part of the head. A study of the embryology of *Pedetes* will be necessary to determine which of these explanations is correct.

The second basic pattern is actually a combination of two patterns, that in which the internal maxillary artery or parts of it originate from the stapedial artery, and that in which the internal maxillary artery or parts of it originate from the anterior end of the external carotid artery. The presence of both these origins for the internal maxillary artery in *Sciurus*, the Heteromyidae, and in certain subfamilies of the Cricetidae necessitates the grouping together of these patterns. The pattern found in *Sciurus* can easily be changed either into a pattern similar to that found in *Eliomys* by the loss of a short section of the stapedial artery (*a* in Fig. 1), or into a pattern similar to that found in *Mesocricetus* by the loss of a short section of the internal maxillary artery (*b* in Fig. 1). The differences in carotid pattern within the Gliridae, Heteromyidae, and Cricetidae do not coincide with the divisions of these families made in current classifications. This may indicate that these families are in need of taxonomic revision but a more extensive study would be necessary to determine this.

The second basic pattern is found in every member of the suborder Myomorpha as well as in the families Sciuridae and Ctenodactylidae. The lack of a stapedial artery in *Sciuravus* eliminates this form from the direct ancestry of the Myomorpha but does not eliminate the possibility of a sciuravid origin for the Myomorpha as proposed by Wood (1959). The similarity of the pattern found in the Sciuridae to that found in the Myomorpha is an example of parallelism; this group originated from the Paramyidae and not the Sciuravidae (Wood 1959). The resemblance between the patterns found in the Sciuridae and Ctenodactylidae may indicate a common origin for these two groups as suggested by Wood (1955).

The third basic pattern is that in which the internal maxillary artery arises from the external carotid artery before the latter artery turns laterally across the tympanic bulla. This pattern or variations on it is probably found in all members of the suborders Caviomorpha, Hystricomorpha, Bathyergomorpha, Castorimorpha, and in the families Aplodontidae and Geomyidae. All the rodents in this group lack a stapedial artery and all except the Geomyidae and Castoridae have a dual origin for the ophthalmic artery as indicated in Table 1. According to Wood (1959) all these groups except the Geomyidae have arisen from the Paramyidae. The presence of this pattern in the Geomyidae is unexpected. However, this artery is present in the embryo of *Rattus* and probably in the embryos of most rodents. The dissection of one specimen of *Geomys* and one specimen of *Dipodomys* certainly is not enough to determine the closeness of the carotid pattern of the Geomyidae to that of the Heteromyidae, nor is it enough to determine which basic pattern is the primitive one in this group. Certainly this problem should be studied further.

The pattern found in the Castoridae differs from that found in other members of this group in both the absence of a connection between the ophthalmic artery and the circle of Willis and in the presence of an internal carotid artery. The Bathyergidae, as previously noted, differ from other rodents in the path taken by the external carotid artery. These differences as well as the geographic isolation of the Hystricomorpha from the Caviomorpha (Wood and Patterson 1959) indicate the probability of separate origins of the suborders included in this group from the Paramyidae.

A uniform ancestral pattern within the Rodentia may never have occurred in adult rodents but only in their embryos. The presence of the third pattern in many descendants of the paramyids as well as the evidence for the presence of a stapedial artery in this group may indicate that more than one basic pattern was present in adult members of the Paramyidae.

SUMMARY

The major variations of the carotid circulatory pattern in the Rodentia are described, these differences in pattern occurring mostly at or above the family level. Variations in pattern are attributed to the retention of different combinations of embryonic arteries in different groups of rodents. Reduction to one origin for each artery from the multiple origins found in the embryo

usually occurs, but whether one pattern has any advantage over another is not known. The variation in circulatory pattern found in the Rodentia may eventually be useful in determining phylogeny, but further work on the extent and embryological development of this variation must be done before the significance of variation in carotid pattern can be properly assessed.

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By Craig C. Black

CAMBRIDGE, MASS., U.S.A.
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No. 11 — *Miocene Rodents from the Thomas Farm Local Fauna, Florida*

By Craig C. Black[1]

During the last several years a considerable number of rodent specimens have been recovered from the early Miocene Hawthorn formation at the Thomas Farm locality, Gilchrist County, Florida. For the most part only isolated teeth have been found but sufficient numbers of these are now available to increase considerably our knowledge of this rodent assemblage.

Rodents from the Florida Miocene south of the town of Midway were first described by Wood (1932). At that time he described *Proheteromys floridanus* and *P. magnus.* In 1935 this material was reviewed by Wood but no new specimens were then available to supplement his earlier work. In 1947, he described additional specimens of both species from Thomas Farm and also recorded the presence of a cricetid at this locality as well as the presence of *Mesogaulus* in the Miocene at Midway, Florida. *Mesogaulus* was represented by a single premolar, Florida State Geological Survey No. V-5422, which has since been lost. The presence of a cricetid was indicated by several fragmentary limb bones and a number of incisors.

The present collection includes two isolated cricetid molars, several *Proheteromys magnus* teeth, a large number of *Proheteromys floridanus* teeth (which, for the first time, make possible a complete description of the dentition of this species), four squirrel teeth, and one prosciurine M^3. The last two forms are new to the fauna. Unfortunately, no new mylagaulid material has been found.

I would like to thank Mr. Stanley J. Olsen and the Florida Geological Survey for the loan of the types of *Proheteromys floridanus* and *P. magnus* as well as many additional specimens, Dr. Clayton E. Ray of the University of Florida for the loan of material in his care, and Dr. A. S. Romer for the loan of specimens in the collections of the Museum of Comparative Zoology, Harvard University. The illustrations are by Mr. Richard Lang and were made possible by a grant from the Gulf Oil Corporation. All measurements are in millimeters.

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[1] Gulf Curator of Vertebrate Fossils, Carnegie Museum, Pittsburgh, Penn.

The following abbreviations are used throughout:

F.S.G.S., Florida State Geological Survey; K.U., University of Kansas, Museum of Natural History; M.C.Z., Museum of Comparative Zoology, Harvard University; U.F., University of Florida; a-p, anteroposterior; tr., transverse.

Order RODENTIA

Family PARAMYIDAE

Subfamily PROSCIURINAE

PROSCIURUS? sp.

Figure 1

Material. F.S.G.S. V-5952, a right M^3.

Description. Although the enamel on this tooth has been damaged, the crown pattern is still clear. The tooth is broadly triangular with the protocone filling the lingual margin. The anterior cingulum is broad and rises to a well-developed parastyle. The protoloph is complete with some indication of a protoconule but the presence of this cusp cannot be determined with certainty. There are indications of several ridges running down the anterior and posterior slopes of the protoloph. A well-defined metaloph is present passing obliquely from the protocone to the postero-buccal corner. The metaloph is lower than the protoloph and is partially constricted on both sides of the large metaconule. A short mesoloph lies between the protoloph and metaloph and passes internally to fuse with the metaloph at the base of the metaconule.

Discussion. This specimen is referred to the Prosciurinae because of the complex ridging developed behind the protoloph. The development of a metaloph and/or a mesoloph on M^3 is seen in some members of the Sciuridae particularly in *Cynomys* and to a lesser degree in some species of the subgenus *Citellus*. However, in both these cases this pattern appears to be a late Cenozoic development, no Tertiary North American sciurids being known which show this pattern. The presence on M^3 of a metaloph, well-developed metaconule, and mesoloph are common features of *Prosciurus,* however, and tend to ally the Florida specimen with that genus. *Prosciurus* is a rather common element of many Oligocene faunas in western North America but it had not been reported from the Miocene until recently. The genus

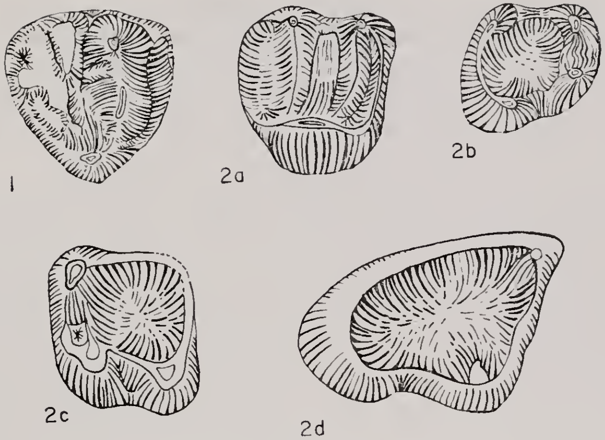

FIG. 1. *Prosciurus?* sp. F.S.G.S. V-5952, RM^3, x10. Figure 2. *Tamias* sp. 2a. F.S.G.S. V-6021, LM$^{1 \text{ or } 2}$, x15. 2b. F.S.G.S. V-6020, RP$_4$, x15. 2c. U.F. No. 3873, LM$_1$, x15. 2d. F.S.G.S. V-5951, RM$_3$, x20.

is now known from the basal Miocene of South Dakota (Macdonald, pers. com.), and also from the early Miocene in Wyoming (Black, 1960). It is somewhat surprising, therefore, to find this genus in the later part of the early Miocene of Florida. The presence of *Prosciurus* in Florida at a later date than it is known to occur in the Great Plains lends support to the suggestion made by Wood (1947) in regard to the mylagaulid tooth, that Florida may have been isolated from the main center of evolution of these families and acted as a refugium for the more primitive forms.

Measurements

	a-p	tr.
RM^3	2.85	2.85

Family SCIURIDAE

TAMIAS sp.

Figure 2

Material. U.F. No. 3873, partial mandible with LM$_1$; F.S.G.S. V-5951, RM$_3$; V-6021, LM$^{1 \text{ or } 2}$; V-6020, RP$_4$.

Description. The upper molar is unworn and shows a high, somewhat compressed protocone. The anterior cingulum is broad and joins the protocone at its base, well below the level of the protoloph. Buccally, the anterior cingulum bears a small parastyle. The protoloph and metaloph are low and complete, merging with the protocone about halfway down its buccal slope. A small metaconule is present in the metaloph. The posterior cingulum is narrow but expands slightly where it joins the protocone. A small mesostyle is present at the base of the paracone.

The diastema of the mandible is long in relation to overall size and the diastemal depression shallow. P_4 has a trapezoidal shape with the protoconid and metaconid separated by a narrow notch. There is no indication of an anterior cingulum or anteroconid. The posterolophid is somewhat elevated and passes in a gentle curve from the hypoconid to the entoconid with the entoconid submerged within the posterolophid. There is no mesostylid present. The ectolophid is low and weak and bears no trace of a mesoconid. M_1 is square in outline with an angular entoconid corner. A small anteroconid is present on the anterior cingulum. The metalophid is complete and the small trigonid basin completely enclosed. The posterolophid is low. The entoconid is submerged in the posterolophid. The ectolophid is low and weak and the buccal valley is shallow. No mesostylid is present. The M_3 is extremely elongate, more so than in any other sciurid and it is quite possible that this is not a chipmunk M_3 and should not be associated with the other material described here. However, the tooth bears no resemblance to that of the prosciurines and on the basis of size alone it is here tentatively referred to *Tamias*. Most of the enamel on the tooth is missing and the crown pattern obliterated.

Discussion. These specimens, with the possible exception of the M_3, are scarcely separable from the isolated chipmunk teeth known from the Miocene of the Great Plains. Although they are somewhat smaller, the compressed high protocone, partially elevated posterolophid, and entoconid submerged within the posterolophid are characters which agree closely with those of the South Dakota and Wyoming Miocene chipmunks.

Measurements

	a-p	tr.
$LM^{1 \text{ or } 2}$	1.3	1.5
RP_4	1.1	1.0-1.2
LM_1	1.2	1.2-1.2
RM_3	1.8	1.4-1.3

Family CRICETIDAE

Subfamily CRICETINAE

Tribe Hesperomyini

Genus and species indet.

Figure 3

Material. F.S.G.S. V-6019, RM^1; U.F. No. 3940, RM$_1$.

Description. The first upper molar is mesodont with prominent lophs. About one-third of the anterior portion of the tooth is missing; however, the overall tooth outline can be reconstructed (Figure 3a) with some degree of accuracy. This anterior section was constricted transversely as is indicated by the narrowing of the tooth just posterior to the break. The presence or absence of a shallow reentrant between the protocone and anteroloph cannot be ascertained in this specimen. The rest of the tooth shows three transverse, obliquely oriented lophs and two transverse valleys both extending almost the complete width of the occlusal surface. The anterior loph passes anterobuccally from the protocone and probably connected the protocone and the anteroloph. The second loph parallels the first and connects the hypocone and paracone while the third loph passes from the posterior cingulum to the metacone. The anterior valley is composed of two segments and with further wear would be interrupted at the center of the tooth resulting in the formation of a deep lingual valley between the paracone and anteroloph. The latter valley would rapidly disappear with further wear. The second transverse valley arises between the paracone and metacone and passes internally to the midline of the tooth where it bends posteriorly and ends near the posterior border at the base of the hypocone. The occlusal surface of M^1 is terraced with the buccal cusps elevated and the lingual cusps flattened.

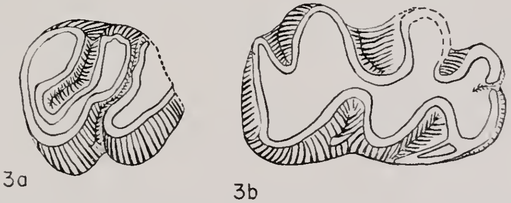

FIG. 3. Hesperomyines, genus and species indet. 3a. F.S.G.S. V-6019, RM^1, x20. 3b. U.F. No. 3940, RM$_1$, x20.

The enamel is partially chipped and the metaconid is broken on M_1. The tooth is somewhat lower crowned and the cusps more prominent than in the upper molar. The anterolophid is weakly bilobed and connects with the metalophid along the midline of the tooth. The four major cusps are slightly offset with the metaconid and entoconid lying forward of the protoconid and hypoconid. The anterior protoconid arm passes obliquely across the tooth to the metaconid. There is also a broad connection with the entoconid through the posterior protoconid arm. The anterior hypoconid arm parallels that of the protoconid passing anteriorly to the entoconid. The anterior reentrant between the anterolophid and protoconid is partially closed by a crest passing from the anterolophid towards the base of the protoconid. The posterior buccal and lingual reentrants are of nearly the same size and depth and both turn anteriorly as they pass toward the midline of the tooth. The anterior lingual reentrant is shallow and narrow and is directed posteriorly. The four major cusps are approximately equal in size, with the entoconid and probably the metaconid elevated above the protoconid and hypoconid. The posterior cingulum is short and narrows to a thin ledge behind the entoconid.

Discussion. These teeth clearly demonstrate the presence of hesperomyine cricetids in the Thomas Farm fauna. The absence of a mesoloph and mesolophid on the two molars might be taken to indicate a relationship with the phyllotine or sigmodont hesperomyines rather than with the *Peromyscus-Oryzomys* group (Hershkovitz, 1955). However, Hooper (1957) has shown that, in *Peromyscus* at least, these two structures are variable both inter- and intraspecifically. As regards the two Florida molars one, M^1, does seem to resemble those of the sigmodont cricetids in most characters while the other, M_1, appears to be that of a *Peromyscus*-like form.

The first upper molar is higher crowned than M_1 and the lophs are more completely developed. In this respect the tooth resembles M^1 of *Sigmodon.* The confluence of the anterior buccal and lingual reentrants, lying between the paracone and anteroloph and the protocone and hypocone respectively, is duplicated in the unworn first upper molars of *Sigmodon* but I have not seen this condition in any other hesperomyine. In *Sigmodon* the anterior reentrant between the protocone and anteroloph is deep and the anterior margin of the protoloph is directed across the crown almost at a right angle to the long axis of the tooth. In

F.S.G.S. V-6019, however, what is preserved of the lingual margin of the protoloph is directed antero-buccally. Thus, if an anterior reentrant were present, it would not pass directly across the tooth as it does in *Sigmodon*. The terraced crown of the Florida specimen is not found in *Sigmodon* but is seen in the more bunodont and brachyodont dentition of *Hesperomys*. However, in other details of crown pattern M^1 bears little resemblance to that of *Hesperomys*, and its closest affinities seem to be with *Sigmodon*.

The first lower molar is more bunodont and somewhat lower crowned than the upper molar and in this respect more closely resembles that of *Peromyscus* and *Hesperomys* than that of *Sigmodon*. The bilobed anteroloph seen in U.F. No. 3940 is present to a slight degree in *Hesperomys* and is well developed in *Perymyscus* but absent in *Sigmodon*. The principal cusps do not appear to be as prominent as are those of *Peromyscus, Oryzomys,* and *Onychomys,* although this may be partially due to the extreme state of wear, nor are they as completely incorporated into transverse lophs as they are in *Sigmodon* or *Phyllotis*. The terraced occlusal surface seen on the M^1 from Thomas Farm is not as pronounced on the lower molar but is present to a slight degree. The shallow depth and the direction of the reentrants correspond to the condition in *Peromyscus, Hesperomys,* and to a less extent in *Reithrodontomys* but differ from that in *Sigmodon* and *Phyllotis*. The shallow reentrant between the posterior cingulum and the entoconid corresponds to the condition in *Peromyscus* and *Oryzomys*. In general, the lower molar resembles that of *Peromyscus* and possibly *Hesperomys* more closely than any other hesperomyine.

Both of these teeth indicate the presence of hesperomyine rodents at Thomas Farm. One of the teeth is more highly specialized than any others yet reported from the Miocene or early Pliocene. *Peromyscus* has been reported from the late Miocene (Hall, 1930, Hoffmeister, 1959) but, to the best of my knowledge, no member of the Hesperomyini has previously been reported from an earlier horizon. One of the Florida species, represented by the M^1, appears to be closely related to cotton rats which today are distributed through the southern portion of North America and the grass and scrubland area of northern South America (Hershkovitz, 1955). The other Florida species would appear to be most closely allied to the more generalized hesperomyines of the genus *Peromyscus*.

Measurements

	a-p	tr.
M^1	1.4 approx.	1.3
M_1	2.1	0.8-1.1-1.2

Family HETEROMYIDAE

PROHETEROMYS FLORIDANUS Wood

Figure 4

Proheteromys floridanus Wood, 1932: 45; 1935:166; 1947:489.

Type. F.S.G.S. V-5329, jaw fragment with LP_4-M_1.

Hypodigm. P^4-F.S.G.S. V-6012, V-6015, V-6026, V-6031, V-6034, M.C.Z. Nos. 8480, 8482, U.F. Nos. 3872, 3941, 4061, 4062, 4075, 4076; $M^{1 \text{ or } 2}$-F.S.G.S. V-5330, V-5331, V-6000, V-6002, V-6003, V-6004, V-6005, V-6016, M.C.Z. Nos. 8452, 8454, 8458, 8466, 8467, 8468, 8469, 8470, 8471, 8472, 8474, 8475, 8483, U.F. Nos. 3867, 4057, 4058, 4060, 4064, 4074, 4079, M.C.Z. Nos. 7134, 7139; M^3-F.S.G.S. V-6001, V-6017, V-6028, V-6029, U.F. Nos. 4067, 4078, 4080; RdP_4-M.C.Z. No. 8450; LdP_4-M.C.Z. No. 8478; P_4-F.S.G.S. V-6014, V-6027, M.C.Z. Nos. 7137, 8450, 8457, 8470, 8478, 8485, U.F. Nos. 3871, 4077; $M_{1 \text{ or } 2}$ F.S.G.S. V-5334, V-6006, V-6007, V-6008, V-6009, V-6010, V-6011, V-6013, V-6035, M.C.Z. Nos. 7136, 8449, 8451, 8453, 8456, 8459, 8462, 8463, 8464, 8473, 8477, 8479, 8481, U.F. Nos. 4059, 4063, 4065, 4066, 4068, 4069; M_3-F.S.G.S. V-6030, V-6032, V-6033, M.C.Z. Nos. 8448, 8455, 8460, 8461, 8465, 8484, U.F. Nos. 3869, 4070, 4071.

Emended diagnosis. Smaller than *Proheteromys sulculus, P. matthewi,* and *P. thorpei;* cheek teeth bilophodont with cusps not as prominent as in *Mookomys;* P^4 with single cusp on protoloph, three cusps on metaloph; central valley in $M^{1 \text{ or } 2}$ closed lingually by fusion of styles; P_4 generally with low median crest connecting metalophid and hypolophid but crest not as prominent as in perognathines; P_4 without anteroconid but generally with accessory hypoconulids.

Description. The fourth upper premolars all show a single cusp on the protoloph, the protoconid, and a three cusped metaloph, composed of the metacone, hypocone, and entostyle. The protocone lies well below the level of the metacone and hypocone in all specimens and is only weakly connected to the metaloph

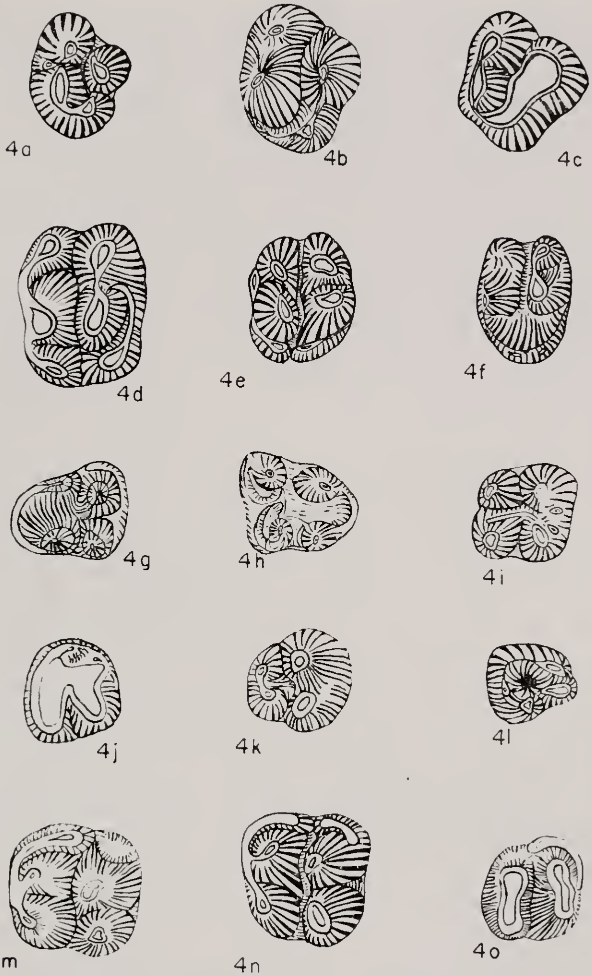

Fig. 4. *Proheteromys floridanus*, all approximately x20. 4a. F.S.G.S. V-6031, RP^4. 4b. F.S.G.S. V-6015, RP^4. 4c. F.S.G.S. V-6026, RP^4. 4d. F.S.G.S. V-6016, $RM^{1\text{ or }2}$. 4e. M.C.Z. No. 8470, $LM^{1\text{ or }2}$. 4f. F.S.G.S. V-6028, LM^3. 4g. M.C.Z. No. 8450, RdP_4. 4h. M.C.Z. No. 8478, LdP_4. 4i. F.S.G.S. V-6014, RP_4. 4j. U.F. No. 3871, LP_4. 4k. M.C.Z. No. 7137, RP_4. 4l. M.C.Z. No. 8485, LP_4. 4m. M.C.Z. No. 8481, $RM_{1\text{ or }2}$. 4n. M.C.Z. No. 8473, $RM_{1\text{ or }2}$. 4o. M.C.Z. No. 8484, LM_3.

through the entostyle. Buccally, no protocone-metaloph connection would appear until an extreme stage of wear had been reached at which time all traces of cusp pattern would be obliterated. There is some variation in the size of the entostyle and in the connecting arms passing from it to the protocone and hypocone. In an unworn condition the arms to both the protocone and the metacone are extremely thin and would remain so even after considerable wear. In M.C.Z. No. 8482, however, there is a thickening of the arm from the entostyle to the hypocone which gives the appearance of the addition of a fourth cusp to the metaloph. In one specimen, M.C.Z. No. 8480, there is a small cusp lying well down on the anterior face of the metaconid.

The numerous additional first and second upper molars add little to the description already given by Wood (1932, 1935). There is very little variation in this sample with only minor differences, such as a slight variation in the height of the styles, apparent. The central valley does not pass completely across the teeth but is closed lingually by the fusion of the styles. Both anterior and posterior cingula are present. M^3 is reduced with the major cusps fused together to form a ring around the central basin. The central cusp of the protoloph stands slightly higher than the other cusps and is the last cusp to be completely incorporated in the ring.

There are two dP_4s in the collection. Each has four principal needle-like cusps corresponding to the four cusps of the permanent premolar. The anterior border of the tooth is marked by a high, thin ridge which arcs from the mesoconid to the protoconid. The posterior border is similarly enclosed by the elevated posterior cingulum which passes from the hypoconid completely across the back of the tooth to the postero-lingual corner of the entoconid. On M.C.Z. No. 8478 a short crest runs forward from the mid-point of the posterior cingulum between the hypoconid and entoconid and merges into the anterior base of the hypoconid. On this tooth there are also present short, low crests running from the protoconid to the base of the entoconid and from there to the base of the hypoconid. These crests are entirely absent on M.C.Z. No. 8450.

The fourth lower premolars show a considerable amount of variation and the new material necessitates a number of additions to the original description (Wood, 1932, 1935). The only P_4 previously described is extremely worn and as Wood has pointed out the crown pattern is obscured. In this tooth the metalophid and hypolophid surround a shallow central basin and there is no indication of a median arm passing from the metalophid to the hypolophid. However, the central basin is not as deep as are the buccal and lingual valleys which separate the two lophids. Hence, with further wear, the metalophid and hypolophid would fuse first in the midline of the tooth thus presenting a broad X-pattern which is characteristic of later perognathines. However, the perognathine premolars are higher crowned than those of *Proheteromys floridanus* and wear to the X-pattern much earlier in the life of the tooth. The premolars in the present collection show (with one exception) a low to prominent central crest passing from the metalophid to the hypolophid. The one tooth which does not show this pattern, M.C.Z. No. 8485, has a deep central pit and a very high crest along the buccal margin which fuses the mesoconid and hypoconid. The valley between the protoconid and entoconid in this tooth is deep and no accessory cusps are present. In all the premolars, an anteroconid is absent; and there is no indication of a hypostylid. Several of the premolars have two small cusps set between the hypoconid and entoconid along the posterior margins of the teeth. In all the premolars the mesoconid and hypoconid are set closer together than are the protoconid and entoconid. One premolar, U.F. No. 3871, is worn and shows clearly the broad median connection of the lophids and the initial fusion of the mesoconid and hypoconid leaving a small, shallow pit between the buccal margin of the tooth and the median crest.

M_{1-2} are narrower in relation to their length than are M^{1-2}. The metalophid on these teeth is considerably higher than the hypolophid with the protoconid and metaconid submerged within the metalophid to a greater degree than the hypoconid and entoconid are within the hypolophid. The anterior cingulum passes from the antero-internal corner of the metaconid around the protoconid and ends in a small but distinct protostylid. The median valley is deep and completely separates the two lophids. The hypoconid and entoconid are of approximately the same size while the hypostylid is much smaller. M_3 agrees in occlusal pattern with M_{1-2} except in the development of the stylar cusps. The protostylid is reduced and the entostylid absent.

An analysis of the measurements of the teeth here assigned to *P. floridanus* is given below. The variation seen is slightly more than one might expect to find for a sample taken from a single mammalian population, but not as high as one would expect if the sample were a mixture of two species.

Statistical data on cheek teeth of *P. floridanus*

		N	O.R.	M	S	V
P^4	anteroposterior	10	.7-1.0	.81±.016	.05	6.7±1.48
	width metaloph	10	.9-1.1	1.03±.016	.05	4.9±1.09
$M^{1 \text{ or } 2}$	anteroposterior	20	.7-.9	.81±.011	.05	6.2±.98
	width metaloph	20	.9-1.1	1.04±.011	.05	5.0±.79
M^3	anteroposterior	6	.6-.7	.71±.016	.04	5.6±1.60
	width metaloph	6	.7-1.0	.90±.033	.08	8.8±2.25
dP_4	anteroposterior	2		.77		
	width hypolophid	2		.70		
P_4	anteroposterior	7	.6-.7	.67±.019	.05	7.5±2.00
	width hypolophid	7	.6-.7	.70±.016	.04	5.7±1.52
$M_{1 \text{ or } 2}$	anteroposterior	23	.7-1.0	.83±.010	.05	6.0±.88
	width metalophid	23	.8-1.0	.91±.010	.05	5.7±.87
M_3	anteroposterior	10	.6-.8	.73±.013	.04	5.5±1.22
	width metalophid	10	.7-1.0	.79±.016	.05	6.3±1.40

Discussion. As Galbreath (1953, p. 98) and Wilson (1960, p. 78) have pointed out, it has become increasingly difficult to fit the early Miocene species of heteromyids into the present definitions of the known genera, *Heliscomys, Mookomys,* and *Proheteromys.* As more material becomes known, there is an increasing overlap in size and occlusal pattern between species assigned to these three genera.

Galbreath (1953, pp. 63-65) has clearly demonstrated a considerable range of structural variation in the dentition of *Heliscomys vetus* from the Orellan of Colorado; and, if the Thomas Farm sample of *P. floridanus* described here is truly representative of a single species, this range of variation, particularly in the premolars, would appear to be true for the genus *Proheteromys.* Wilson (1960, pp. 75-79) found the same variation in specimens from the Martin Canyon Quarry A local fauna. Aside from several larger heteromyid specimens which he believes represent a species close to *P. magnus,* he discusses three smaller populations which he refers to *Proheteromys, Florentiamys?,* and *Mookomys.* In his discussion, he has assigned the more extreme variants in his sample to *Florentiamys?* and *Mookomys,* and the bulk of the material to *P. sulculus.* As a result, the structural variation found in *P. sulculus* is rather small compared to that in *P. floridanus.* However, if the five specimens referred to *Mookomys* sp. cf. *M. formicorum* and the single upper molar referred to *Florentiamys?* sp. were considered as variants of *P. sulculus* (a possibility which Wilson acknowledges in both cases), the variation in the Colorado species and in *P. floridanus* would be of a similar degree and would parallel the variation seen in *Heliscomys vetus*. If these early Miocene species are as variable as the samples of *P. floridanus* and *P. sulculus* may indicate, then, it would be almost impossible to distinguish species of *Proheteromys* from those of *Mookomys*.

The other species of *Proheteromys*, *P. parvus* and *P. matthewi* (excepting *P. magnus* which is clearly distinct), are known from such fragmentary material that their relationship to *P. floridanus* and *P. sulculus* cannot be determined.

P. floridanus closely resembles *P. sulculus* but differs from the Colorado species in being somewhat smaller and in possessing the median arm on P_4. The new material shows that *P. floridanus* is not as heteromyine in structure as Wood (1932, 1935) believed. This fact would support Wilson's belief (1960, p. 78) that the Heteromyinae and Perognathinae are not separable in the early Miocene and that *Proheteromys* in a broad sense could be structurally ancestral to both subfamilies.

PROHETEROMYS MAGNUS Wood

Figure 5

Proheteromys magnus Wood 1932, p. 46; 1935, p. 168; 1947, p. 490.

Type. F.S.G.S. V-5332, LP^4.

Hypodigm. Type and LdP^4-F.S.G.S. V-5336; RdP^4-F.S.G.S. V-6018; RP^4-M.C.Z. No. 7138; $LM^{1 or 2}$-F.S.G.S. V-6025; LP_4-F.S.G.S. V-6024; $RM_{1 or 2}$-F.S.G.S. V-5333, V-6022; $LM_{1 or 2}$-F.S.G.S. V-6023, U.F. No. 3868, M.C.Z. No. 3694.

Emended diagnosis. Largest species of genus; P^4 with single cusp on protoloph, three cusps on metaloph and a cusp-like expansion of crest from entostyle to hypocone; central valley completely bisects the upper molars; P_4 with median crest; anteroconid present on P_4; stylids small on lower molars; posterior cingulum short but prominent on lower molars.

Description. There is one deciduous upper premolar, F.S.G.S. V-6018, in the present collection which agrees in all details with one previously described for this species (Wood, 1935). There is one cusp in the anterior row and there are three in the posterior row with the central cusp being most prominent. The deciduous tooth is slightly smaller than the permanent premolar but it is probably too large to be the dP^4 of *Proheteromys floridanus*. Wilson (1960, p. 80) has described the dP^4 of a species from the Pawnee Creek formation which he believes is related to *P. magnus.* This tooth, KU10237, displays three rows of cusps and is somewhat larger than the permanent premolar. He suggests that the tooth considered a dP^4 of *P. magnus* by Wood (1935) is too small to be the deciduous premolar of that species. It is quite true that deciduous premolars in heteromyids are generally as large as or larger than the permanent premolars. However, F.S.G.S. V-5336 and V-6018 are probably too large to be the deciduous premolars of *P. floridanus* and there is no other species known from the Florida Miocene with which they could be associated.

Fig. 5. *Proheteromys magnus,* all approximately x20. 5a. M.C.Z. No. 7138, RP^4. 5b. F.S.G.S. V-6025, LM$^{1 \text{ or } 2}$. 5c. F.S.G.S. V-6024, LP$_4$. 5d. F.S.G.S. V-6022, RM$_{1 \text{ or } 2}$. 5e. U.F. No. 3868, LM$_{1 \text{ or } 2}$.

The anteroloph of the permanent premolar is composed of one cusp and the posterior loph of three large cusps and an expanded crest between the entostyle and the hypocone. I agree with Wilson's (1960, p. 79) interpretation of these cusps and can state that the P^4 of *P. magnus* is not five cusped as Wood (1932, 1935) thought. The entostyle has moved forward and lies closer to the protocone than the hypocone but it is more strongly connected to the latter than to the protocone. The crest from the entostyle to the hypocone is expanded and somewhat cusplike. There is no ridge from the protocone to the base of the crown as there is in *Proheteromys* sp. cf. *P. magnus* from Colorado.

Both the anterior and posterior cingula are extremely narrow on the first and second upper molars, much more so than in *P. floridanus*. These teeth also differ from those in *P. floridanus* in that the central valleys pass completely across the crowns and are open both buccally and lingually. The cingular crests are short and narrow and converge toward the central cusps on both the anterior and posterior lophs. The central cusp of each loph is large while the buccal and lingual cusps are smaller and anteroposteriorly compressed.

There is one P_4 in the present collection but the enamel is severely damaged and missing from the tips of all the cusps and along the midline of the tooth. An attempt has been made in Figure 5c to reconstruct the probable crown pattern but the shape and position of the median crest is somewhat doubtful. Four principal cusps were certainly present together with a small anteroconid and a low, narrow ridge running from the base of the entoconid backward to the posterior edge of the tooth. The buccal and lingual valleys are both deep and buccally a high enamel wall is preserved connecting the hypoconid and mesoconid towards the midline of the crown. This enamel wall is missing at the internal end of the lingual valley but was probably present before the tooth was damaged. It would appear therefore that a broad median crest connected the anterior and posterior lophids as in *Perognathus* and *Cupidinimus*. This median lophid was probably considerably stronger than that seen in *P. floridanus*.

The additional lower first or second molars add little to the descriptions already given by Wood. The anterior and posterior lophids are completely separated for most of the crown height by a deep central valley. On both lophids the stylids are very small. There is a prominent but short posterior cingulum between the hypoconid and entoconid which fuses with the bases of these cusps and cuts off a small basin between them.

Measurements

	a-p	tr.
dP^4	1.6	1.4
P^4	1.8	2.1
$M^{1 \text{ or } 2}$	1.5	1.8
P_4	1.4	1.4
$M_{1 \text{ or } 2}$	1.6, 1.6, 1.4	1.6, 1.6, 1.5

Discussion. The additional material of both *P. magnus* and *P. floridanus* makes it clear that these two species, and probably the genus as presently defined, cannot be assigned to any of the three living subfamilies with any degree of accuracy. Structurally they are somewhat more advanced than the species of *Heliscomys* but there are no observable trends leading towards the specializations seen in the Heteromyinae, Perognathinae, or Dipodomyinae. This lack of specialization is perhaps more apparent in *P. floridanus* than in *P. magnus* but the latter is still inadequately known and the range of structural variation in the premolars of *P. magnus* may prove to be as great as that in *P. floridanus.* It would appear that *P. magnus* is nothing more than a large heteromyid with essentially the same molar structure as in *P. floridanus.*

Wilson (1960, p. 80) has suggested an entoptychine relationship for *P.* sp. cf. *P. magnus* and hence has implied the same possible relationship for the Florida species. The entoptychine genera *Entoptychus, Gregorymys* and *Grangerimus* are first much higher crowned than is *P. magnus* and secondly both the upper and lower premolars are much more complex than are those of *P. magnus.* The other entoptychine genus, *Pleurolicus,* has high crowned cheek teeth, but the premolars are not as complex as in the other genera of the subfamily and approach more closely the condition seen in *P. magnus* although there is still a considerable difference between the two. The species of *Pleurolicus* are for the most part older than *P. magnus.* A common Oligocene ancestry for *Pleurolicus* and *Proheteromys magnus* is possible. However, in view of the great structural similarity between *P. magnus* and *P. floridanus,* I would hesitate in placing *P. magnus* in the Entoptychinae on the basis of size alone.

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