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BATS OF THE GENUS STURNIRA IN THE LESSER ANTILLES

J. KNOX JONES, JR., AND CARLETON J. PHILLIPS

Yellow-shouldered bats of the Neotropical genus *Sturnira* first were reported from the Lesser Antilles by Glover Allen (1911:223) based on two specimens taken on the island of Dominica in 1906 by A. E. Verrill. Referred by Allen to *Sturnira lilium* at a time when that species was thought to be monotypic, these specimens were variously ignored or associated with a continental subspecies of *lilium* by catalogers (see Miller, 1924; Miller and Kellogg, 1955; Hall and Kelson, 1959) in the more than half a century that elapsed between Allen's paper and the time when additional material from the Lesser Antilles was reported.

In 1966, de la Torre (1966:271) named *Sturnira angeli* based on eight specimens (including the two collected by Verrill) from Dominica and one from Martinique, and de la Torre and Schwartz (1966:299, 301) named *Sturnira thomasi* and *Sturnira paulsoni* based on single specimens from Guadeloupe and St. Vincent, respectively. More recently, Koopman (1968:4) recorded additional material from Martinique and Dominica, Jones and Phillips (1970:135) mentioned series obtained by them in 1966 and 1967 on Dominica, St. Vincent, and St. Lucia, and Genoways and Jones (1975:924) reported four specimens of *thomasi* taken on Guadeloupe in 1974.

The material that has been accumulated in the last decade or so as a result of zoological exploration in the Antillean region brings to more than 75 the known specimens of *Sturnira* from that area, and allows for a more complete assessment of variation in the several insular populations than could have been undertaken previously. Currently, then, extant populations of *Sturnira* are known from Guadeloupe, Dominica, Martinique, St. Lucia, and St. Vincent in the Lesser Antilles. The genus has not been recorded from Grenada, but does, of course, occur on Trinidad and the adjacent South American mainland. Elsewhere in the Antillean region it has been recorded only from Jamaica, whence Dobson (1878:540) listed two specimens that were collected more than a century ago. Koopman and Williams (1951: 23) suggested that these might represent an accidental occurrence. The possibility exists, too, that the data associated with these two specimens are incorrect and that they actually originated from some place in tropical America other than Jamaica. In any event, it seems almost certain that *Sturnira* does not now occur on that island.

As a result of our study of Lesser Antillean populations, we tentatively retain *S. thomasi* of Guadeloupe as a distinct species, but relegate all others to subspecific status under *S. lilium*. Two new subspecies are described, one from Martinique and the other from St. Lucia.

In the accounts beyond, all measurements are given in millimeters, and weights are reported in grams. Measurements of embryos are of crown-rump length. We are grateful to Karl F. Koopman of the American Museum of Natural History (AMNH) for the opportunity to examine specimens housed in that institution. Specimens in the collection of the Museum of Natural History at The University of Kansas (KU) were collected under the sponsorship of the Bredin-Archbold-Smithsonian Biological Survey of Dominica and the Kansas University Endowment Association; those housed in The Museum of Texas Tech University (TTU) were obtained under the aegis of a grant (GB-41105) from the National Science Foundation. Stephen L. Williams and Thomas Swearingen assisted with preparation of the illustrations.

Sturnira lilium

Common Yellow-shouldered Bat

Sturnira angeli de la Torre and Sturnira paulsoni de la Torre and Schwartz were described in different publications issued on the same day. Both were compared with *lilium* but, unfortunately, were not compared with each other. S. angeli was alleged to differ from *lilium* "in being smaller, in having a completely different skull shape, and in having low, rudimentary metaconids and entoconids." S. paulsoni was described as morphologically similar to *lilium*, differing from it in certain details of molar construction. We find, with more abundant material available for study, that both cranial and dental morphology are variable in Antillean populations here assigned to *lilium*, and that, in any event, such differences as can be discerned among them, and TABLE 1.—Comparative measurements (averages and extremes) of adults of four insular populations of S. lilium in the Lesser Antilles. Superscript numbers indicate fewer specimens measured than indicated in column headings.



FIG 1.—Dorsal views of skulls of *Sturnira lilium*: upper left *S. l. parvidens* from 1 km. N, 2 1/2 km. W Villa Somoza, Nicaragua (KU 110976, ?); upper right, *S. l. lilium* from Tataracual, 31 km. E Cumana, Venezuela (KU 118571, ?); lower left, *S. l. lilium* from Guayaguayare, Trinidad (KU 117413, ?); lower right, *S. l. paulsoni* from Clifton Hill, St. Vincent, Lesser Antilles (KU 110144, ?), greatest length of skull, 22.7. Illustration by T. Swearingen.

between them and adjacent mainland populations of *lilium*, are relatively minor in nature.

Except for rather modest differences in some dimensions (Table 1), we cannot separate cranially the insular populations from each other, nor do they differ markedly from mainland samples when geographic variation from throughout the range of *lilium* is taken into account (see Fig. 1). In comparison with *S. l. lilium* of Trinidad, however, all tend to have a somewhat longer and lower rostrum. Some trends in variation among the Antillean populations are discussed below.

Maxillary Dentition

The upper molars, especially the first and second, are geographically variable in *Sturnira lilium* in the Lesser Antilles. In specimens from Dominica and Martinique, the first upper molars are characterized by having a small labial shelf anteriorly and a prominent metacone, the latter resulting in a posterolabial extension of the tooth (Fig. 2). The metacone is most prominent in the population on Martinique. In specimens from St. Lucia, the anterior labial shelf is better developed than in individuals from Martinique and Dominica. The extreme in development of the anterior labial shelf of the first upper molar is seen in specimens from St. Vincent (Fig. 2) wherein the shelf extends beyond the labial edge of the metacone. The first upper molar does not vary consistently in size from island to island.

In the second upper molar, the anterior labial shelf is best developed in specimens from Martinique (Fig. 2). In size, the second upper molar averages larger in bats from Martinique and St. Lucia than it does in those from Dominica and St. Vincent. The third upper molar varies geographically in size, averaging smallest in bats from Dominica and largest in bats from St. Lucia.

Geographic trends in the upper dentition, as outlined above, seem to be constant enough to be useful in taxonomic considerations. For example, of 24 specimens from Dominica, 15 clearly fit the pattern for that island as shown in Fig. 2, whereas eight Dominican specimens and one of eight examined from Martinique were considered by us as intermediate between the typical morphological conditions for those populations. We found no specimens that could be considered structurally intermediate between Martinique and St. Lucia samples as depicted in Fig. 2. Two of eight specimens from St. Lucia and three of six from St. Vincent are intermediate between the examples illustrated for those islands in Fig. 2.

Mandibular Dentition

The first and third lower molars are the most variable of the mandibular teeth in Antillean populations of *S. lilium*. Specimens can be placed into two groups on the basis of morphological features of the first lower molar. In those from Dominica and Martinique, the paraconid is located at least as near the center line of the tooth as it is the 6



FIG. 2.—Graphic illustrations of right upper and lower molar toothrows of *S. lilium* from Lesser Antilles and Trinidad. Illustration by C. J. Phillips.

lingual edge (Fig. 2); in fact, in some individuals the paraconid actually is in the center of the anterior end of the tooth. In all specimens from St. Lucia and St. Vincent examined by us, however, the paraconid is located on the lingual edge of the first molar with the consequence that the paraconid, metaconid, and entoconid nearly form a linear lingual sequence. Furthermore, in specimens from St. Lucia and St. Vincent the entoconid is a well-defined and elongate cone, whereas in individuals from Dominica and Martinique the entoconid of the first molar is low crowned and generally not much more than a well-defined ridge. In *lilium* from Trinidad, the paraconid is located near the anterior midline of the tooth and the entoconid is relatively low and long, as in specimens from Dominica and Martinique.

The second lower molar does not vary geographically so much as does the first, and individual specimens cannot be identified on the basis of morphological features of this tooth. In general, however, the metaconid is slightly longer in individuals from St. Lucia and St. Vincent than in specimens from Dominica and Martinique.

The third lower molar varies both individually and geographically. On the average, this tooth is smallest in specimens from Dominica and Martinique and largest in specimens from the two southern islands. Morphologically and dimensionally, the third molar varies considerably on an individual level. Furthermore, it occasionally is lacking in specimens from the northern islands. In 24 specimens from Dominica, one lacked the tooth on both sides and another lacked it on the left side only. Out of eight specimens from Martinique, two lacked a third molar on one side but not the other.

The third lower molar is reduced least among our samples in specimens from St. Lucia. Indeed, in one remarkable individual (KU 110147) it is rectangular, as in the first two molars, and retains all of the cusps (paraconid, metaconid, entoconid, protoconid) found on those teeth. In the other specimens from St. Lucia, however, the crown is reduced and lacks a paraconid.

Size

Antillean *S. lilium* fall generally within the size range, both externally and cranially, of other populations of the species as known to us from material from both Middle and South America. There is, however, some variation (Table 1) between insular samples, although no clinal geographic trends are apparent. For example, bats representing the population on St. Vincent tend to be the largest cranially among specimens examined from the islands, whereas individuals from Martinique are proportionately broader across the zygomatic arches and have a longer maxillary toothrow than do those in other samples.

Externally, specimens from Dominica average slightly more in length of forearm than do others, but we note no other differences in external proportions. Ranges in other external measurements of our Dominican (largest) sample are typical for the insular populations: head and body, 64 to 72; hind foot, 15 to 17; ear, 16 to 18.

Color

Antillean S. lilium average somewhat darker than do those that we have examined from Trinidad and adjacent Venezuela and fall generally into two groups, bats from Dominica and Martinique being darker, especially dorsally, than those from St. Lucia and St. Vincent. The former tend to be dark brownish or dark brownish buff rather than grayish brown or yellowish brown. The differences among pop-

readings (ranges in paren-	•
Mean	
-E 2.—Color reflectance readings for specimens of Sturnira lilium from four Antillean islands. N	theses) are given. See text for discussion.
TAI	

	Green	9.0 (6.0-11.0)	6.8 (5.0-10.0)	10.5 (9.0-13.5)	11.1 (10.0-13.0)	
Venter	Blue	7.9 (6.5-10.0)	6.4 (5.0-9.0)	8.9 (7.0-11.5)	9.7 (9.0-10.0)	
	Red	17.4 (15.0-21.0)	15.8 (11.0-19.0)	18.9 (15.0-26.0)	20.7 (19.5-21.5)	
	Green	<i>Dominica</i> 4.6 (3.5-6.5)	Martinique 4.1 (2.5-5.5)	<i>St. Lucia</i> 7.0 (6.0-9.0)	<i>St. Vincent</i> 6.6 (6.0-7.0)	
Dorsum	Blue	4.6 (4.0-5.5)	3.8 (3.0-5.0)	6.3 (5.5-7.5)	6.0 (5.0-7.0)	
	Red	13.6 (10.0-16.0)	11.0 (9.0-13.0)	16.7 (14.0-20.5)	17.6 (16.5-18.5)	
	N	14	12*	7	e	

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ulations are best illustrated in Table 2, in which reflectance readings are recorded as a percentage of pure white (taken with a Photovolt Photoelectric Reflection Meter, Model 610, with red, green, and blue filters). Readings were taken on middorsal and midventral areas of each museum study skin. Specimens from Martinique, which were all in spirits, were fully dried with an air hose prior to making color determinations. Greater reflectance readings indicate paler color, and it is evident from the table that bats from the two northern islands are darker than those to the south, both dorsally and ventrally. Overall, bats from Martinique are darkest, and those from St. Vincent are palest.

Summary

Koopman (1968:4) and Jones and Phillips (1970:134-135) have suggested that all small bats of the genus *Sturnira* in the Lesser Antilles, which the genus evidently entered from the south, ought to be referred to the species *lilium*. Study of the more abundant material now available confirms, in our minds at least, that this is the correct course of action. Characters used to erect *angeli* and *paulsoni* as species distinct from *lilium* now can be shown to be either individually or geographically variable, and the relationship of the populations on Dominica, Martinique, St. Lucia, and St. Vincent is best elucidated by referring all to *lilium*. The species has not yet been reported officially from the southernmost island in the Lesser Antilles, Grenada, but we have it on good authority that specimens have been taken there in the course of epidemiological work in recent years. When material is available for study from Grenada, we believe it will further strengthen our case.

Antillean populations of *lilium* generally fall into two groups, with bats from St. Lucia and St. Vincent bearing a close relationship to each other and, similarly, those from Dominica and Martinique having a number of characteristics in common. Nevertheless, the differences separating each insular population from the others are sufficient to warrant subspecific distinction for all. Thus, we recognize four subspecies of *S. lilium* as outlined below. If forced to synonymize the Antillean populations by applying ever greater minimal conditions for recognition of subspecies, we first would place the new subspecies from St. Lucia with *panlsoni* of St. Vincent, next place the new subspecies from Martinique with *angeli* of Dominica, and finally place all together as a single subspecies, for which *angeli* is the first available name. The distribution of Antillean *Sturnira* is shown in Fig. 3.



F1G. 3.—Distribution in the Lesser Antilles of the genus *Sturnira*: 1, *S. thomasi* (Guadeloupe); 2, *S. l. angeli* (Dominica); 3, *S. l. zygomaticus* (Martinique); 4, *S. l. luciae* (St. Lucia); 5, *S. l. paulsoni* (St. Vincent).

Sturnira lilium angeli de la Torre, 1966

Holotype.—Adult male, skin and skull, USNM 361881, from 6 mi. NE Roseau, 1000 ft., St. Paul Parish, Dominica; obtained by R. F. Klinikowski on 21 February 1962, original no. AS 5354.

Distribution.—Known only from Dominica.

Diagnosis.—Size medium for Antillean subspecies (see Table 1), zygomatic region relatively narrow; first upper molar with small anterior labial shelf and fairly prominent metacone (see Fig. 2); third upper molar relatively small; paraconid of first lower molar located as near center line as lingual border, entoconid low crowned and generally no more than a well-defined ridge; third lower molar relatively small; overall color dark (see Table 2), dorsum dark brownish to grayish brown, slightly paler ventrally.

Specimens examined (24).—DOMINICA: Clarke Hall Estate, 100 ft., St. Joseph Parish, 24 (KU 104781-91, 110121-33).

Additional records.—DOMINICA: 6 mi. NE Roseau, 1000 ft., St. Paul Parish (de la Torre, 1966:272); no specific locality (Allen, 1911:233; de la Torre, 1966:272).

Sturnira lilium zygomaticus, new subspecies

Holotype.—Adult male, in spirits but with skull removed, AMNH 213972, from Balata, Martinique; obtained by Harry Beatty and Peter Martin on 19 March 1967, original no., if any, unknown.

Distribution.---Known only from Martinique.

Diagnosis.—Resembling *S. I. angeli*, but zygomatic region broader and maxillary toothrow longer (see Table 1); metacone well developed on first upper molar, resulting in prominent posterolabial extension of tooth (see Fig. 2); second and third upper molars relatively large; lower molars much as in *angeli*; color darkest among Antillean populations (see Table 2).

Specimens examined (20).—MARTINIQUE: Balata, 20 (AMNH 213959-78). Additional records.—MARTINIQUE: Morne Rouge (de la Torre, 1966:272).

Sturnira lilium luciae, new subspecies

Holotype.—Adult male, skin and skull, KU 110137, from 1/2 mi. SE Bogius, 100 ft., Dauphin Parish, St. Lucia; obtained by J. Knox Jones, Jr., on 28 August 1967, original no. 5415.

Distribution.---Known only from St. Lucia.

Diagnosis.—Size small to medium among Antillean subspecies (see Table 1); anterior labial shelf of first molar well developed but metacone not so prominent as in insular populations to the north (see Fig. 2); second and third upper molars large: first lower molar with paraconid located at lingual border, entoconid well defined and elongate; second lower molar with well-developed metaconid; third lower molar relatively large; color grayish brown to yellowish brown, paler than that in *angeli* or *zygomaticus*, but darker than in *paulsoni* (see Table 2).

Specimens examined (8).—ST. LUCIA: 1/2 mi. SE Bogius, 100 ft., Dauphin, 7 (KU 110135-41); Union Agricultural Station, 100 ft., Gros-Islet (KU 110134).

Sturnira lilium paulsoni de la Torre and Schwartz, 1966

Holotype.—Adult female. skin and skull, USNM 361882, from Lowrt, 1000 ft., St. Andrew Parish, St. Vincent; obtained by D. R. Paulson on 30 December 1961, original no. AS 5333.

Distribution.—Known only from St. Vincent.

Diagnosis.—Similar in external and cranial dimensions to *S. 1. luciae* but averaging somewhat larger on basis of specimens examined (see Table 1, but also see smaller measurements of holotype in original description): color averaging paler than in *luciae* (see Table 2), palest among Antillean populations; first upper molar essentially as in *luciae*, but second and third smaller; lower molars much like those of *luciae*, but last two averaging smaller.

Specimens examined (6).—St. VINCENT: Clifton Hill, 400 ft., St. George Parish, 6 (KU 110142-47).

Additional record.—St. VINCENT: LOWRT, 1000 ft., St. Andrew Parish (de la Torre and Schwartz, 1966:301).

Natural History

Little is known of the natural history of *S. lilium* in the Lesser Antilles. On St. Vincent, we netted yellow-shouldered bats over a small stream between banana groves, in a pastured clearing near

Dates	No. females examined	No. pregnant	Size embryos	No. lactating
	De	ominica		
22-29 March	7	7	20.1 (16-24)	0
4-22 April	4	4	25.0 (22-28)	0
29 August-				
1 September	5	0		1
	Ма	urtinique		
17-20 March	13	11	18.6 (9-23)	0
	Si	t. Lucia		
27-28 August	3	2	25.0 (24-26)	1
	St.	Vincent		
23 August	1	0		0

TABLE 3.—Summary of reproductive status of young adult and adult females ofSturnira lilium from the Lesser Antilles.

bananas, on a rise near the bend of a tree-lined stream, and in a natural flyway between trees. The holotype was "trapped in a net [set] across a 20-foot wide mountain stream . . . in an area adjacent to rain forest" (de la Torre and Schwartz, 1966:302). On St. Lucia, we took one specimen in a net set across a trail through forest, six others in a net across a truck road that separated a banana grove from adjacent second-growth vegetation, and one in a net over a river. On Dominica, individuals were netted in a variety of situations, but most were taken along trails separating cocoa or banana groves from adjacent forest or over a gravel bar in the Layou River. The series of angeli reported by de la Torre from 6 mi. NE Roseau was taken in nets set across streams "in rain forest with no adjacent cultivated areas." Bats taken along with S. lilium on various islands included Ardops nichollsi, Artibeus jamaicensis, Brachyphyllum cavernarum, Glossophaga longirostris, Monophyllus plethodon, and Myotis dominicensis.

Testes of seven August-taken adult males from St. Lucia and St. Vincent averaged 6.4 (5 to 8) in length, whereas those of three young adults measured 3, 3, and 4. Similarly, four adults taken on Dominica in late August and early September had testes 4, 7, 7, and 8 in length, with those of subadults and young adults from the same period measuring 2.5, 3, 3, and 4. Reproduction in females is summarized in Table 3. The few data do not permit generalizations, but early spring does appear to be one peak reproductive period.

Antillean S. lilium collected by us were parasitized externally by as yet unidentified mites and by the following bat flies: Aspidoptera

Measurement	USNM 361883 (adult 6)*	TTU 19904 (yg. adult ?)	TTU 19905 (juvenile 9)	TTU 19906 (adult ?)	TTU 19907 (adult ?)
Length of head and body	80	82	73	80	81
Length of hind foot	16	13	13	15	15
Length of ear	18	19	16	17	19
Length of forearm	48.1	45.9	46.4	46.1	47.7
Greatest length of skull	26.2	25.3	24.4	24.9	25.1
Condylobasal length	24.7	23.3	22.4	22.9	23.6
Zygomatic breadth	12.7	12.1	11.9	12.2	12.5
Mastoid breadth	12.1	11.7	11.2	11.7	11.8
Breadth of braincase		9.8	9.5	9.8	9.6
Interorbital constriction	6.3	5.7	5.5	5.9	6.0
Postorbital constriction	6.0	5.7	5.6	5.5	5.9
Length of maxillary toothrow	7.7	7.0	6.7	6.9	6.9
Breadth across upper molars Length of mandibular	8.2	8.1	7.7	8.0	8.0
toothrow (i-m2)	7.8	7.7	7.7	7.7	7.8

TABLE 4.	External	and	cranial	measu	ements	of	the five	known	specimens	of
Sturnira thomasi.										

*Measurements after de la Torre and Schwartz (1966:301).

sp. on Dominica and St. Lucia; *Megistopoda* sp. on St. Lucia and St. Vincent; and *Metalasmus pseudopterus* on Dominica, St. Lucia, and St. Vincent.

Sturnira thomasi de la Torre and Schwartz, 1966

Guadeloupe Yellow-shouldered Bat

Holotype.—Adult male, skin and skull, USNM 361883, from Sofaïa, 1200 ft., Guadeloupe; obtained by R. Thomas on 26 January 1963, original no. AS 5413.

Distribution.—Known only from Guadeloupe.

S. thomasi was named and described by de la Torre and Schwartz (1966:299-301) on the basis of a single adult male, which remained the only reported specimen of this taxon until Genoways and Jones (1975:924) recorded four additional individuals, all taken in the summer of 1974. Measurements of the five known specimens are given in Table 4.

This bat is distinctive among Antillean populations of *Sturnira* by virtue of its large size and long, narrow skull (Fig. 4). It may well be, as Koopman (1968:4) has suggested, that, with the acquisition of additional material, *thomasi* will prove to be best regarded as a sub-



FIG. 4.—Dorsal, ventral, and lateral views of skull of *Sturnira thomasi* (TTU 19907, 9). Illustration by S. L. Williams.

species of *lilium*. We are presently disposed, however, tentatively to retain specific status for *thomasi* because it differs to a much greater degree from *Sturnira* occurring on other West Indian islands than any of those populations differ from each other, albeit mostly in quantitative characteristics. Koopman (1968:4) was "inclined to re-

gard *paulsoni*, *angeli*, and even *thomasi* as successive modifications of *lilium* out of contact with other species of *Sturnira*."

Some support for Koopman's view is generated by the fact that none of the four recently taken females from Guadeloupe is so large as the male holotype. Nevertheless, discounting the one juvenile listed in Table 4, the greatest length of skull in *thomasi* ranges from 24.9 to 26.2 as opposed to a range of 22.1 to 23.9 in recorded Antillean samples of *lilium* (see Table 1; de la Torre, 1966:272; de la Torre and Schwartz, 1966:302), and the breadth measurements of the skull are relatively or actually narrower than in *lilium* (zygomatic breadth ranging from 12.1 to 12.7 in *thomasi* as opposed to 12.5 to 13.8 in samples of *lilium*, for example). The maxillary toothrow is long (6.9 to 7.7), as claimed in the original description, but the holotype has a much greater value for this measurement than do other specimens. In color, *thomasi* generally resembles *lilium* from Dominica and Martinique, being dark brownish dorsally and somewhat paler ventrally.

The holotype lacks a third lower molar, which was mentioned by the describers as a possibly distinctive feature. This condition is not constant in the four recently obtained specimens, however. Two of these lack a third lower molar on both sides, one lacks the tooth on the right side only, and the fourth has a small m3 in both lower jaws. As noted previously, one of 24 specimens of *lilium* from Dominica also lacked third lower molars, and one specimen from that island and two of eight skulls examined from Martinique lacked this tooth in one mandibular row. Evidently, an evolutionary trend resulting in the loss of the much reduced third lower molar is best developed in *thomasi*.

The male holotype was trapped in a mist net set "in a deep ravine" that cut through dense forest. Four females collected in July 1974 were netted as follows: one over a boulder-strewn river in rain forest; two over a large stream lined with gallery forest; and the fourth on a mountainous slope where banana groves gave way to tall forest. Two of the females were lactating adults, one was a young adult, and one a juvenile with unfused phalangeal epiphyses. Other bat species netted with *thomasi* included *Ardops nichollsi*, *Artibeus jamaicensis*, *Brachyphylla cavernarum*, and *Molossus molossus*.

Specimens examined (4).—GUADELOUPE: 2 km. E Saint-Claude, 1 (TTU 19904); 1 km. W Vernon, 2 (TTU 19905-06); 2 km. S, 1 km. W Vernon, 1 (TTU 19907).

Additional record.—GUADELOUPE: Sofaïa, 1200 ft. (de la Torre and Schwartz, 1966:299).

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Addresses of authors: J. K. JONES, JR., Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, 79409; C. J. PHILLIPS, Department of Biology, Hofstra University, Hempstead, New York 11550. Received 3 September, accepted 22 October 1975.







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