SOME ENDOPARASITES OF THE HERPETOFAUNA OF DOMINICA, WEST INDIES, AND THEIR USE AS CLUES TO HOST ZOOGEOGRAPHY

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The endoparasites of the herpetofauna of Dominica, West Indies, were studied to see if they would be of value in determining host zoogeography. Thirteen of the fifteen species of herptiles occurring on the island were collected. Examination of the hosts yielded two trematodes, one cestode, one acanthocephalan, six nematodes and one pentastomid. One of the trematodes is described as a proposed new genus and new species. Problems of host-parasite zoogeography are discussed. Two of the eleven parasites proved to be of significance in understanding host zoogeography. It was suggested that host-parasite relationships will be of greater value as knowledge of the distribution of parasites and hosts is broadened.

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CHAPTER I

INTRODUCTION

A concomitant and comparative study of hosts and parasites in different parts of the world has been labelled the "von Ihering method" after the first scientist to use parasites as indicators of relationships and geographical distributions of host species (Noble and Noble, 1964). This method has received wide criticism and is plagued with many pitfalls where cases of recent acquisition, divergent evolution, convergent evolution and discontinuous distribution make it impossible to use the parasites as unerring guides to the origins of the host. Noble and Noble (1964) have suggested that von Ihering's facts were both inaccurate and inadequate in relating the occurrence of a nematode in wilde Canidae in Europe and South America as indicative that it had existed in their upper Miocene ancestors.

Host-parasite zoogeography has been applied to amphibians by Metcalf (1923, 1929 and 1940) who studied the opalinids of the frog family Leptodactylidae in order to trace their evolution and dispersal. Dunn (1925) and Noble (1925) have both criticized Metcalf's methods and conclu-

sions. Other applications of the "von Ihering method" in varying degrees include the host-parasite groups of flagellate Protozoa of termites (Kirby, 1937); cestodes of birds (Baer, 1948); Metastrongylidae (lung nematodes) of mammals (Doughterty, 1949); Mallophaga of birds (Kellogg, 1913; Harrison, 1914; Hopkins, 1942); Anoplura of mammals (Ewing, 1926); strigeid trematodes of vertebrates (DuBois, 1938); and digenetic trematodes of fish (Manter, 1955).

Mayr (1957) has warned against the use of parasites as indicators of host relationships because of the exchanges of parasites which may occur among hosts. Darlington (1957) states that animals and their parasites can have different geographical histories; a fact that Darlington believes is sometimes not appreciated by host-parasite zoogeographers.

The lack of extensive host-parasite studies in herptiles offers an open area for research. In spite of the criticisms of the "von Ihering method", a study of the endoparasites of the herpetofauna of Dominica might prove to be of value to the accepted zoogeographical patterns which have been based primarily on the morphology of the host species. This report will describe the endoparasitic helminths of the herpetofauna, discuss the problems of

host-parasite zoogeography, and draw some conclusions as to host zoogeography as related to their parasite complement.

CHAPTER II

MATERIALS AND METHODS

Host specimens were collected on Dominica from February to June 1966. The frogs and snakes were collected by hand. The lizards were captured by hand, noose or shot. The specimens of Iguana were obtained by purchase from local natives as this species is rare. Collected animals were usually preserved in 10% formalin the same day of collection.

Systematic dissections were performed in search of endoparasitic helminths. The complete digestive tract and associated organs, respiratory system and all body cavities were explored for the presence of specimens. The majority of dissections were performed on preserved individuals and this was disadvantageous in that the parasite specimens were frequently preserved in a twisted or contorted fashion. As parasite specimens were discovered, they were passed through a series of solutions in Stender dishes. The solutions were: 10% formalin; water; 30% ethanol; 50% ethanol and 70% ethanol. The specimens were kept in each dish from 30 minutes to one hour. The 10% formalin was used to ensure complete fixation and as a wash to remove any materials adhering to the specimen. The water washed out the preserving

agent, and the alcohol series was used to bring the specimen up to the concentration of the storage solution. Each individual parasite or group of parasites, depending on size and number, were stored in vials containing 70% ethanol and 5% glycerine. For each vial, a file card was made in duplicate containing the following information: name of host; host number; host sex; host collection locality; location of parasite; fixing reagent; storing reagent; date; and name of collector. Inside each vial was placed a piece of paper with a number which corresponded with that on the pertinent file card.

Stored parasite specimens were processed for mounting and identification in the following manner:

Trematodes. Stored trematode specimens were returned from the storage solution to water by passage through an alcohol series of 70%, 50%, and 30% ethanol. Material was kept in each solution from 20 min. to one hour. Specimens were washed thoroughly in distilled water and stained for one hour in Harris' hematoxylin. Stained material was washed in 3 changes of tap water and destained in 35% acid-alcohol until the blue color changed to pink. The stain was intensified in ammonia water for 20 min. Specimens were then washed in several changes of tap water and dehydrated by passage up through a standard alcohol series. Methyl

salicylate was used as the clearing agent. Specimens were mounted directly from the clearing medium into Permount on glass slides. When sufficiently hardened, slides were cleaned in 95% ethanol and labelled.

Cestodes. Tapeworms were handled in the same manner as trematodes, except that the cleared specimens were cut into sections of appropriate lengths and mounted, a whole worm to one slide.

Nematodes. Nematodes are extremely difficult to stain, dehydrate and mount in the usual manner because of their impervious cuticle. Staining methods were tried on several specimens with only mediocre results. Best results were obtained by mounting the specimen unstained. This was done in the following manner: the cuticle of each specimen was pricked several times with a fine needle to allow better exchange of fluids; specimens were dehydrated up to 100% ethanol and cleared in a combination of methyl salicylate and 100% ethanol, gradually increasing the concentration of the methyl salicylate to 100% over a period of time. Material prepared in this manner could be mounted in Permount without the specimen turning opaque. Slides were cleaned and labelled as above. Several en face views were prepared.

Acanthocephalans. The thorny-headed worms are also very resistant to the penetration of fluids. However, fair

results were obtained with the following method. Stored specimens were washed with 70% ethanol and the body wall was pricked with a fine needle. The specimen was hydrated by passage down through an alcohol series and stained with Ehrlich's acid hematoxylin. Stained specimens were dehydrated to 70% ethanol and destained in 70% acid-alcohol until pink in color. Destained specimens were intensified with 70% alkaline-alcohol until blue in color. Specimens were then dehydrated to 100% ethanol, cleared in methyl salicylate, and mounted in Permount. Slides were cleaned and labelled as above.

Pentastomids. Tongue worms were cleared directly from the storage solution in phenol-ethanol or after dehydration in methyl salicylate. Methyl salicylate was found to give the best results. Specimens were not stained or mounted, but observed directly in the clearing medium.

Preliminary identification of parasites was done with the aid of keys in Systema Helminthum vol. I, II, III, and V by Yamaguti (1958 - 1963).

Distribution of parasites and hosts were based on published lists.

CHAPTER III

DESCRIPTION OF STUDY AREA

The West Indies lie east of Central America, between North and South America, and mostly within the edge of the tropics. The largest islands running in an east-west direction compose the Greater Antilles. The Lesser Antilles, running in a north-south direction, form an irregular chain between the Greater Antilles and Trinidad, and are composed of relatively small islands.

Dominica, the third largest island in the Lesser Antilles, lies between 15°10' - 15°40' north latitude and 61°44' - 61°30' west longitude, equidistant between the larger islands of Gaudeloupe and Martinique and about 30 miles from each (see fig. 1). The island's maximum length is about 28 miles, the maximum width close to 15 miles, with a total area of about 304 square miles. Like the majority of the volcanic Caribees, Dominica's complex mountainous axis has a north-south trend. All of this land is very rugged and precipitous.

The vegetation of Dominica is fairly diverse. Four primary types of vegetation were recognized by Hodge (1943). These are: (1) the pantropical vegetation of the seabeaches

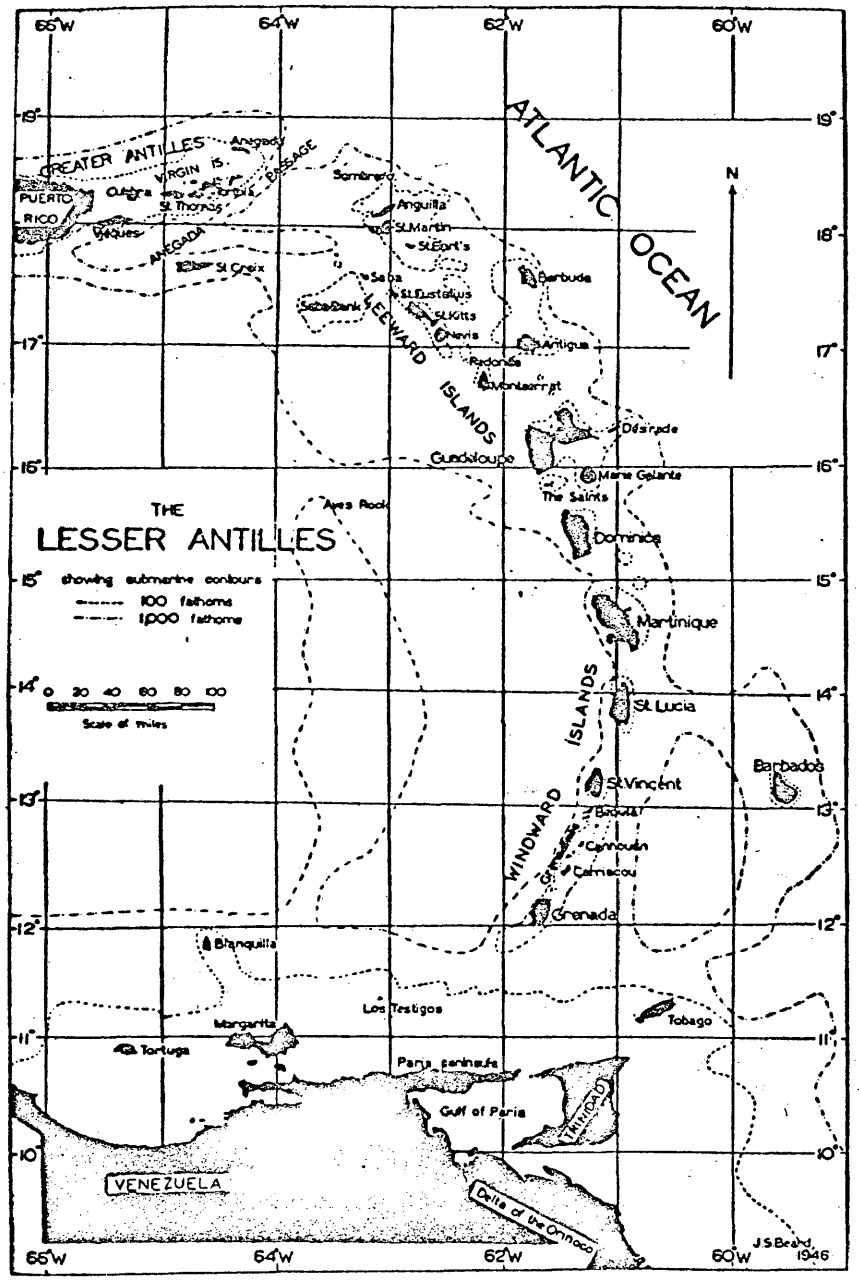

FIGURE 1

THE LESSER ANTILLES SHOWING THE POSITION OF DOMINICA

and coastal thickets, which differs from the other three types in being primarily edaphic, not climatic; (2) the xerophytic vegetation of the lower leeward slopes, characterized by a low deciduous, dry tropical forest occupying a region of seasonal rainfall; (3) the mesophytic vegetation of the mountainous interior, characterized by a high-stemmed, broad-leafed, evergreen rain forest occupying a zone of heavy rainfall; and (4) the vegetation of the upper slopes of the highest peaks, characterized by a medium low, tangled, mossy forest occupying a zone of almost constant mists and rains. For a more detailed description see Hodge (1954).

CHAPTER IV

DESCRIPTION OF HOST SPECIES

The herpetofauna of Dominica is composed of two species of frogs in one family, eight species of lizards in four families, and five species of snakes in three families (see Table 1). The herpetological fauna of the Lesser Antilles shows no genera which are not present in South America (Dunn, 1934a).

The family Leptodactylidae is widely distributed in the Australian region, and in Central and South America. A few species reach the southern United States and one genus occurs in South Africa. The genus Eleutherodactylus, with more than 200 recognized species, is widely distributed and dominant in Central America and especially the West Indies, forming the main part of the frog fauna there. E. martinicensis is wide-spread and abundant in the Lesser Antilles. It has been recorded from as far north as St. Martins (Dunn, 1934a) and is apparently present on all of the islands to the south. Leptodactylus is a Central and South American genus, but also reaches the West Indies (Darlington, 1957). There are about 52 species in this genus (Terent'ev, 1961). L. fallax was recorded from St. Kitts and

TABLE 1

Classification of the herpetofauna of Dominica, W. I.

ORDER	FAMILY	SPECIES
Anura	Leptodactyliae	*Eleutherodactylus martinicensis*
		Leptodactylus fallax
Squamata	Gekkonidae	*Hemidactylus mabouia*
		Sphaerodactylus fantasticus fuga
		Sphaerodactylus vincenti monilifer (2)
		Thecadactylus rapicauda
	Iguanidae	*Anolis oculatus oculatus* (1)
		Anolis oculatus cabritensis (1)
		Anolis oculatus montanus (1)
		Anolis oculatus winstoni (1)
		Iguana delicatissima
	Scincidae	*Mabuya mabouia mabouia*
	Teiidae	*Ameiva fuscata* (1)
	Boidae	*Constrictor constrictor nebulosus*
	Colubridae	*Alsophis antillensis sibonius*
		Clelia clelia clelia (2)
		Dromicus juliae juliae
	Typhlopidae	*Typhlops dominicana* (1)

Note: species listed are regarded as occurring on Dominica by Dr. Albert Schwartz (1965).
(1) species endemic to Dominica.
(2) species not collected during this study.

Antigua by Dunn (1934a), but seems to have been exterminated from all Lesser Antillean islands with the exception of Dominica and Montserrat. Goin and Goin (1962) state that the members of the family Leptodactylidae are advanced types known to be adept at "island hopping".

The true geckos, family Gekkonidae, form a large tropicopolitan family of about 70 genera and more than 200 species. The genus Hemidactylus has about 35 species occurring in southern Europe, southeast Asia, Africa, Polynesia and tropical America (Terent'ev, 1961). H. mabouia is listed as occurring in the Lesser Antilles and northeastern South America by Burt and Burt (1933). The American genus Sphaerodactylus, which are only two inches long, are probably the smallest living lizards. There are 26 species in Central and South America, the West Indies, and Florida (Terent'ev, 1961). Burt and Burt (1933) list S. fantasticus from Martinique, and Boulenger (1885) gives its range as northern Venezuela. Other species of Sphaerodactylus are given as ranging through northern South America, and occupy almost every island in the Lesser Antilles chain (Baskin and Williams, 1966). S. vincenti which is regarded as occurring on Dominica was not collected by the author. Thecadactylus rapicauda is wide-spread through the West Indies, the mainland of South America,

except for the southern part, the Dutch Leeward Islands and Central America (Burt and Burt, 1933). The only other species in this genus is recorded from Torres Strait Islands (Terent'ev, 1961).

The family Iguanidae is the largest family of lizards in the New World, to which it is almost totally restricted. There are about 50 genera, hundreds of species, mostly in the tropics of Central and South America and the West Indies, but a few are found in the temperate zones (Darlington, 1957). The genus Anolis on Sombrero demonstrates its presence on every bank of islands in the Lesser Antilles. A. oculatus is endemic to Dominica, and four subspecies have been described by Lazell (1962). Dunn (1934b) states that neither of the two species of the genus Iguana are known from the Greater Antilles. I. iguana occurs on the South American mainland, in the Lesser Antilles on the Virgins, St. Croix and Saba, and from Isles des Saintes south to the South American continent. I. delicatissima occurs from Anguilla to Isles des Saintes, and together with I. iguana on Dominica according to Dunn (1934b), however, I. iguana is no longer considered as part of the Dominican fauna. Iguanas are articles of commerce and are also very good swimmers thus their spread through the Lesser Antilles is not surprising. I. delicatissima is endemic to the Lesser Antilles.

The family Scincidae, the skinks, are found in all tropical and warm-temperate areas of the world, but are most numerous in Australia, the islands of the western Pacific, the Oriental Region and Africa. Skinks are poorly represented in the New World. There are nearly 50 genera and more than 600 recognized species (Goin and Goin, 1962). The genus Mabuya, with more than 80 species, is in Africa and Madagascar, southern Asia to New Guinea, and South and Central America, southern Mexico and the West Indies. It is the only genus of the family on the continent of South America (Dunn, 1935).

The family Teiidae is exclusively found in the New World. There are about 46 genera and 160 species in South America. One genus reaches the United States and at least 6 genera, especially Ameiva, extend into Central America (Goin and Goin, 1962). Only Ameiva is wide-spread and abundant in the West Indies (Darlington, 1957 and Lazell, 1964a). Ameiva fuscata is endemic to Dominica (Baskin and Williams, 1966).

The family Boidae, constricting snakes, can be found in all tropical and some temperate regions of the world. The family is divided into four subfamilies by Darlington (1957) as recognized by Romer (1956). The subfamily Boinae includes the boas, anacondas and related smaller forms of tropical American, South and Central America and the West

Indies. There are about 7 genera and 20 species. Constrictor constrictor occurs only on two islands in the Lesser Antilles, St. Lucia and Dominica, and is the only South American species occurring on the continental islands of Trinidad and Tobago (Lazell, 1964b).

The family Colubridae is a huge, cosmopolitan group which includes the great majority of the snakes of the world. Alsophis antillensis is wide-spread in the Lesser Antilles (Boulenger, 1893 and Lazell, 1964a) as is the genus Dromicus (Lazell, 1964a). The genus Dromicus has 23 species in the Antilles, Galapagos Islands, Chile and Peru (Terent'ev, 1961). The colubrid snake Clelia clelia which is supposed to be on Dominica was not collected by the author.

The family Typhlopidae, worm snakes, occurs in all tropical and warm-temperate areas of the world. There are 4 genera and close to 200 species. Typhlops occurs throughout the range of the family, with about 164 species (Terent'ev, 1961) in Africa and Madagascar, southern Asia, the Indo-Australian Archipelago and Australia, but not Tasmania and relatively few in America from southern Mexico to Argentina and in the West Indies (Darlington, 1957). T. dominicana is endemic to Dominica.

CHAPTER V

DESCRIPTION OF PARASITE SPECIES

The endoparasites of the herpetofauna of Dominica are rather diverse, if not numerous in species. The herptiles were found to harbor two trematodes, one cestode, one acanthocephalan, six nematodes and one pentastomid (see TABLE 2).

The trematode family Brachycoeliidae includes several multispecies genera, all parasitic in the small intestine of amphibians and reptiles. There are 3 genera found in reptiles from this family but only the genus Mesocoelium was found in Dominican hosts. Mesocoelium is the largest genus having about 16 species described from lizards and snakes collected in Africa, Asia, Australia, the Orient, North and South America. The genus appears to be widespread with regard both to hosts and geography. No genera in common to Dominican hosts are recorded, except for Mabuya as host in the Philippines (Yamaguti, 1958). Mesocoelium sp. was found to parasitize Anolis, Mabuya and Thecadactylus on Dominica (see TABLE 3).

The trematode family Plagiorchiidae is parasitic in fish, amphibians, reptiles, birds and mammals. The subfamily

TABLE 2

Classification of parasites of Dominican herpetofauna.

PHYLUM	CLASS	ORDER	FAMILY	SPECIES
Platyhelminthes	Trematoda	Digenea	Brachycoeliidae	*Mesocoelium* sp.
			Plagiorchiidae	*Omnipharynx anolis* n.g. n.sp.
	Cestoda	Proteocephalidea	Proteocephalidae	*Ophiotaenia* sp.
Acanthocephala		Giganthorhynchidea	Oligacanthorhynchidae	unidentified sp.
Aschelminthes	Nematoda	Ascarididea	Heterocheilidae	*Terranova* sp.
		Filariidea	Filariidae	*Hastospiculum* sp.
		Oxyuridea	Cruziidae	*Cruzia* sp.
			Oxyuridae	*Ozolaimus megatyhlon*
				Pharyngodon sp.
				Thelandros sp.
Arthropoda	Pentastomida	Porocephalida	Porocephalidae	*Porocephalus* sp.

TABLE 3

Distribution of parasites among Dominican herpetofauna, and percent of infestation.

HOSTS	N	PARASITES										
		Mesocoelium	Omnipharynx anolis n.g. n.sp	Ophiotaenia	Oligacanthorhynchidae	Terranova	Hastospiculum	Cruzia	Ozolaimus megatyhlon	Pharyngodon	Thelandros	Porocephalus
Eleutherodactylus	15	—	—	—	—	33im	—	—	—	—	33	—
Leptodactylus	10	—	—	—	—	30im	—	—	—	—	—	—
Hemidactylus	16	—	—	—	—	—	—	—	—	—	19	—
Sphaerodactylus fantasticus	3	—	—	—	—	—	—	—	—	—	67	—
Thecadactylus	6	50	—	—	—	—	—	—	—	—	50	—
Anolis oculatus oculatus	17	82	—	—	6im	—	—	—	—	59	—	—
A. o. cabritensis	17	—	—	—	53im	—	—	—	—	—	76	—
A. o. montanus	13	15	15	—	77im	—	—	—	—	—	—	—
A. o. winstoni	16	6		—	88im	—	—	—	—	—	69	—
Iguana	2	—	—	—	—	—	—	—	100	—	—	—
Mabuya	10	50	—	—	—	—	—	—	—	—	—	—
Ameiva	19	—	—	—	—	—	—	74	—	—	—	—
Constrictor	9	—	—	—	11im	—	11	—	—	—	—	100
Alsophis	6	—	—	—	100im	—	—	—	—	—	—	—
Dromicus	15	—	—	87	—	100	—	—	—	—	—	—
Typhlops	2	—	—	—	—	—	—	—	—	—	—	—

(im = immature)

Astiotrematinae is parasitic in fish and reptiles. Yamaguti (1958) lists 8 genera under this subfamily. The trematode from Anolis oculatus montanus (see TABLE 3) does not fit any of the recorded generic descriptions. Accordingly, this trematode is being described as a new genus and species in the subfamily Astiotrematinae (see APPENDIX A).

The cestode family Proteocephalidae is a very large group of tapeworms parasitizing fish, amphibians and reptiles. The genus Ophiotaenia is one of the larger genera of the family and is the characteristic tapeworm of colubrid snakes (Wardle and McLeod, 1952). There are approximately 47 species of Ophiotaenia from reptiles, 15 species from amphibians and only a few species listed from fish. The geographic distribution of the genus is worldwide. Wardle and McLeod (1952) divide the genus into ten species-groups. The tapeworm from Dromicus (see TABLE 3) falls into Group V which includes 8 species, 2 from fish, 5 from snakes and one from a turtle. All species in Group V have similar morphological characteristics of more than 200 testes, cirrus pouch one-third or less the segment width, and uterine branches less than 30 on each side. The plerocercoid larva of Ophiotaenia most likely uses Eleutherodactylus as intermediate host as this frog was frequently found in the gut of Dromicus upon dissection.

The acanthocephalan family Oligacanthorhynchidae is an intestinal parasite of birds and mammals. The family has about 10 genera with 17 recognized species of worldwide distribution. There are about 11 species generis incertae sedis in the family (Yamaguti, 1963). Terrestrial reptiles never harbor adult acanthocephalans, but frequently serve as paratenic hosts for juveniles which usually encyst in the intestinal mesenteries. On Dominica, Anolis, Constrictor, and Alsophis were found to be intested with Oligacanthorhynchidae juveniles (see TABLE 3). As the generic location of these juveniles is dependent upon their relative characteristics as adults, it is impossible to place them in a specific genus.

The nematode family Heterocheilidae is a parasite of fish, amphibians, reptiles, birds and mammals. The genus Terranova is a parasite of fish, reptiles and mammals. There are about 12 species described from fish, 2 species from mammals and 3 species from reptiles (Yamaguti, 1961). The geographic distribution is worldwide. Terranova sp. was found to be parasitic in the stomach of Dromicus (see TABLE 3). The life cycles of heterocheilid nematodes may involve more than one intermediate host, the first usually being an invertebrate, and the second a vertebrate (Cheng,

1964). The life cycle of Terranova probably involves Eleutherodactylus as a second intermediate host, as this nematode was found encysted in this frog's intestinal mesenteries in an immature form (see TABLE 3). This frog was frequently found in the gut of Dromicus upon dissection. Leptodactylus (see TABLE 3) is probably an accidental second intermediate host as it does not compose part of the diet of Dromicus, except, perhaps only at a very young age.

The nematode family Filariidae includes a large group of long slender worms parasitic in the lymph glands, tissues, and body cavities of their amphibian, reptilian, avian and mammalian hosts. The genus Hastospiculum is composed of large worms (the only specimen examined in this study, a female, measured 204 mm) parasitic in the serous membranes of reptiles. Yorke and Maplestone (1926) give the length of the male genotype, H. varani, as 140 mm, but do not give the length of a female specimen. Yamaguti (1961) lists 8 species with wide host and geographic distribution. Hastospiculum sp. was found in the coelomic peritoneum of Constrictor from Dominica (see TABLE 3). Chitwood (1932) described H. oncocercum in Constrictor imperator from the National Zoological Park, Washington, D. C.

The nematode family Cruziidae is a parasite of amphibians, reptiles and mammals. There are 4 genera in the family;

one each restricted to amphibians, reptiles and mammals and the genus Cruzia found in both reptiles and mammals. The family is unusual in that its geographic distribution is almost totally restricted to South and Central America, except for a few records from southern North America, and the genus Pseudocruzia with only one species described from pigs in India. Cruzia is restricted to the New World. The genus is a small one with only 6 species described from mammals and 3 species from reptiles (Yamaguti, 1961). The representatives from mammals are divided equally with 3 species from marsupials (opossums) and 3 species from edentates (armadillos). The 3 species representative from reptiles are described as one species each from a lizard (Mexico), a colubrid snake (Brazil) and a box turtle (Texas). The Dominican host of Cruzia sp. is Ameiva (see TABLE 3). Wolfgang (1951) described C. cameroni in Didelphis marsupialis insulans, the Large American opossum, from Trinidad. D. marsupialis insulans also occurs on Dominica, however, it was not collected.

The nematode family Oxyuridae parasitizes fish, amphibians, reptiles, birds and mammals. Their geographic distribution is worldwide. There are 4 subfamilies and 17 genera of oxyurids described from reptiles (Yamaguti, 1961). The subfamily Oxyurinae is well represented in the parasite fauna of

Dominica with 3 genera, Ozolaimus, Pharyngodon, and Thelandros, being present (see TABLE 2).

Ozolaimus is parasitic only in Iguana. There is only one species described, O. megatyhlon, in I. tuberculata from Mexico, Venequela, Brazil and Cuba (Yamaguti, 1961). The nematode in Iguana from Dominica fits the description of the genotype, O. megatyhlon (see TABLE 3).

Pharyngodon is a large genus with about 34 species described from a wide range of reptilian hosts with worldwide distribution. Pharyngodon sp. was found to parasitize Anolis oculatus oculatus from Dominica (see TABLE 3). Chitwood (1934) has described P. anolis in Anolis cristatellus from Puerto Rico.

Thelandros is another large genus with about 31 species described from a wide range of reptiles and a few amphibians. Geographic distribution is worldwide. Thelandros sp. is the most widely distributed parasite among Dominican herptiles. This nematode was found to parasitize Eleutherodactylus, Hemidactylus, Sphaerodactylus, Thecadactylus, Anolis oculatus cabritensis and Anolis oculatus winstoni (see TABLE 3). The only recorded host species in common with the Dominican fauna is Hemidactylus. T. maplestoni is described in H. flavoviridis from India and Burma (Yamaguti, 1961).

The class Pentastomida, tongue worms, is parasitic in the respiratory tract and lungs of vertebrates. Over 50 species

of pentastomids have been reported (Cheng, 1964). The family Porocephalidae is composed of worms parasitic in the lungs of reptiles. The genus Porocephalus is confined exclusively to snakes as definitive hosts. Porocephalus sp. was found in Constrictor from Dominica (see TABLE 3). Sambon (1922) describes 3 species from the Neotropical Region, P. crotali, P. clavatus and P. stilesi. Self and McMurry (1948) have pointed out that there is little to distinguish between the 3 species except for host records. P. crotali was described Crotalus (rattlesnake), P. clavatus from Boa and P. stilesi from Lachesis (bushmaster). Porocephalus sp. in Constrictor differs from the above reported species. First, the presence of auxiliary hooks attached to the outside pair was not found. This same condition was noted by Self and McMurry (1948) in their specimens. They suggested that further comparative studies need to be made to determine whether their specimens should be placed in a distinct species, or whether the auxiliary hooks should be eliminated as a generic characteristic. Since the present specimen is a second case of absence of the auxiliary hooks, it appears that the genus most certainly needs revision. Second, the length of the worm from Constrictor is considerably shorter than those recorded for the described species. While the ranges in length overlap for P. crotali, P. clavatus and P. stilasi, the longest female from Constrictor

is 15 mm shorter than the shortest length reported by Sambon (1922). *Porocephalus* from *Constrictor* most closely resembles *P. clavatus* in habitat and shape, except for size. One other species, *P. sublifer*, has been described in *Naja* from tropical and north Africa.

CHAPTER VI

HOST-PARASITE SPECIFICITY

Host specificity refers to the peculiar mutual adaptation which restricts a parasite to its host species. Most parasites are specialized and live in a specialized environment for which they have evolved through time and association with the host. Unnecessary organs and systems may have been lost and their functions replaced by those of the host species. Obviously this could lead to a rather high degree of host specificity.

No parasite lacks host specificity, but it is seldom absolute and often varies dependent upon the stage of the life cycle. Thus, one must show caution in interpretation of specificity of parasites in determining the phylogeny of hosts. For a large number of parasite species exist only in bottles on museum shelves based on variations of a minute character and represent a subjective judgment on the part of the worker who described them. Cameron (1964) states that the "genus" in parasitology is completely subjective and represents a grouping of convenience. Thus classification on an "either or" basis is phylogenetically significant only in its higher characteristics. Because parasites must have a host, their

phylogeny and classification should be interpreted only in terms of the phylogeny and classification of the host (Cameron, 1964). While the parallel evolution of hosts and parasites exists, "its uncritical application can result in grossly erroneous conclusions" (Stunkard, 1937).

Noble and Noble (1964) describe two categories of host-parasite specificity. Ecological specificity exists when the parasite may be able to live in a foreign host, but is prevented from doing so by some ecological barrier. Physiological specificity exists when the parasite is physiologically compatible with the normal host and physiologically incompatible with a foreign host. When physiological specificity results from behavior patterns, it may be called ethological specificity. Physiological specificity often means the parasite and its host have evolved together over evolutionary time resulting in phylogenetic specificity, a situation which may be used to help solve problems of host taxonomy.

Cameron (1964) has analyzed host-parasite associations and has arrived at eight type situations: (1) animals with comparable food habits have similar parasites; (2) only some groups of parasites show high host specificity; (3) old established hosts have numerous species of related parasites; (4) related hosts have a tendency to have related parasites;

(5) more highly specialized hosts have more highly specialized parasites and a more restricted fauna; (6) related parasites have evolved from a common ancestor whether in related hosts or not; (7) related parasites in unrelated hosts have developed divergent evolutionary lines; and (8) unrelated host groups with numerous related parasites must have lived together in their earlier days of evolution. Noble and Noble (1964), however, caution that as more intensive research discloses the existence of larger numbers of parasites, species once considered strictly host specific are often found not to be so.

Usually parasitic worms with direct life cycles such as nematodes show less host specificity than do worms with indirect life cycles such as digenetic trematodes and cestodes. A notable exception is monogenetic trematodes which are highly host specific but have direct life cycles. Worms with indirect life cycles usually show greater specificity for the intermediate host than for the definitive host.

Trematodes. Because of the complex life histories of digenetic trematodes one might expect them to be highly host specific, however, when distribution records are analyzed, one finds that specificity is not marked in all families. Although specificity exists to a great extent, closely related species may exhibit great differences in the degree of specificity.

Genera that show a wide host tolerance are usually limited to hosts which are ecologically related. Adult specificity is generally less than larval or juvenile specificity (Cheng, 1964).

Cestodes. Tapeworms are classified mainly on the basis of the different kinds of adhesive organs on the scolex which are adaptations to parasitism. The fact that they vary in different groups suggests that the modern classification is, on broad general lines, a phylogenetic one. The phylogenetic significance lies in the fact that series of similar types tend to occur in series of related hosts (Yamaguti, 1959). Baer (1952) states, "the data indicate that ecological specificity has been replaced by phylogenetic specificity, a much more intimate type of association that arose thousands of centuries ago when cestodes first became parasitic in the ancestors of species which today serve them as hosts." Snakes possess distinct and characteristic species of tapeworms (Noble and Noble, 1964). The host range of cestodes is often generic rather than specific. In colubrid snakes the characteristic tapeworm genus is the proteocephalan Ophiotaenia (Wardle and McLeod, 1952).

Acanthocephalans. Acanthocephalans seem to vary considerably as to host specificity. The Pacific pilotfish and the closely related Atlantic pilotfish each harbor a distinct

species of the same acanthocephalan genus (Noble and Noble, 1964). Cheng (1964) states that a single species can exist in more than one species of host, in fact, the same species may occur in several different families of a host species, but never occurs in different orders of host species. Nicholas (1967) also states that acanthocephalans show a remarkable lack of specificity towards a definitive host within orders. He cites examples where one species of acanthocephalan was found to use 84 species of birds as hosts, another used 11 species of mammals, and a third used 57 species and subspecies of fish as definitive hosts. Adult acanthocephalans occur as parasites of freshwater teleost fish and turtles, amphibia, birds and mammals. They are rare in marine fish and never occur as adults in terrestrial reptiles such as lizards and snakes. Juvenile acanthocephalans are often found encapsulated in the bodies of vertebrates that feed on the invertebrate intermediate host. These vertebrate hosts are known as paratenic hosts and are not necessary for the completion of the life cycle, but serve as transport host in the food chain to bring the juvenile acanthocephalan to a suitable definitive host. Lizards and snakes often serve as paratenic hosts.

Nematodes. There is little evidence of parallel evolution of hosts and their nematode parasites (Noble and Noble,

1964). The basic physical organization of nematodes seems to be suitable for a variety of environments. Parasitism has not lead to specialization as reflected by nematode morphology and life cycles which are simple and similar to free-living forms. The lack of specialization is indicative of the slight host specificity shown by nematodes (Rogers, 1962). However, Cameron (1964) states that definite distribution patterns exist among different groups of animals. The dominant nematodes of snakes and lizards are the oxyurids. Ascarids are rare in lizards, but common in snakes.

Pentastomids. Pentastomids appear to be highly host specific for poikilothermic vertebrates with 93% of the known genera using them exclusively as hosts. The remaining genera occur in tortoises, birds and mammals, and a large number of this percent are parasites of tortoises which are poikilothermic. Of the 93% of genera parasitizing poikilotherms, 43% are in snakes, 22% in crocodiles and 14% in lizards (Cheng, 1964).

CHAPTER VII

HOST-PARASITE ZOOGEOGRAPHY

The trematode genus Mesocoilium is unsuitable for the study of host phylogeny and zoogeography. The genus is not host specific and has worldwide distribution. From Dominica the same species of Mesocoelium was found to utilize three different families of lizards as definitive hosts. The infection of adult hosts apparently must depend on food habits, as all of the Dominican hosts are insectivorous and most likely have common items in their diets. This is an example of the first type of association as given by Cameron (1964), that is, animals with comparable food have similar parasites.

The cestode genus Ophiotaenia is an example of a genus which presents problematic questions with respect to host-parasite zoogeography. Harwood (1933) states that the Ophiotaenia group is almost certainly of monophyletic origin. Tapeworms are parasites that supposedly have a relatively high degree of host specificity (Baer, 1952; Yamaguti, 1959). Ophiotaenia is the characteristic tapeworm genus of colubrid snakes and was found in the colubrid Dromicus from Dominica. However, on the basis of Wardle and McLeod's (1952) species-groups, the worm in Dromicus is most morphologically similar to 8 species of Ophiotaenia described from fish, a mammal and

several families of reptiles. The problem can be approached from two directions. First, if the morphological similarity is indicative of the closeness of phylogenetic relation, then it must be assumed that little host specificity exists as reflected by host distribution. Second, if morphological similarity is not indicative of the closeness of phylogenetic relation, then each of the 8 species could be host specific as a result of convergent evolution of morphology without concurrent change in host specificity. Whichever is the case, the value of this parasite to host zoogeography is minified. There is no doubt that Ophiotaenia is the characteristic genus in the family Colubridae. It is probable that this cestode has evolved with this family of snakes, and that other hosts are the result of accidental infestation becoming permanent. However, because morphology is the only practical basis for determining the phylogenetic relations between parasites, the parasites have little value as an indicator of host phylogeny when they are very similar, but the hosts obviously not even closely related.

The nematode genera Terranova, Hastospiculum, Pharyngodon and Thelandros appear to be of little use to host zoogeography. They are all widely distributed as to hosts and geographic range. However, there are definite distribution patterns of nematodes among different groups of animals

to which this study adds supporting evidence. Ascarids are common in snakes, and the Dominican colubrid Dromicus was found to be parasitized by the ascarid Terranova. Oxyurids are the dominant nematodes of lizards. The Dominican lizards Hemidactylus, Sphaerodactylus, Thecadactylus and Anolis were found to harbor either the oxyurid Thelandros or Pharyngodon. These broad patterns indicate the lack of host specificity that is generally attributed to nematodes.

The zoogeography of the nematode genus Cruzia is very unusual. While this worm does not appear to be host specific, it is nonetheless localized geographically in South and Central America. The mammalian hosts of the genus are strictly New World animals. The family Didelphidae, American opossums, is confined to South, Central, and eastern North America, and the family Dasypodidae, armadillos, is confined to South and Central America, and north into the southeastern United States (Darlington, 1957). The recorded reptilian hosts, while not geographically limited at the family level, are limited at the generic level. The colubrid snake Erythrolamorus is confined to tropical America, Mexico and Texas, and the box turtle, Terrapene, ranges through eastern and central United States and Mexico (Terent'ev, 1961). The only other species of Cruzia described in reptiles was from an unidentified lizard taken in Mexico (Yamaguti, 1961).

Cruzia was found in Ameiva from Dominica. The family Teiidae to which Ameiva belongs is exclusively found in the New World. It appears that this nematode has evolved in the New World and has utilized New World hosts. The specificity of Cruzia is most likely determined by the food habits of the hosts, however, no life cycles have been determined. Opossums are most commonly omnivorous, whereas armadillos feed on insects, other invertebrates and some small vertebrates (Walker, 1964). Ameiva is carnivorous, feeding on snails, slugs and other invertebrates. The complex zoogeography of Ameiva in the West Indies has been recently re-evaluated by Baskin and Williams (1966). While the occurrence of Cruzia in Ameiva can add nothing to the knowledge of its' zoogeography per se, it adds further evidence to the obvious population of the West Indies by South American fauna.

The zoogeography of Ozolaimus and its host, Iguana, is readily apparent. Yamaguti (1961) lists this nematode as occurring only in I. tuberculata, synonym for I. iguana, from Brazil, Venezuela, Mexico and Cuba. O. megatyhlon is the only species in this genus (O. cirratus is a synonym for O. megatyhlon, Yamaguti, 1962). The nematode in Iguana delicatissima from Dominica fits the description of O. megatyhlon. Ozolaimus is evidently highly host specific for Iguana, suggesting that this parasite and host have been in

association for a long time and that the nature of this specificity is of significance to host phylogeny. I. delicatissima is closely related to and evolved from the mainland species I. iguana. The fact that both species harbor the same nematode is indicative of a common ancestor or cohabitation of the same area in the past. Dunn (1934b) suggests that Iguana delicatissima has evolved endemically to the islands in the middle of the Lesser Antilles chain, as I. iguana is found on the northernmost islands in the chain and on the continent to the south. It would be interesting to examine I. iguana from a northern island and see if it is also parasitized by Ozolaimus.

The genus Porocephalus (Pentastomida) is not highly host specific. It appears that any snake feeding on mammals, which serve as the secondary host for the larva, could be a possible definitive host. A thorough revision of the genus is needed to determine the significance of the auxiliary hooks. These two facts make it readily apparent that the presence of Porocephalus in Constrictor is of no phylogenetic or zoogeographic significance at the present state of knowledge.

CHAPTER VIII

CONCLUSIONS

The results of this study revealed that in two of eleven cases parasites were somewhat indicative of host zoogeography. *Cruzia* in *Ameiva* and *Ozolaimus* in *Iguana* add supporting evidence to a South American origin of the herpetofauna of Dominica and the Lesser Antilles. No parasite evidence was found to indicate possible colonization from Africa. The cosmopolitan genera *Hemidactylus* and *Mabuya* which are thought to have entered the New World through the West Indies from Africa on drift show no parasitological evidence of doing so. Based on host morphology, the herpetofauna of the Lesser Antilles reflects qualitatively, but not quantitatively, the fauna of South America. Darlington (1957) has written on the approximate relation of area to the number of species of herptiles present on certain West Indian islands. The situation on Dominica fits roughly into this schema. The Lesser Antilles are generally thought to have been populated from the southern end of the chain with South America being the source (Darlington, 1957, *Leptodactylus*; Baskin and Williams, 1966, *Ameiva*; and Lazell 1964b, *Constrictor*). However, the history of *Eleutherodactylus* cannot be traced (Darlington, 1957) and

Anolis from Dominica northward has clear Greater Antillean affinities (Williams, 1962). Thus the possibility of a northern route of colonization for some species from the Greater Antilles and ultimately Central America is more than just surmise. The author would suggest that a survey of the parasites of the herpetofauna of all major islands in the Lesser Antillean chain might provide more concrete evidence as to the direction of colonization.

Application of the "von Ihering method" appears to be limited until questions concerning degree of specificity, recognition of actual species of parasites, and geographic and host range of parasites are answered. As more and more hosts are examined for the presence of parasites, it has been found that parasites which were originally thought to be highly host specific are not as specific as assumed. Often in flatworms, the specific host will influence the morphology,on which species of parasites are usually based (Stunkard, 1957). Cheng (1964) conjectures that "the number of currently recognized species will be reduced because species reported from different hosts and established on that basis may be found to be infective to various hosts and thus shown to be identical. . . ." The differences in morphology of closely related species could represent intraspecific variation and not species characteristics. As records of

parasite geographic and host range become more complete the host-parasite zoogeographer will be able to arrive at more meaningful patterns of host relations and zoogeography. It is my opinion that the "von Ihering method" is a useful tool when applied with care and consideration of the available knowledge, and that its value as a tool will increase in the future as knowledge of distribution of parasites and hosts is broadened.

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APPENDIX

APPENDIX A

Four trematodes were found in the small intestine of Anolis oculatus montanus (WM-3063). A published description could not be found in the literature, therefore, the specimens are described by the following diagnosis and shown in FIGURE 2 as a proposed new genus and new species.

GENERIC DIAGNOSIS.-Plagiorchiidae, Astiotrematinae: Body long lanceolate, widest at level of testes, 5.1 to 7.1 mm. long by 1.28 to 1.43 mm. wide. Body covered with spines. Oral sucker moderately developed, subterminal, 0.37 to 0.45 mm. long by 0.28 to 0.31 mm. wide. Acetabulum in anterior one-fourth of body, 0.24 to 0.27 mm. round. Pharynx well developed, 0.27 to 0.34 mm. long by 0.22 to 0.25 mm. wide. Esophagus very small. Ceca moderately wide and terminating near posterior extremity. Testes large, entire, equal and tandem in posterior third of body and separated by uterine coils. Cirrus pouch large, 0.61 to 0.82 mm. long by 0.17 to 0.23 mm. wide, curved, extending back of acetabulum and enclosing a large winding seminal vesicle and ovoidal prostatic complex. Protrusible cirrus ? Genital pore slightly out of median line and preacetabular. Ovary postequatorial and nearer to anterior testes than to acetabulum. Receptaculum seminis dorsal and posterior to ovary. Shell gland posterior to ovary. Laurer's canal present. Uterus in transverse coils, passing between the two testes and reaching to near cecal ends, mainly intercecal, but overlaps in spots. Eggs numerous, oval, 0.023 to 0.027 mm. long by 0.0013 to 0.015 mm. wide. Metraterm ? Vitelline follicles extending in lateral fields from midway between ovary and acetabulum to near cecal ends. Excretory vesicle Y-shaped ?, arms reaching almost to oral sucker. Intestinal parasite of Iguanidae.

The new worm needs only to be differentiated from the genus Parallopharynx (see Yamaguti, 1958, p. 427 for generic description). The new trematode has a long lanceolate body

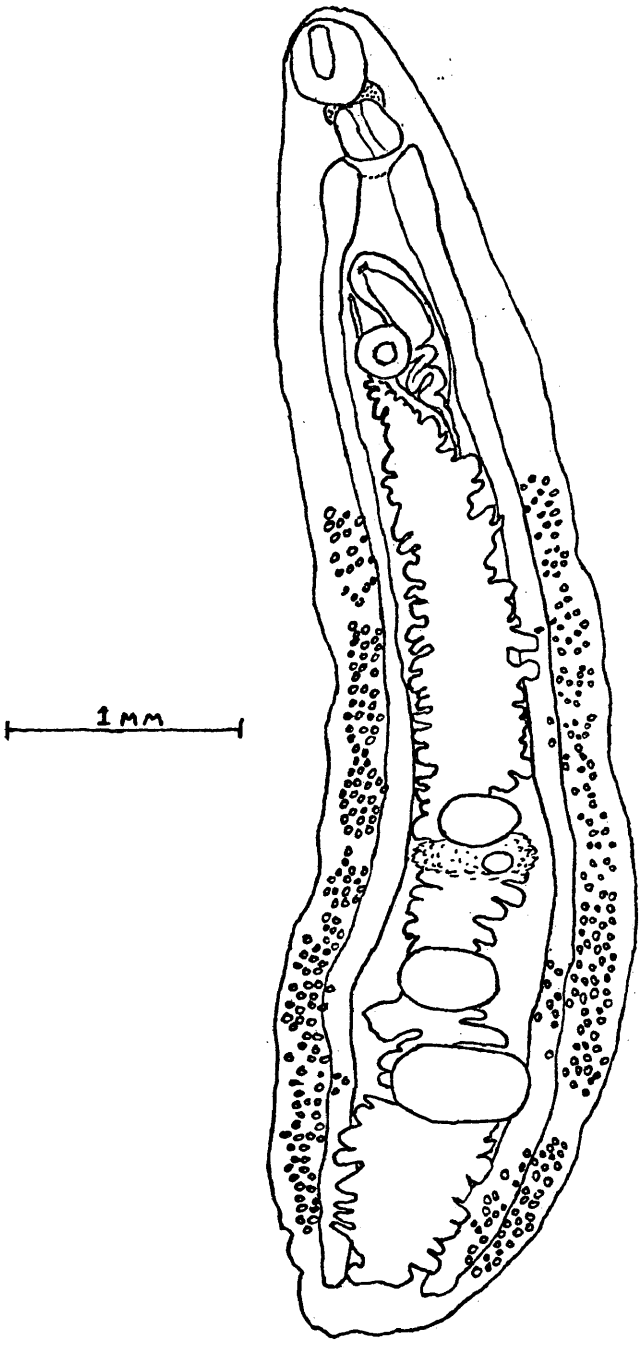

FIGURE 2

Omnipharynx anolis n.g. n.sp.

covered with spines as opposed to a more slender, flattened cylindrical body without spines in Parallopharynx. A prepharynx is absent in the new trematode. The remaining features of the two worms are very similar. Both worms are intestinal parasites in Iguanidae as opposed to the trend of the subfamily to parasitize chelonians and fish. There is only one species in the genus Parallopharynx, P. arctus, described from the small intestine of Basiliscus vittatus from Guatemala (Yamaguti, 1958).

The new genus has been designated Omnipharynx on the basis of the new prominence of a pharynx in a digestive system where a prepharynx is absent and where the esophagus is practically absent. Also, to add to the conformity of nomenclature, the name will serve to associate it with the genus Parallopharynx and the genus Allopharynx which are in the same subfamily. The genotype has been named O. anolis to indicate its genotypic host.

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