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Earthworms of the British Solomon Islands Protectorate

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Fifteen species of earthworms are known from the British Solomon Islands. Of these, 11 are referred to the megascolecid genus *Pheretima* and one to each of the megascolecid genera *Pontodrilus*, *Dichogaster* and *Ocnerodrilus*, and the glossoscolecid genus *Pontoscolex*. Four species of *Pheretima* are known only from the Solomons; all other species are widely distributed peregrine forms. Reasons are given for regarding *Pheretima bifida* Gates and *P. lavangguana* Gates as synonyms of *P. solomonis* (Beddard). *Pontodrilus matsushimensis* Iizuka is recorded from the intertidal zone of Solomons shores. It is also known from the shores of other Pacific islands and is probably dispersed by ocean currents.

Within the Solomons there is no apparent relationship between the distribution of earthworms and contemporary geographic barriers. The small number of species, predominance of peregrines associated with man, and lack of evidence of endemism and adaptive radiation indicate that most, if not all, the species (except *P. matsushimensis*) have probably been introduced by man. Geological evidence does not favour former land connexions between the Solomons and any of the adjacent large land masses. The character of the earthworm fauna indicates that any such connexions are most unlikely to have existed. The earthworm fauna is examined in relation to various biogeographic theories, including the equilibrium theory of MacArthur & Wilson (1963, 1967). It is concluded that the earthworms of the Solomons have not attained a state of equilibrium in the sense of these authors' theory, and that factors not considered in the equilibrium theory are primarily responsible for the present constitution of the earthworm fauna.

Some aspects of the ecology of the intertidal earthworm *P. matsushimensis* are discussed.

Introduction

During the Royal Society Expedition to the British Solomon Islands, 1965, large numbers of earthworms were collected by the author and others from the islands of Guadalcanal (Mt Gallego, Mt Popomanaseu, and terraces south of Honiara), San Cristobal (near Wainoni in the catchment areas of the Warahito and Huni Rivers), Ugi, Kolombangara, Santa Isabel, San Jorge, and from islets in Thousand Ships Bay. Much of the sampling was from inland sites in mountainous terrain, but coastal sites were also sampled and a search was made for intertidal species in beach sands. Sorting and identification of the collections are not yet completed, and a detailed taxonomic study will be published in a later paper.

Gates (1959) studied collections of earthworms made by the Danish (1951) and British (1953) expeditions to Rennell Island, south of Guadalcanal. He found six species of *Pheretima* Kinberg and one of *Dichogaster* Beddard. Gates recorded three previously unknown species of *Pheretima*, but the remainder were common pantropical species and he concluded that it could not be assumed that Rennell Island had any endemic earthworms and considered it most likely that all the earthworms found were probably introduced, by man, from lands to the west.

Gates's paper is the only comprehensive study of any section of the Solomon Islands earthworm fauna. Small collections from widely separated localities have been examined by other authors. Beddard (1899) described *P. solomonis* from the New Georgia Islands and from Guadalcanal he recorded *P. loriae*, a species described previously from New Guinea (Rosa 1898). Michaelsen (1913) recorded the pantropical *P. posthuma* (L. Vaill.) from Santa Cruz. Gates (1938) described two new species, *P. bifida* and *P. copulata*, from Ugi, and recorded from Santa Cruz the common Pacific Islands species *P. esafatae* (Beddard). Cernosvitov (1942) found three pantropical species, *Ocnerodrilus occidentalis* Eisen and *Pontoscolex corethrurus* (Muller) in collections from Tulagi, and *Dichogaster bolaui* (Michaelsen) from Tulagi and Guadalcanal.

The present paper concerns the general constitution of the earthworm fauna of the British Solomon Islands, and the distribution and biogeographic relationships of the species.

Constitution of the earthworm fauna

Species of earthworms recorded from the British Solomon Islands by previous authors and in the present collections are listed in table 19.

Synonymy of Pheretima solomonis, P. bifida *and* P. lavangguana

P. bifida and *P. lavangguana*, described by Gates (1959), are distinguished from *P. solomonis* principally on the basis that:

(1) *P. solomonis* has one pair of spermathecae in each of v, vi, vii, viii, and ix; *P. bifida* has two pairs in each of v, vi, vii, viii and ix; *P. lavangguana* has two groups of spermathecae, with one to five in each group, in each of v, vi, vii, viii and usually in ix.

(2) *P. solomonis* has a median ventral unpaired female pore; the female pores of *P. bifida* and *P. lavangguana* are paired, close together.

(3) The number and arrangement of tubercula pubertatis varies.

(4) The testis sacs of *P. bifida* are said to be U-shaped, one per segment, while those of *P. solomonis* and *P. lavangguana* are separated median ventrally (i.e. there are two per segment).

In the present collection there are specimens that correspond with the descriptions of each of the three species, but in a large series of specimens collected near the mouth of the Huni River, in eastern San Cristobal, there are specimens with the characters of each of the species as defined and other specimens with various combinations of the characters of the three species. There would seem therefore to be no basis for retaining the three species and *P. bifida* and *P. lavangguana* must be regarded as synonyms of *P. solomonis*. Results of a detailed study of variation in *P. solomonis* will be published in a later paper. Taking *P. bifida* and *P. lavangguana* as synonymous with *P. solomonis* a total of 15 species of earthworms has now been recorded from the British Solomons.

Endemism

The species recorded may be divided into four groups:

(1) *Pheretima posthuma*, *P. hawayana*, *Dichogaster bolaui*, *Ocnerodrilus occidentalis* and *Pontoscolex corethrurus*, which are among the most widely distributed earthworms of tropical regions.

(2) *Pheretima esafatae*, *P. upoluensis*, *P. montana*, and the intertidal earthworm *Pontodrilus matsushimensis*, which are widely distributed in lands of the western and south-western Pacific.

TABLE 19. SPECIES OF EARTHWORM RECORDED FROM THE BRITISH SOLOMON ISLANDS

species	Solomons collection localities: previous records and references	Solomons collection localities: present collection	distribution outside Solomons
Fam. MEGASCOLECIDAE			
G. *Pheretima*			
1. *P. solomonis* (Beddard)	New Georgia (Beddard 1899)	Guadalcanal; Kolombangara; San Cristobal	not known elsewhere
2. *P. bifida* Gates	Ugi (Gates 1938)	Guadalcanal; Kolombangara; San Cristobal	not known elsewhere
3. *P. lavangguana* Gates	Rennell (Gates 1959)	Guadalcanal; Kolombangara; San Cristobal	not known elsewhere
4. *P. copulata* Gates	Ugi (Gates 1938)	—	not known elsewhere
5. *P. rennellana* Gates	Rennell (Gates 1959)	—	not known elsewhere
6. *P. pickfordi* Gates	Rennell (Gates 1959)	Guadalcanal	not known elsewhere
7. *P. loriae* (Rosa)	Guadalcanal (Beddard 1899)	—	New Guinea
8. *P. posthuma* (L. Vaill.)	Santa Cruz (Michaelsen 1913)	—	cosmopolitan in tropics
9. *P. esafatae* (Beddard)	Santa Cruz (Gates 1938) Rennell (Gates 1959)	—	widespread in western and south-western Pacific Islands
10. *P. upoluensis* (Beddard)	Rennell (Gates 1959)	—	widespread in western and south-western Pacific Islands
11. *P. montana* Kinberg	Rennell (Gates 1959)	—	widespread in western and south-western Pacific Islands
12. *P. hawayana* (Rosa)	—	Guadalcanal	cosmpolitan, especially in Pacific area
13. *P. sangirensis* (Michaelsen)	—	Kolombangara	Indonesian area
G. *Pontodrilus*			
14. *P. matsushimensis* Iizuka	—	San Cristobal; Santa Isabel	widespread intertidal species of Pacific Islands
G. *Dichogaster*			
15. *D. bolaui* (Michaelsen)	Tulagi; Guadalcanal (Cernosvitov 1942); Rennell (doubtful record; Gates 1959)	Guadalcanal; Kolombangara	cosmpolitan in tropics
G. *Ocnerodrilus*			
16. *O. occidentalis* Eisen	Tulagi (Cernosvitov 1942)	—	cosmopolitan in tropics
Fam. GLOSSOSCOLECIDAE			
G. *Pontoscolex*			
17. *P. corethrurus* (Muller)	Tulagi (Cernosvitov 1942)	Kolombangara	cosmopolitan in tropics

(3) *Pheretima sangirensis* and *P. loriae*, known from the Indonesian–Melanesian area to the west of the Solomons.

(4) *Pheretima solomonis*, *P. copulata*, *P. rennellana*, and *P. pickfordi*, known only from the Solomons.

Only the last of these four groups can be regarded as possibly endemic. Very little is known of the earthworms of New Guinea and its surrounding islands, and much remains to be learned of those of Indonesia. Further knowledge of the earthworms of these regions may show that the four species at present known only from the Solomons are more widely distributed. At present it can only be said that they may be confined to the Solomons.

Distribution and biogeographic relationships

Distribution within the Solomon Islands

The distributions of the fifteen species known from the Solomon Islands show no clear relationship to geographical barriers between or within islands, nor to altitudinal zonation of soils and vegetation.

Pheretima copulata is known only from Ugi Island, off the coast of San Cristobal, and *P. rennellana* only from Rennell Island. However, the apparent isolation of two species, each on a particular island, is slight evidence on which to base any generalization on the effects of geographic isolation on speciation, particularly when other species are widely distributed on various islands and when earthworm collections have not been made from much of the area of the Solomons. Other species at present known from only one island in the Solomons have all been recorded from areas outside the Solomons and no inferences concerning distribution within the Solomons archipelago can be drawn from them.

A series of collections made on Kolombangara Island during the Expedition clearly illustrates the lack of correlation generally found between species of earthworms and altitudinal zonation of soils and vegetation. Earthworms were collected along a transect about 10 miles long from sea level at Dolo Cove, on the south coast, to the south summit of Kolombangara at 5540 ft. The transect covered a sequence of vegetation types from swamp forest and grassed village areas on the coastal platform through lowland rain forest, montane rain forest, to upper montane mossy rain forest. Populations were small and among the 219 specimens collected only four species, *Pheretima solomonis* (including forms similar to *P. lavangguana* Gates), *P. sangirensis*, *Dichogaster bolaui*, and *Pontoscolex corethrurus*, were found. *P. corethrurus* was found only under grassland on the coastal platform and in lowland forest close to Kuzi village, while the distribution of the other three species showed no relation to altitude and forest zonation. At well-drained sites on the coastal platform and in the lowland forest at about 200 ft. altitude earthworms were found in the upper 3 in. of the mineral soil, but at all other sites sampled earthworms were collected only from above-ground habitats; they were found in rotting logs, under bark of trees, in clumps of moss, and most commonly in accumulations of organic matter at the bases of epiphytes and between the leaf bases of living Pandanaceae and of some palms. The smallest species (*D. bolaui*) was most common, probably because it can most easily live in the confined spaces where most earthworms were found.

Biogeographic relationships

The earthworms of south-east Asia, western and south-western Pacific lands are predominantly Megascolecidae. It seems most likely that megascolecid earthworms have spread from the Indo–Malayan area, south-eastward (Lee 1959), as have many other groups of animals and plants (Fleming 1962, 1964; Darlington 1965; and many other authors).

Gressitt (1956) discusses distribution patterns of Pacific Islands animals, especially beetles. He concludes that the islands of the Pacific basin, apart from New Zealand, Lord Howe, Norfolk, Chatham, and the islands south of New Zealand, should be regarded as part of the Oriental region, which would also include New Guinea and the Cape York Peninsula in Queensland. The remainder of Australia, New Zealand, Lord Howe, Norfolk and Chatham Islands are grouped in an Australian region. Gressitt subdivides the Pacific portion of the Oriental region into a number of subregions. He includes the Solomon Islands in a Papuan subregion, with the Cape York Peninsula, New Guinea, the Bismarcks, eastern Celebes, and small islands adjacent to New Guinea. The oceanic Pacific islands are assigned to a Polynesian subregion, with a composite fauna that represents a gradual attenuation of the fauna of the Papuan subregion and to a lesser extent of those of the Philippine, 'Wallacea', Malayan, and other subregions. He places New Caledonia and its adjacent islands in the Oriental region as a division of the Polynesian subregion. Evidence from the distribution of earthworms supports Gressitt's conclusions, except that New Caledonia would seem to be distinct, with a high degree of endemism, especially in the genus *Acanthodrilus* (see Michaelsen 1913), which is confined to New Caledonia, the neighbouring island of Maré, and Raoul Island in the Kermadecs. The New Caledonian earthworms are more nearly allied to those of New Zealand than to those of the Oriental region as defined by Gressitt (Lee 1959), and would be better included with those of Gressitt's Australian region.

The megascolecid earthworms of Gressitt's Indo-Chinese, Malayan, and other subregions of the Oriental region eastward into the Pacific Basin (except the New Caledonian division) include a variety of genera, but are probably best characterized by the genus *Pheretima*. There is a large number of species of *Pheretima* in south-east Asia, the Philippine and Indonesian archipelagos, and in New Guinea, and a few species, most of them very widespread, in the islands to the eastward, including the Solomon Islands. Gressitt's Australian region is also characterized by a variety of megascolecid genera, some shared with the Oriental region, but including a high proportion of endemic genera, especially in New Zealand, where 14 of the 27 megascolecid genera are confined to New Zealand and adjacent islands (Lee 1959).

Darlington (1957) states that the occurrence of animals on islands depends on many things, including the nature and powers of dispersal of different animals; comparative ecology (degree of favourableness and diversity) of different animals; the direction of winds and currents, now and in the past; the nature of the nearest mainland (whether old or new land, whether ecologically favourable, whether inhabited by a large or small fauna, whether with rivers discharging drift, etc.); the effect of competition or reduction on the fauna; the area of the particular islands to be colonized; the distance to be crossed from the source to the island. He notes that some of these factors are so complex and difficult to measure that their significance cannot be assessed, but points out that for some animals on some islands area and distance can be shown to be critical factors. In later papers Darlington (1959, 1965) discusses evidence from many groups of animals and plants and concludes that there is a correlation of number of species in different places with area and with climate. Direction of dispersal is more from large to small areas and from favourable to unfavourable climates than the reverse.

MacArthur & Wilson (1963, 1967) have emphasized the importance of island area and distance from a source of immigrants in determining species diversity in island faunas, and have shown that area and distance from a source of immigrants can account for much of the observed pattern of island distribution in some of the examples they have selected. They have put forward a number of hypotheses and have developed mathematical models relating area and distance to rates of immigration and extinction of species, and rates of immigration and extinction to species numbers and many aspects of the ecology of island faunas. Their hypotheses do not allow for differences in climate or habitat diversity, which Darlington has shown to be important, but these are not easily quantified. Given a series of islands reasonably similar physically, with similar climate (such as the series from New Guinea to the Solomons and other south-west Pacific archipelagos with rain-forest vegetation), habitat diversity must vary roughly in proportion to island area. There is therefore likely to be a reasonable correlation between diversity of species of some animal groups, especially those that have well-developed behavioural adaptations for dispersal, and island area, as MacArthur & Wilson have shown. The correlation that is found may, however, be primarily with habitat diversity but may be manifest as such only in a less similar series of islands; such a correlation would appear to be directly with area where differences in climate and habitat diversity are minimal. The Solomons earthworms show no recognizable relationship of species diversity to island areas as suggested by MacArthur & Wilson's hypotheses.

MacArthur & Wilson put forward an equilibrium model that relates the rate of entry of new species into an island to the rate of species extinction on the island. When these two rates are equal, a state of equilibrium is attained and the number of species present is in equilibrium. That such equilibria must exist is almost axiomatic, and is implicit in a passage from Darwin (1859), quoted by Darlington (1965, p. 57). However, MacArthur & Wilson have attempted to bring some precision to the concept and to develop hypotheses that have general application to island biogeography. For the equilibrium model to apply to any particular group of animals (or plants) it is essential that a state of equilibrium must have been attained. The time required for equilibrium to be reached must depend on many attributes of an animal group, including the availability of immigrant species able to colonize an island, the means of dispersal available to the animals, and their ability to survive in transit to the island. It seems likely that earthworms are an ancient and slowly evolving group of animals (Lee 1959). Also it is known that, with the exception of a few species, megascolecid earthworms are unable to survive immersion in sea water. These two factors greatly affect their present distribution and their dispersal to isolated land areas. It is unlikely that anything approaching a state of equilibrium in the sense of MacArthur & Wilson's model has been attained by Solomon Islands earthworms. At present there are only fifteen species known from the Islands, and of these only four are not known elsewhere and five are among the most widely distributed earthworms of tropical regions. There is no evidence of the high degree of adaptive radiation or ecological specialization characteristic of megascolecid earthworms in New Caledonia (Michaelsen 1913) and New Zealand (Lee 1959). Darlington (1957) considers that the level of endemism shown by a group of animals on an island indicates whether they have dispersed across wide ocean gaps by natural means or have been carried by man. If they have dispersed naturally it is reasonable to assume that they have been arriving for as long as suitable conditions for their dispersal and establishment have existed, i.e. in the case of the Solomons probably since mid-Tertiary times, and there should be a high level of endemism on the islands, as in the megascolecid earthworms of New Caledonia and New Zealand. If they have been carried by man they can have been on remote islands for at most only a few thousand years, and the level of endemism should be low, as in the megascolecid earthworms of the Solomon Islands. Gates (1959) concluded that six species of *Pheretima* that he identified from Rennell Island have probably been introduced by man from the large land masses to the west, while *Dichogaster bolaui*, the only other earthworm known from Rennell, has probably been similarly introduced and must have originated from America or Africa. Of the 15 Solomons species it seems likely that most, if not all, the species of *Pheretima* have been introduced from the west and spread within the Solomons archipelago by Melanesian and Polynesian man, that *Dichogaster bolaui*, *Ocnerodrilus occidentalis* and *Pontoscolex corethrurus* have been introduced in the same way, or possibly by European man as they apparently have been in many tropical countries, and that only the intertidal earthworm *Pontodrilus matsushimensis* has reached the Solomons by natural means, dispersed by ocean currents.

The equilibrium hypothesis of MacArthur & Wilson is not affected by the mode of migration of species that reach an island. It is sufficient that the species arrive, by whatever means. However, the modes of migration available to any particular group of animals do affect the chances of arrival in any given time, and so affect the rate of immigration in MacArthur & Wilson's equilibrium model. For a group of animals such as earthworms, greatly restricted in their ability to cross ocean gaps, the time required for equilibration on isolated islands must be very long, long enough that though there has apparently been land in the Solomons area since mid-Tertiary times, earthworms are still in a preliminary stage of establishment and spread and these considerations apparently outweigh all others in determining the present distribution pattern. By contrast, for animals such as birds and flying insects, with well-developed powers of dispersal across ocean gaps, the time required to attain equilibrium would be expected to be relatively short. That such groups do fit MacArthur & Wilson's hypotheses reasonably well is shown in some of the examples chosen to illustrate their thesis. Lee (1968) discusses the distribution of megascolecid earthworms on sub-antarctic islands. The islands (apart from Auckland Islands, which have some species related to New Zealand megascolecids) were apparently depopulated during the Pleistocene glaciations. A small group of euryhaline species of *Microscolex* has apparently spread, carried by the West Wind Drift, in an easterly direction from South America. On individual islands there are only one or two species of *Microscolex*, and in the absence of competition they have spread through various habitats from the intertidal zone to upland soils. They are analogous to *Pontodrilus matsushimensis* in the Solomon Islands. Subsequently, two species of Lumbricidae have been introduced, apparently by man. These species are analogous to the widely distributed species that make up the remainder of the Solomons fauna.

MacArthur & Wilson's equilibrium model takes no account of the order in which events occur. Nemertine worms are found living in terrestrial habitats on some isolated islands and not on others. Apparently they can only become established in the absence of land planaria, so that the order of arrival of immigrants is critical for some animal groups. It seems likely that MacArthur & Wilson's hypotheses apply to some groups of animals on some islands, but as a general theory to explain the biogeographic relationships of island faunas and floras they may prove to be inadequate.

It is apparent from the constitution of the earthworm fauna of the Solomon Islands that there can have been no continuous land connexion between the Solomons and any other substantial land mass such as New Guinea, New Caledonia or Australia. To explain the present distribution of figs (*Ficus* spp.) Corner (1967) has postulated a series of former land connexions, probably in Jurassic times, connecting the Solomons to New Guinea, New Caledonia, the New Hebrides, and eastward across the Pacific Ocean to tropical South America. If these land connexions existed, megascolecid earthworms would have spread along them into the Solomons and should by now have radiated and given rise to a wide variety of endemic species, as they have in New Caledonia (Michaelsen 1913) and New Zealand (Lee 1959). That there is no evidence of such radiation indicates that land connexions could not have existed. The Solomons are separated by deep ocean from other land areas, and are of volcanic, volcanically derived sedimentary, or organogenic origin; there is no geological evidence of possible former land connexions.

The intertidal earthworm *Pontodrilus matsushimensis*

Pontodrilus matsushimensis was originally described (Iizuka 1898) from the intertidal zone of beaches in Japan. It has since been found on the shores of many Pacific islands. In the Solomon Islands the species was found sporadically in beach sands on the shores of eastern San Cristobal and at Santa Isabel. It was always confined to a narrow zone not more than 2 to 3 ft. wide under stranded leaves, branches and algae at high-water mark, and most specimens were collected from wet sand just above the level of the water table.

On the north-eastern shore of the bay at the mouth of the Huni River in eastern San Cristobal, *P. matsushimensis* was collected from pockets of coral sand among low coral outcrops. Forest trees, growing on a low coastal coral platform, overhung high-water mark. *Pheretima solomonis* was collected from the shallow rendzina under forest on the coral platform, and specimens were found right down to the narrow strip of deep litter that had accumulated along the base of the coral platform. Specimens were found down to 1 in. above high-water mark. *Pontodrilus matsushimensis* was confined to the coral sand immediately below the litter layer. The relationship of the two earthworm species to the edge of the sea and the coastal platform is shown in figure 47.

Freshwater springs are commonly found along shore lines close to high-water mark, and the ground-water of sands inhabited by *P. matsushimensis* may frequently have a salinity lower than that of sea water. To test the ability of *P. matsushimensis* to live in sea water specimens were taken from sand at high-water mark and put into a small pool of sea water among coral outcrops exposed at low tide. All specimens showed immediate signs of irritation; they writhed and exuded coelomic fluid from dorsal pores and nephridiopores, but within 10 min of being placed in sea water they relaxed and then burrowed into the coral sand on the bottom of the pool. The initial response is similar to that evoked in most megascolecid and in lumbricid earthworms when placed in sea water, but this behaviour is followed in the majority of species by paralysis and death instead of relaxation and burrowing as in *P. matsushimensis*. The behaviour of *P. matsushimensis* indicates that it is able to adjust rapidly to the osmotic conditions of sea water. Absence of the species from soil and litter slightly above high water mark (figure 47) indicates that although it can tolerate higher levels of salinity than 'normal' earthworms it cannot adjust to the low levels normally found in soil and litter. In this respect it differs from *Microscolex* spp. of subantarctic islands.

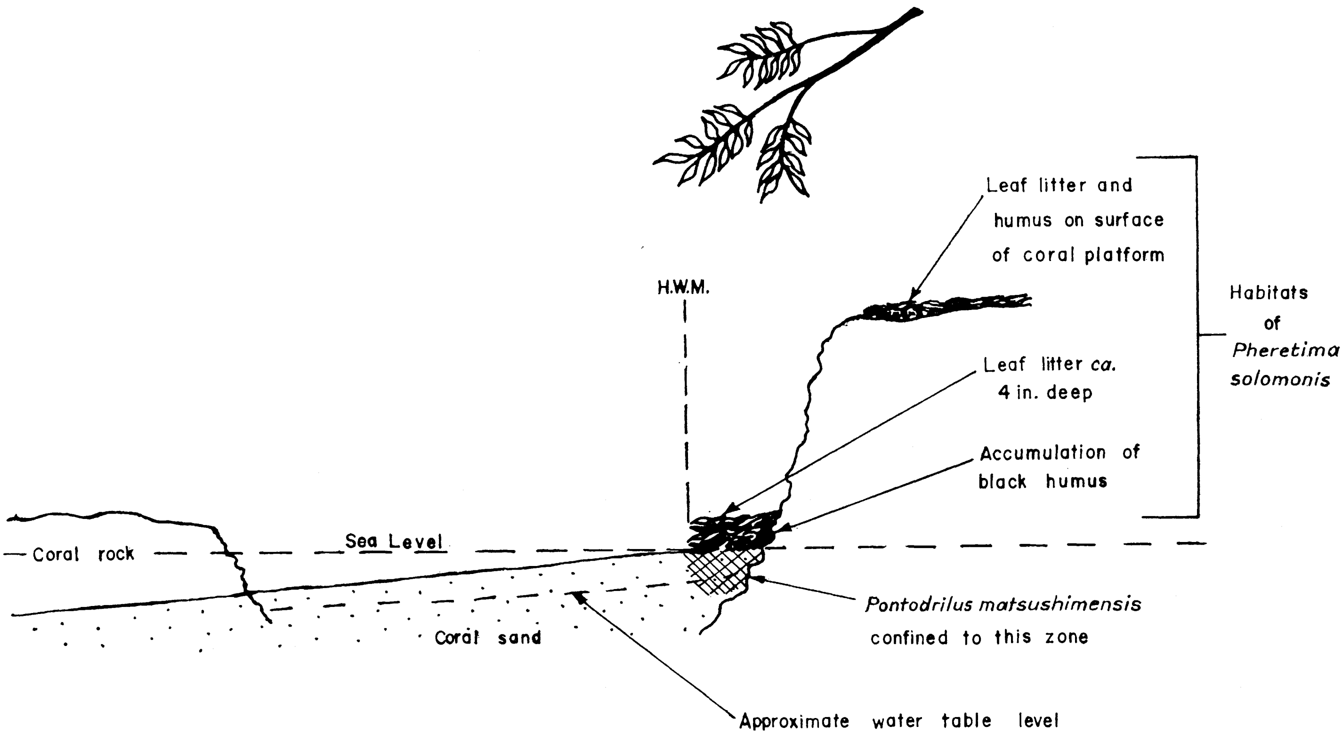

FIGURE 47. Habitats of *Pontodrilus matsushimensis* and *Pheretima solomonis* on and adjacent to the shore, eastern San Cristobal.

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