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The Present Distribution of the Onychophora, a Group of Terrestrial Invertebrates

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CONTENTS

PREFACE

A close study of the geographical distribution of almost any class of animals emphasizes certain features which are obscured, or sometimes entirely masked, in the geographical distribution of other types, and it is therefore essential, if we would lay a firm foundation for zoögeographical generalizations, that the details of the distribution of all types should be carefully examined.

Not only do the different classes of animals vary in the details of their relationships to the present land masses and their subdivisions, but great diversity is often found between families of the same order, and even between genera of the same family. Particularly is this true of nocturnal as contrasted with related diurnal types.

As a group the onychophores have been strangely neglected by zoölogists. Owing to their retiring habits they are difficult to find, and few collectors have devoted their attention particularly to them. Thus the majority of the species are known from very few specimens, which often were collected more or less accidentally. For instance the original examples upon which the Rev. Lansdown Guilding based the name *Peripatus juliformis,* creating for the new form the class Polypoda in the phylum Mollusca, were collected by him in St. Vincent in 1825; only once since have specimens of this species been

found—by Mr. H. H. Smith in 1894—though many naturalists, myself among the number, have searched for them.

It is of course impossible to approach a discussion of the distribution of the onychophores in the same way in which one would approach a discussion of the distribution of better known types, for the number of genera and species yet remaining to be discovered is undoubtedly large in proportion to the number of the genera and species which have already been described, while we do not know with any degree of accuracy the range of even a single form.

In many of the zoögeographically most important regions of the world no onychophores have as yet been found, though in some of them they certainly exist. Unidentified species, which were not preserved, have been met with in the Philippines and in Fiji, but none have been reported from New Caledonia, Samoa, the Solomon Islands, Halmahera, Celebes, Borneo, the Sunda Islands east of Sumatra, or Madagascar, where almost certainly they occur, or in southeastern Asia outside of the Malay Peninsula, though there should be representatives of the group in Ceylon and southern India as well as in Burma and Siam and the adjacent lands. Excepting for those in the Cape Colony and Natal we know practically nothing of the African types.

A discussion of the distribution of the onychophores therefore must take the form of a simple exposition of the generally accepted facts in zoögeography and palæogeography, and an exposition of the evidence for or against these facts presented by the species of the group as we know them now.

THE ONYCHOPHORES APPARENTLY AN ANCIENT TYPE

Although we have no palæontological evidence upon which to base our statement, it would appear that the onychophores represent a very ancient type for, like most ancient types, (1) they are strictly nocturnal, (2) they are all built upon the same plan with very little deviation from the mean, and (3) they indicate land connections which we know to have been very ancient.

THE PHYSICAL AND ECOLOGICAL DISTRIBUTION OF THE ONYCHOPHORES

So far as we know, the onychophores are confined within a relatively narrow and circumscribed physical range; that is, they require a fairly uniform temperature within very moderate extremes, and a uniformly high humidity.

This means that many barriers have operated as a check to their dispersal which are readily passed by the great majority of the other terrestrial types, both invertebrate and vertebrate, and suggests that the facts presented by the distribution of the onychophores possesses exceptional value.

Although existing within very narrow physical limits, the onychophores are in certain ways more independent of their immediate surroundings than the great majority of invertebrates, for they are predacious, and apparently feed upon any organisms small enough for them to overcome. This renders them quite independent of the distribution of the plant species, which determines the distribution of many insects, and which in turn is governed to a large extent by the underlying geology of the regions in which the plants occur.

THE THERMAL DISTRIBUTION OF THE ONYCHOPHORES

The mean annual temperature of the portions of the world inhabited by the onychophores varies from 50° to 80° F. (10.00° to 26.67° C.), though certain forms occur locally in average temperatures slightly in excess of both of the extremes given. So far as we are able to calculate from the estimated temperatures of their habitats, most of the species occur between the limits of 60° and 70° F. (15.56° and 21.11° C.), which appears to be the optimum temperature range for the group, suggesting that it was between these temperatures that these animals originated.

A critical study of the recent crinoids shows that their optimum temperature is between 55° and 65° F. (12.78° and 18.33° C.), and I have suggested that it was probably within this temperature range that the post-palæozoic crinoid fauna, at least, attained its greatest development.[1]

Combining the data deduced from the study of these two groups, the one marine, the other terrestrial, we find a coincidence of the optimum conditions for both between 60° and 65° F. (15.56° and 18.33° C.).

GENERAL FEATURES OF THE DISTRIBUTION OF THE ONYCHOPHORES

The most striking feature of the geographical distribution of the onychophores as we know it today is the restriction of all the species

[1] Une étude philosophique de la relation entre les crinoïdes actuels et la température de leur habitat. Bulletin de l'Institut Océanographique (Fondation Albert Ier, Prince de Monaco), No. 294, 20 Juin, 1914.

to the region south of the Tropic of Cancer, and of the great majority of them to the southern hemisphere; only in the West Indies and in Central America do we find an appreciable number north of the equator.

Another very striking feature is the geographical distinctness of the systematic units. Nowhere, so far as we know, do species of the Peripatidæ and of the Peripatopsidæ occur together. The two subfamilies of the Peripatidæ are separated by the entire breadth of the Indian Ocean.

In the subfamily Peripatinæ, *Mesoperipatus* is separated from *Oroperipatus, Macroperipatus, Epiperipatus, Plicatoperipatus* and *Peripatus* by the expanse of the Atlantic Ocean; *Plicatoperipatus* is isolated on the island of Jamaica where, however, *Peripatus* is also found; *Oroperipatus* occurs almost exclusively west of the watershed between the Pacific and the Atlantic in Central and South America; *Peripatus,* however, also occurs within its territory; *Macroperipatus* and *Epiperipatus,* both generally distributed over tropical America east of the Andes, occur over practically the same area, though the former is absent from Tobago and Grenada where the latter occurs; *Peripatus* is found with them over a small area in northern Venezuela. *Peripatus* alone occurs in the Antilles, except on Jamaica, where *Plicatoperipatus* also is found, and on Cuba, Grenada, Tobago and Trinidad, from which islands it is absent.

The two subfamilies of the Peripatopsidæ are entirely separate in the Australian region, one (Peripatopsinæ) being confined to New Guinea and the adjacent islands, the other (Peripatoidinæ) occurring in Australia, Tasmania and New Zealand, though both exist together in South Africa; in each subfamily the genera found in South Africa represent a systematic type markedly different from that found further to the east. The subfamily Peripatoidinæ is represented in Chile.

We are thus able to recognize among the onychophores traces of a zonal distribution such as is suggested by many other types, best marked in the east, the Peripatidæ being equatorial (the Malay Peninsula and Sumatra, central Africa and tropical South and Central America), the Peripatopsinæ intermediate (New Britain, New Guinea and Ceram, Natal, and the adjacent portions of Cape Colony), and the Peripatoidinæ austral (Australia, Tasmania and New Zealand, Natal and the Cape Colony, and Chile).

THE DISTRIBUTION OF THE PERIPATIDÆ

The distribution of the species of Peripatidæ indicates that, so far as the onychophores are concerned, Sumatra and the Malay Peninsula, central Africa and tropical America collectively form a zoögeographical unit.

This agrees with what we conclude from the distribution of other types, most of which, however, fall into two groups, an Afro-American and an Afro-Malayan.

No onychophores have as yet been reported from southern India. On the basis of what we know of other forms we would expect in this region a genus or genera more closely related to African than to Malayan types.

Of the genera inhabiting the zoögeographic area under consideration *Eoperipatus* (belonging to the subfamily Eoperipatinæ) of Sumatra and the Malay Peninsula shows the highest degree of specialization, and is rather abruptly differentiated from the remaining three genera, which collectively form a distinct systematic unit (the Peripatinæ).

Mesoperipatus of central Africa is considerably less specialized than *Eoperipatus,* though more specialized than *Peripatus* of eastern South and Central America, which in its turn is more specialized than the very primitive and worm-like *Oroperipatus* of South and Central America west of the crest of the Andes.

EXPLANATION OF THE DISTRIBUTION OF THE PERIPATIDÆ

In order that the facts brought out by the geographical distribution of the genera and species of the Peripatidæ may be understood, it is necessary first to give a brief sketch of the processes by which the geographical differentiation of animals is brought about.

The physical and economic conditions under which any new animal type arises are naturally the optimum conditions for the perpetuation of that type in its original form, and the generative center, or the center of distribution, of the type will be the locality where the optimum conditions represent the average or mean of a long range of imperceptibly varying conditions, representing all of the conditions under which it is possible for the type to exist, and therefore permitting of progressive deviation from the original type through gradual adaptation for a maximum distance in a maximum number of directions.

Any animal type once evolved will extend itself immediately in every direction as far as the natural barriers to its further dispersal

will permit; but in proportion as it departs from the region where the optimum conditions represent the mean of a wide range of conditions, it will become less and less capable of producing subtypes, for not only is the range of conditions under which it is capable of existing constantly narrowing, at the natural barriers becoming reduced to the vanishing point, but also the time taken in its migration represents so much time lost from its virile and adaptable type youth, and a corresponding advance toward a more or less inert and inflexible type maturity.

On the borders of the range of any type, where the range of the conditions under which it is possible for it to exist is very small, there will be found a great number of localities where the type is able to maintain itself, each of these localities differing slightly from all the others, thermally or economically, or otherwise. Such thermal or economic differentiation is of course also geographical. There will thus result a large number of allied forms which, however, cover collectively a small economic and physical range.

An animal type intruding into a new and favorable area will at once, through the opportunities of existence offered its less efficient individuals, tend toward an excess of individual variation, which may become extreme, until through the pressure of its own increasing numbers, and the constantly increasing severity of its internal competition, it begins to weed out the numerous less efficient varieties, and to narrow them down to a very few, or even to one only, which exist each within very restricted structural limits.

Thus the existence in any area of a great number of closely allied forms indicates either (1) the existence of a very restricted physical or ecological range in which the type can maintain an existence, in which case the corresponding organic varieties will be evidenced as geographical forms (in the strictest sense of the term), or (2) a region newly colonized, in which case a large number of more or less closely related types will be found intermingled, or but partially localized.

The migratory birds offer, in the light of the preceding statements, an instructive study in primary and secondary colonization.

In the summer the temperate regions of the northern hemisphere (and to a much less extent the southern) support many bird types which are divided into a large number of local races, each local race being a direct adaptation to a local enviroment which represents economically or physically a very narrow ecological range, the sum total of these narrow ecological ranges being the total range under

which the type as a whole can maintain itself, a total range which is always duplicated within the tropics.

Bird types which exist only in a great number of local forms cannot be assumed to be living under optimum conditions for the type as a whole. Such bird types, living always within tropical conditions, are probably all of ultimately tropical origin, their progenitors having gradually extended their range outward from the tropics with the annual outward extension of the tropical conditions, and eventually having colonized, though in the summer only, the temperate regions.

To a type with a highly developed power of migration, such as many birds, the temperate regions in the summer represent the border of a tropical habitat, and thus we should expect to find such a type occurring in the temperate regions in summer obeying the laws of peripheral distribution of animal types in general.

In the winter these migratory birds, in order to remain within the economic range necessary for their existence, of necessity withdraw within the tropics (where, as non-breeders, they are perfectly well able to exist) there to remain until, with the advent of summer, the tropical conditions are again extended.

But in the tropics the sum total of the range of each type is duplicated, and conditions are such that there is no closely circumscribed local and ecological differentiation comparable to that which occurs in the temperate regions.

Therefore there is no compelling reason for the various races to maintain their summer segregation, and a number of these races may be found living together.

Many of these bird types have breeding representatives in the tropics, especially on isolated islands where the factors which, after the summer colonization of the temperate regions, caused their extirpation as breeding residents from their original tropical home, have not operated; the non-breeding individuals of many others appear to prefer always to remain within the tropics.

These bird types within the tropics are secondary colonists, returned to their original area of optimum conditions, where they are able to exist as adults in a great number of closely related forms, but where nidification, unless of a newly acquired highly specialized type, or in especially protected localities, has now, thanks to the development of certain enemies, become impossible.

In any area in which the optimum conditions for a given animal type are represented by the mean of the conditions under which that type is able to maintain itself, the progressive development of that

type, after its first appearance, whether by original generation or introduction from outside, will (as in part suggested by the behavior of introduced species) be marked first by individual variation, soon leading to more or less fixed varieties, and finally to the evolution of new species and even new genera, each of which was originally the exponent of conditions more or less different from those under which the type originally appeared.

Now in most large genera we find among the component species one which in its characters occupies the mean between the extremes shown by the other forms, and which typically covers the entire economic, physical, and geographical range of the genus, unless the species on the borders of the generic range are isolated by barriers.

Obviously this is the species best adapted to the conditions of the present day and, if conditions should remain indefinitely as they are now, such a species would gradually succeed, by the mere force of numbers and greater procreative power, which have already enabled it to overrun all the other forms, in exterminating all of the other species of the genus which it was able to reach.

As families and orders are constructively the same as genera, we typically find in them a highly dominant genus, subfamily, or family, which stands in the same relation to them that the dominant species does to the genus.

And among the higher groups the same thing is repeated; thus, for example, we find among the mammals the rodents, among the birds the finches, among the fishes the perches, among the flies the muscoid types, etc., each group including species almost all of which are of small average size, yet never excessively small, representing the dominant types which appear to be on the road to supplanting all the other types through a development from their immediate stock of virile competing forms, and which, were conditions to remain indefinitely as they are at the present epoch, would eventually come to form the entire world fauna.

An appreciation of the normal existence of such a dominant type in each large and widely distributed group is essential for the comprehension of the fact that, given a number of closely related genera occupying a large area, but separated from each other by barriers, the genus occupying the center of distribution will be the most specialized, while that at the periphery will be the least specialized.

Let us suppose a genus recently arisen, occurring uniformly over a very wide area in the center of which the conditions grade very slowly from the optimum to impassible physico-economic barriers in each direction, while at the periphery the conditions grade very

rapidly from those capable of supporting the type to impassible physico-economic barriers.

It is evident that the individuals at the periphery of the area of distribution, living within a very narrow physico-economic radius, would have to restrict themselves within a very small structural compass, while those at the center of the area of distribution, existing in a very wide economic and physical radius, could wander very far away from the optimum structural condition without meeting prohibitive obstacles.

At the periphery of the range the physico-economic belt capable of supporting the type is so narrow that it serves only as the habitat of a single type, a type which will therefore maintain itself near the original type of the organism. Here additional types cannot arise in any one locality, though slightly different types will be found in adjacent localities each one of which differs slightly in its physical and economic characters from the others, but all of which are included within the narrow mean.

At the center of the area of distribution the physico-economic belt is very broad, and it grades imperceptibly away from the mean in either direction. Thus here the original type, instead of being preserved intact as at the periphery, will eventually be supplanted by a type of subsequent origin, and this latter type will be the one which of all the derivative types is capable of covering the maximum number of economic units.

The appearance of such a type, which is represented by the dominant type seen in each genus, family, and higher group, is inevitable; for the original type, occupying the mean of the conditions at the center of distribution, will gradually colonize all possible conditions departing from the mean in every direction, this being rendered easy by the very gradual changes from the optimum, and the very wide separation of the impassible physico-economic barriers. The colonists will be more or less modified to suit their new surroundings and, if the physico-economic belt be broad enough, will divide themselves into new types and subtypes. Eventually a type is certain to appear which will alone be capable of occupying all of the regions occupied by the organism as a whole, and which therefore will gradually supplant and finally exterminate all the other types; and this type will not be a primitive type, such as that which is maintained intact at the periphery of the area of distribution, but a much more specialized type; for though the mean of the conditions which it covers is the same as the physico-economic range in which the peripheral types

live, it is economically much more specialized in its inherent ability to exist over a very wide range. Though much more specialized than the original type, this new dominant type will also be much less specialized than many of the types which it supplants, which will have possessed a very high degree of specialization in order to meet very highly specialized conditions.

The sum of the effect of this organic progress may be expressed by the statement that any animal type, once evolved, will extend itself immediately in every direction as far as the natural barriers to its dispersal; a more specialized form (a dominant type) of the same animal, better fitted for the conditions under which it lives, will sooner or later be evolved somewhere in the central, or most favorable, portion of the territory inhabited by the original type; this new type will at once extend itself as did the original type; but in the meantime there may have arisen certain barriers which the second type cannot cross and beyond which, therefore, the first type is secure. Up to these barriers—high mountains, deserts, newly formed arms of the sea, or whatever they may be—the second type will gradually supplant the first, as a result of its better economic equipment and more perfect physical resistence, and the advantages which this better equipment and resistence give it in the struggle for existence. Thus we shall eventually find a specialized type beyond the limits of which occurs a more generalized type of the same organism. The subsequent evolution of additional types, which will most frequently occur at or near the so-called center of distribution as a natural result of the greater facility for adaptation due to the greater distance apart of the physico-economic barriers and the consequently greater radius of each type, will result in the gradual formation of a dispersal figure which would be ideally represented by a series of concentric circles, each of the circles representing a barrier, the small central circle enclosing the most perfected type and the peripheral band the most generalized, the intervening areas including intermediate types increasing in specialization toward the center.

The distribution of the Peripatidæ represents a sector of such an ideal dispersal figure; the center of distribution for the family is the Malayan region, where the most specialized type occurs; just west of this is the great barrier of the Indian Ocean; in central Africa we find a less specialized type which probably reached its present habitat long before the type now occurring in the Malayan region was evolved, and which has been protected from the encroachment of that type by the submergence of the land over which it originally migrated.

In the case of the onychophores the assumption that the Malayan region is the center of distribution is somewhat arbitrary, though the correctness of this supposition is strongly indicated by the fact that the phylogenetic lines converge there. Under the very nearly uniform conditions which prevailed in the distant past there was no such thing as a center of distribution; new forms arose anywhere, and immediately spread everywhere; but as the surface of the earth became differentiated into warm and cold regions and the mountain ranges attained progressively to greater and greater heights, it happened that, speaking broadly, the Malayan region as a whole remained the region of least diurnal and seasonal variability, and of the most delicately graded temperature differences, and therefore, as the region of the most nearly permanent conditions and of the most gradual differentiation in its physical and economic features, the region of maximum physical and economic radius, and of least interrupted progressive phylogenetical advance.

Among the other groups of terrestrial organisms there are few, if any, for which the Malayan region represents the sole center of distribution as it may almost be said to do in the case of the onychophores. Though in most cases, broadly speaking, the Malayan region may reasonably be regarded as the chief, and possibly ultimate, center of distribution, there are commonly additional centers of distribution each of which partakes more or less of the character of the primary Malayan center.

As has already been explained, it is characteristic of types which have newly entered upon very favorable territory to vary very greatly, and eventually to give rise to a large number of local forms, which, if not subjected to the competition of more efficient intruders, may be supposed, under fixed conditions, to persist for a very considerable length of time, and which will be diversified in direct proportion to the breadth of the physical and economic radius of the area. Such specific abundance therefore indicates not the center of distribution for any given type, but the periphery. Thus the great number of species in the genus *Oroperipatus* occurring west of the crest of the Andes indicates that this region, a region of small physical and economic radius, represents the extreme western limit, and the maximum distance from the generative center, of the area inhabited by the Peripatidæ, while similar conditions in the genus *Peripatus* indicate that their territory is only slightly less far removed from that center.

The explanation of the distribution of the species of the family Peripatidæ, viewed in the light of what we know in regard to the distribution of other animal types, appears to be as follows:

Occurring originally as a uniform or slightly varying organism over a land including the Malayan region (but not the Australian), central Africa, and northern South and Central America, the original prototype of the family became differentiated, taking on the aspect in which we see it today, by the following processes:

The increasing height of the Andes, besides enabling the species living in that region to maintain themselves in the most suitable temperatures, isolated at a very early epoch such individuals as were living west of their crest, rendering them secure from invasion by types of later origin economically more specialized, and fitted to occupy a habitat with a slightly higher average temperature.

A new type, an immigrant from the east, better equipped economically than the original type and with a slightly higher optimum temperature, reached Africa, northern South and Central America, overrunning and extirpating the original type from all the territory east of the crest of the Andes and later in a few places even invading the mountainous region itself. This type subsequently became locally differentiated, through the same processes by which it itself was originally evolved, into five subtypes, the three newer, more specialized and more efficient, extirpating the original immigrant (their immediate ancestor) wherever they were able to reach it.

But before the differentiation of this type into subtypes, though subsequent to the extension of its range westward as far as the Cordillera, Africa became separated from the Malayan region and, at about the same time, also from South and Central America, this latter process involving the submergence, or disruption from other causes, of the Antillean region, resulting in the formation of the West India archipelago.

So far as we know at present no representative of the original immigrant type remains in Africa, though it is quite possible that some eventually will be found there. Its single known derivative in this region, *Mesoperipatus,* though very different, approaches the Malayan type more closely than do any of the American types.

This may be due to either of two causes; southern India and Ceylon maintained a connection with Africa after their separation from the Malayan region, and it is possible that this more efficient type reached this region in or near its present form from the Malayan region just before the separation of the two, subsequently spreading to Africa, but being prevented from extending its range to America by the formation of the Atlantic Ocean; or, which is far more likely, these three types may be all of local development, the African approaching more

closely to the Malayan on account of a greater similarity of the conditions under which it was perfected.

In the Malayan region, subsequent to the separation from Africa, evolution gradually produced, through the processes which have already been given in detail, a more specialized type, *Eoperipatus,* which represents the dominant type under present conditions. It is possible that this represents the only type in the region, for it is the only type we know; but it is probable that subordinate types will eventually be discovered.[1]

THE DISTRIBUTION OF THE AMERICAN SPECIES OF THE PERIPATIDÆ

The details of the distribution of the American species of the Peripatidæ deserve special consideration. In South and Central America we find the very primitive *Oroperipatus* almost entirely confined to the territory west of the watershed of the Andes, only three species (*Oroperipatus bimbergi, O. multipodes* and *O. ciseni*) occurring in the mountainous regions east of the divide, while the remaining territory, including the West India islands, is occupied by the less primitive *Peripatus,* two species of which, in Colombia and Panamá, have gained a foothold in the area otherwise occupied solely by *Oroperipatus.*

While the species of *Oroperipatus* exhibit great uniformity, this is not by any means true of the species of *Peripatus,* which fall into four well marked subgenera; one of these subgenera (*Plicatoperipatus*) is, so far as we know, confined to the island of Jamaica; another (*Macroperipatus*) occurs from Rio de Janeiro northward to Vera Cruz, including the island of Trinidad; the third (*Epiperipatus*), with almost the same continental range, though not known either so far north or so far south, extends to Trinidad, Tobago, and Grenada; while the fourth (*Peripatus*), found in a small area between Caracas and La Guayra and Mérida in Venezuela, near Bogotá in Colombia, in northern Panamá, and in Costa Rica, is eminently characteristic of the Antillean region, being found on Jamaica, Haiti, and Puerto Rico, and on the Lesser Antilles from St. Thomas to and including St. Vincent.

It is worthy of especial mention that, whereas *Oroperipatus,* the most primitive type, is chiefly developed in, and very largely confined to, the cool regions of the high mountains, where very uniform

[1] Since this was written the related genus *Typhloperipatus* has been described from the adjacent portion of Tibet.

conditions of temperature and of humidity prevail, and *Peripatus* finds its optimum conditions in somewhat warmer regions, the two most specialized types, *Macroperipatus* and *Epiperipatus*, are chiefly characteristic of territory which is very warm, and more or less variable both in temperature and in humidity. In other words, increasing warmth of habitat is correlated with increased specialization of the organism, and increased differentiation into subtypes, suggesting that the original temperature under which the onychophores arose was more comparable to the average temperature of the habitat of the American genus occurring in the coolest situations than to that of the habitat of any of the others.

In the light of the preceding, and considered in connection with what we know of the distribution of other animal types, the explanation of the present distribution of this family in America appears to be as follows:

During the time tropical America was inhabited only by the primitive *Oroperipatus* type, before the intrusion of the *Peripatus* type from the east, the Cordillera had attained a height sufficient to prevent the intrusion into that region of the newer and more specialized forms originally developed under, and specialized for, an average temperature somewhat higher than the optimum for the primitive *Oroperipatus*.

This new intrusive type, economically more efficient than the type with which it came into competition, and better suited in every way to meet existing conditions, extirpated the latter as far westward as the crest of the Andes; and so complete was this extirpation that only three species of *Oroperipatus* are known to occur on the Atlantic side of the divide, *Oroperipatus bimbergi,* from Amagatal and Guaduas, Colombia; *Oroperipatus multipodes,* from Rio Amago, Colombia; and *Oroperipatus eiseni,* from the Rio Purus, Brazil, though undoubtedly many more will be discovered in the future. Indeed the intrusive type proved virile enough to enter the region west of the divide in Colombia, Panamá and Costa Rica, for we find *Peripatus* (*Peripatus*) *bouvieri* at Boca del Monte, near Bogotá, Colombia, and *Peripatus* (*Peripatus*) *ruber* at Rancho Redondo, Costa Rica, as well as at Lino, near Bouquete, in the Province of Chiriqui, Panamá.

At this epoch, when the Cordillera and the country to the west was inhabited by the *Oroperipatus* type, and the country to the east by the *Peripatus* type, South (and Central) America became separated from Africa by the formation of the Atlantic Ocean, the accompanying geological changes involving the disintegration of the Antillean region, through submergence or otherwise, into the West India

archipelago, exclusive, however, in the south, of Trinidad, Tobago and Grenada, which still remained united to the mainland.

These fundamental changes in the geological structure of tropical America induced corresponding alterations in the environment of all the terrestrial organisms, and it was possibly as a result of these alterations in environmental conditions that the two subgenera *Macroperipatus* and *Epiperipatus,* both more specialized and economically more efficient than the parent type, were given off from *Peripatus.*

The effect of the economically more efficient *Macroperipatus* and *Epiperipatus* upon the parent type, *Peripatus,* was the same as had been the effect of *Peripatus* upon *Oroperipatus; Peripatus* disappeared from every situation which they were able to reach.

Thus *Peripatus* disappeared almost completely from continental South and Central America, persisting only in the mountains of western Venezuela, Colombia, Panamá, and Costa Rica, from which territory we know the following species—*Peripatus* (*Peripatus*) *sedgwicki,* Caracas, San Esteban, La Moka, Las Trincheras, and La Guayra, Venezuela; *Peripatus* (*Peripatus*) *brölemanni,* Tovar, Raxto Casselo, and Puerto Cabello, Venezuela; *Peripatus* (*Peripatus*) *bouvieri,* Boca del Monte, near Bogotá, Colombia; and *Peripatus* (*Peripatus*) *ruber,* Rancho Redondo, Costa Rica, and Lino, near Bouquete, in the Province of Chiriqui, Panamá. But the very process which caused *Peripatus* to disappear almost completely from the mainland of South America resulted in making it the characteristic type in the Antilles from Jamaica and Haiti eastward and southward to and including St. Vincent, for, thanks to the water barrier, *Macroperipatus* and *Epiperipatus* were not able to reach these islands, though they could, and did, reach Trinidad, Tobago, and Grenada, which at this time were a part of the mainland.

It is possible that the origin of *Macroperipatus* was subsequent to that of *Epiperipatus,* so that it was prevented from reaching Tobago and Grenada by the separation of those islands from the mainland after the intrusion of *Epiperipatus.*

The subgenus *Plicatoperipatus* appears to be, so far as we are able to see at present, of local origin in the island of Jamaica; it is quite possible, however, that it occurs in Haiti also.

The occurrence of *Epiperipatus* upon Grenada, Tobago, and Trinidad, and of *Macroperipatus* upon Trinidad, the very close relationship between the species of *Epiperipatus* upon Tobago and Trinidad,[1] and

[1] Piccole Note su degli Onychophora. Zool. Anzeiger, Bd. 42, Nr. 6, S. 253-255. 18 Juli 1913.

the absence of *Peripatus* from these islands, may be thus accounted for.

Grenada lies not upon the ridge supporting Trinidad and Tobago, but upon the ridge supporting St. Vincent, St. Lucia, and the islands beyond. There is no evidence that it ever was connected with Trinidad or with Tobago. Certain elements in the fauna of Grenada, such as *Epiperipatus* among the onychophores, and very many types among the other groups of organisms, recall the fauna of Tobago and Trinidad, and separate Grenada sharply from the islands to the north. I believe that the island of Grenada, including the Grenadines to the northward as far as Bequia, first became separated from St. Vincent by the formation of a deep channel between them, and at a considerably later epoch, after the fauna of Grenada had become further modified by additions direct from South America (and not by way of Trinidad and Tobago), it became separated from South America, to which it had been joined in the general region of Margarita Island.

The fauna of Barbados (including, so far as we know, no onychophores) is the fauna of an oceanic island purely, being composed entirely of representatives of the most widely ranging and most easily transported of the organisms of the adjacent islands. Barbados has been entirely submerged since it formed a part of the ancient Antillean land.

No onychophores have ever been found in Cuba, though they have been diligently sought for there by a number of competent naturalists. If any are ever discovered it will be interesting to see whether they will belong to the subgenus *Peripatus,* like those on the other islands, or to *Epiperipatus,* like those on Grenada and Tobago, or to both *Epiperipatus* and *Macroperipatus,* like those on Trinidad.

The uniformity of the onychophores throughout the West India archipelago, both in the Greater Antilles and in the Lesser, is of much interest in indicating the original and fundamental unity of the entire group of islands. They do not indicate a zoögeographical division into a Greater and a Lesser Antillean fauna for the reason that their genera are uniformly distributed both in South and Central America, so that the same faunal elements would enter either group of islands in the event of a continental connection.

The close faunal affinity between the Antilles and the mountain region of western Venezuela, Colombia, Panamá, and Costa Rica indicated by the species of the subgenus *Peripatus* is not a true faunal affinity. It merely shows that in the Antilles and in the mountain region *Peripatus* has in exactly the same way been protected by barriers which have prevented the intrusion of the more efficient com-

peting forms which everywhere else have succeeded in extirpating it, in one case by barriers of water, in the other by barriers of mountain ranges.

THE DISTRIBUTION OF THE PERIPATOPSIDÆ

The family Peripatopsidæ includes fewer, but far more diverse, types than the singularly homogeneous Peripatidæ. It ranges from New Britain, New Guinea, and Ceram (in the Moluccas) to Australia, Tasmania, and New Zealand, and thence to southeastern and southern Africa, and to Chile.

The subfamily Peripatopsinæ inhabits New Britain, New Guinea, and Ceram, and also Cape Colony and Natal. At first sight this distribution appears to be quite anomalous, but in reality it agrees perfectly with what we know of the distribution of a number of other organisms, confirming the evidence presented in other groups of a past land connection between the Moluccas, New Guinea, and New Britain, and southeastern Africa.

The Peripatopsinæ and the Eoperipatinæ are not at present known to occur together anywhere in the east, being separated by a line passing west of the Moluccas.

This line, which separates the Peripatidæ from the Peripatopsidæ as well as the Eoperipatinæ from the Peripatoidinæ, is the equivalent of the famous Wallace's line, for it separates the Australasian from the Indo-Malayan types.

Unfortunately we cannot as yet, on the basis of the onychophores, say what the exact location of this line is; we only know that the genus characteristic of New Britain and New Guinea (*Paraperipatus*) occurs also on Ceram, and therefore the line must pass somewhere to the westward of Ceram, between Ceram and Sumatra, where the easternmost representative of the Peripatidæ occurs.

The distribution both of the Peripatidæ and of the Peripatopsinæ confirms the presence in the distant past of a land mass extending from the Malayan region westward and southwestward to central and southern Africa; and it is reasonable to suppose that the same land mass, though possibly at different epochs, served for the migration of both types, one passing over the more northern portion, the other over the more southern. The Peripatidæ passed over Africa into America, but the more specialized Peripatopsinæ, possibly later arrivals, went no farther than Africa.

In the Peripatidæ the most specialized type is that in the Indo-Malayan region, but in the Peripatopsinæ we find the most specialized

types in South Africa and the least specialized types in New Britain, New Guinea, and Ceram. This would appear to indicate that the headquarters of the group was originally somewhere between New Guinea and South Africa, and that New Guinea and the adjacent islands became very early detached and separated by a water barrier so that the endemic onychophores were protected from the intrusion of later and more efficient types, exactly as were the species of the genus *Oroperipatus* west of the Andes. If this view is correct, Madagascar should support a more specialized type of this subfamily than either South Africa or New Guinea and the adjacent islands.

We do not know any onychophores from the Cape York peninsula in Australia; it is probable that such forms as occur there belong to the Peripatopsinæ, and are related to the forms in New Guinea and the adjacent islands.

The distribution of the subfamily Peripatoidinæ is very interesting; this subfamily occurs in New Zealand, Tasmania, southern and western Australia, South Africa, and southern South America.

The forms occurring in Australia, New Zealand, and Tasmania collectively make up a very closely knit faunal unit, indicating the fundamental faunal homogeneity of these areas; Tasmania, however, lacks the less specialized component of the fauna of Australia and New Zealand, a fact which may or may not be significant. It is most probable that this type will eventually be found there.

There are two possible explanations for this distribution; (1) the species of this subfamily may have been extirpated from all the more desirable localities by more efficient and more aggressive species of the other groups, or (2) the subfamily may have attained its present distribution through following a more southern route.

The first of these alternatives seems untenable, for if it were so we should expect to find species of Peripatoidinæ north as well as south of the species of the other groups, and also occurring in isolated situations, such as mountain tops, where the other species could not penetrate. But nothing of the kind occurs. Moreover the species of the Peripatoidinæ are very highly specialized, so much so that if they came into competition with the species of the other families they probably would, other things being equal, prove themselves dominant.

Therefore we must tentatively accept the second alternative, namely, that the Peripatoidinæ attained their present distribution through originally having been widely spread over a southern land which at one time or another included within its boundaries New Zealand, Tasmania and southern South America, as well as South

Africa. This hypothesis, moreover, accords with what we know of the distribution of many other southern types.

As the American species of Peripatoidinæ are far more specialized than the American species of Peripatidæ, we may assume that the connection between southern South America and the Australian region persisted to a much later date than that by which the Peripatidæ arrived from Africa.

Although, judging from what we know of the other elements of the faunas of Australia, Tasmania, and New Zealand, it is easy to understand how the Peripatoidinæ entered southern South America from the Australian region, it is not so easy to understand how they entered South Africa, unless we are willing to assume that there has been a connection between South Africa and Antarctica by way of the Crozet and Kerguelen Banks, which was more or less contemporaneous with that between southern South America and Antarctica.

The African genus *Opisthopatus* is very closely allied to the American *Metaperipatus,* the alliance being much more close than in the case of the African and American genera of the Peripatidæ. These two genera are less specialized than are the other genera of the Peripatopsidæ, and the explanation at once suggests itself that, besides being later arrivals in America than the genera of the Peripatidæ, they, like *Oroperipatus,* indicate the extreme limits of the area over which their group (the Peripatoidinæ) was at one time dominant, and exist at present in localities with a physico-economically very restricted radius which approaches the physico-economical conditions of the original habitat of their subfamily more closely than does the habitat of any of the more specialized Australian genera, so that they have had but little incentive to change in order to meet new conditions.

If this were so, it would suggest of itself that the Peripatoidinæ in the past had their headquarters in the extreme south, in contrast to the primarily tropical Peripatidæ.

The sharp separation in the distribution of the Peripatoidinæ and the Peripatopsinæ in the East Indian and Australian regions suggests a long and complete separation of the land of which the Moluccas, New Guinea, and New Britain (and southeastern Africa) were once an integral part, from Australia (including Tasmania and New Zealand, but possibly excepting the Torres Strait region), this separation long antedating the separation of Australia from Antarctica, but being subsequent to the isolation of the Malayan region from the Moluccas and the islands farther east.

THE DISTRIBUTION OF THE SPECIES, GENERA AND HIGHER GROUPS OF THE ONYCHOPHORES IN DETAIL

Order ONYCHOPHORA: Malay Peninsula and Sumatra; Ceram; New Guinea; New Britain; Australia, Tasmania and New Zealand; central and southern Africa; Central and South America from Tepic, Mexico, southward to Chile, including the West Indies.

Family PERIPATOPSIDÆ Bouvier, 1904: New Britain, New Guinea and Ceram, Australia, Tasmania and New Zealand; Natal and Cape Colony; Chile.

Subfamily PERIPATOIDINÆ Evans, 1901: Southern Queensland, New South Wales, Victoria and Western Australia; Tasmania and New Zealand; Natal and the adjoining portion of Cape Colony; Chile.

Section I: Southeastern (southern Queensland, New South Wales and Victoria) and Western Australia, Tasmania and New Zealand.

Genus *Peripatoides* Pocock, 1894: Southern Queensland, New South Wales, Victoria and Western Australia, Tasmania and New Zealand.

Viviparous species; *Peripatoides.*

Peripatoides orientalis (Fletcher): Wollongong, Blue Mountains, Moss Vale District, Tamworth, Cassilis (banks of Mounmoun Creek), Burrawang, Colo Vale (near Mattagong), Moree, Illawarra, and Dunoon (near Richmond River), New South Wales; ?Cardwell, ?Brisbane, ?Wide Bay, Queensland; ?Cunningham's Gap, Northern Territory of South Australia.

Peripatoides occidentalis (Fletcher): Bridgetown, Island of Perth, Western Australia.

Peripatoides gilesii Spencer: Lion Mill and Armadale, near Perth; Mundaring Weir, Darling Ranges; and Kimberley, Western Australia.

Peripatoides novæ-zealandiæ (Hutton): Wellington, Dunedin, Nelson, Porirua, Stephen's Island and Oropibush (near Taranga), Otago, Woodville, and Jararua, New Zealand.

Peripatoides suteri (Dendy): Stratford and Taranaki, north New Zealand.

Oviparous species; *Ooperipatus.*

Peripatoides leuckarti (Sänger): Northwest of Sydney, New South Wales; Macedon, Sassafras Gully, Ferntree Gully, and Gembrook, Victoria.

Peripatoides spenceri Cockerell: Mt. Wellington, district of Lake St. Clair, Tasmania.

Peripatoides viridimaculatus (Dendy): End of Lake Te Anau, Clinton Valley, south New Zealand; ?near Te Aroha, north New Zealand.

Oviparous species; *Symperipatus.*

Order Onychophora—Continued.
Family Peripatopsidæ Bouvier, 1904—Continued.
Subfamily Peripatoidinæ Evans, 1901—Continued.
Section I—Continued.
Genus *Peripatoides* Pocock, 1894—Continued.
Peripatoides oviparus (Dendy): Warburton (on the upper Yarra), Brown Hill (near Ballarat), Macedon, Valhalla, Mt. Baw Baw, Pyalong, Warragul (Gippsland), Victoria; Mt. Kosciusko (Wilson's Valley, at an altitude of 5,000 feet, and also at an altitude of 5,700 feet), and between Exeter and Bundanoon (Moss Vale district), New South Wales; Cooran, Cardwell and Brisbane, Queensland; Cunningham's Gap, northern territory of South Australia.
Section II: Natal, and the adjoining portion of Cape Colony; Chile.
Genus *Opisthopatus* Purcell, 1899: Natal, and the adjoining portions of Cape Colony.
Opisthopatus cinctipes Purcell: Vicinity of Dunbrody, Uitenhage Division, Cape Colony; Doornek, Zuurberg Range, Alexandria Division, Richmond and Durban, Natal.
Genus *Metaperipatus* A. H. Clark, 1913: Chile.
Metaperipatus blainvillei (Blanchard): Chiloë Island; near Villa Rica; near Corral; Enero, in the Cordillera Pelada, province of Valdivia; Contulmo, Cordillera of Nahuelbuta, which separates the provinces of Malleco and Arauco; valley of Buchoco, between Lake Lanalhue and the sea, south of Cañete, 10 kilometers from Contulmo; all the localities are in southern Chile.
Metaperipatus umbrinus (Johow): Near Zapallar, on the coast of Aconcagua province, in 32° 33′ 20″ S. lat.
Subfamily Peripatopsinæ Evans, 1901: New Britain, New Guinea and Ceram; Natal and Cape Colony.
Section I: Cape Colony and Natal.
Genus *Peripatopsis* Pocock, 1894: Cape Colony and Natal.
Peripatopsis sedgwicki Purcell: Plettenberg Bay (Knysa), Port Elizabeth and Grahamstown, Cape Colony.
Peripatopsis moseleyi (Wood-Mason): Vicinity of King William's Town, East London, Katberg Forest (50 miles northwest of King William's Town), Pirie Bush (near King William's Town), Dias, and vicinity of Port Elizabeth, Cape Colony; Pietermaritzberg and vicinity, Eastcourt and vicinity, Richmond, Aslockton (Dronkvlei, near Umzimkulu River, Ixopo District), and Riet Vlei (in the west of Umvoti District), Natal.
Peripatopsis clavigera Purcell: Knysa, eastern part of Cape Colony.

Order Onychophora—Continued.
Family Peripatopsidæ Bouvier, 1904—Continued.
Subfamily Peripatopsinæ Evans, 1901—Continued.
Section I—Continued.
Genus *Peripatopsis* Pocock, 1894—Continued.
Peripatopsis leonina Purcell: Lions Hill, and the shores of Table Bay.
Peripatopsis balfouri (Sedgwick): Vicinity of Cape Town; Table Mountain; Platteklip and Newlands ravines, Table Mountain; ravines near Camp's Bay and Hout Bay; Simons Town, St. James, on the shore of False Bay; Cedar Mountains; Clanwilliam, at Boschkloof waterfall; Constancia (Plettenberg Bay), Cape Colony.
Peripatopsis capensis (Grube): Vicinity of Cape Town, Constancia, Mowbray, Table Mountain, Platteklip, St. James (False Bay), Wynberg, Newlands, Randebosch, Frenchhoek (division of Paarl), Caledon, Houw Hoek, Hottentots Holland Mountains (division of Caledon), and Swellendam, Cape Colony.
Section III: New Britain, New Guinea and Ceram.
Genus *Paraperipatus* Willey, 1898: New Britain, New Guinea and Ceram.
Paraperipatus novæ-britanniæ (Willey): New Britain.
Paraperipatus schultzei Heymons: German New Guinea, on a mountain in the interior at an altitude of 1,570 meters.
Paraperipatus schultzei var. *ferrugineus* Heymons: German New Guinea, on a mountain in the interior at an altitude of 1,570 meters.
Paraperipatus lorenzi Horst: South Dutch New Guinea, in the Wichmann mountains, at an altitude of 10,000 feet.
Paraperipatus papuensis Sedgwick: North Dutch New Guinea, in the Arfak mountains at Sarayu, at an altitude of 3,500 feet.
Paraperipatus ceramensis (Muir and Kershaw): Peroë (Piru), western Ceram.
Family Peripatidæ Evans, 1902: Malay Peninsula and Sumatra; French Congo; tropical America from Tepic, Mexico, southward to Sorata, Bolivia, and eastward, on the Atlantic coast ranging from Rio de Janeiro to and throughout the West Indies.
Subfamily Eoperipatinæ A. H. Clark: Sumatra and the Malay Peninsula.
Genus *Eoperipatus* Evans, 1901: Sumatra and the Malay Peninsula.
Eoperipatus weldoni Evans: Malay Peninsula; Mt. Bukit Besar, on the border between Nawngchick and Jalor, 1,000 meters; Larut, 1,220 meters.

Order Onychophora—Continued.
Family Peripatidæ Evans, 1902—Continued.
Subfamily Eoperipatinæ A. H. Clark—Continued.
Genus *Eoperipatus* Evans, 1901—Continued.
Eoperipatus horsti Evans: Malay Peninsula; Kuala Aring, state of Kelantan.
Eoperipatus sumatranus (Sedgwick): East coast of Sumatra.
Genus *Typhloperipatus* Kemp, 1913: Extreme southeastern corner of Tibet.
Typhloperipatus williamsoni Kemp: Near Rotung, on the banks of the Dihang River (in Tibet, very near the northern corner of Assam); 1,200 to 2,500 feet.
Subfamily Peripatinæ Evans, 1902 (emended A. H. Clark, 1913): tropical America; French Congo.
Genus *Mesoperipatus* Evans, 1901: French Congo.
Mesoperipatus tholloni (Bouvier): Ngômô, Ogôoué, French Congo.
Genus *Peripatus* Guilding, 1825: Tropical America, except in a few localities in the mountains of Colombia, Panamá and Costa Rica east of the Atlantic-Pacific watershed, from Vera Cruz, Mexico, and Guatemala on the north to Rio de Janeiro on the south, including the West India islands.
Subgenus *Macroperipatus* A. H. Clark, 1913: Rio de Janeiro, Brazil, French and British Guiana, and Trinidad, westward to Panamá, and northward to Vera Cruz, Mexico.
Macroperipatus ohausi (Bouvier): Near Rio de Janeiro, Brazil.
Macroperipatus geayi (Bouvier): French Guiana; La Chorrera, Panamá.
Macroperipatus guianensis (Evans): Demerara, British Guiana.
Macroperipatus torquatus (von Kennel): Trinidad.
Macroperipatus perrieri (Bouvier): Vera Cruz, Mexico.
Subgenus *Epiperipatus* A. H. Clark, 1913: Santarem, Brazil, French, Dutch and British Guiana, Trinidad, Tobago and Grenada, westward to Central America, ranging northward to Guatemala.
Epiperipatus brasiliensis (Bouvier): Santarem, Brazil, Mérida, Venezuela and San Pablo, Panamá.
Epiperipatus simoni (Bouvier): Island of Marajó, at the mouth of the Amazons; Caracas, Venezuela.
Epiperipatus edwardsii (Blanchard): French and Dutch Guiana, and possibly Trinidad, westward to Panamá and Darien.
Epiperipatus imthurmi (Sclater): British, French and Dutch Guiana.
Epiperipatus evansi (Bouvier): Demerara, British Guiana.
Epiperipatus trinidadensis (Stuhlmann): Trinidad.

Order Onychophora—Continued.
Family Peripatidæ Evans, 1902—Continued.
Subfamily Peripatinæ Evans, 1902 (emended A. H. Clark, 1913)—Continued.
Genus *Peripatus* Guilding, 1825—Continued.
Subgenus *Epiperipatus* A. H. Clark, 1913—Continued.
Epiperipatus trinidadensis var. *broadwayi* A. H. Clark: Tobago.
Epiperipatus barbouri (Brues): Grenada.
Epiperipatus isthmicola (Bouvier): Costa Rica.
Epiperipatus biolleyi (Bouvier): Costa Rica; ?British Honduras.
Epiperipatus biolleyi var. *betheli* Cockerell: Puerto Barrios, Guatemala.
Epiperipatus nicaraguensis (Bouvier): Nicaragua.
Subgenus *Plicatoperipatus* A. H. Clark, 1913: Jamaica.
Plicatoperipatus jamaicensis (Grabham and Cockerell): Jamaica.
Subgenus *Peripatus* Guilding, 1825: West India islands of Jamaica, Haiti, Puerto Rico, Vieques, St. Thomas, Antigua, Guadeloupe, Dominica and St. Vincent; mountains of western Venezuela westward to Colombia, northward to Panamá and Costa Rica.
Peripatus swainsonæ Cockerell: Jamaica.
Peripatus haitiensis Brues: Near Furcy, Haiti.
Peripatus manni Brues: Furcy, Haiti.
Peripatus juanensis Bouvier: Puerto Rico and Vieques.
Peripatus danicus Bouvier: St. Thomas.
Peripatus antiguensis Bouvier: Antigua.
Peripatus bavayi Bouvier: Guadeloupe.
Peripatus dominicæ Pollard: Dominica.
Peripatus juliformis Guilding: St. Vincent.
Peripatus brölemanni Bouvier: Tovar, Raxto Casselo and Puerto Cabello, Venezuela.
Peripatus sedgwicki Bouvier: Caracas, San Esteban, La Moka, Las Trincheras and La Guayra, Venezuela.
Peripatus bouvieri Fuhrmann: Boca del Monte, near Bogotá, Colombia.
Peripatus ruber Fuhrmann: Rancho Redondo, Costa Rica; Lino, near Bouquete province of Chiriqui, Panamá, 4,100-4,500 feet elevation.
Genus *Oroperipatus* Cockerell, 1908: Excepting for localities in Colombia and western Brazil, restricted to the Pacific watershed of tropical America, from Tepic, Mexico, southward to Sorata, Bolivia.
Oroperipatus eiseni (Wheeler): Tepic, Mexico, south to the Rio Purus, Brazil.
Oroperipatus soratanus (Bouvier): Sorata, Bolivia.
Oroperipatus intermedius (Bouvier): Sorata, Bolivia.

Order Onychophora—Continued.
Family Peripatidæ Evans, 1902—Continued.
Subfamily Peripatinæ Evans, 1902 (emended A. H. Clark, 1913)—Continued.
Genus *Oroperipatus* Cockerell, 1908—Continued.

Oroperipatus balzani (Camerano): States of Coroico and Chulumani, Bolivia.

Oroperipatus corradoi (Camerano): Quito, Balzar and Guayaquil, Equador; Ancon, Panama Canal Zone.

Oroperipatus belli (Bouvier): Duran (Guayas River), Equador.

Oroperipatus quitensis (Schmarda): High regions of Equador.

Oroperipatus cameranoi (Bouvier): Cuenca and Sigsig, Equador.

Oroperipatus lankesteri (Bouvier): Paramba, near Quito, Equador.

Oroperipatus ecuadoriensis (Bouvier): Bulim, northwestern Equador.

Oroperipatus tuberculatus (Bouvier): Popayan, Colombia.

Oroperipatus multipodes (Fuhrmann): Rio Amago, Colombia.

Oroperipatus bimbergi (Fuhrmann): Amagatal (900-1,800 meters) and Guaduas (800 meters), Colombia.

Oroperipatus goudoti (Bouvier): Mexico.