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ECOLOGICAL BIOGEOGRAPHY IN THE PHYLUM ONYCHOPHORA

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ABSTRACT.- The ecological biogeography of onychophorans has been the subject of some qualitative observations, but the results have been inconsistent. This paper presents the results of (1) statistical analyses of 172 geographic quadrats for both onychophoran families (worldwide) and (2) independent graphic analyses of most South African and Australian species. Both types of analysis produced different results, including a correlation of occurrence with Pleistocene vegetation, which does not imply causation. Although altitude and rainfall correlate with the distribution of some South African and Australian taxa, each of the following factors failed to explain by itself the barriers that limit onychophoran distribution at the global level; mean annual rainfall and temperature, photosynthesis, and types of climate, vegetation and biome. The barriers seem to be a product of several ecological factors which depend on the onychophoran taxon.

KEY WORDS.- Onychophora, Distribution, Biogeography, Pleistocene Refugia, South Africa, Australia.

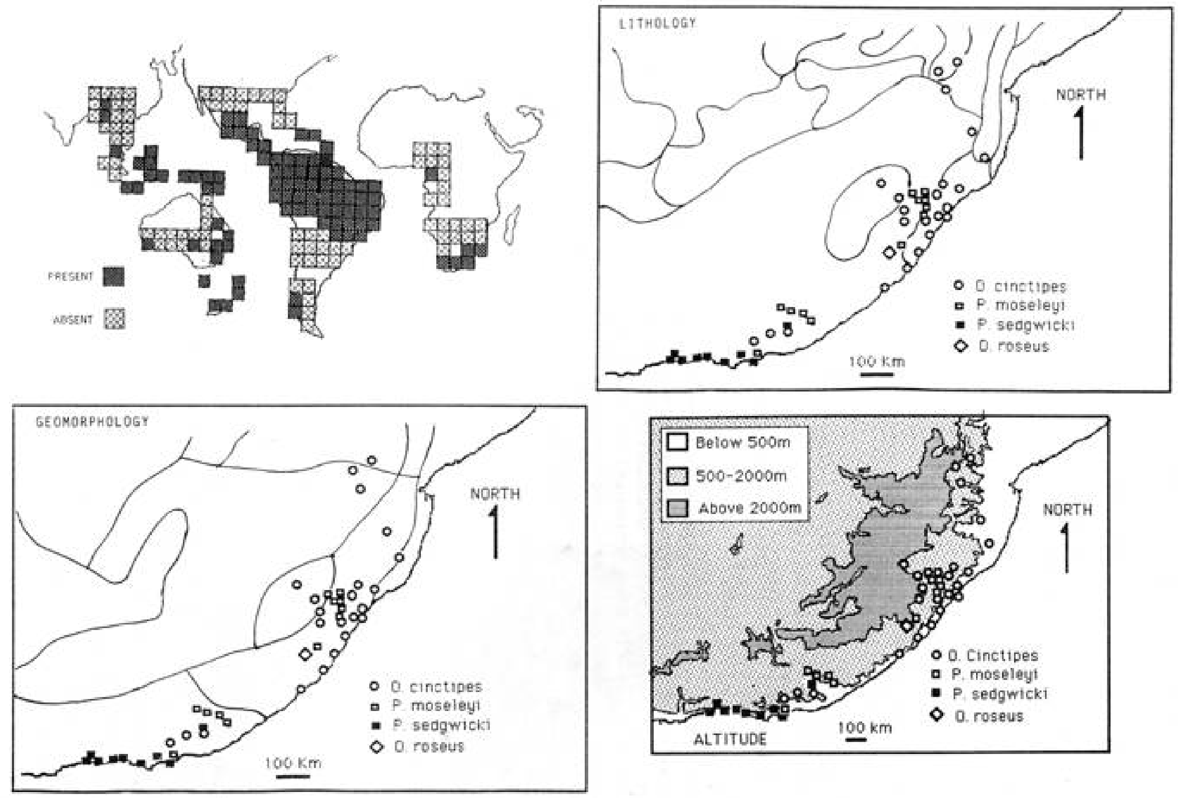
RESUME.- La biogeographic écologique des Onychophores a Cté le sujet des queiques observations qualitatives, cependant les résuitats sont peu consistants. Cet article prCsente les résultats de (1) lanalyse statistique de 172 quadrats geographiques pour les deux families d'Onychophores a léchelle mondiale, et une analyse graphique indCpendante concernant Ia majorité des espèces d'Afrique du Sud et dAustralie. Les deux types danalyse apportent divers resultats, et en particulier montrent une correlation de repartition avec la vegetation du Pléistocène, ce qui nimplique pas de causalité. Bien qualtitude et precipitation puissent être correlées avec Ia distribution de quelques taxa sud-africains et australiens, les facteurs tels que precipitation annuelie moyenne, temperature, photosynthese, types de climat, vegetation et biomes, narrivent pas a justifier deux-mCmes les barrières que limitent Ia distribution des Onychophores a lchelle mondiale. Ces demières semblent être le produit de differents facteurs ecologiques dont depend Ic taxon Onychophora.

MOTS-CLES.- Onychophora, Distribution, Biogeographic, Pleistocene, Refuge, Afrique du Sud, Australie.

INTRODUCTION

The phylum Onychophora is a rare group of invertebrates which has undergone little morphological change since the late Cambrian (RUHBERG, 1985, MONGE-NAJERA, 1994). It includes two families with disjunct distribution in the tropics and southern subtropics (VACHON, *1953,* MONGE-NAJERA, 1994).

Onychophorans are a good group for biogeographic research because they are poor dispersers and their distribution probably reflects phylogenetic relationships (SEDGWICK, 1908). They were used as an example to support the concept of continental drift *(e.g.* CLARK, 1915, BRUES, 1923, GRAVIER & FAGE, 1925) although there was disagreement *(e.g.* BRINCK, 1956).



Figs. 1-4. Distribution of the phylum Onychophora. 1.Onychophoran distribution in Asia- Oceania(left), America(center) and Africa(right). The maps were divided in quadrats which inculded areas where the onychophorans occur and adjacent regions for comparison. Quadrats with about half of the area occupied by onychophoran are excluded because it was difficult to decide if they should recorded as "presence" or "absence". 2-4. Distribution of South African onychophorans in relation with borders in the lithology, geomorphology and altitude.

DISPERSAL AND BIOTIC FACTORS

Dispersal over land is normally assumed (BRUES, 1925) but the possibility of rafting across the sea, discarded by some (BRUES, 1925; BRINCK, 1956), should be reconsidered (S.B. PECK, 1992 pers. comm.; MONGE-NAJERA et al., 1993; MONGE-NAJERA, 1994). Similarly, anthropic transport was not accepted by earlier authors (e.g. BRUES, 1925; BRINCK, 1956) but was reported later for Wallacea and Galapagos (vAN DER LANDE, 1991; H. RUHBERG, 1991 pers. comm. based on specimens collected by S.B. PECK).

There are no studies of how their distribution may be affected by predators, prey and internal parasites (reviews: READ, 1985; RUHBERG, 1985; MONGE-NAJERA et al., 1993), but in contrast with such biotic factors, habitat characteristics have received some biogeographic consideration and are reviewed below.

Temperature

Today onychophorans may occupy climatic conditions similar to those of the ancestral stock (CLARK, 1915). They are not limited to narrow temperature or altitude ranges (NEWLANDS & RUHBERG, 1978), but individual survival is reduced if temperatures are allowed to fluctuate rapidly (CLARCK, 1915; BRINCK, 1956; RUHBERG, 1985). They can survive adverse climate by becoming inactive in favourable microhabitats (BRINCK, 1956; RUHBERG, 1985).

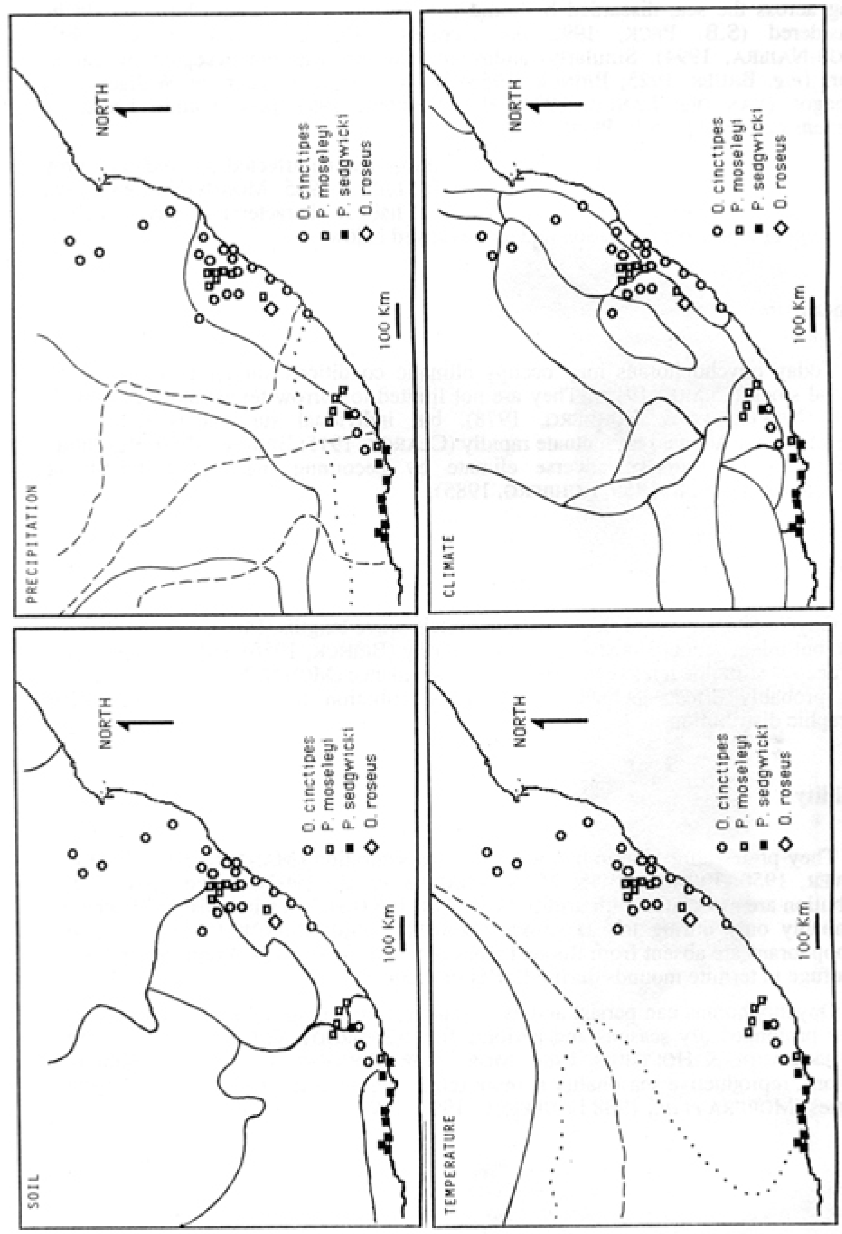
Light

Onychophorans avoid strong light of certain wave lengths (MONGE-NAJERA *et al.,* 1993), but this reaction decreases at high humidity (BRINCK, 1956) and light appears to be a "decoy' stimulus related with dessication avoidance (MONGE-NAJERA *et al.,* 1993). Light probably affects behavior and microdistribution more than it may affect geographic distribution.

Humidity

They prefer atmospheric humidity close to saturation (MANTON, 1938; BURSELL & EWER, 1950; BRINCK, 1956; MONGE-NAJERA *et al.,* 1993). Large gaps in their distribution are associated with aridity (VACHON, 1953) and so when dispersal occurs it is probably only during moist periods (BRINCK, 1956). BRINCK (1956) stated that onychophorans are absent from flooded areas but CARVALHO (1942) reported that some find refuge in termite mounds during floods in Brazil.

Onychophorans can persist and even remain active in apropriate isolated patches despite prolonged dry seasons and periodic fires (ENDRODY-YOUNGA & PECK, 1983; VAN DER LANDE & HOLTHUJS, 1986; MOlRA & MONGE-NAJERA, 1990). Similar to scorpions, reproductive seasonality is more related with climate than with phylogenetic affinities (MORERA *et al.*, 1988 LOURENcO, 1992, 1994 pers. com.).



Figs. 5-8. Distribution of South African onychophorans in relation with soil, rain precipitation, temperature and climate borders.

Vegetation and soil

A relative independence of onychophorans upon specific vegetation has long been recognized and related with their predatory habits *(e.g.* CLARK**,** *1915).* Their environmental requirements often but not always associate them with old forests, and some local gaps in their distribution might be caused by recent deforestation **(**BRINCK**,** 1956; RUHBERG**,** 1985).

Soil requirements for the onychophorans are unknown, but probably the capacity to hold humidity and the presence of microcaverns are important factors **(**RUHBERG**,** 1985; MESIBOV **&** RUHBERG**,** 1991; MONGE-NAJERA & MORERA, 1994).

ECOLOGICAL CORRELATES OF DISTRIBUTION

Until now, the general biogeographical conclusion has been that humidity is the overriding factor in onychophoran distribution, but admitedly the knowledge of the onvchophoranss ecology is poor, fragmentary and rarely reaches a quantitative level (see RUHBERG**,** 1985). More recently it was stated that the role of temperature or rainfall seasonality *per se* on onychophoran distribution is uncertain (VAN DER LANDE, 1993).

A visual examination of maps suggests that The Andes, the Cape Mountains, the Himalayas and the Australian Great Dividing Range are topographic barriers to onychophoran dispersal, and that climatic barriers act in southern Brazil, northeast South Africa, India and southwestern Australia, but this is only a subjective impression.

OBJECTIVE

There is little doubt that current onychophoran distribution reflects (as for scorpions; LOURENCO, 1985) ancient associations of land masses **(**CLARK**,** 1915; RUHBERG**,** 1985), and their large scale distribution in six disjunct areas of the World has been reviewed recently with a **historical** biogeography approach (MONGE-NAJERA, 1994). Rather than repeating that analysis, this study is an attempt to go beyond the qualitative approach in the **ecological** biogeography of the Onychophora. It applies factor analysis and quadrat assessment, techniques that have proved useful for other groups (MONGE-NAJERA & MORERA, 1987; CURRIE, 1991), as well the traditional graphic analysis, to identify factors which may define distributional barriers. The basic question examined is: Can any of the environmental factors considered here explain by itself onychophoran distribution? One novelty is that one historical factor, Pleistocene vegetation, is also considered quantitatively and simultaneously. It must be remembered that the combined effect of several factors is difficult of test statistically because of the binomial (presence/absence) nature of information currently available for the phylum.

MATERIAL AND METHODS

Quadrats were superimposed on an updated map of Onychophoran distribution (original and sources in MONGE-NAJERA, 1994) only including places where onychophorans occur, and surrounding areas for comparison (Fig. 1). This was done to prevent consideration of appropriate but historically unreachable areas. For each quadrat the following variables were recorded from World maps (ANONYMOUS, 1979; COX & MOORE, 1985; ANONYMOUS, 1988): climate type, mean annual rainfall, current vegetation type, Pleistocene vegetation type (18 000 ybp), annual mean temperature, biome type, and primary productivity as reflected by photosynthesis (g carbonlm2/year). The complete matrix is available from the author. A multiple regression analysis done originally was not used when it was noticed that the data were not adequate (see JAMES & MCCULLOCH, 1990), yet the nonparametric tests detailed in Table I gave the same result by identifying Pleistocene vegetation as an important correlate for both families. Multiple correspondence analyses (Carrol and GREEN 1988) was applied to each family but failed to produce a graphic output because Pleistocene vegetation was independent of the next most correlated variables. Independent graphic analyses were done for South African onychophorans (Figs. 2-12, based on ANONYMOUS, 1977, 1979, 1988), whose distribution is relatively well known (NEWLANDS & RUHBERG, 1978). The distribution of humans and onychophorans in Australia was included (Fig. 13, based on ANONYMOUS 1979; RUHBERG, 1985 ; ROWELL *et* a!., 1994) after noticing their similarity.
,Table I. Contingency coeficients X 100 (C) and chi-square significance X 1000 (S) for seven *factors* in relation with occurrence of onychophoran families (NS = not significant.).

RESULTS

The highest correlation of occurrence was with Pleistocene vegetation and climate in Peripatidae, and with biome and Pleistocene vegetation in Peripatopsidae (Table 1). Considering both families, onychophorans tend to be absent in areas which 18000 years ago were covered by steppe, desert, damp temperate or hot damp rainforest vegetation. In contrast they occur today where Pleistocene vegetation was primarily drought seasonal forest and tall grassland, tropical and subtropical rain forest or subtropical drought deciduous woodland (Tables II and III). The graphic analysis only showed a correlation between distribution and altitude in South Africa (Figs. 2-12). The distribution of onychophorans in Australia greatly corresponds with human occupation (Fig. 13).

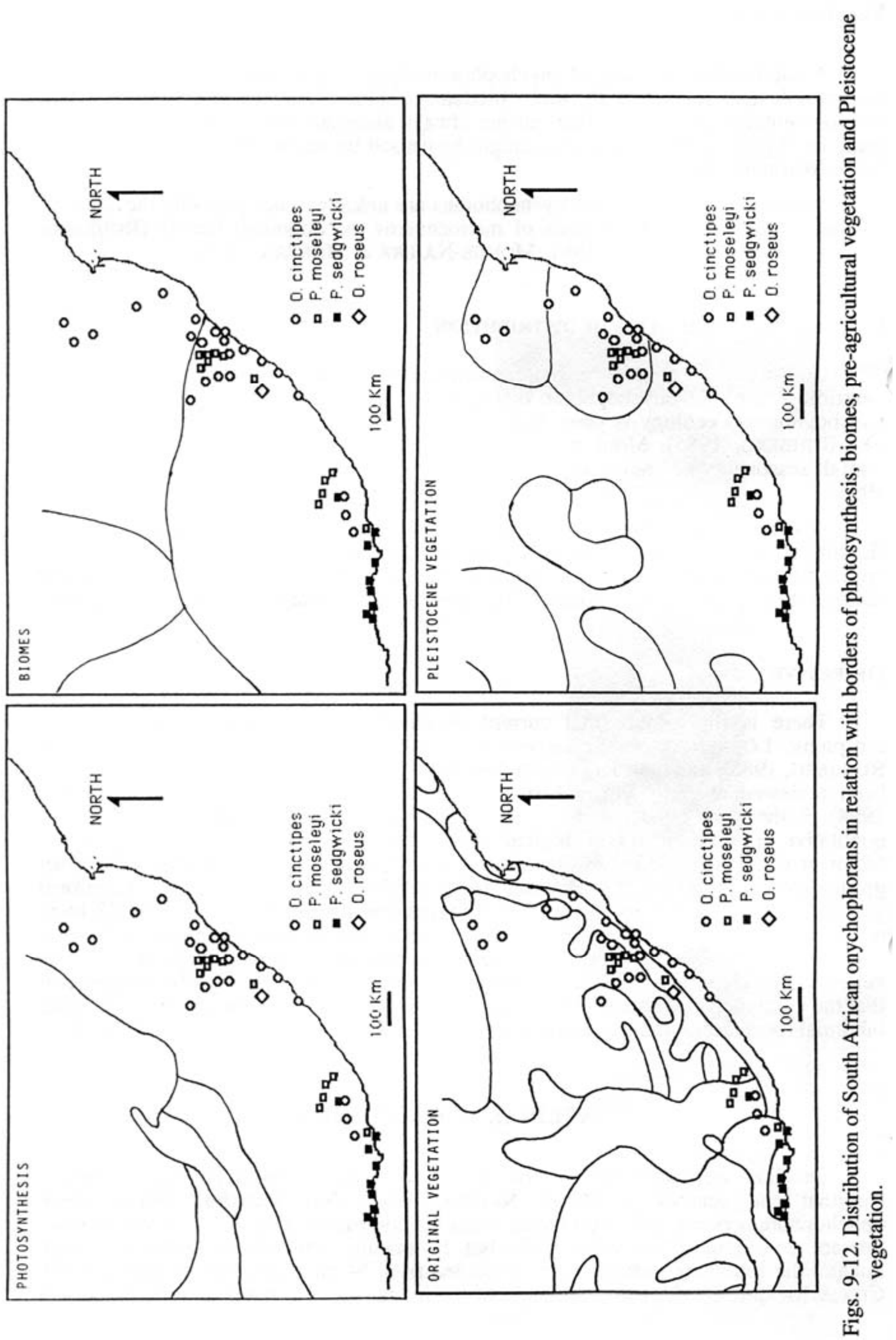
DISCUSSION

LIMITATIONS OF THIS STUDY

The study is based on several assumptions about the maps and statistical tests. One of them is that the maps are correct: this seems reasonable considering the modern status of cartography, but the map of onychophoran distribution is certainly less precise *(e.g.* two quadrats marked “with onychophorans” coincided with desert, in which the phylum is absent). Nevertheless new collections in the last fifty years have changed very little this map (compare BRUES, 1923 with MONGE-NAJERA, 1994). Although no statistical analysis can be considered definitive, the tests used in the present paper are adequate for this sort of data (JAMES & MCCuLL0CH, 1990).

Both types of analysis produced different results, which suggests that despite the relative biological homogeneity of the group (reviews in RUHBERG, 1985 and MONGE-NAJERA, 1994), global distribution patterns do not correspond well with those of specific areas such as South Africa or Australia. This suggestion is supported by the statistical analysis: the correlation values of ecological factors were not the same in the two families, although Pleistocene vegetation was highly correlated in both. This will be analyzed below.

	Peripatidae		Peripatopsidae	
Factor	C	S	C	S
Biome	45	0000	48	0000
Climate	50	0000	30	NS
Fotosynthesis	40	0000	14	NS
Pleist. vegetat.	63	0000	35	0035
Precipitation	33	0001	28	0296
Temperature	31	0000	33	0054
Vegetation	43	0000	29	NS



Figs. 9-12. Distribution of South African onychophorans in relation with borders of photosynthesis, biomes, pre-agricultural vegetation and Pleistocene vegetation.

Fig. 13. Distribution of onychophorans (circles) and humans (grey) in Australia.

FACTORS WITH LOW OR NO CORRELATION

When two factors show a low correlation, or lack it, it is probable that one is not a significant cause of the other. Each of the following factors failed to explain by itself the barriers that limit onychophoran distribution at the global level: mean annual rainfall and temperature, photosynthesis, and types of climate, vegetation and biome.

This result is surprising. Onychophorans require high humidity and this low association with average rainfall might mean that the yearly distribution of precipitation (not considered here) is more significant that its amount (see Cox & MOORE, 1985). The low correlation with temperature was also unexpected because the species from tropical areas (Peripatidae) were considered independently of those from temperate regions (Peripatopsidae). Obviously there is high variation even within families. Finally, although earlier writers had suspected that the taxonomic composition of vegetation was not important **(CLARK,** 1915*;* BRINCK, 1956) the type of plant formation often allows the experienced collector to predict onychophoran occurrence, but this factor was only slightly correlated in the Peripatidae and unsignificant in the Peripatopsidae.

Similar results were obtained for other organisms when quantitative techniques were applied. In several cases, factors such as range shape, habitat diversity, climate type, climate variability, habitat heterogeneity, history, competition, predator disturbance and habitat disturbance have surprisingly failed to correlate with some biogeographic trends (RYDIN & **BORGERGARD,** 1988; CURRIE, 1991).

CORRELATED FACTORS

When high correlation does exist, causation can be suspected but not proved. In this case, altitude and rainfall correlate with the distribution of some South African and Australian taxa, respectively, and at the global level, Pleistocene vegetation appeared significantly correlated with the distribution of both families. If these correlations reflect a real cause-effect relationship, it means that (1) globally onychophoran ranges are limited to areas which conserved appropriate microclimates during the general decrease in moisture and temperature about 18000 years ago, as known for highland plants (SIMPSON, 1974) and in agreement with the debated refugia model (see LOURENCO, 1987), and (2) that locally the specific boundaries are marked by other factors such as altitude or rainfall according to the taxon and as suggested previously (BRINCK, 1956; NEWLANDS & **RUHBERG,** 1978; MESIBOV & **RUHBERG,** 1991). This interpretation implies that little expansion has taken place since the Pleistocene and may be taken as support to the idea of refugia. On the other hand, the Pleistocene effect (as well as the correlations with altitude or rainfall) may simply be coincidental, a possibility that must be addressed in future studies. The Australian case interestingly suggests that humans and onychophorans are affected similarly by dry conditions which prevent the development of forest (MESIBOV, 1994, pers. comm.) although it may also reflect that most sampling is done near populated areas (G. PONT, 1993 pers. Comm., University of South Wales).

Overall these results answer the basic question of this study negatively: the global distribution of the phylum onychophora does not correspond with any of the single ecological factors considered here. The biogeographical barriers seem to be a product of ecological factors which depend on the taxon and may often act in combination, with none clearly overriding the others. A proper test of how factors interact will have to wait until density data become available.

Table II. Number of geographic quadrats for each environmental category in which the family Peripatidae is absent or present.

Biome	1	2	3	4	5	6	7	8	9			
Absent	17	17	16	8	4	18	3	15	7			
Present	2	2	0	9	3	15	0	31	5			
Climate	1	2	3	4	5	6	7	8	9	10		
Absent	20	14	19	17	18	7	5	4	0	1		
Present	2	0	8	32	5	19	0	0	1	0		
Photosynthesis	1	2	3	4								
Absent	16	30	46	13								
Present	0	5	35	27								
Pleist.veg.	1	2	3	4	5	6	7	8	9	10	11	12
Absent	6	33	24	12	5	6	3	1	2	12	1	0
Present	0	0	3	0	2	0	11	0	0	14	36	1
Rainfall	1	2	3	4	5							
Absent	18	13	22	29	23							
Present	1	1	13	29	23							
Temperature	1	2	3									
Absent	12	64	29									
Present	0	30	37									
Vegetation	1	2	3	4	5	6	7	8	9	10	11	
Absent	11	3	7	7	3	24	12	13	22	2	1	
Present	0	2	2	0	0	41	8	1	13	0	0	

Biomes. 1:desert, 2:temperate grassland, 3:temperate decidous and rain forest, 4:tropical decidous forest, 5:tropical scrub forest, 6:tropical grassland and savannah, 7:mountains, 8:tropical rain forest, 9:Mediterranean.
Climate. 1:steppe, 2:desert, 3:damp temperate, 4:hot damp rainforest, 5:warm with dry winters, 6:periodically dry savannah, 7:cold with wet winters, 8:warm with wet winters, 9:tundra, 10:warm with dry summers.
Photosynthesis (carbon: glm2lyear). 1: 0-100, 2: 101-400, 3: 401-800,4: above 800.
Pleistocene vegetation. 1:mesic grassland, 2:cold decidous broad-leaved forest and woodlands, 3:arid grasslands and shrublands, 4:subtropical drought decidous woodlands, 5:evergreen needle-leaved forest and woodlands, 6:tundra, 7:drought seasonal forests and tall grasslands, 8:polar desert and ice, 9:cold decidous needle-leaved forest and woodlands, 10:tropical and subtropical rain forest, 11 subtropical drought decidous woodlands, 12:tropical grassland and savannah, 13:tropical decidous forest, 14:mountains, I 5:Mediterranean.
Mean annual rainfall (mm). 1:25 or less, 2:28-51, 3:53-102, 4:103-202, 5:203 or higher.
Mean annual temperature (C). 1:-12 or less, 2:-13 to -7, 3:-8 to 4,4:5-15,5:16-27,6:28 or higher.
Current vegetation. 1 desert shrub and waste, 2:scrub and thorn forest, 3:temperate and subtropical forest, 4:temperate grasslands, 5:coniferous forest, 6:tropical rain forest, 7:unclassified highlands, 8:steppe (shortgrass), 9:tropical grasslands (savannah), 10:Mediterranean mixed forest.

Table III. Number of geographic quadrats for each environmental category in which the family Peripatopsidae is absent or present (Simbology as in Table 2).

Biome	1	2	3	4	5	6	7	8	9			
Absent	19	18	7	17	7	31	3	40	5			
Present	0	1	9	0	0	2	0	6	7			
Climate	1	2	3	4	5	6	7	8	9	10		
Absent	21	14	18	43	15	26	5	4	1	0		
Present	1	0	9	6	8	0	0	0	0	1		
Photosynthesis	1	2	3	4								
Absent	14	33	66	34								
Present	2	2	15	6								
Pleist.veg.	1	2	3	4	5	6	7	8	9	10	11	12
Absent	6	21	23	12	5	5	12	1	2	22	37	1
Present	0	12	4	0	2	1	2	0	0	4	0	0
Rainfall	1	2	3	4	5							
Absent	19	12	28	55	33							
Present	0	2	7	3	13							
Temperature	1	2	3									
Absent	5	82	60									
Present	7	12	6									
Vegetation	1	2	3	4	5	6	7	8	9	10	11	
Absent	10	5	5	5	3	57	20	12	28	1	1	
Present	1	0	4	2	0	8	0	2	7	1	0	

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