

Onychophora: past and present. Edited by M. H. Walker and D. B. Norman

Phylogeny, biogeography and reproductive trends in the Onychophora

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A cladistic analysis places the Onychophora between Polychaeta and Arthropoda. The 'Uniramia' concept is not supported. No justification was found for either onychophoran family to be considered ancestral. A cladogram of fossil genera indicates the common ancestor to have long oncopods, armoured plates and an annulated body. Later forms show adaptations to life in reduced spaces. Physiological data suggest that the Onychophora became adapted to land via the littoral zone, before the Late Ordovician. Adhesive glands evolved for defence on land. Peripatopsidae and Peripatidae were distinct by the late Triassic. The occurrence of onychophorans probably dates from post-Pliocene in New Guinea and southern Australia, and post-Early Cretaceous in Chile, the southern half of Southeast Asia, Mesoamerica and the Caribbean. After the Early Cretaceous, the peripatids of tropical Africa lost terrestrial contact with those of South America. A new biogeographic technique, formalized here under the name retrovicariance, indicates that the Peripatidae of Equatorial Africa and the Neotropics are sister-groups. Typical inbreeding adaptations found in some onychophorans include: female-biased sex ratios; gregarious development; relatively constant time of development and number of offspring in each clutch; male polygamy and shorter life span; frequent sibmating in the microhabitat of development, and sperm storage by females, so that a single insemination fertilizes all ova.

ADDITIONAL KEY WORDS:—Cambrian lobopods — vicariance — retrovicariance — fossil — oncopodophores — mating systems — cladistics — evolution.

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INTRODUCTION

There are about one hundred described onychophoran species, classified in two families: the Peripatopsidae (found in Chile, South Africa and Australasia) and Peripatidae (found in the Antilles, Mexico, Central America, northern South America, West Equatorial Africa and Southeast Asia) (Bouvier, 1905, 1907; Ruhberg, 1992 personal communication).

Onychophorans usually inhabit dark and moist microhabitats chiefly in forest litter and soil, rotten logs and bromeliads (Picado, 1911; Endrody-Younga & Peck, 1983). They feed on small invertebrates which are captured with the help of an adhesive substance, which is also expelled as a defence.

They share many characters with annelids and arthropods. These characters have caused much debate regarding their phylogenetic position (see Sawyer, 1984; Ballard *et al.*, 1992). The group, however, is generally regarded as having phylum status (e.g. Brusca & Brusca, 1990). To date, its evolution has not been comprehensively analysed, to the extent that no phylogenetic tree exists for onychophoran families and genera (see Ruhberg, 1985a), including related fossil and living forms. Cladistic analyses for onychophoran taxa, including related fossil and living forms, are not available. The

last palaeobiogeographic study of their distribution was done about 40 years ago (Vachon, 1953, 1954). Their mating systems have not been analysed from a current evolutionary approach, with the exception of a few suggestions by Ghiselin (1985).

In this paper, the relationships of onychophoran families to Annelida, Tardigrada, Arthropoda and several fossil oncopodophores are analysed using cladistic techniques, and the implications for evolutionary trends within the group are discussed. A new approach based on palaeogeographical and ecological reconstructions is used to analyse their distribution. Finally, current evolutionary theory is used to evaluate the relationship of microhabitat adaptations, mating systems and parental investment. Original results from ongoing research are also presented to supplement the theoretical analysis.

Cladistic analysis

In 1949, Vandel summarized onychophoran evolution as follows: "Onychophorans can be considered highly evolved annelids, adapted to terrestrial life, which announced prophetically the Arthropoda. They are a lateral branch which has endured from ancient times until today, without important modifications".

In a comprehensive study, Ruhberg (1985a) reviewed the biology of the phylum and examined the taxonomy of the Peripatopsidae. She concluded that a detailed cladistic analysis was unjustified, on the basis of data then available. Several traditional phylogenetic trees linking Annelida, Onychophora and Arthropoda have been proposed (e.g. Sharov, 1966; Manton, 1977; Dzik & Krumbiegel, 1989) but they differ significantly (Fig. 1). A new insight has been gained from a recent cladistic analysis which places the Onychophora in an intermediate position between the Polychaeta and the Tardigrada-Arthropoda clade (Brusca & Brusca, 1990).

None of these phylogenies dealt with the relative position of groups within the Onychophora. Bouvier (1900, 1905, 1907) and Ruhberg (1985a) believed that the Peripatidae is the less derived family, while Marcus (1937) and Peck (1975, 1982) suggested the opposite, based on some of the same characters.

Fossils which have been proposed as being related to the Onychophora (Ramsköld & Hou, 1991) include species of *Luolishania* Hou & Chen, *Hallucigenia* Conway Morris, *Cardiodictyon* Hou, Ramsköld and Bergström, *Microdyction* Chen, Hou and Lu, *Onychodictyon* Hou, Ramsköld and Bergström, *Xenusion* Pompeckj, *Aysheaia* Walcott, and *Helenodora* Thompson & Jones. Other possible oncopodophores were not included for lack of sufficient data (see Cloud & Bever, 1973; Donovan & Paul, 1985; Dzik & Krumbiegel, 1989; Hou & Chen, 1989b; Hou, Ramsköld & Bergström, 1991). Little is known about the biology of these extinct oncopodophores, which occurred in shallow coastal communities, including algae as primary producers, and deposit-feeding collectors, suspension feeders, carnivores and scavengers (Conway Morris, 1986; Hou, Ramsköld & Bergström, 1991).

Biogeography

The geographic distribution of Onychophora has received attention since the beginning of this century. The idea of a former land connection between southern hemisphere populations was accepted by Clark (1915) and supported by Croizat (1958; see also Brink, 1957). Both families have mutually exclusive geographic ranges: recent reports of passive transport-resulting from human activity-across the 'latitudinal barrier' have been reviewed by van der Lande (1991).

The existence of temperate onychophoran fossils indicated a former wide range (Vachon, 1953), and suggested that the families separated as a result of past isolation in Laurasia and Gondwana. Accordingly, both families were later forced southward by climatic changes and are currently isolated by arid belts in America and Africa, and by sea in Asia and Oceania (Vachon, 1954).

A new analysis is presented here, which indicates that both were defined before the separation of Gondwana and Laurasia.

Reproductive systems

Organisms from isolated biotopes often adapt to small territories and to inbreeding, particularly if they live in confined, dark, humid microhabitats (Hamilton, 1967). Apparently, a high genetic variability is unnecessary in such stable microhabitats (Hamilton, 1967; Ramírez, 1987) and this leads to similar

adaptations in phylogenetically unrelated organisms (Hamilton, 1967; Ramírez, 1987) and here I will examine whether these adaptations occur in onychophorans, which are often found in such microhabitats.

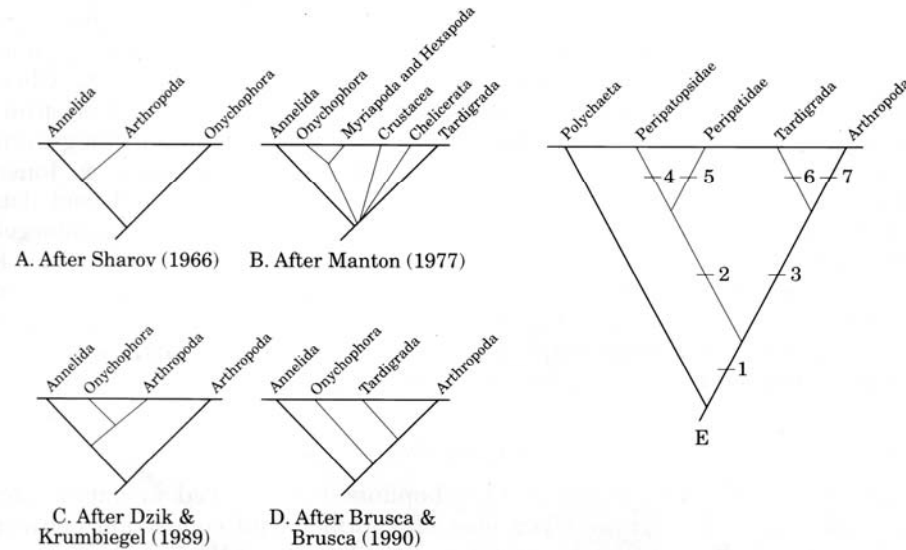


Figure 1. Phylogenetic relationship of the Onychophora, according to some authorities. Traditional dendrograms have been redrawn as cladograms. In E, the result of this analysis, the derived characters states are the following:

1. Poorly defined cephalic region, chitinous cuticle, growth by moulting, dorsal folds in body wall, reduced metamerization? oncopods, small number of locomotory appendages, walking pads, reduced coelom? cross-striated muscle? body pigment soluble in alcohol, oral papillae, dorsal open heart, coxal glands, loss of palps, two developed centres in antennal nerves, developed scalariform junctions in active transport epithelium, excretory ducts with cuticular walls renewed by moulting, loss of unicellular epidermal glands, non-septate, haemocoel, unicellular sensory setae in epidermis, deutocerebrum defined, short sperm duct, short oviduct, gonopore near penultimate pair of oncopods, absence of sex reversal, cuticular impregnation, egg fertilized in ovary, vesicula copulatrix, loss of larvae, centrolecithal eggs, uniform blastoderm comprising low cuboidal cells, extraembryonic blastoderm, elongate dorsal gonads.

2. Loss of external segmentation? loss of striated muscle except in mandibles, oblique muscle layer in body wall, subcutaneous haemal channels, oral papillae, salivary gland reservoir, pre-digestion of prey, terrestrial habits, crural glands, loss of cirri, body papillae and scales, adhesive glands, non-migratory gastrulation, onychophoran coxal glands and tracheal system.

3. Cuticular plates, sclerotized locomotory appendages, Malpighian tubules (those of Tardigrada may not be homologous with those in Arthropoda).

4. Reduction of last oncopod pair, body pigmentation not soluble in alcohol, ovoviviparity, viviparity, gonopore behind penultimate pair of oncopods, 'penis', vesicula copulatrix reduced or lost, egg fertilised in oviduct in some species, irregular dorsal folds in some species.

5. Primary and secondary papillae, increased and variable number of oncopods (more in females), inner mandible diastema, crural glands lost in males, loss of oviparity, attachment- type placenta, elongated sperm duct, probable loss of cuticular impregnation.

6. Buccal stylets, miniaturization and related characters, digits or increased number of claws (perhaps not homologous to other claws), telescopic legs, tolerance to environmental extremes, pseudolarvae, loss of mandibles, heart, antennae, nephrostomic flagellar system, transport epithelia and respiratory structures? These characters might also suggest aschelminth affinities.

7. Lateral compound eyes, rarely calcified cuticle, discrete sclerites, articulated appendages, more ventrally positioned appendages, greater regional specialization in the gut, cephalic ecdysial glands, loss of motile cilia and flagella except in sperm, (characters for node 7 are illustrative only and are from Brusca & Brusca, 1990, because the Arthropoda were not included in this study).

MATERIAL AND METHODS

Cladogram

A variety of names has been used for the same group of animals ancestral to onychophorans, e.g. 'lobopod animals', 'lobopodophores' and even 'lobopods'. To avoid confusion, the following distinctions are made in this paper: the 'lobopod' is a hypothetical ancestral leg in the form of a simple body evagination. More complex and annulated, but non-articulated legs with claws, similar to those of onychophorans, are 'oncopods' (Ruhberg, 1992 personal communication). Oncopod-bearing animals are here called 'oncopodophores'. Onychophorans are living representatives of the oncopodophore clade (see Bergström, 1991; Hou, Ramsköld & Bergström, 1991).

Here, to substantiate the cladograms, the most significant data are presented in tabular form (Appendices 1—6). The blanks in the appendices readily pinpoint worthwhile subject areas for new

research. Although an attempt has been made to give credit to the original authors, in some cases recent reviews are cited, to reduce the list of references. All hypotheses presented are supported by clearly stated data and their testable implications are enumerated.

Doubtful characters referred to in the literature were verified by examining specimens from the Museum of Zoology, University of Costa Rica. Fossil characters not mentioned by authors were recorded from original photographs and illustrations in the literature.

Many characters were considered, comprising traditional morphology, as well as physiology, ecology and behaviour (Appendices 1—5). By considering characters in much detail, rather than clumping them in broad categories such as 'legs present', the danger of ignoring convergence is reduced.

Previously, suggestions of 'primitive' versus 'advanced' conditions, as well as proposals about phylogenetic affinities, have been presented on the basis of isolated characters, with contradictory results (e.g. Bouvier, 1900; Marcus, 1937; Cave & Simonetta, 1975; Thompson & Jones, 1980; Robison, 1985). Besides consideration of isolated characters, confusion has been created by assuming that every oncopodophore character which resembles an arthropod character is derived (see Manton, 1973; Boudreaux, 1979; Brusca & Brusca, 1990). For example, an author observing only onychophorans and arthropods can argue that holoblastic cleavage, which occurs in both, indicates a close phylogenetic relationship. This would be incorrect, because annelids also have holoblastic cleavage, which therefore is a symplesiomorphy for the group. Nevertheless, this type of reasoning has often been applied to onychophorans.

The conclusion that a character is derived in any taxon is unjustified unless it is simultaneously true that such a character is different in the appropriate outgroup (see Brusca & Brusca, 1990). In this paper, rigorous outgroup comparison is used to define character polarity, as recommended by Stevens (1980). Even if annelids developed segmentation independently, there are good reasons to believe that they are close relatives of onychophorans (see Brusca & Brusca, 1990), which makes them an acceptable outgroup (see Stevens, 1980). For the present analysis, Polychaetes were selected as the outgroup for onychophores and other oncopodophores, because other annelids are derived forms adapted to terrestrial life (Marcus, 1937; Brusca & Brusca, 1990). For living groups, Polychaeta and Tardigrada were used to establish character polarity. Polychaeta and Onychophora were similarly used as outgroups for fossil oncopodophores.

Many characters were formally found to be symplesiomorphies and were consequently excluded, facilitating construction of the cladograms. These were constructed by hand (see procedure in Funk & Stuessy, 1978).

Hypothesis tests and other observations

Observations were carried out on *Epiperipatus biolleyi* Bouvier, collected in Coronado, San José, Costa Rica. They are found during daytime in logs and shallow galleries in the soil. The methods and results of these observations will be presented in detail in another paper.

To assess population density and to record associations of individuals in the field, appropriate microhabitat quadrats were selected using a table of random numbers. Each quadrat was searched to extract all onychophorans. Sex was determined by counting legs (in this species, females have more than 29 pairs).

The behaviour of the adhesive was tested by making the animal eject glue directly under fresh (tap) water and sea water (30 ppt) from the Pacific coast of Costa Rica. An empty petri dish was used as control ('air'). Reactions of living animals were tested by placing them in petri dishes with each type of water. Burrowing capacity was tested by placing them in terraria with loose commercial soil and exposed to daylight. Similar terraria with moss were used as a control and all treatments were randomly assigned. Locomotory speed was measured of onychophorans walking away from a light source on the surface of standard bond paper.

Solubility of body pigments in alcohol was examined in Polychaeta, Onychophora and Crustacea in the collection of the School of Biology, and in the collection of Tardigrada, Faculty of Microbiology, University of Costa Rica.

Biogeography

Biogeography comprises three lines of thought, each with its own methodology and assumptions: (1) dispersalism, (2) panbiogeography and (3) vicariance biogeography (Nelson & Platnick, 1980). Dispersalism attempts to identify routes of dispersal from the original range of each taxon (see Nelson & Platnick, 1980). Panbiogeography identifies geographic areas with related biotas (Croizat, 1958). Vicariance biogeography uses phylogenies to establish the sequence of separation among geographic areas (see Cracraft, 1983).

The assumed limited vagility of the Onychophora suggests that, within families, geographically close species could also have close phylogenetic relationships (Sedgwick, 1908; Brues, 1923; Ruhberg, 1985a). Because the phylogenetic relationships of onychophoran genera are unknown, it was decided to make systematic predictions based on geographic affinities. This fourth biogeographic approach, which has been implicit in biogeographic comments of earlier authors, is here named 'retrovicariance' (an example appears together with the results). The maps are based on review of geological botanical and zoological information from the Permo-Triassic transition to the present (references cited in figure captions). By plotting current onychophoran ranges, new biogeographic inferences were obtained, which will be considered separately for each family.

Reproductive trends

A total of 38 characters related to confined microhabitats (some of them specifically associated with inbreeding, Appendix 7) were considered, according to the data and sources detailed in Appendices 1–5.

RESULTS AND DISCUSSION

Cladistic analysis

The following interpretation, as in any cladistic study, is a description of what the branching sequence implies regarding biological characters and the geologic time of cladogenesis. Of course, if new data permit modification of the cladogram, several implications could prove to be erroneous. For the moment, the inferences presented below are consistent with current data.

Phylogenetic position

The phylogenetic relatedness of Onychophora and Arthropoda is suggested by a large set of characters (Fig. 1). The cladogram, which does not support the Uniramia concept of Manton (1973), is consistent with that of Brusca & Brusca (1990), which used fewer characters and did not consider onychophoran families individually. Surprisingly, only three characters were found to relate the Tardigrada with the Arthropoda (Fig. 1), and even these are not very significant, for three reasons: (1) cuticular plates could be defensive convergence, armouring occurs in many unrelated invertebrates (see Brusca & Brusca, 1990); (2) the sclerotized legs of tardigradans are telescopic, not articulated as in arthropods (Appendix 2), and (3) the Malpighian tubules of tardigradans may not be homologous with those of arthropodans (see Brusca & Brusca, 1990). This result will please those who believe that tardigrades are more closely related to the Nematoda.

Characters believed to indicate a derived condition in either onychophoran family (see Peck, 1982; Ruhberg, 1985a) were mostly valueless for the following reasons:

(1) Number of leg pairs. It is often assumed that having fewer leg pairs is derived, possibly because insects are derived and have only three. Additionally, a trend toward leg loss also occurs in Crustacea (e.g. Branchiopoda to Decapoda) and Chelicerata (Xiphosura to Arachnida). Unfortunately, that character is cladistically invalid because of overlap: some peripatopsids have more leg pairs than some peripatids. Similarly, gonopore position is practically intermediate in tardigrades, and it is to some extent subjective to decide that it resembles more closely either the peripatid or the peripatopsid position. Nevertheless, this argument is invalid if tardigrades are not related to onychophorans. A study of fossil onychophorans may be useful on this regard.

(2) Intraspecific variation in number of leg pairs. The number of leg pairs is fixed in peripatopsids and variable in peripatids. The character is fixed in tardigradans. I ignore if polychaetes have a variable number, a prerequisite to considering the peripatopsid condition to be derived.

(3) Heart details. The derived condition cannot be examined since tardigrades lack a heart. If equivalent data are obtained for polychaetes and appropriate arthropods, the issue could be re-examined.

(4) The following characters are known only in one group, and seem to constitute autapomorphies: (a) reduction of last leg pair (only found in some peripatopsids and secondarily in highly modified polychaetes); (b) body pigment solubility in alcohol (insoluble pigments only occur in peripatopsids); (c) crural glands (they appear to occur only in onychophorans) and (d) placental viviparity (found only in peripatids).

(5) Salivary gland reservoir and coxal glands. It has recently been found that such structures occur in peripatopsids (H. Ruhberg, 1992 personal communication).

Both families have 8–9 known autapomorphies, and 1–2 possible derived characters shared with tardigrades. It must be admitted that they are so similar, that labelling any as derived or ancestral does not seem justified with current data.

The cladogram (Fig. 2) indicates that oncopodophores had an ancestor bearing long oncopods (possibly each with two claws), armour plates, and body and oncopod annulation. The morphological similarities between Onychophora and *Aysheaia* have frequently caused the Onychophora to be labelled as a 'living fossil', a term opposed by several authors (e.g. Schopf *et al.*, 1975; Schopf, 1984). While retaining an ancestral body plan, like many other organisms (Brusca & Brusca, 1990), onychophorans present some new characters, such as the proteic adhesive, and in Peripatidae, a placenta and a genome rich in adenine and thymine (Mora, 1992). Peripatids also appear to have extraordinarily small mitochondrial genomes and material frequently organized in tandem (see Hebert *et al.*, 1991; Mora, 1992). Their geographic distribution has also been interpreted as 'primitive' (Fig. 3; review in Ruhberg, 1985 a).

Feeding-related adaptations and papillation

No evidence is available to support or reject carnivory and a terminal mouth as ancestral conditions. The reports of sponge-feeding and terminal mouth in living 'pro-onychophores' (Sundara Rajulu & Gouri, 1988a, b, 1990) are suspect (Jayaraman, 1989). If *Aysheaia* fed on sponges (Whittington, 1978), it is strange that no sponge spiculae were preserved in the digestive tract. Such spiculae are obvious in the tract of polychaetes that feed by applying an eversible proboscis to sponges (Manton, 1967). It may be that some oncopodophores were carnivorous, as are living onychophorans, but heads and mandibles are missing in most fossils (Appendix 6). Onychophoran mandibles are strikingly similar to some conodonts (Fig. 4). The term conodont defines a variety of microfossils (Briggs, Clarkson & Aldridge, 1983) which without evidence is usually assumed to belong to a single type of animal (see Aldridge & Briggs, 1986).

How a conodont functioned is debated. Some authors suggest a biting action (e.g. Schmidt, 1934; Bengtson, 1980) and others oppose it (e.g. Lindström, 1964; Hitchings & Ramsay, 1978). The morphological similarity with onychophoran mandibles may give hints of their function. Onychophoran mandibles basically move backwards, tearing the prey exoskeleton (Manton, 1953, 1973). Conodonts may have functioned similarly, but they do not represent homologous structures, because conodonts seem to be early chordate structures (Aldridge & Briggs, 1986). If the proboscis has been properly identified in palaeontological reconstructions, it was apparently lost late in the history of lobopodophores (Fig. 2), perhaps in relation to life in reduced spaces. In polychaetes, a proboscis is frequent in vagile ('errant') families but absent in burrowing and sedentary species (Appendix 3).

The anal segment (pygidium) may have been lost during oncopodophore evolution, and certainly is not visible in fossils of *Onychodictyon* and related forms, although a small anal cone occurs in onychophorans (see Anderson, 1973; Boudreaux, 1979; Robison, 1985).

Annulation is often associated to the function of elongation and compression. It may have developed for burrowing (see Dzik & Krumbiegel, 1989) and in oncopods, to facilitate locomotion (see Manton, 1953).

Body papillae were present in Cambrian oncopodophores at least before the branching of *Onychodictyon* (Fig. 2) and possibly had the same tactile function as the papillae of living onychophorans (see Robson, 1964). Primary papillae of living onychophorans are larger on the dorsal surface of the oncopods, perhaps related to a greater sensitivity. It is unknown if the same applies to papillae from fossil oncopodophores.

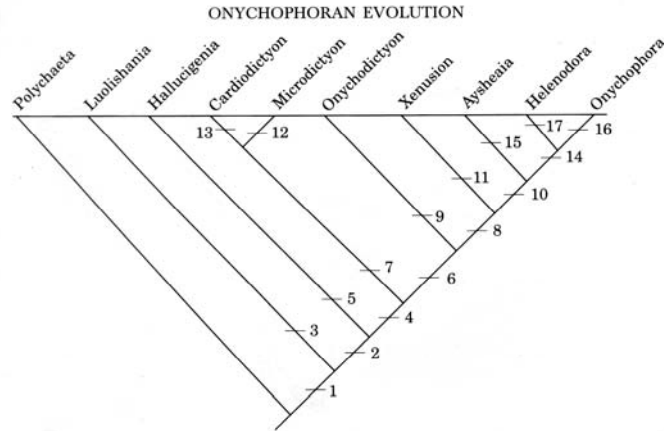


Figure 2. Cladogram of fossil and extant legged invertebrates (non-arthropod), based on the characters of Appendix 6 (Whittington, 1978; Thompson & Jones, 1980; Chen, Hou & Lu, 1989; Dzik & Krumbiegel, 1989; Hou & Chen, 1989a, b; Hou, Ramsköld & Bergström, 1991; Ramsköld & Hou, 1991). Characters with asterisk possibly appeared earlier in the cladogenesis, but here appear where indicated by current data.

1. Elongated oncopods, plate armouring, body and oncopod annulation. 2. Two claws in each leg?, body plates enlarged, trunk spines. 3. Increase in number of claws, to 4 or 5. 4. Oncopod spines reduced in length (?). 5. Seven pairs of long and strong dorsal spines. 6. Body papillation*, medium length oncopods, oncopodial spines. 7. Synapomorphies yet undetermined. 8. Reduction in plate size. 9. Long dorsal and ventral papillae(?). Eleven pairs of annulated legs with rearward direction of claws reversed in the posterior legs. 10. Proboscis lost, loss of trunk spines and plate armouring. 11. Large body size (20 cm). 12. 'Netted' scales, 13. 21—24 pairs of lateral plates pointed ventrally. 14. Loss of oncopodial spines, reduction of oncopod length, mandibles*. 15. 6—7 claws per oncopod, branched antennae. 16. Adhesive glands. 17. *Helenodora* autapomorphies yet to be identified.



Figure 3. Natural geographic distribution of recent Onychophora and fossil oncopodophores(*); 1—3 Peripatidae, 4—6 Peripatopsidae (Ruhberg, 1985a; van der Lande & Holthuis, 1986; van der Lande, 1991).

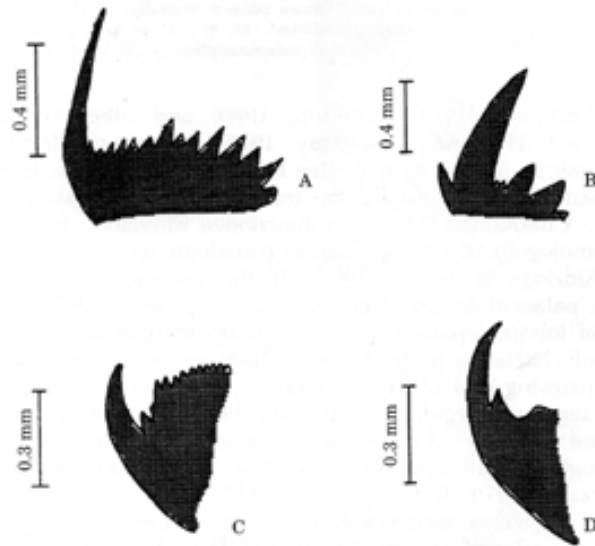


Figure 4. Some euconodonts (A and B) convergently resemble the mandibles of Onychophora (C and D). Conodonts based on Gould (1985); onychophoran mandibles from Morera-Brenes & Leon (1986).

Oncopods and armouring

Dark bands along the oncopods of *Onychodictyon* might represent internal structures, although they have not been interpreted this way by other researchers (see Hou, Ramsköld & Bergström, 1991). There is an internal rod (aciculum) in polychaete parapodia, but it is unlikely that a similar structure existed in oncopodophores (see Manton, 1967). Manton (1953, 1967) and Anderson (1973) believed that articulated legs, oncopods and parapodia originated independently from ancestral lobopods, in opposition to Sharov (1966).

The number of claws fluctuates along the cladogram (Fig. 2). Most authors assumed that oncopodophores did not dwell on muddy bottoms, because they had claws (Chen, Hou & Lu, 1989), but this was not necessarily so, for living onychophorans use their walking pads on a smooth surface and use claws only for hard, rough substrates (Ruhberg, 1985b). Additionally, tardigrades with claws dwell in abyssal muddy bottoms (H. Dastych, 1992 personal communication).

Manton (1967) stated that spines on walking appendages would hinder rather than favour locomotion. Their possible role in anchoring, climbing (Whittington, 1978) or defence is unknown, and it would be useful to study their function in extant Heterotardigrada, which also bear them (H. Dastych, 1992 personal communication).

A trend for shorter oncopods began with *Onychodictyon*. Long legs are generally associated with rapid locomotion, which is more necessary in open exposed habitats than in tunnels. Some crustaceans are known to walk more slowly under water than on land (Manton, 1953), because of the resistance of water (see Brusca & Brusca, 1990). This suggests that Cambrian oncopodophore speed was below the mean 3.45 mm/s (mm. 1, max. 5.6) of *E. biolleyi* (Monge-Nájera, unpublished observation).

The cladogram (Fig. 2) suggests that the ancestral animal probably had a radial mouth and moulted (some fossils of later forms are believed to represent exuviae, see Appendix 6). *Xenusion* may have moulted following a split of integument along a ventral line (see Dzik & Krumbiegel, 1989; and Jaeger & Martinsson, 1967 for the contrary opinion), which is very different from living onychophorans (see Campiglia & Lavallard, 1989 for a review).

Besides allowing growth, moulting may have been favoured in evolutionary history as a mechanism to shed ectoparasites (see Lavallard & Campiglia, 1975a). No previous report of onychophoran ectoparasites has been found by the author, but presumably phoretic acari have recently been reported to occur in onychophorans (Mesibov & Ruhberg, 1991). Possibly specialized bacteria, which do not appear elsewhere on the exterior of the animal's body, have been found reproducing in pits located near the midline of an undescribed *Epiperipatus* from Costa Rica (Monge-Nájera, in preparation).

Their mode of fossilization (Hou *et al.*, 1991) suggests that oncopodophores had an active life on the sea substratum, which probably exposed them to errant predators. The development of a spiny armour is not surprising, because it has evolved many times as a defence against predators in groups as different as lepidopterans, dinosaurs and mammals. Larger Carboniferous diplopods, unable to hide in the litter,

developed spines and sometimes gigantism (Shear & Kukalová-Peck, 1990), which might explain the large size of *Xenusion* (Appendix 6).

It has been hypothesized that *Xenusion* could assume a defensive curled posture, while the shorter *Aysheaia* could not (Dzik & Krumbiegel, 1989). Some living onychophorans curl while resting (Ruhberg, 1985a, and personal observation of *E. biolleyi*), which is consistent with this hypothesis. In contrast, the relative body length of *Aysheaia* could hardly have prevented it from curling-up, because even shorter millipedes can roll-up (a Paleozoic example is illustrated in Shear & Kukalová-Peck, 1990).

Apparently, the development of oncopod spines preceded a trend toward smaller body plates (*Xenusion*) and the final loss of plates and spines (*Aysheaia*). With *Helenodora*, which is more similar to living onychophorans and perhaps was even semiterrestrial, spines disappeared altogether and oncopods became even shorter and similar to those of living onychophorans (Fig. 2). This trend to eliminate armouring may be one of the most significant in the evolution of oncopodophores. One hypothesis is that they changed from exposed life on the marine substratum to new microhabitats with reduced space, such as tunnels, crevices or even sponge canals (although reconstructions show *Aysheaia* crawling on the outside of sponges (Whittington, 1978), a lack of armour would better suit life inside the canal system of the sponge). Some predictions of the reduced space hypothesis are: (1) elimination of structures hindering forward movement, such as spines and prominent plates, (2) reduction of oncopod length, and (3) increase in body flexibility. Current data on *Aysheaia*, *Helenodora* and Onychophora do not allow rejection of this hypothesis (Manton, 1958; Thompson & Jones, 1980; Robison, 1985). In small spaces where many predators cannot follow, a rigid spiny armour appears both unnecessary and a hindrance (see Manton, 1958). The loss of metameric internal organization of the body is associated with the functionality of a fluid skeleton (Boudreaux, 1979), which is useful for life in tunnels (Manton, 1958).

Internal fertilization and flexible body

The evolution of internal fertilization and a direct life cycle is frequent in marine invertebrates with vagile adults which live in unstable environments (Brusca & Brusca, 1990). This could suggest that internal fertilization occurred in tidal zone oncopodophores and that it favoured land colonization for onychophorans, because direct gamete transfer provides an appropriate environment even out of water (see Brusca & Brusca, 1990). Accompanying internal fertilization, some crural glands and nephridia became modified as accessory genital glands (Purcell, 1900; Ruhberg & Storch, 1978). Similar structures occur in Heterotardigrada (Renaud-Mornant, 1982).

Manton (1958) insisted that a hard exoskeleton never evolved in the Onychophora because the ability to change body shape was favourably selected as an adaptation to move through reduced spaces. This capacity, related to the absence of striated muscle (which does not bend easily) allows them to escape from predators and unfavourable conditions and implied that a tentorium could not develop (Manton, 1958, 1973). From those ideas it can be hypothesized that one of the prerequisites for a rigid mandibular apparatus with a tentorium has not been developed in the group. Without a tentorium, strong predatory mandibles cannot function, explaining why adhesive glands are particularly useful to dominate the prey and for defence. The maintenance of a flexible body imposes severe limitations on body size, precision of movements, defence and speed (Brusca & Brusca, 1990), a generalization which fits the Onychophora (Appendices 1—5).

The transition to land

The stages that onychophorans may have followed during adaptation to land are illustrated by some anomuran and brachyuran decapods: some burrow to avoid desiccation; others to control blood density and drink; additionally to these adaptations, others use water-absorbing structures (see Barrington, 1979).

Onychophoran adaptations correspond to the most advanced decapod stage (see Manton & Ramsay, 1937; Campiglia & Maddrell, 1986; Campiglia & Lavallard, 1978; Barrington, 1979; Ruhberg & Nutting, 1980). Perhaps burrowing occurred in late Cambrian oncopodophores (as suggested by loss of armouring) and was used in the intertidal zone to prevent desiccation during low tides.

Burrowing is a key survival factor in living onychophorans, which are thought to be unable to make tunnels, although this has not been formally studied (see Ruhberg, 1985a for a review). Experiments in progress indicate that *E. biolleyi* is incapable of making burrows even in soft soil (Monge-Nájera, unpublished observation).

Because the ancestors of onychophorans lived in shallow marine environments, they may have adapted to land via the intertidal zone. A transitional freshwater stage could also be hypothesized, because the adhesive substance functions when experimentally ejected under freshwater (see below). From Barrington (1979), I have extracted the following characters that indicate a direct sea-land transition: (1)

development of major water retention mechanisms, (2) water drinking behaviour, (3) ultrafiltration, (4) high surface permeability, (5) high blood osmotic pressure and (6) uricotelly. All occur in the Onychophora (see Manton & Ramsay, 1937; Campiglia & Maddrell, 1986; Campiglia & Lavallard, 1978; Barrington, 1979; Ruhberg & Nutting, 1980) and clearly suggest that they adapted to terrestrial life via the littoral zone. Since the first arthropods were marine (Shear & Kukalová-Peck, 1990), and the Tardigrada are also aquatic (Brusca & Brusca, 1990), the Onychophora probably occupied land independently of the Arthropoda (Fig. 1). The cladogram suggests that they originated before the terrestrial arthropods (Fig. 1), which appeared in the late Ordovician (Shear & Kukalová-Peck, 1990).

Fossil oncopodophores have only been found in northern continents, while Recent onychophorans have a Tropical-Austral distribution (Fig. 5). Location on maps of the corresponding geologic periods shows that marine oncopodophores inhabited shallow waters in the subcontinental areas of Baltica, China and North America (Cambrian tropical and temperate belts) and later, in North America and Europe (Carboniferous tropical belt; Monge Nájera, in preparation).

On land, a waxy body cover that reduces desiccation is not advantageous in organisms that experience daily temperature changes (Barrington, 1979), a fact that could suggest that onychophorans, which lack an external wax layer, adapted to land in a habitat characterized by strong daily fluctuations in temperature. On the other hand, Ruhberg & Nutting (1980) suggested that onychophorans colonized land in a temperate region, because cooler climates have water richer in oxygen and reduce xeric stress. Both hypotheses deserve elaboration and testing.

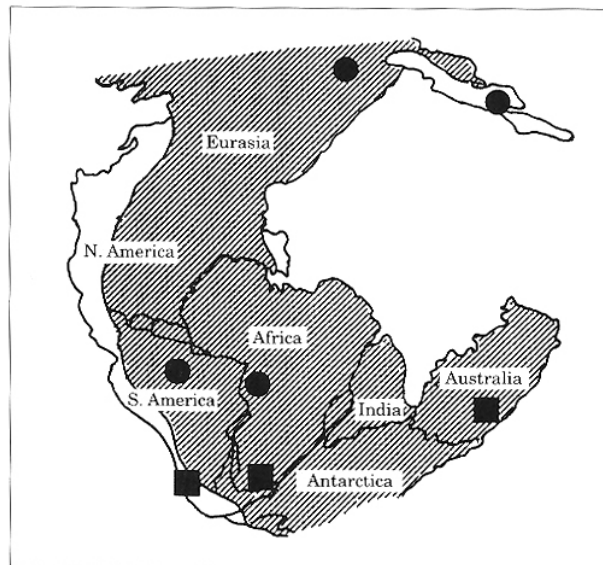


Figure 5. Paleogeographic World maps. Permo-Triassic transition (245 Myr before present). There was a single landmass (Pangaea) with generally warm and slightly dry conditions in the northern (Laurasia) and southern parts (Gondwana). Nevertheless, eastern Pangaea received more moisture and the southern half of Gondwana suffered strong seasonal fluctuations of temperature (and probably of aridity). The western coast of the American continents and much of SE Asia were submerged under an epicontinental sea. Reptiles inhabited the land. A mass extinction had decimated diversity in the Permian seas. In this series of maps (Figs 5–8), submerged land areas (usually controversial or ignored in reconstructions) are based on distributions of marine and terrestrial organisms, including ammonites, belemnites, hermatypic corals, bivalves, foraminiferans, brachiopods, ostracods, bryozoans, arthropods, fishes, amphibians, reptiles and other vertebrates, as well as plants (based on MacKerras, 1970; Heitzler, 1976; Kurtén, 1976; Hallam 1973, 1981; Schuster, 1976, 1983; Pielou, 1979; Coney, 1982; Gómez, 1982; Bussing, 1985; Seyfried & Sprechman, 1985; Alvarado, 1988. Climatic reconstructions and plate tectonic maps follow Cox, 1974; Barron & Washington, 1982; Condie, 1982; Hay, Behensky, Barron & Sloan, 1982; Parrish & Curtis, 1982; McKenzie, 1986; Alvarado, 1988; van der Voo, 1988; Horgan, 1989; Gyllenhaal *et al.*, 1991; Parrish, Ziegler & Scotese, 1982; Patzkowsky *et al.*, 1991; Piccoli *et al.*, 1991; Wang & Chen, 1991). Circles: centres of current Peripatid geographic ranges. Squares: centres of current Peripatopsid geographic ranges. Shaded areas = emerged land.

Gas exchange and feeding on land

Terrestrial gas exchange also posed a problem, which was solved through the development of tracheae. Onychophoran tracheae must be analogous to those of the Arthropoda (Fig. 1). Nevertheless, histological evidence needs to be obtained, because Manton (1967) mentioned that onychophoran tracheae resemble those of some centipedes. The independent development of similar structures is to be expected because onychophoran tracheae are also similar to cutaneous invaginations found in terrestrial polychaetes (Marcus, 1937; see also Bicudo & Campiglia, 1985). No branchiae have been found in fossil

oncopodophores although body evaginations in *Onychodictyon* (see illustration in Hou *et al.*, 1991) might have been respiratory structures. Thus it is more likely that the tracheae used on land evolved secondarily after aquatic cutaneous gas exchange.

There was no tendency towards mechanical protection from desiccation which is chiefly avoided through nocturnal and photonegative behaviour (Manton & Ramsay, 1937; Holliday, 1942; Morrison, 1946b; Endrody-Younga & Peck, 1983; Lavallard *et al.*, 1975). As a result, onychophorans are restricted to moist habitats and some populations may easily become isolated in small areas (Lavallard *et al.*, 1975; van der Lande, 1978; Morera-Brenes & Monge-Nájera, 1990; Mesibov & Ruhberg, 1991). Habitat restriction has been found to favour inbreeding adaptations in other organisms (Ramírez, 1987), as discussed later.

In onychophorans, the lack of a strong protection against desiccation imposes significant restrictions. Food needs to be obtained within a very limited time (a few hours per day) and space (nearly moist microhabitat). The resulting selection for a low cost/benefit ratio explains their predatory behaviour, compared with other feeding habits that provide less energy (see Brusca & Brusca, 1990). There is evidence that *Peripatus acacioi* Marcus & Marcus may be undernourished in nature (Campiglia & Lavallard, 1989), suggesting the importance of feeding restrictions.

Captive *Peripatoides gilesii* Spencer have fed in daylight (van der Lande, 1978). If onychophorans feed during daytime in nature, it may represent an adaptation to moist temperate microhabitats with many day-active prey (Ruhberg & Nutting, 1980). Nocturnal pulmonate molluscs sometimes become active during daytime hours when rain increases the atmospheric humidity (personal observations) and some onychophorans may behave similarly.

It has been suggested (Robison, 1985) that the development of adhesive glands took place on land, because the adhesive substance would have been inoperative in the sea. In fact, the adhesive substance of *E. biolleyi* dissolves quickly in sea water, dries in air after a few seconds, and remains operative for hours in fresh water (Monge-Nájera, in preparation). Adhesive glands are probably modified crural glands (see Ruhberg & Storch, 1977), although Anderson (1966) disagreed.

Apparently no model has been published about the evolutionary development of onychophoran adhesive glands, which are used both to capture prey and for defence. A hypothesis that may encourage future analysis is that the original function was defence. This is suggested because chemical defence is widespread in animals, including many invertebrates (see Brusca & Brusca, 1990) and mammals (Eisenberg, 1981), while a hunting adhesive is only known in onychophorans (some arachnids use adhesive, although the mechanism is different; see Lavallard & Campiglia, 1971). Ancestral onychophorans might have secreted from their crural glands a viscous substance which interfered with the mandibular action of small predators. In this way, the original apparatus could be functional from an early stage, requiring only improvements in the viscosity, amount and distance that the substance could be expelled. This defensive substance would in turn also be useful for hunting, if the original condition consisted of capturing some prey directly with the mandibles, as still occurs when onychophorans handle small prey. The adhesive substance probably allowed the entanglement of larger and therefore more nutritious prey.

The glands produce an adhesive substance which, when expelled, is guided with the help of a pair of eyes with large chitinous lenses and a well-developed retinal layer. Although onychophoran vision was traditionally thought to be poor (Cuénot, 1949), it is noted that the ability to distinguish leg joints and fangs mentioned by Read & Hughes (1987) indicates otherwise. Food is digested extra-corporally with the help of enzymes in saliva produced by modified nephridia (Buxton, 1913; Storch, Alberti & Ruhberg, 1979).

The adaptation to subterranean life

Cave dwelling organisms often have elongated appendages, lack eyes and cuticular pigmentation and occur in small and isolated geographic ranges. In tropical and subtropical areas they probably evolved from non-troglobitic ancestors living in dark and humid habitats (Holsinger, 1988). This suggests that the Onychophora, all adapted to dark humid microhabitats, are well suited to produce troglobitic species. However, only two are known: the peripatopsid *Peripatopsis alba* Lawrence of South Africa Lawrence, 1931 and the peripatid *Speleoperipatus spelaeus* Peck, 1975 from Jamaica. *Typhioperipatus williamsoni* Kemp, 1914 from India and *Tasmanipatus anophthalmus* Ruhberg, Mesibov, Briscoe & Tait, 1991 from Tasmania, both of which live under forest litter, are eyeless; the former retained normal pigmentation, but pigmentation is reduced in *T. anophthalmus*. Some *Peripatoides indigo* Ruhberg, 1985 and *Peripatoides novaezealandiae* Hutton, 1876 from New Zealand have been found in caves but do not have troglobitic characters (Ruhberg, 1985a; Newlands & Ruhberg, 1978).

Troglobitic ecosystems depend on external energy and often sustain only small populations (Holsinger, 1988). They often have species with low respiratory rates which are slower and less aggressive than related non-cave species (Lawrence, 1962). The population size of both *S. spelaeus* and *P. alba* was very small (Lawrence, 1931; Peck, 1975).

Biogeography

The implications of the biogeographic analysis are presented separately for each family (Figs 5—8).

Paleobiogeographic reconstruction

Peripatopsidae. The occurrence of Peripatopsidae in New Guinea and adjacent islands (but not New Zealand), as well as in eastern Australia and Tasmania, must represent a post-Pliocene colonization because those areas were submerged in the Oligocene-Pliocene (Fig. 8B, references in figure caption). Chilean peripatopsids probably reached their current range after the early Cretaceous, because the area which is currently Chile was previously submerged (see Figs 6 and 7; sources stated in Fig. 5). The separation of peripatopsid populations which originally inhabited southern Gondwana began not later than the Early Cretaceous, when South Africa became separated by a water gap (Fig. 7). A terrestrial connection remained between South America and Australia until the end of the Cretaceous via Antarctica (but see below).

Peripatidae. The exact range of the Onychophora in Southeast Asia is not known, but current data indicate that at least part of the area may have been submerged in the Oligocene-Pliocene (Fig. 8) suggesting a later colonization. The southern half was submerged in the Lower Cretaceous (Fig. 7) and must have been colonized after that time. If the Mexican, Central American and Antillean Onychophora have a South American origin, as is widely believed (see Cuénot, 1949), these areas must have been reached after the Early Cretaceous for the same reason (Figs 7 and 8).

According to the reconstruction presented here, *Mesoperzatus* Evans lost any remaining terrestrial contact with South American onychophorans after the Lower Cretaceous (Fig. 7). The time of separation for the Asian population is more difficult to assess. The last terrestrial connection between a joined South America—Africa landmass and Asia, occurred in the early Jurassic via North America. Another possibility is that Asian onychophora originated in the early Jurassic, when India was in contact with South American and Africa. If such was the case, the Indian onychophorans (Figs 6—8) were carried north and colonized Southeast Asia when India collided with Asia. Marcus (1937) suggested that, in the past, onychophorans were widespread in India, until they became extinct during the geomorphologic and climatic change that caused the extinction of many Indian organisms.

This biogeographic model (Figs 5—8) suggests that the two extant families, Peripatopsidae and Peripatidae, were fully distinct and had wide longitudinal distributions in Triassic—Jurassic times. This contradicts Vachon (1953, 1954), who did not have access to the detailed paleogeographical information now available.

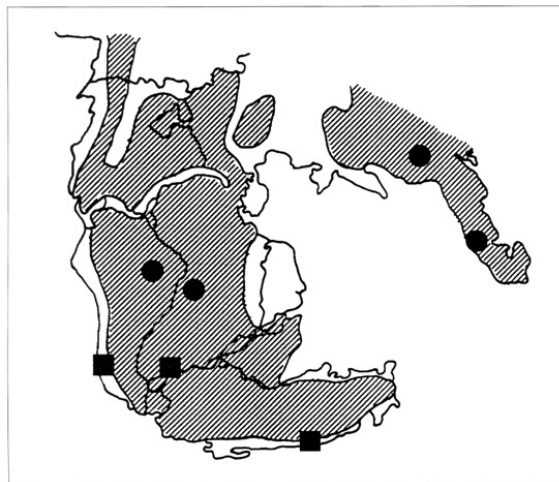


Figure 6. Early Jurassic (194 Myr before present). The separation of Laurasia and Gondwana has begun, with a connection remaining via the Iberian Peninsula. Many areas, including much of Europe, were submerged, but eastern Asia was connected by land to North America. The climate was warm and dry and dinosaurs and flying reptiles inhabited the land (sources and symbols as in Fig. 5).

Figure 7. A, Lower Cretaceous (116 Myr before present). The connection of North America with East Asia, and the proximity of North America to Gondwana via Africa, may explain some of their present biotic similarities. The pattern of epicontinental seas had changed and Africa became separated by water from India and Antarctica, while connected indirectly to them and to Australia by South America. In general, the climate was very warm and dry, conditions which would become harsher in the mid Cretaceous. B, Upper Cretaceous (87 Myr before present). North America was divided by sea into eastern and western landmasses. The western was connected to East Asia until late in the period, and the eastern connected to western Europe. Africa was composed of two large islands fully separated from Madagascar and India, a large island itself at about 72 Myr before present: a brief island connection existed between South and North America, via the Antilles, which were moving eastward. New Zealand separated from West Antarctica. The climate was, in general, very warm and dry (sources and symbols as in Fig. 5).

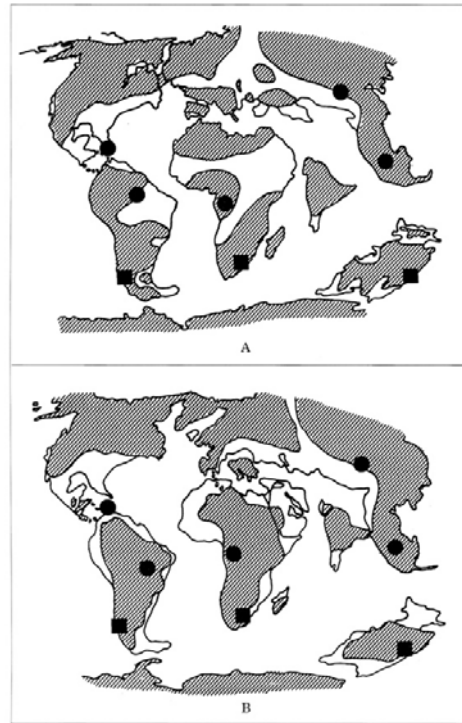


Figure 8. A, Paleocene-Eocene (Tertiary) (59—40 Myr before present). The distribution of epicontinental seas changed significantly. Asia was connected with North America and Europe by what probably was an island arc. The Antilles were close to their current position and Central America was represented by another island arc. South America and Australia were separating from Antarctica (which was still forested). Much of Africa was submerged, but the northern part was in contact with the Iberian Peninsula. The relative position of India appears here as indicated by palaeomagnetic evidence (Condie, 1982), although fossil data indicate contradictory relationships: closer to Asia (animals: Hallam, 1981) and closer to South Africa (plants: Schuster, 1983).

B, Oligocene-Pliocene (Tertiary) (28—3.4 Myr before present). There was a continuum of land uniting Asia, North America, Greenland and Europe, although there was still no direct connection between Europe and Asia. Island arcs connected South with North America, and Europe with Africa. India was rapidly approaching Asia and epicontinental seas covered great areas and may have even invaded the Amazon basin and more of Africa than shown here. Temperature and aridity fluctuated widely. In the Oligocene, plate collisions elevated the Himalayas and the Alps: the Miocene was a time of great vulcanism and increasing aridity, with forests being substituted by grasslands. In the Pliocene the temperatures fell significantly and the Central American Isthmus fully united South and North America (sources and symbols as in Fig. 5).

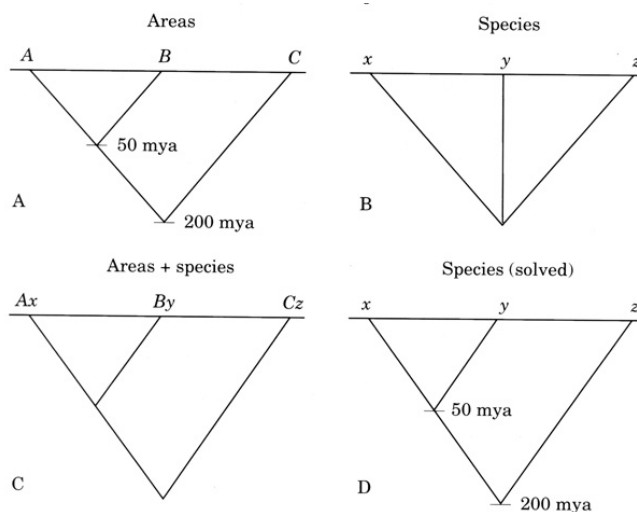


Figure 9. The technique of retrovicariance biogeography. Area cladograms are useful to produce phylogenetic hypotheses. In this imaginary example, geologic evidence indicates that areas A and B were joined more recently, while area C had separated earlier (A). The phylogenetic relationship of three taxa, x, y and z, is unknown (B), but as their distribution is plotted in the area cladogram, a hypothesis of their phylogenetic relationship results: x is the sister group of y, while z represents a clade that speciated earlier (C). When the geologic time of the area separations is known, the time of cladogenesis can be suggested (D).

Retrovicariant analysis

Sedgwick (1908) cautioned that many taxonomic characters seem to reappear haphazardly in onychophoran taxa. This can complicate cladistic analysis. Without a cladogram, a vicariance analysis is impossible. Recent biochemical data suggest that several 'species' described on the basis of morphological characters are in fact species groups (Hebert *et al.*, 1991; Ruhberg, 1992). The biological validity of at least some genera also remains to be demonstrated (see Ruhberg, 1992).

Retrovicariance biogeography uses area cladograms, produced from geological data, as the basis for constructing biogeographic, systematic and even paleontological hypotheses; these can be tested against nonbiogeographical evidence when it becomes available. Consider the example of Fig. 9. Geological evidence indicates the time of separation of areas A, B and C (Fig. 9A). The phylogenetic relationship of three taxa, x, y and Z, is unknown (Fig. 9B). If each taxon ranges exclusively in each geographic area, distribution can be plotted in the area cladogram, resolving the phylogenetic relationship. In this example, x is the sister group of y, while z is the extreme of a clade that was separated earlier (Fig. 9C).

When the geologic time of the area separations is known (Fig. 9A), the probable lower time limit for cladogenesis can be assessed (Fig. 9D) and evaluated if there is a fossil record. For example, if fossils of taxon y were found in strata significantly older than 50 Myr ago, the retrovicariant cladogram could be rejected.

The requirements of retrovicariance are the same as for vicariance (see Nelson & Platnick, 1980; Craw, 1982) and include evolution by cladogenesis, monophyletic taxa and non-composite geographic areas.

Retrovicariant cladograms are hypotheses: they must be consistent with their data and make clear taxonomic predictions. For that reason, they can be tested and refined as new data and interpretations become available (e.g. new palaeogeographic reconstructions, estimations of biochemical distance and molecular clock analysis). In the future, when detailed palaeo-biome maps become available for all geographic areas and geologic periods, retrovicariance will significantly increase in accuracy, by considering appropriate biome connections and not exclusively emerged land connections.

The usefulness of retrovicariance is not limited to taxa for which no phylogenetic trees exist (such as Onychophora). The technique produces cladograms which can indeed be tested against existing phylogenies based on traditional or other phylogenetic procedures. Circular reasoning, in which area cladograms based on phylogenies are used to 'support' phylogenies, must of course be avoided.

Retrovicariance applied to onychophoran genera

By applying the retrovicariant procedure to the areas inhabited by onychophorans (Fig. 6A) in accordance with the sequence of geographic separations shown in Figures 5—8, a phylogenetic hypotheses for both families was produced (Fig. 10). The resulting cladogram (Fig. 10B) indicates for the Peripatidae a common ancestor for the taxa of Equatorial Africa and the Neotropics (contradicting Purcell, 1900), while the Asian taxa represent their sister group which separated earlier. This contradicts Kemp's (1914) opinion that the Indian genus *Typhiperipatus* Kemp is most closely related with

Neotropical onychophorans. An African relationship is more likely from their relative positions (Fig. 6). Similarly, the Peripatopsidae of Australia and adjacent islands, and those of Chile, appear more closely related between themselves than with those of South Africa (Fig. 10). This result contradicts important morphological evidence (Ruhberg, 1985a, and 1992 personal communication) and might mean that onychophorans from Australia and adjacent islands had become isolated even earlier, when a large dry area covered Antarctica and much of Australia (see map in Hay *et al.*, 1982). The separation of the lineage leading to South African *Opisthopatus* Purcell and *Peripatopsis* Pocock has an early Cretaceous date. The lineage of Chilean *Metaperipatus* Clarck and *Parapisthopatus* has a Paleocene start (Fig. 10A, B).

At the beginning of the Upper Jurassic, the lineage of Indian *Typhioperipatus* and Malaysian *Eoperipatus* Evans branched from the clade leading to Equatorial African *Mesoperipatus* Evans (which split in the Upper Cretaceous) and the Neotropical peripatids (Fig. 10A, B).

In the Caribbean, Jamaica, Hispaniola, Puerto Rico and the Lesser Antilles were probably colonized by trans-oceanic dispersal, raising the question of how onychophorans react to the marine environment. When placed in sea water, individuals of *E. biolleyi* die and sink after a few minutes (Monge-Nájera, unpublished observation). But onychophorans must be able to reach islands on rafts of logs, soil and vegetation. Bates (1864) noted that such rafts commonly leave the mouth of the Amazon River; moreover, marine currents flow from eastern South America to the Antilles. In the Caribbean, the distance that onychophorans can travel across water is at least 165 km, the gap separating the oceanic island of Barbados (see Peck & Peck, 1980) from Saint Vincent, the nearest neighbour island with onychophorans. Cuba was not isolated from adjacent land until the Oligocene (Alvarado, 1988). The absence of onychophorans in Cuba might mean that they did not occur in nearby islands previous to that time. This agrees with recent biochemical evidence suggesting that some onychophorans reached Jamaica between 20 and 7 Myr ago (Hebert *et al.*, 1991). The Pliocene is suggested as the oldest limit for the establishment of Mesoamerican populations if they arrived from South America, because most of Mesoamerica was underwater until the Oligocene (some parts emerged as islands and were available for terrestrial organisms).

Both systematic and timing hypotheses resulting from my work fit the current data but can be tested when new information becomes available. For example, a protein analysis might indicate both the branching sequence and the approximate dates for onychophoran speciation (see Havel, Wilson & Hebert, 1989).

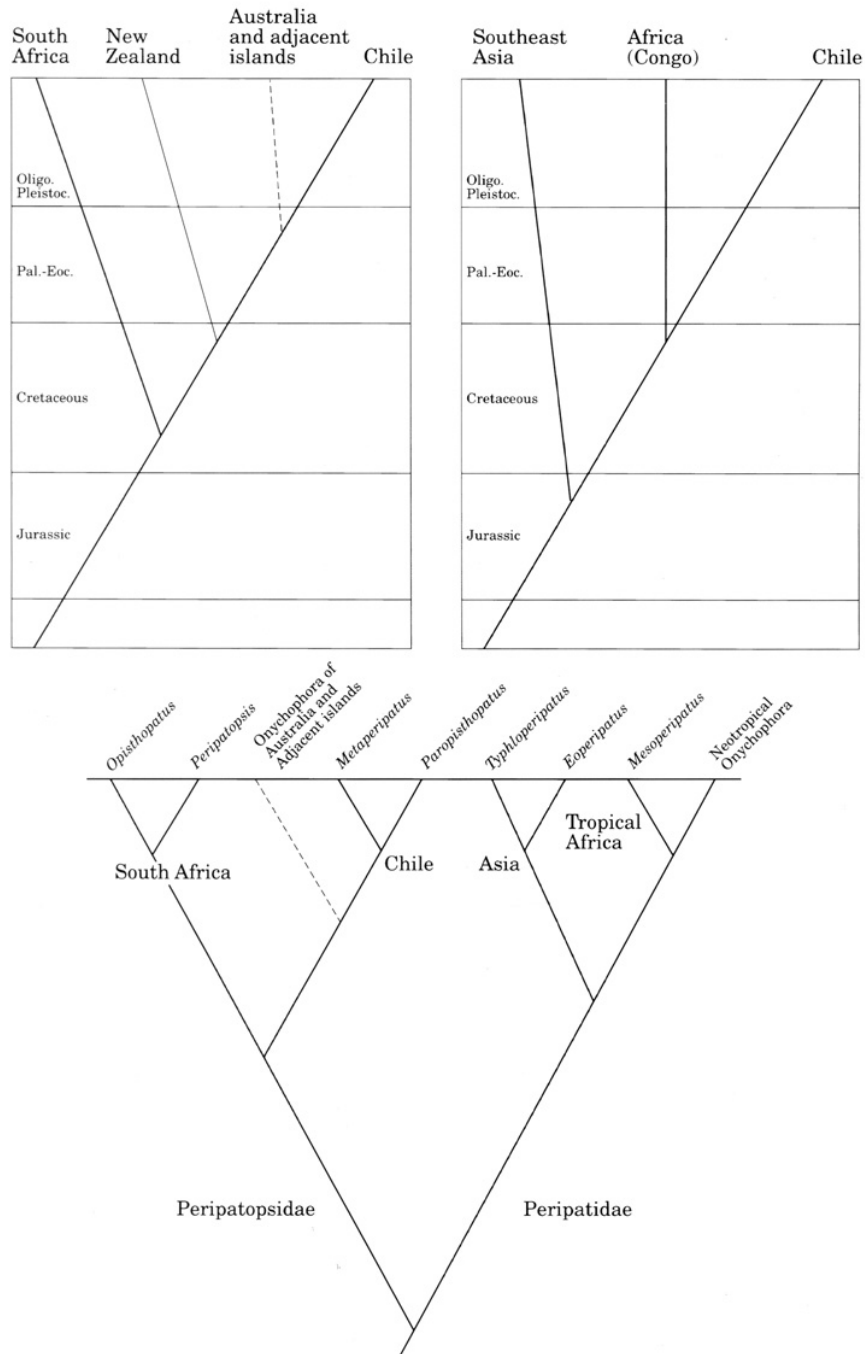


Figure 10. A, Area cladograms for land masses inhabited by Peripatopsidae (left panel) and Peripatidae (right panel). B, A retroviciant cladogram for the Onychophora. The species from Australia and adjacent islands represent a highly heterogeneous group. Broken line indicates doubtful information.

Ecological biogeography

The significance of humidity in the distribution of Onychophora was recognized early (Clark, 1915) and it is reasonable to expect a coincidence between appropriate habitats and onychophoran ranges. Several maps have therefore been examined: photosynthetic potential (map supplement to *National Geographic* 174 (6), 1988); vegetation, temperature and rainfall (Hammond, 1979) and Holocene vegetation (map supplement to *National Geographic* 174 (6), 1988). None correspond to the present day geographic distribution of the Onychophora, although photosynthetic potential is always high in onychophoran habitats. The restricted range of *Mesoperipatus* Evans in Equatorial Africa is puzzling as there are similar habitats surrounding it (possibly isolated at present because of deforestation).

Insufficient collecting and the possibility that onychophorans were unable to cross the Congo River also require further consideration.

No onychophorans have been found in central eastern Australia (yet they occur in southern Queensland and northern New South Wales). This is an arid barrier isolating moist relict refuges (see Cracraft, 1983) during widespread desertification in the Pleistocene, as reflected, for example, by bird distribution and vicariant analysis. This indicates that *Austroperipatus* and *Ooperipatus* from northern Queensland became isolated from other Australian onychophorans after the late Cenozoic.

Reproductive systems

Stable microhabitats and genetic diversity

Climatically stable and isolated microhabitats often have organisms with low genetic variability which inbreed, such as has been shown for fig wasps and bee parasites (Hamilton, 1967; Ramírez, 1987; Brusca & Brusca, 1990). These conditions are analysed for onychophorans which often inhabit the same type of habitat. This applies particularly to peripatids, which seem to fit the characters in Appendix 7 better than most peripatopsids. A tendency, rather than a perfect fit of characters was expected for two reasons: (1) onychophoran microhabitats basically include rotting logs and litter, which are not as stable as figs and bee cells; (2) onychophorans are not totally isolated, because they probably disperse during moist periods and some even occur widely in humid grasslands (Lavallard *et al.*, 1975; Endrödy-Young & Peck, 1983).

Do the facts agree with the hypothesis? A high DNA content in the genome of the peripatid *E. biolleyi* has been discovered, substantiating the hypothesis of evolution in a stable environment (Mora, 1992). Certain adaptations to isolation in confined microhabitats do not occur in peripatids; nevertheless, they have smaller males which are probably neotenic and mate precociously (Appendices 5 and 7). Low genetic diversity can explain the lack of allozyme variation in *Macroperipatus insularis* Clark (see Hebert *et al.*, 1991). Another testable prediction of the low genetic diversity hypothesis, when data become available, is that a higher proportion of the characters presented in Appendix 7 will be found in populations from drier habitats, where onychophorans are forced to concentrate in small moist patches.

Nevertheless, of the 15 general inbreeding characters (Hamilton, 1967), nine are known or suspected to occur in the Onychophora, particularly in the Peripatidae: namely female-biased sex ratios (as adults : ratio at birth is 1: 1), gregarious development, relatively constant time of development and number of offspring in each clutch, male polygamy and shorter life span, frequent sibmating in microhabitat of development, and female storage of sperm through which a single insemination fertilizes all eggs (Appendix 7). Only five inbreeding characters are unknown or suspected not to occur in the Onychophora (Appendix 7). Furthermore, another extreme adaptation to isolated stable microhabitats, parthenogenesis (Hamilton, 1967), has been vaguely reported in *Epiperipatus imthurni* Sclater (Read, 1985). Perhaps some species for which no males have been collected (Ruhberg, 1985a) are also parthenogenic.

Mating systems

Most frequently, single individuals are found in the field. How do the sexes meet for fertilization? Two possible patterns are: (1) there is a single fertilization early in a female's life, or (2) there is periodic fertilization, either during meetings of two individuals or in larger aggregations. For example, *P. acacioi* belongs to pattern 1 (see Lavallard & Campiglia, 1975b), and is more likely to fit the low diversity-inbreeding model than *Opisthopatus cinctipes* Purcell, in which females are fertilized periodically (see Walker, 1992b).

P. gilesii in Australia (van der Lande, 1978), *Tasmanipatus barretti* Mesibov & Ruhberg in Tasmania (Mesibov & Ruhberg, 1991) and *E. biolleyi* in Costa Rica (personal observation) are sometimes found in clusters. There is evidence that such clusters represent kin, which is in agreement with the hypothesis of sibmating. In captivity *P. gilesii* neonates group with adults during the first days after birth; *T. barretti* clusters found in nature are composed of young individuals of similar sizes (Mesibov & Ruhberg, 1991). Harris (1991) reported extraordinarily high densities of up to 36 individuals per log in New Zealand, but did not give their sex or the age/size composition of the colony. Nevertheless, some clusters of *Plicatoperipatus jamaicensis* Grabham & Cockerell were certainly not mother-offspring groups (Hebert *et al.*, 1991).

It has been suggested that onychophoran males which mate at an early age may be favoured over those which wait until a larger size is reached (Ghiselin, 1985). This can explain why males are smaller and grow more slowly, as reported by Lavallard & Campiglia (1975a, b). Nevertheless, it remains to be explained why there is moulting not only shortly after birth, but even before birth (see Manton, 1938; Holliday, 1944; Morera-Brenes, Monge-Nájera & Saenz, 1988).

The possible function of body colouration (including patterns visible only in the infrared, similar to the ultraviolet patterns of insects; see Silberglied, 1979), and pheromones in onychophoran mating has not been studied and may open a new field of research. Van der Lande (1978) noticed that *P. gilesii* is hard to see in litter, which suggests that the brownish colouration of many species may have a cryptic value.

Parental investment

Internal fertilization ties the female to the zygote and allows the male to abandon the female and search for more females (Dawkins & Carlisle, 1976). This probably applies to onychophorans, in which polygyny is suspected (see references in Appendix 5). The evolution of increased parental investment leading to ovoviviparity and viviparity in onychophorans could be the result of significant pressure from parasites and predators, as in other groups (see Gross & Shine, 1981). In Tasmania, oviparous species are mostly found in litter, while viviparous species occur mostly in logs (R. Mesibov, 1992 personal communication). This hypothesis could be tested by measuring the relative abundance of predators in litter and logs. Predation pressure should be higher in logs where viviparous onychophorans are found. No data are yet available, but the ratio is 1.8 predator species for each prey species in logs associated with Costa Rican *Epiperipatus hilkae* Morera & Monge-Nájera (B. Morera, 1990 personal communication). A quantitative synecological analysis of *E. biolleyi* ecosystem is now in progress and equivalent data from other regions would be of great value.

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APPENDICES

Appendix 1

General characters of onychophoran families and extant related taxa (Appendices 1–5 constructed from data in Marcus, 1937; Holliday, 1944; Morrison, 1946a,b; Choonoo, 1947; Cuénot, 1949; Vachon, 1953, 1954; Milne & Milne, 1954; Krishnan, 1970; Daly, 1972; Campiglia & Lavallard, 1973, 1989; Lavallard & Campiglia, 1973, 1975a,b; Hackman & Goldberg, 1975; Schroeder & Hermans, 1975; Locke & Huie, 1977; Newlands & Ruhberg, 1978; Lavallard, 1981; Dyrce, 1982; Peck, 1982; Renaud-Mornant, 1982; Ruhberg, 1985a,b; Nylund *et al.*, 1987; Read & Hughes, 1987; Rubberg & Storch, 1988; Havel, Wilson & Hebert, 1989; Ruhberg, 1990; Walker & Campiglia, 1990; Brusca & Brusca, 1990; Storch & Ruhberg, 1990; Walker, 1992a,b).

	Polychaeta	Peripatopsidae	Peripatidae	Tardigrada
Fossil history	Cambrian ¹	No data	No data	Cretaceous ²
Diversity (number of species)	Over 12000	About 40 ²	About 50	Above 680
Size	5–10 cm; rarely 0.1–100 cm	10–80 mm but varies as individual moves	10–150 mm but varies as individual moves	0.1–1.7 mm
Body shape	Cylindrical and several modifications	Cylindrical	Cylindrical	Short cylinder
Cephalic region (compared to trunk)	Poorly to well defined	Poorly defined	Poorly defined	Poorly defined
Cuticle	Thick, thin or absent	Thin	Thin	Thin
Cuticle composition	Mainly collagen	Alpha-chitin, protein, others	Alpha-chitin, protein, others	Chitin, others
Cuticular permeability	To O ₂ , H ₂ O, glucose, etc.	To O ₂ and H ₂ O	To O ₂ and H ₂ O	To O ₂ and H ₂ O
Moulting	Absent	Present	Present	Present
Plates in cuticle	Absent	Absent	Absent	In some species
Body wall colouration	Vivid (depends on group and habitat)	Vivid	Brownish, reddish	Varied
Dorsal folds per segment	–	12–18	12–24	Present
Arrangement of dorsal folds	–	Irregular, regular	Regular	Regular
Papillae	Absent?	Single	Double	Absent
Metamerization (based on body compartmentalization)	Important	Present, not strong	Present, not strong	Reduced (or separately evolved)

¹Some Ediacara (Pre-Cambrian) fossils are thought to represent Polychaeta, and some are superficially similar to *Spinther*, considered ancestral by Sharov (1966) but derived by Manton (1967).

²Perhaps over 90 species, according to biochemical evidence (H. Ruhberg, 1992 personal communication).

Appendix 2

Locomotion and muscular system in onychophoran families and related taxa (sources as in Appendix 1).

	Polychaeta	Peripatopsidae	Peripatidae	Tardigrada
Type of 'leg'	Bilobulate parapodia (depending on family: uniramous or subbiramous).	Oncopods	Oncopods	Telescopic
Number of 'leg' pairs	Few to hundreds	13-29	19-43	4
Variability in number of legs	None?	None	High	None
Claws	Absent ¹	2	2	4-8; structure diff. from Onychop.
Walking pads	Absent	Present	Present	Present (possibly not homologous with those of Onychophora)
Locomotion	Walking, swimming, burrowing	Walking	Walking	Walking
Locomotory contractions of body	Present	Present	Present	Reduced
Coelom	Normality developed, reduced in a few cases	Reduced ² (plesio- morphically?)	Reduced ² (plesio- morphically?)	Never ² present?
Circular muscle	Present	Present	Present	Absent?
Longitudinal muscle	Present	Present	Present	Present
Muscular bands	In parapodia	In oncopods	In oncopods	Present, generalized
Muscle striation	Oblique and cross- striated	Oblique	Oblique	Smooth, oblique and cross-striated
Smooth muscle	Absent (there is epithelial muscle)	Present	Present	Absent
Last pair of legs	Developed in most	Reduced?	Developed	-
Heart 'SR'	?	Developed	Poorly developed	Absent
Mitochondria in heart z-material	?	Clustered	Evenly distributed	Absent
Heart innervation	?	Large dorsal nerve bundle	Dorsal nerve bundle and two dorsolateral bundles	Absent
Body pigment soluble in ethanol	Yes	No	Yes	No

¹ Some polychaetes have hardened setae modified as hooks.

² Coelom developed in hydrostatic skeleton, authors disagree on whether this is a real reduction.

Appendix 3

Feeding and digestion in onychophoran families and related taxa (sources as in Appendix 1).

	Polychaeta	Peripatopsidae	Peripatidae	Tardigrada
Mandibles	Originally absent At least 4 ¹	4	4	Absent
Composition of mandibles ¹	Chitin	Chitin	Chitin	Mandibles absent
Inner mandible diastema	Absent?	Absent	Present	Mandibles absent
Mouth	Ventral	Ventral	Ventral	Subterminal or ventral
Oral Papillae	Absent?	Present	Present	Present
Proboscis	Often present (vagile families)	Absent	Absent	Present
Buccal stylets	Absent	Absent	Absent	Present
Slime glands	Absent	Present	Present	Absent
Salivary gland reservoir	Absent	Present	Present	Absent? (but salivary glands are present)
Food pumping	Varied	Present	Present	Present
Diet	Carnivorous, suspension and detritus feeders	Carnivorous	Carnivorous	Carnivorous, herbivorous, omnivorous and detritivorous.
Digestive tract	Can be short ² , depending on group	Short ²	Short ²	Short ²
Digestion	In midgut	In body of prey and in intestine	In body of prey and in intestine	In gut
Anus	Terminal	Terminal	Terminal	Between last pair of lobopods, or absent
Faeces	Pellets coated with mucus	Hard parts in peritrophic membrane	Hard parts in peritrophic membrane	Sometimes abandoned in exuvia, probably not peritrophic
Kin foraging	Absent	Present?	Present?	Absent?
Mandible movement	Along body axis	Along body axis	Along body axis	-
Jointed mandibles	No ²	No	No	-

¹Polychaetan mandibles originated in the foregut and are not homologous with those of the Onychophora, which are modified limb tips.

²'Short' means length of digestive tract similar to body length (i.e. unfolded).

Appendix 4

Ecophysiology in onychophoran families and related taxa (sources as in Appendix 1).

	Polychaeta	Peripatopsidae	Peripatidae	Tardigrada
Geographic distribution	Some cosmopolitan	Austral disjuncts (restricted)	Tropical disjuncts	Some cosmopolitan
Habitat	Marine, fresh water, rarely terrestrial	Terrestrial	Terrestrial	Aquatic (marine and freshwater)
Density (individuals/m ²)	Up to thousands	e.g. Up to 10 in South Africa ¹ and 0.05 in Tasmania ²	e.g. 0.037 in Trinidad ³ and 2.0 in Costa Rica	Up to 14 million
Tolerance to desiccation	Very low	Low	Low	High, but depends on group
Anaeromorphy	?	Strong	Strong	?
Phototropism	Strongly negative, except during mating in some groups	Strongly negative	Strongly negative	May occur in some
Circulation	Pumping vessels	Dorsal heart	Dorsal heart	Without vessels
Blood pigments	Originally absent?	Absent?	Absent?	?
Gas exchange	Originally diffusion?	Chiefly tracheae	Chiefly tracheae	Diffusion
Coxal vesicles	Absent	Infrequent	Present	Absent
Osmoregulation	Originally protonephridia	Nephridia	Nephridia	'Malpighian tubules'
Brain	Bilobed	Bilobed	Bilobed	2-4 lobes
Nerve cord	Double, usually fused, with ganglia	Double, ladder-like	Double, ladder-like	Double, with ganglia
Eyes	Originally none? (1-many)	2	2	Basically 2
Ocular lens	Present in some	Present	Present	Present in some species
Eye organization	Extremely variable, similar to Onychophora in some cases	Everse, cuticular lens	Everse, cuticular lens	Very simple
Antennae ⁴	Present	Present	Present	Absent
Nuchal organs	Present in some families	Absent	Absent	Absent
Cirri	Mostly present	Absent ⁵	Absent ⁵	May be present
Setae	Mostly present	Absent	Absent	May be absent?
Statocyst	Present in a few families	?	?	?
Palps	Often present	Absent	Absent	Absent
Crural glands	Absent?	Often present in both sexes	Present only in males	Absent
Nephridia organized in segmental pairs	Yes	Yes	Yes	Absent?
Two developed centres in antennal nerves	No	Yes	Yes	Antennae absent
Flagellar propulsion in nephrostome	Present	Present	Present	Absent
Urinary vesicle without cuticular enclosure	Present	Present	Present	-
Scalariform junctions in active transport epithelia	Not developed	Developed	Developed	-
Excretory duct with a cuticular wall renewed by moulting	Absent	Present	Present	Present
Cuticular pore canals	Absent	Absent	Absent	Probably absent
Single epidermal gland cells	Present	Absent	Absent	-
Cuticle calcification	No	No	No	Probably not
Ciliated reproductive tract	Yes	Yes	Yes	-

¹ S. B. Peck personal communication.

² R. Mesibov, 1992 personal communication; Harris (1991) reported numbers equivalent to an abnormal density of 2000/m².

³ Calculated by author from data in Read (1985) and Read and Hughes (1987).

⁴ Antennae of these groups are not homologous.

⁵ Sensory 'hairs' at tips of main papillae might be equivalent to setae (S. B. Peck, 1992 personal communication), but their cellular ontogeny is unknown.

Appendix 5

Reproduction and development in onychophoran families and related taxa (sources as in Appendix 1).

	Polychaeta	Peripatopsidae	Peripatidae	Tardigrada
Oviparity	Present	Present	Absent	Present
Ovoviviparity	Originally absent	Present	Absent	Absent
Viviparity	Originally absent	In most	All species	Absent
Placenta	Absent	Absent	Present	Absent
Testes	–	Elongated?	Elongated	Sacular
Sperm duct	Often absent	Unpaired part short to medium	Unpaired part long	Short (single or double)
Ovaries	–	–	–	Sacular
Oviduct	Often absent	Two, short	Two, short	Single, short
Receptaculum ovarum	Often absent	Present, sometimes reduced	Present	?
Location of genital pore	No specialized genital pore	Between or behind last pair of lobopods	Between penultimate pair of lobopods	Cloacal or near anus, between penultimate and last pair
Sex reversal	Present	Absent	Absent	Absent
Hermaphroditism	At least in fresh-water taxa	Absent	–	In few species
Courtship	Present	Unknown	Unknown	Known in one sp.
Penis or equivalent	Originally absent	Secondarily developed in some	Absent	Originally absent
Copulation	Originally absent	Absent? Few data	Probable	Poorly known, apparently present
Sexual pheromones	Present	?	?	?
Cuticular impregnation	Originally absent	Known in <i>Peripatopsis</i>	Probably absent	In a few species
Spermatophore	Only in some groups	Present	Present	Absent
Male first mating	Some shortly after birth	e.g. at 9–11 months	e.g. shortly after birth	?
Female first mating	e.g. from before eclosion to at least 4 years age	e.g. at 9–24 months	e.g. at 5–9 months	?
Female first reproduction	e.g. one year	e.g. 2–3 years	1.4–1.9 years	?
Site of egg fertilization	Originally outside the body	Oviduct	Oviduct?	Ovary or outside the body
Egg nourishment by sperm	?	Present	?	?
Vesicula copulatrix	Originally absent	Reduced or absent	Ovoid	Absent?
Receptaculum seminis	Absent	Present in some	Present	Sometimes present
Number of inseminations in female's life	One in some	One?	One	?
Females inseminated in population	Up to 90%	?	e.g. 61%	?
Egg vitelin content	Variable, often low	Medium to large greatest in oviparous taxa	Very low?	?
Egg size (diameter)	Ovum 1.4 mm (Originally small)	Largest in oviparous taxa (1.3–1.9 mm)	Very small (250–380 μ)	Upto 120 μ m
Developmental time	e.g. 7–16 days	Egg: 6–17 months Others: 11–13 months	e.g. 12 months	Up to 14 days

Appendix 5 (continued)

	Polychaeta	Peripatopsidae	Peripatidae	Tardigrada
Embryo association with mother	In egg	In later stages free in maternal duct	Attached to mother by placental stalk (50% of development time)	In egg
Larva	Trochophore	Absent	Absent	Pseudolarva
Number of offspring	Few-hundreds	6-23/year	1-8/year	1-30 eggs each time
Maternal investment	?	?	× 12.6 (2.5-34)%	?
Number born each time	-	1-2	1	?
Extremity born first	-	Either	Head	-
Coloration of young	-	Lighter than adult	Lighter than adult	Lack adult coloration
Independence of young	Originally total	High	High	Complete
Brooding	Originally absent?	?	?	Absent?
Egg sex ratio	Female biased in some spp.	?	?	Various?
Embryo sex ratio	?	?	1:1	?
Neonate sex ratio	?	1:1 in oviparous spp.	Male biased in at least one sp.	?
Adult sex ratio	Female biased in some	Often female biased	Normally female biased	Often female biased
Male mating	?	?	Multiple?	?
Mating seasonality	?	Some yearly, others year round	?	?
Breeding seasonality	Present in some species (rest year round)	Some yearly, other year round	Long season (excludes dry period)	Probably periodic, during moist time
Neonate sexual dimorphism	?	Little	Little	?
Adult sexual dimorphism	Dwarf males in some species	Little only in oviparous spp.	Females bigger	Dwarf males in some species.
Number of legs per sex	?	Similar in oviparous spp.	More legs in females	Same in both sexes
Offspring sex periodicity	Absent?	?	Absent?	?
Mortality per sex	Similar?	Higher in males	Higher in males	?
Life span per sex	Similar? (e.g. 1-4 years)	Longer for females? (e.g. 3-7 years)	Longer for females (e.g. 3.5-5 years)	Similar?
Organization of egg vitellus	Iso or homolecithal	Centrolecithal	Centrolecithal	-
Uniform blastoderm of low cuboidal cells	No	Yes	Yes	-
Egg type	-	-	-	Holoblastic
Segmentation	Spiral	Superficial	Superficial	Superficial, total and equal
Cleavage	-	Intralecithal, total equal	Intralecithal, total, equal	Holoblastic
Development	Indirect, determinate	?	?	Direct

Appendix 6

Characters of fossil taxa apparently related to the Onychophora. Polychaeta and Onychophora are included to establish character polarity (from Hutchinson, 1969; Whittington, 1978; Thompson & Jones, 1980; Robison, 1985; Conway Morris, 1986; Chen, Hou & Lu, 1989; Dzik & Krumbiegel, 1989; Hou & Chen, 1989a,b; Brusca & Brusca, 1990; Hou, Ramsköld & Bergström, 1991; Ramsköld & Hou, 1991).

	Polychaeta	<i>Hallucigenia</i>	<i>Xemusion</i>	<i>Luolishania</i>	<i>Microdyction</i>
Mouth type	Radial	—	Radial	—	—
Mouth location	Ventral	Terminal?	Terminal?	—	—
Oral papillae	Absent?	—	—	—	—
Mandibles	Originally absent	—	—	See note 1	See note 1
Diet	Carnivorous and others	—	Carnivorous (parasitic on sponges)?	Carnivorous	—
Moult	Absent	—	Present	—	Present
Length (cm)	Most species 5–10	Around 2	20	1.5	Up to 8
Leg length*	Originally short	Long	Long	Long	Long
Lobopodial spines	Absent	Absent	Present	Absent	Absent
Annulation	In many species	Absent?	In body and lobopods	In body and lobopod	In body
Body papillae	Absent?	Absent	Present	—	—
Claws	Originally absent	2?	Absent?	4 or 5	1?
Trunk spines	Originally absent	Present	Present	Absent	Present in some
Armoured plates	Absent	Paired, large	Paired, intermediate size	Paired, small	10 pairs in some large
Leg pairs	From few to hundreds	7	12–20 or more	15	10
Antennae	Present	—	—	—	—
Distribution	Cosmopolitan	British Columbia	Sweden: Germany	Yunnan	Cosmopolitan
Occurrence	Mid-Cambrian to present	Mid-Cambrian	Lower Cambrian	Lower Cambrian	Lower Cambrian- Mid-Ordovician
Proboscis	Long	Long, and bulbous ²	Long	—	—
Habitat	Originally marine, varied types of water	Marine shallow anoxic water muddy bottom	Marine, quiet water with little bacterial and scavenging activity	Marine, quiet water, soft bottom	Marine, quiet water, soft bottom?
Associated biota	Benthic invertebrates	Algae, molluscs, sponges, echinoids, coelenterates, priapulids, polychaetes, arthropods	—	Priapulids, annelids, arthropods, molluscs, sponges	Jellyfish
Pygidium or equivalent	Present	—	Present?	Present?	Present?

Appendix 6 (continued)

	<i>Cardiodictyon</i>	<i>Aysheia</i>	<i>Onychodictyon</i>	<i>Helenodora</i>	Onychophora
Mouth type	–	Radial?	Radial?	–	Radial
Mouth location	–	Terminal	Anteroventral?	–	Ventral
Oral papillae	–	Present	See note 2	Present	Present
Mandibles	See note 1	Present	Absent	Present	Present
Diet	–	Carnivorous (parasitic on sponges)?	–	–	Carnivorous
Moultling	Present?	Present	Present?	–	Present
Length (cm)	0.30	1–6	5–6	Up to 6.4	2–20
Leg length*	Short	Medium	Medium	Short	Short
Lobopodial spines	Absent	Present	Present ³	Absent	Absent
Annulation	Absent	In body and lobopods	In body and lobopods	Present	In body and oncopods
Body papillae	Absent?	Present	Present ¹	Present	Present
Claws	4 or 5	6 or 7	2 large, 1 small?	2	2
Trunk spines	Present	Absent	Present	Absent	Absent
Armoured plates	21–24 pairs, large	Absent	10 dorsal some large	Absent	Absent
Leg pairs	21–24	10	10–11	21	13–43
Antennae	–	Branched	–	Present?	Present
Distribution	Yunnan	British Columbia, Utah	Yunnan	Illinois	Tropical and Austral disjuncts
Occurrence	Lower Cambrian	Mid-Cambrian	Lower Cambrian	Carboniferous	Present
Proboscis	Absent	Absent	Absent	Absent	Absent
Habitat	Marine, quiet water, soft bottom	Marine, shallow anoxic water	Marine, quiet water, soft bottom	–	Terrestrial (originally marine)?
Associated biota	Priapulids, annelids, arthropods, molluscs, sponges	Algae, molluscs, sponges, echinoids, coelenterates, priapulids, polychaetes, arthropods	Priapulids, annelids, arthropods, molluscs, sponges	Hydrozoans, molluscs, echiurans, polychaetes	Terrestrial invertebrates
Pygidium or equivalent	Absent	Absent	Absent	Absent?	Present

Note 1. Yunnan oncopodophores had mandibles (X. Hou, in prep.).

Note 2. Supposed oral papillae of *Onychodictyon* proved to be leg papillae after further preparation (L. Rämssköld, 1991 personal communication).

¹Rows of elongated protrusions, like elongated papillae, occur in dorsal and ventral sides of *Onychodictyon*.

²If head is at the right (not left) extremity of reconstruction in Rämssköld and Hou (1991: fig. 4), as might be thought by claw orientation, the proboscis of *Hallucigenia* was not bulbous but elongated and similar to that of *Xenusion*.

³(L. Rämssköld, 1991 personal communication).

Appendix 7

Convergent characters in three groups with isolated populations from stable habitats (data on wasps and acari from Ramirez (1987), onychophoran information from Appendices 1-5).

	Wasps (Agaonidae)	Acari (<i>Varroa jacobsoni</i>)	Onychophora
1. Species specific relationships developed	+	+	-
2. Sex ratio female biased*	+	+	+
3. Developmental synchronization of host and associate	+	+	-
4. Unfertilized eggs produce males*	+	+	?
5. Precise sex ratios	+	+	?
6. Females modify the developmental period of the host	+	?	-
7. Gregarious development*	+	+	+
8. Development occurs in a dark and humid environment (claustral habitat)	+	+	+
9. Few females colonize hosts microhabitats	+	+	?
10. Females usually produce a constant number of offspring	+	+	+
11. Male eggs usually laid at the beginning of the sequence	+	+	-
12. Development time from eggs to adult is nearly constant*	+	+	+?
13. Quite constant progenies reared per host	+	+	?
14. Males born before females*	+	+	-
15. Neotenic males	+	+	+?
16. Smaller males	+	+	+
17. Shorter male lifespan*	+	+	+
18. Adult males do not feed	+	-	-
19. No fighting by males	+	+	?
20. No oedemery of male's front legs	+	+	-?
21. Mating occurs before female emergence	+	?	-
22. Polygamous males*	+	+	?
23. Sibmating more common than outcrossing*	+	+	+?
24. Mating in same place of development*	+	+	+?
25. Precocious local mating	+	?	+
26. Females are lethargic before and at mating	+	?	?
27. No males successfully mate outside their own group*	+	+	?
28. No abandonment of place of development by most males (claustrophilic males)*	+	+	?
29. Females store sperm*	+	+	+
30. One insemination serves to fertilize the whole egg production*	+	+	+
31. Finding of new host only by females*	+	+	?
32. Large peritremata in females and males	+	+	-
33. Protruding respiratory structures	-	+	-
34. Fighting of females at oviposition	+	+	-?
35. Competition for resources biases the sex ratio	+	+	-?
36. Local resources competition (LRC)	+	+	+?
37. Nonrandom searching for hosts	+	+	?
38. Differential mortality of developing females occurs with superparasitism	+	+	-

*Characters originally identified by Hamilton (1967).