

Millipede (Diplopoda) distributions: A review

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Abstract

In spite of the basic morphological and ecological monotony, integrity and conservatism expressed through only a small number of morphotypes and life forms in Diplopoda, among which the juloid morphotype and the stratobiont life form are dominant, most of the recent orders constituting this class of terrestrial Arthropoda are in a highly active stage of evolution. This has allowed the colonisation by some millipedes of a number of derivative, often extreme and adverse environments differing from the basic habitat, i.e. the floor of temperate (especially nemoral), subtropical or tropical forests (in particular, humid ones). Such are the marine littoral, freshwater habitats, deserts, zonal tundra, high mountains, caves, deeper soil, epiphytes, the bark of trees, tree canopies, ant, termite and bird nests. Most of such difficult environments are only marginally populated by diplopods, but caves and high altitudes are often full of them. To make the conquest of ecological deviations easier and the distribution ranges usually greater, some millipedes show parthenogenesis, periodomorphosis or morphism.

Very few millipede species demonstrate vast natural distributions. Most have highly restricted ranges, frequently being local endemics of a single cave, mountain, valley or island. This contrasts with the remarkable overall diversity of the Diplopoda currently estimated as exceeding 80 000 species, mostly confined to tropical countries. There are few places on the globe where a local diplopod fauna, or faunule, exceeds two dozen species, the world record being a patch of rainforest in central Amazonia where 33 millipede species have been revealed.

Such a highly mosaic distribution of the diversity in Diplopoda over the globe is rooted in the group's general structure, biology, ecology and phylogeny. This particular combination has long made the Diplopoda a group most attractive for biogeographical reconstructions.

Keywords: Diplopoda, distribution, diversity, ecology, extreme environment, life form, speciation

1. Introduction

With over 12 000 described species in 145 families and 16 orders (Adis 2002, Shelley 2002c, Sierwald & Bond 2007, Shelley 2007), and an estimated global fauna of more than 80 000 species, the Diplopoda (millipedes) is the third largest class of terrestrial Arthropoda following Insecta and Arachnida. A major component of terrestrial ecosystems throughout the temperate, subtropical and tropical zones of the world, they are ecologically important as detritivores (= saprophages, or consumers of dead plant material), and are important biogeographical indicators because of their profound diversity and geological age, as well as low vagility (Hopkin & Read 1992).

Millipedes, whose population density in forest soil sometimes exceeds 1000 individuals per square metre, are estimated to consume 10–15% of the annual leaf fall in temperate forest. Detritivores predominating, only a few species can be qualified as omnivores, even fewer as carnivores, e.g. *Apfelbeckia insculpta* (C. L. Koch, 1867) (Callipodida: Schizopetalidae) feeding on earthworms (Stoev & Enghoff 2008). Coprophagy is quite common in this animal group, including the consumption of their own pellets and exuvia (Minelli & Golovatch 2001).

The oldest fossil millipedes, apparently detritivores (Crawford 1992), are known from the mid-Silurian and Devonian, while since the Carboniferous they became quite diverse. Those early diplopods represented six extinct orders and are recognised as fully terrestrial, because of the presence of a tracheal system (visible spiracles). The fossil superorder Arthropleuridea is remarkable in having contained both gigantic (over 2 m long) and tiny species (a few mm long). It is only since the Mesozoic, however, that fossil millipedes tend to be classified within extant orders and families (Sierwald & Bond 2007). Despite the long fossil record of Diplopoda, it remains so fragmentary that only few extinct species appear to be relevant to modern millipede distributions.

Modern millipede taxonomy is largely based on male genitalia (= gonopods), i.e., legs 8, legs 8 and 9 or legs 9 and 10 transformed into spermatopositors. Gonopods are characteristic of all Helminthomorpha, a hopelessly heterogeneous assemblage covering the bulk of millipede diversity, but still kept as opposed to the compact, far less diverse but unquestionably monophyletic Penicillata (3–4 families in one order, Polyxenida) and the Pentazonia (three orders, Glomeridesmida with a single family and genus, Sphaerotheriida with four families, and Glomerida with three families).

Spermatopositors basically function as a pipette, being involved in the so-called indirect-direct sperm transfer. They first receive sperm from the gonopores placed just behind or even on top of male coxae 2, then store it and place it into the female vulvae during mating. Gonopods are usually highly complex in structure, their minor details reflecting differences between species. A similar pattern of sperm transfer is observed at least in some Pentazonia (Glomerida), but the role of spermatopositors is taken up by unmodified mouthparts. The only modified legs are the last 2–3 pairs, of which the last two are totally suppressed in the female, and either both legs 20 and 21 (Sphaerotheriida) or only the caudalmost pair 19 (some Glomerida) are/is enlarged to form the so-called telopods. These function as pincers to grasp and immobilise the female during copulation. Since telopods are not involved in sperm transfer per se, they are usually not as complex and diverse as gonopods, reflecting taxonomic differences only at the generic level. Finally, in Polyxenida there are no sex-linked leg

modifications. Sperm transfer is entirely indirect, because first the male weaves and spreads a small web of silk threads (secreted by special glands in the gonopore region), then he deposits a few droplets of sperm on the web and spins a trail of signal threads. A mature female recognises the signal threads with her antennae, follows one towards the web to pick up the sperm droplets directly with her everted gonopores (Hopkin & Read 1992).

Ghilarov (1970) considers changes in the patterns of sperm transfer in terrestrial arthropods as an evolutionary trend in their adaptations to terrestrial life, in response to an increasing water deficit. An indirect mode of sperm transfer thus seems to be basal in diplopods, first replaced by an indirect-direct one without specially modified legs and then with the origins of special spermatopositors. Direct sperm transfer culminating in the development of a true penis, as in insects, is absent from Diplopoda. Their sperm is always aflagellate, i.e., another hint to the group's strict association with land.

In general, millipedes are typical of the forest floor, where they find not only enough food and shelter like leaf litter or dead wood, but also a sufficiently high humidity. These animals are usually quite sensitive to water deficit, being meso- to hygrophiles. In addition, many are calciphiles as well. Ecologically, most of the diplopods reveal poor compensatory capacities, i.e., when exposed to a single limiting factor, they fail to overcome it and die, even if other ecological factors are favourable (Golovatch 1994). Despite this relative stenotopy, millipedes occur on all continents except Antarctica, and nearly in all terrestrial environments. Most of the higher diplopod taxa can be considered as flourishing groups at a stage of very active speciation and evolutionary progress. Due to anthropochorism, some species have attained vast, up to ubiquitous distributions.

2. Environments and habitats, millipede morphotypes and life forms

The environment that can be postulated as the most typical of the Diplopoda is temperate (especially deciduous), subtropical or tropical forest (in particular, humid ones). The most typical habitats are leaf litter, the litter/soil interface, the uppermost soil, and dead wood. All kinds of milder environments and habitats can be considered as rather typical, such as boreal forest (= taiga), compost, dung, greenhouses etc.

Millipedes, however, can also dwell high in the mountains (above timberline), in grasslands, in caves, deeper in the soil, under the bark of trees, in the desert and even in environments which can be regarded as extreme for this arthropod group (see below).

Such ecological preponderances and deviations among Diplopoda seem to be rooted in the body construction plans, or morphotypes, on the one hand, and their life forms, or ecomorphotypes, on the other hand. The former category is above all morphological, whereas the life-form is an autecological rather than a morphological term. A life form is a set of organisms inhabiting more or less the same ecological niche and showing a complex of similar morphophysiological characters which have arisen under the influence of similar factors of natural selection (Kime & Golovatch 2000).

Following Manton's (1977) approach in distinguishing locomotory-based ecomorphotypes in Diplopoda, Hopkin & Read (1992) summarised the following five millipede life forms:

- (1) bulldozers or rammers, represented chiefly by the long-bodied orders Julida, Spirobolida and Spirostreptida;
- (2) wedge types, or litter-splitters, with short-bodied Polydesmida equipped with strong paraterga being the most typical order;
- (3) borers, typified by the chiefly flat-bodied orders Chordeumatida, Polyzoniida, Platydesmida and Siphonophorida;
- (4) rollers, represented by Glomerida and Sphaerotheriida capable of conglobation; and
- (5) bark dwellers, typified by the tiny, soft-bodied and swift Polyxenida.

A slightly different system has been proposed by Kime & Golovatch (2000). It is based on the following hierarchy of diplopod morphotypes:

- (1) polyxenoid, solely with Polyxenida, corresponding to 'bark dwellers';
- (2) glomeroid, with Glomerida and Sphaerotheriida, corresponding to 'rollers';
- (3) juloid, represented by Juliformia and corresponding to 'bulldozers' or 'rammers';
- (4) polydesmoid, corresponding to the 'wedge type'; and
- (5) platydesmoid, corresponding to 'borers'.

These diplopod morphotypes are distributed among the following universal terrestrial arthropod life forms:

- (1) stratobionts, restricted to litter and the uppermost soil, dominant in the Diplopoda and represented by all five morphotypes;
- (2) pedobionts, or geobionts, mainly restricted to mineral soil and represented by the smaller juloid, glomeroid and polydesmoid morphotypes, usually implying body miniaturisation or elongation, shortening of appendages, often also decoloration of the teguments and loss of eyes;
- (3) troglobionts, likewise represented by the juloid, glomeroid and polydesmoid morphotypes, but usually implying a drastic elongation of the extremities, depigmentation of the teguments, blindness, sometimes mouthpart modifications, often also 'cave gigantism';
- (4) under-bark xylobionts, or subcorticoles, represented by all five morphotypes, but either particularly flat-bodied (polydesmoids, platydesmoids) or miniature (polyxenoids, glomeroids), often also especially thin (juloids); and
- (5) epiphytobionts, again with all five morphotypes involved, but usually characterised by very small body sizes. A life-form of epiphytobionts is still too vaguely delimited to consider it unquestioned; moreover, since life forms of arboricoles (= dendrobionts), symbionts of ants or termites, deserticoles etc. are habitually even less conspicuous, none of them seems to warrant the recognition of a separate life form.

Fig. 1 summarises the relations between, and characteristics of, millipede life forms. As one can see, life forms display adaptations that are not characteristic of Diplopoda alone. Millipedes have evolved the same well-known adaptations as a number of ecologically similar arthropod taxa (e.g. certain Acarina, Collembola, Isopoda, Coleoptera etc., where stratobionts tend to be the main and primary life form), when adapting to life in the soil or in caves, for example.

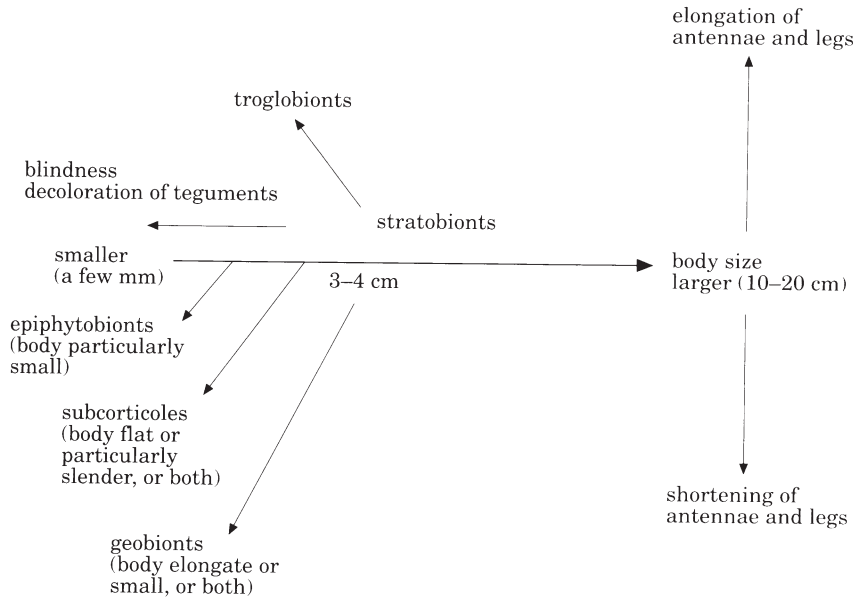


Fig. 1 Relations between and characteristics of millipede life forms (after Kime & Golovatch 2000).

We can assume that early in their evolution Diplopoda were detritivores living on the forest floor, and that this still applies to the majority. Cylindrical burrowers (juloids), flat-backed litter-splitters (polydesmoids) and rollers (glomeroids) are known already since the Palaeozoic. These were mainly large, spiny or crested forms, hence unquestioned stratobionts (Kime & Golovatch 2000).

Fig. 2 schematically depicts the main trends in, and pathways of, diplopod ecological evolution. The biomes are arranged according to their age along two vectors of past climatic/biotic change, one showing deterioration from bad to worse conditions (overcooling from subtropical to boreal forest), and the other from warm to hot conditions (overheating, from subtropical to tropical forest) since the end of the so-called 'warm Earth', i.e., terminal Oligocene (Zherikhin 2003).

As one can see, arrows '1' showing primary stratobionts appear the most prominent, indicating their dominance, except in the hylaea biome, which is the only humid forest type almost entirely devoid of a litter stratum. This is a relatively young, as well as the world's least entropy-producing biome (Zherikhin 2003), where diplopod arboricoles (which have failed yet to develop a separate life-form) and subcorticoles (already as a special life form) prevail (arrows '2'). Elsewhere they definitely decline toward the taiga belt. Being restricted to suspended soils, epiphytobionts (arrows '3') decline northward even more markedly; as a life form they are missing already from the nemoral (= broadleaved deciduous) forest belt.

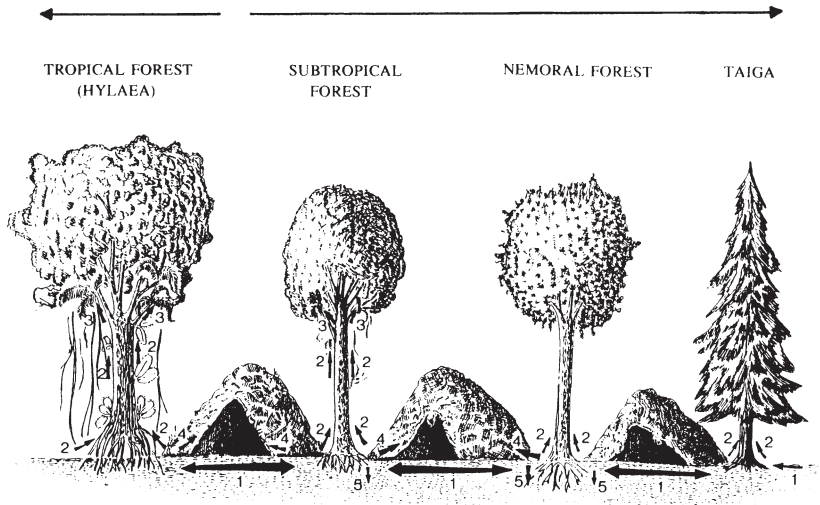


Fig. 2 Main trends in the ecological evolution of Diplopoda. All are life forms except for arboricoles. 1: stratobionts; 2: trunk and crown arboricoles, as well as subcorticolous xylobionts; 3: epiphytobionts; 4: troglobionts; 5: geobionts. NB. The thickness of numbered arrows roughly corresponds to the share of the respective ecological grouping along a gradient of biome succession with age (uppermost arrows, the gap between them indicates the primary biome whence developed all the main extant biomes). Further explanations in the text (after Kime & Golovatch 2000).

The proportions of diplopod troglo- and geobionts show a different trend (arrows '4' and '5', respectively), suggesting their synchronous evolution. True troglobionts are not too common in tropical countries, but geobionts are nearly missing there, probably due to the generally very poor soils of tropical forest. The only notable exceptions are the 2–3 known species of the order Siphoniulida, all tiny and hitherto encountered only in the uppermost soil and inside thick litter. Both true geo- and troglobionts seem more characteristic of subtropical and, especially, nemoral belts, totally declining towards the taiga biome.

Speaking even more generally, all derivative life forms, i.e., subcorticoles, epiphyto-, troglo- and geobionts, might have evolved from the main stratobionts more or less simultaneously, relatively recently, probably already since the onset of the Plio-Pleistocene glaciations. The few and rather indistinctly defined life forms in Diplopoda seem to support this opinion.

One must not confuse the age of a taxon and that of a life form, for some highly relict taxa have managed to survive only as relatively young life forms (numerous examples among diplopod troglobites, maybe also the order Siphoniulida as possibly geobionts). It is the great climatic/biotic change during the past 2–3 Ma that appears to have especially affected the ecological evolution of millipedes (and similar groups), which had either to adapt to some (micro)habitats like caves, the soil, subcortical crevices, or die. Even the tropical belt has probably gained in epiphytobionts due to the same events.

To summarise, only a few millipede life forms can be distinguished. Diplopoda, a group of soil/litter macrofauna too markedly sensitive to water deficit, often calciphilous as well, appear to have failed beyond a certain measure, both morphophysiologicaly and ecologically, to conquer the environments and habitats significantly deviating from a forest floor (Kime & Golovatch 2000).

3. Extreme environments

Despite the group's pronounced ecological integrity and monotony, Diplopoda have managed, at least marginally, to populate a considerable number of difficult to extreme habitats. Below is a slightly updated review of millipedes at the extreme (Golovatch 2009).

Marine littoral

Sea water is generally considered as an insurmountable barrier for millipedes. Still there are a few exceptions that can be termed as littoral species: *Thalasssobates littoralis* (Silvestri, 1903) and *Orinisobates soror* Enghoff, 1985 (both Julida: Nemasomatidae). The former species is amphi-Atlantic, living under stones and seaweeds, in rock crevices, or among shingle in or shortly above the tidal zone, sometimes also in coastal caves around the Mediterranean, around the British Isles, reported also from the coasts of Sweden and the eastern U.S.A. (Massachusetts and Virginia) (Enghoff 1987a). This species is basically considered European, with a secondary, likely anthropochorous colonisation of North America. *O. soror* is common among shingle and debris on the shores of Sakhalin and Kuril Islands, Russia (Mikhaljova 2004). In the very large western Mediterranean and Macaronesian genus *Dolichoilulus* Verhoeff, 1900 (Julida: Julidae), while several species occur in coastal areas (Enghoff 1992), only *D. tongiorgii* (Strasser, 1973) is characteristic of the littoral (Mauriès 1982).

In the large European genus *Leptoilulus* Verhoeff, 1894 (Julida: Julidae), *L. belgicus* (Latzel, 1884), found in various terrestrial habitats in Western Europe, is particularly common along river banks and has been observed in large numbers in dunes and under stones on coastal beaches in the intertidal zone well below the high watermark in Wales (personal observations of the second author).

Similarly, among all 28 hitherto known species of the Australian genus *Lissodesmus* Chamberlin, 1920 (Polydesmida: Dalodesmidae), only *L. orarius* Mesibov, 2006 occurs just above sea-level in dune scrubs, tea-tree forest and tea-tree scrub along a narrow strip of the west coast of Tasmania. Remarkably, this small species is usually quite abundant, its distribution extends down to the high tide line, and at the type locality it was found together with intertidal crabs under driftwood surrounded by sedge and grass (Mesibov 2006).

In addition, there is a strong association of certain species of Polyxenida with maritime habitats such as shingle beaches in Italy (Verhoeff 1941).

Some more examples are given in the paper by A. Barber in this volume (Barber 2009).

No special studies have been conducted to reveal the mechanisms of salt tolerance in these diplopods, but all these species represent the juloid, polydesmoid or polyxenoid morphotype.

Freshwater habitats

Examples of millipedes tolerant to freshwater habitats are likewise few. Several European diplopods can stand submersion, especially those adapted to life in floodplains. Thus, in the laboratory conditions at 4 °C, *Polydesmus denticulatus* C. L. Koch, 1847 (Polydesmida: Polydesmidae) can stay alive underwater for 75 days (Zulka 1996). But none of such species can be termed as semi-aquatic. In Europe, millipedes survive in floodplains simply using a 'risk strategy', combining high reproduction rates, dispersal and re-immigration following catastrophic events (Adis & Junk 2002).

The only truly semi-aquatic millipede known to date from a relatively cold environment is *Serradium semiaquaticum* Enghoff, Caoduro, Adis & Messner, 1997 (Polydesmida: Polydesmidae), both subadults and adults. This troglobitic species from northern Italy is remarkable in showing modified, broom-like mouthparts, combined with hydrophobic microtrichia in the spiracles, the adaptations that enable it to remain submerged for up to 4 weeks (Adis et al. 1997).

Selminosoma chapmani Hoffman, 1977 (Polydesmida: Paradoxosomatidae), a montane troglobite from Papua New Guinea, is likewise well adapted not only to cavernicolity, but also to immersion in water (Hoffman 1977). A closer unidentified, epigeal species of Paradoxosomatidae from the mountains of southern China has been observed entering water without any difficulties (L. Deharveng, in litt.).

In the tropics and subtropics, apparently due to a geologically far longer and stable evolution, numerous terrestrial arthropods, including a few millipedes, have developed special adaptations to life under water (Adis 1997). Perhaps the best-known example is *Myrmecodesmus adisi* (Hoffman, 1985) (Polydesmida: Pyrgodesmidae) endemic to a patch of blackwater inundation forest near Manaus, Central Amazonia, Brazil. Advanced juveniles and subadults of this tiny species can live submerged over the annual flood period of 5–7 months, up to almost a year, actively grazing on algae growing on tree trunks. Their entire cuticula, including the spiracles, is covered with a white secretion layer (cerotegument) supported by microtuberculi, so that a thin air casing is held below the cerotegument. This enables the so-called plastron respiration which is lost, however, with the final moult into adults, because their cerotegument no longer covers the spiracles. Unsurprisingly, the adults are only restricted to the terrestrial phase of the water pulse. In contrast, a sympatric congener from upland (= non-inundated) forests, *M. duodecimlobatus* (Golovatch, 1996), cannot withstand submersion at all (Adis & Junk 2002). Millipedes lacking any morphological and/or physiological adaptations must rely on vertical migrations along the tree trunks to survive the flood period (Adis et al. 1996, Adis 1997, Minelli & Golovatch 2001).

Similar observations concern another tiny species of Pyrgodesmidae, *Aporodesminus wallacei* Silvestri, 1904, which has both a cerotegument for plastron respiration and the mouthparts adapted for food uptake under water. Furthermore, it shows such a highly sporadic distribution (St. Helena Island, Atlantic Ocean, creeks in the environs of Sydney, Australia, Tahiti, Polynesia and the Hawaiis, Pacific Ocean) that zoochory (= ornithochory) has been suggested as a possible mechanism of dispersal. The closely related species *Cryptocorypha ornata* (Attems, 1938) shows not only a similar cerotegument, but also a very similar distribution (St. Helena Island, the Hawaiis, the Cook Islands, the Marquesa Islands, Tahiti and Hong Kong) (Adis et al. 1998).

In Amazonia, only few diplopod species have vast distributions ranging along the Amazon/Solimões River, sometimes from about the Andes to the delta region. Such are *Pycnotropis tida* (Chamberlin, 1942) (Polydesmida: Aphelidesmidae), *Poratia obliterated* (Kraus, 1960) and *P. insularis* (Kraus, 1960) (Polydesmida: Pyrgodesmidae), *Mestosoma hylaeicum* Jeekel, 1963 (Polydesmida: Paradoxosomatidae), *Epitrogoniulus cruentatus* (Brölemann, 1902) (Spirobolida: Trigoniulidae) etc. All are more characteristic of inundated forests than upland woodlands, their life histories being fitted to the river's flood pulse (Adis 1992, 1997, Hoffman et al. 2002, Golovatch et al. 2004, Bergholz et al. 2005). Their downstream distribution could largely be accounted for by transportation on floating debris (see below).

Nothing is known yet about the way of life of another millipede from Guyana, *Pandirodesmus disparipes* Silvestri, 1932 (Polydesmida: Chelodesmidae), but this small species (adults about 13 mm long) is so remarkable that it suggests a special ecology associated with fresh water. The most striking, largely unique morphological features are as follows.

Heteropody. All legs are extremely long, but every posterior leg-pair on the diplosegments is considerably (by 1/4) longer than the anterior pair. Extremely long legs alternate with shorter ones all along the body (Fig. 3).

The spiracles are upright and tubiform, possibly to facilitate respiration on/near water surfaces or, occasionally, even under water.

The legs and sternites are beset with dendroid, apparently hydrophobe setae.

The distalmost part of the tibia and the basalmost part of the tarsus are enlarged to form a nod-shaped junction similar to that observed in numerous Arachnida, but nearly missing in other Diplopoda.

Based on this evidence, despite the absence of both a cerotegument and of microtrichia inside the tubes of the spiracles, *P. disparipes* possibly represents a good climber, swimmer and/or glider. If this proves to be the case, the monobasic genus *Pandirodesmus* would represent another, highly special life form among the millipedes (Silvestri 1932, Adis & Golovatch 2000). If this species is a glider, the strange heteropody might be useful so that the adjacent legs of differing lengths would not interfere during rowing.

It is noteworthy that all diplopods proven or suggested to be strongly associated with freshwater habitats appear to belong to the polydesmoid morphotype.

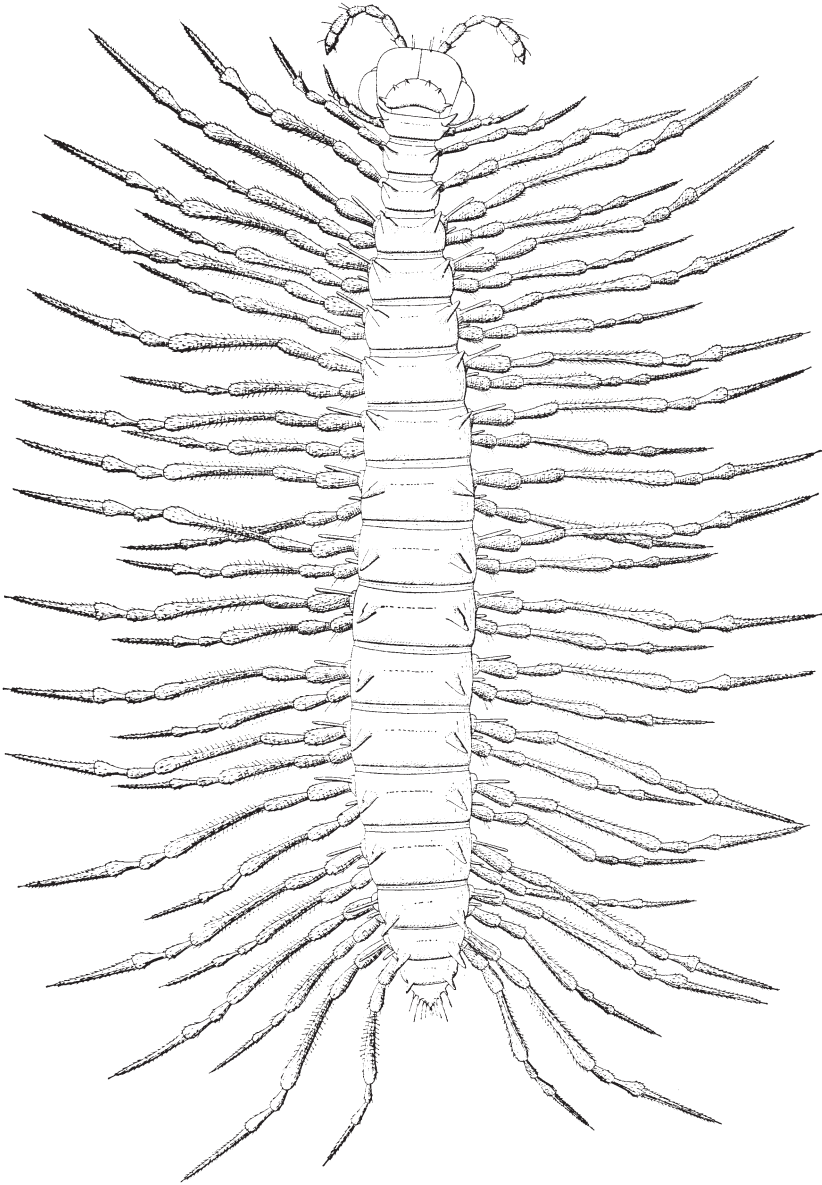


Fig. 3 Habitus of *Pandirodesmus disparipes* Silvestri, 1932 (after Silvestri 1932).

Deserts

Deserticolous millipedes are also scarce, but some of them inhabit the globe's harshest deserts such as the Sonora and Kalahari.

Perhaps the best-known example is *Orthoporus ornatus* (Girard, 1853) (Spirostreptida: Spirostreptidae), a species living from the southern U.S.A. (from Arizona to Texas and New Mexico) to northern Mexico. Among the adaptations to arid environments, this large species (up to 185 mm long) shows a low rate of water loss due to a rather impermeable cuticle, waxy epicuticle, ability of water uptake from unsaturated air, protection of eggs in pellets to prevent water loss, and use of cracks, burrows, stones and other shelters to buffer the wide temperature oscillations that occur in deserts. In addition, the animals remain dormant deep in the soil most of their life, with the most active periods coinciding closely with periods of rain, when swarming is often observed. As a behavioural adaptation, individuals may thermoregulate by alternate basking and retreating into cool shelters (Crawford 1979, Crawford et al. 1987).

Similar observations concern the large spirostreptid *Archispirostreptus syriacus* (DeSaussure, 1859) in Israel where, depending on locality, the life span varies from 9 to 11 years (Bercovitz & Warburg 1985).

Orthoporus Silvestri, 1897 is a very large American genus, in which most species inhabit woodlands and/or savannoid environments like serrado or pampas. *O. ornatus* is the northernmost, peripheral representative, being already characteristic of desert (Crawford 1976). *Archispirostreptus* Silvestri, 1895 is a smaller but still fairly large, basically East African genus, with about 15 species or subspecies known to date. Most of them are rather typical of savannas, but three (one in Yemen, one more in Yemen and Saudi Arabia, and the third, *A. syriacus*, in Israel and the West Bank) are deserticoles.

Such examples suggest an evolutionary trend to the colonisation or in-situ adaptation of deserticolous Diplopoda from savanna- or oasis-dwellers (Dangerfield & Telford 1996).

Among three large species of Spirostreptida that Crawford et al. (1987) studied in deserts on three continents, two become active with the onset of rains, while one, in a winter-rainfall desert, hibernates in winter and forages during the long dry summer. As soon as microclimates exceed a certain level of moisture, millipedes and other macrodetritivores are limited in activity only by extreme temperatures and their own life history constraints (Crawford & McClain 1983, Crawford 1992). Their large size seems to be an advantage as heat gain and loss is less rapid, as is water loss (Hopkin & Read 1992). The soil, however, must always be loose enough to penetrate, especially by active burrowers (Minelli & Golovatch 2001).

Representatives of the juloid morphotype usually dominate the savanna biome as well, largely due to species of Spirostreptida. However, at least in southern Africa, the savanna diplopod fauna is far richer (nearly 17 % of the total) and encompasses species from the polyxenoid, polydesmoid and glomeroid morphotypes as well (Hamer et al. 2006). Similarly, the millipede fauna of the serrado-dominated State of Mato Grosso, Brazil (Por et al. 2005) is fairly rich and diverse (at least 85 species from 34 genera, seven families and four orders). However, only a few large Spirostreptidae predominate in the Pantanal, the globe's largest wetland which is affected by a harsh, sharply continental climate, with huge areas alternately flooded or dry for several months every year. During the dry phase, all diplopods in the Pantanal remain dormant (Golovatch et al. 2005).

Unsurprisingly, the most conspicuously deserticolous diplopods belong to the juloid morphotype. Among polydesmoids, only few, usually small to tiny, apparently ephemeral species can thrive in deserts (Shear & Shelley 2007). Larger polydesmoids are seldom observed in deserts, e.g. *Cnemodesmus riparius* Shelley & Crawford, 1996 (Polydesmida: Paradoxosomatidae) from riparian forests of the Namib Desert, Namibia. The crucial factor for the survival of these animals seems to be moist silt remaining in the dry river bed at least for one month following the previous 'flood' event (Shelley & Crawford 1996).

All of the main morphotypes except perhaps the platydesmid one appear to occur in the desert biome.

Recent evidence (Nguyen Duy-Jacquemin 2000, 2006, Prisnyi 2002, Alexander 2006, Kime & Enghoff 2010) reveals polyxenidans to be species of sheltered microsites on exposed surfaces sufficiently open to sunlight to permit the growth of algae and lichens. These occur on exposed rocks in situations where succession to denser vegetation is unable to proceed due to the exposure experienced on rocky coasts and also inland on rocky crags, including in the Sahara Desert, basically part of the epiphyte and saxicole invertebrate assemblage. Relict populations in the South of the Middle-Russian Upland live in hard shrubby litter on limestone denudations (Prisnyi 2002).

Zonal tundra

At the opposite end, Diplopoda seem to be absent from the waterlogged and cold tundra belt of the Northern Hemisphere. Furthermore, they are missing to marginal in the adjacent northern parts of the boreal forest (= taiga) biome.

The northernmost records of millipedes in Eurasia are for the subcorticolous species *Proteroiulus fuscus* (Am Stein, 1857) (Julida: Blaniulidae). This parthenogenetic, basically European species even occurs slightly north of the Arctic Circle, both in Fennoscandia (Andersson et al. 2005) and in the forested tundra sub-belt of the Yamal Peninsula, Russia (Golovatch 1992a).

The only other millipede that has been encountered north of the Arctic Circle in Scandinavia is *Polyxenus lagurus* (Linnaeus, 1758) (Polyxenida: Polyxenidae), another basically European species, which is strictly parthenogenetic at these high latitudes (Andersson et al. 2005). The widespread Siberian species *Angarozonium amurense* (Gerstfeldt, 1859) (Polyzoniida: Polyzoniidae) also crosses the Arctic Circle, in particular along the Yana River in Yakutia (Sakha), Russia (Mikhaljova 2004).

In the entire Holarctic, the taxonomic richness of Diplopoda generally decreases from south to north, from deciduous (Europe and the Russian Far East), subtaiga (Siberia) or (sub)tropical forest (U.S.A) towards the tundra belt, it also decreases from north to south through forested steppe (= sparse woodlands), steppe (= grasslands), semi-desert to desert (Golovatch 1992a, 1997a, 1997b, Kime & Golovatch 2000, Mikhaljova 2004).

The most apparent ecological factor that limits the distribution of Diplopoda in boreal ecosystems seems to be the presence of superficial permafrost (Minelli & Golovatch 2001). The congruence between the northernmost range limits of millipedes and the distribution of permafrost in Asia might look weak (Fig. 4), but in fact quite convincing on finer geographical scales. Since millipedes require soil for oviposition and larval development, very often also as a shelter against adverse weather conditions, the absence of permafrost is

crucial. Unsurprisingly, not only the great polar deserts of northern Canada, Alaska and northern Russia, but also the tundra or boreal forest ecosystems on permafrost are devoid of any diplopods.

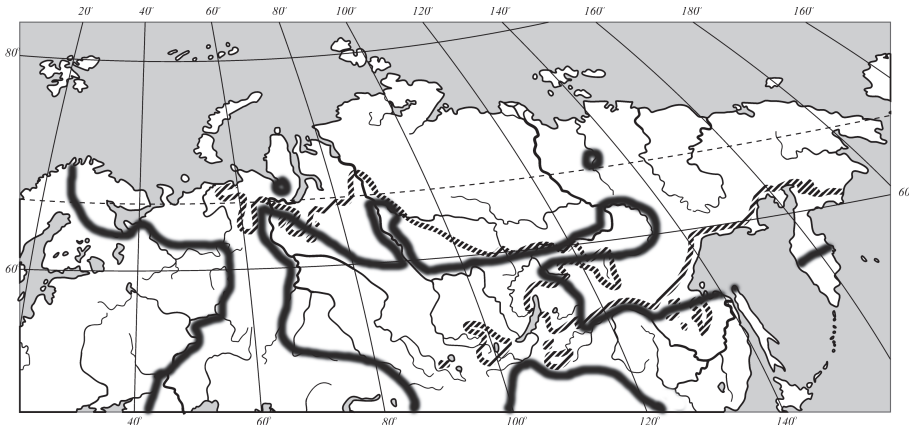


Fig. 4 Distribution of *Diplopoda* in northern Eurasia (thick contours) against the background of permafrost (dashed lines).

This, however, is hardly the sole reason explaining the absence of *Diplopoda* from some boreal regions. Thus, the entire West Siberian Lowland (between Irtysh and Yenisey rivers), except for its southernmost parts overgrown with forested steppe, seems to support no millipedes (Striganova & Poryadina 2005). This picture is all the more striking as diplopods are quite common in the boreal woodlands east of Yenisey River, as well as in the Urals to about Ekaterinburg in the north (Fig. 4). A causal reason for such a huge millipede-free lacuna in Siberia might be rooted in the entire region having been inundated during some of the Pleistocene interglacials (Markov et al. 1965), and even at present very swampy and heavily waterlogged. In addition, most of the northern areas of this region support superficial permafrost (Fig. 4).

The most apparent pathways for the northernmost penetrations of *Diplopoda* in Eurasia are rivers, because their valleys are geologically old enough and mostly devoid of permafrost, even in Siberia. In addition, such a direction of dispersal is favoured by numerous rivers over Eurasia running from south to north.

In contrast, the alpine belts of the high mountains of Europe and Siberia, but obviously not of Canada and the adjacent parts of the U.S.A., that support tundra or tundroid habitats without permafrost often appear to be rich in *Diplopoda*, both numerically and faunistically (e.g. Shelley 2002b, Mikhaljova 2004).

All of the main morphotypes except the glomeroid one appear to occur in high latitudes.

High mountains

Many mountains of temperate and tropical lands are to be regarded as natural foci and refugia for millipedes. As in the case of latitudinal zonation, they normally show a succession of vertical belts. One or more forest belts, depending on geographical location and elevation, are usually followed by subalpine to alpine grasslands. Open habitats lying above the timberline are usually termed as high-montane, or orobiome (Beron 2008).

In Siberia, these highest habitats are referred to as montane tundra which, when devoid of permafrost but rich in snow, support especially abundant populations in numerous species of Chordeumatida (Mikhaljova 2004). These are mainly the 'winged' Diplomaragnidae representing the polydesmoid morphotype. Like virtually any Chordeumatida, they are highly hygrophilous, yet hardly thermophilous, still finding sufficiently favourable conditions to be considered as a diplopod family in a very active phase of speciation. Its representatives are strictly Palaearctic, ranging from the Kama River region, European Russia in the West to Japan and Taiwan in the East (Mikhaljova 2000).

Similarly, the high-montane faunas of Europe and Central Asia are dominated by species of Chordeumatida (Read & Golovatch 1994, Spelda 1996, Kime & Golovatch 2000). In the Himalayas, where the timberline lies well above 4000 m a.s.l., the diversity of Diplopoda is quite pronounced, with over half of the about 200 described species of Polydesmida. The fauna is composed of elements of various origins, mainly oriental/tropical and Palaearctic/subtropical to warm temperate. The share of Chordeumatida is relatively small (less than 30 species). In most of the large genera, especially basically Palaearctic or belonging to Palaearctic families, such as *Tianella* Attems, 1904 (Chordeumatida: Cleidogonidae), *Usbekodesmus* Lohmander, 1933 (Polydesmida: Polydesmidae), *Anaulaciulus* Pocock, 1895 and *Nepalmatoiulus* Mauriès, 1983 (both Julida: Julidae) etc., the vertical distribution of the constituent species usually shows a wide range of altitudinal preponderances (Golovatch & Martens 1996). Thus, among the 17 species of *Nepalmatoiulus* currently known from the Himalayas, *N. ivanloebli* Enghoff, 1987 occurs between 2200 and 4800 m a.s.l., representing perhaps the highest millipede record globally (Enghoff 1987b). Closer unidentified Diplopoda have been observed in Nepal even at 5300 m a.s.l. (Beron 2008). This contrasts with some other terrestrial invertebrates in the region, e.g. spiders, which have been encountered at nearly 6000 m a.s.l. (Martens 1993).

In the Andes, the highest records probably belong to *Mestosoma alticolum* Attems, 1931 (Polydesmida: Paradoxosomatidae), from between 3900 and 4700 m a.s.l. in Bolivia. In tropical Africa, *Sphaeroparia petarberoni* Mauriès & Heymer, 1996 (Polydesmida: Fuhrmannodesmidae) has been recorded from Mt Ruwenzori, Uganda, from 3000 to 4200 m a.s.l. (Mauriès & Heymer 1996, Beron 2008). It is generally not known whether these species extend down to lower elevations. However, at least *S. petarberoni* and *N. ivanloebli* have been recorded not only from the orobiome, but also from below the timberline. Many European diplopods have large altitudinal ranges from the alpine zone down to the lower forest belts.

In northern Eurasia and Canada, mountains are too cold to harbour many or even any millipede species. Among the more than 40 diplopod species currently known from Canada, only 1–2 appear to be endemic (Shelley 2002b). So, unsurprisingly, there seem to be no truly boreo-alpine patterns in millipedes at all. In contrast, most of the mountains lying at or closer to the southern periphery of the Holarctic, such as the Pyrenees, Alps, Dinaric Alps,

Apennines, Balkans, Caucasus, Kopet Dagh, Tien-Shang, Pamirs-Alai, Altai, Sayan, Sikhote-Alin, Rockies, Appalachians etc., have long been known as so-called 'long-term', or Tertiary, refugia. They all represent areas of more or less pronounced diplopod diversity and endemism associated with nemoral and/or derivative boreal forests (Kime & Golovatch 2000).

There are few millipedes endemic to high-montane habitats alone. These are mainly chordeumatidans, apparently because cold-hardiness is very low in other orders (David & Vannier 1997). So it is hardly surprising that the overwhelmingly cold Siberia is dominated by species of Chordeumatida (Mikhaljova 2004).

In the Pyrenees, species of *Pyreneosoma* Mauriès, 1959 (Haplobainosomatidae) and *Ceratosphys* Ribaut, 1920 (Opisthocheiridae) are cold-hardy orobionts, as is *Marboreuma* Mauriès, 1988, a relictual monotypic genus of uncertain family placement (Mauriès 1975, 1988). In the Alps, all the few species of *Trimerophorella* Verhoeff, 1902 (Neoatractosomatidae) are nivicoles, as is the monotypic genus *Janetschekella* Schubart, 1954 (Craspedosomatidae), living between 2200 to more than 3000 m a.s.l. in rocky crevices among ice and snow far above the timberline (Geoffroy 1981, Pedroli-Christen 1993). *Niphatrogleuma* Mauriès, 1986, another relictual monobasic genus of uncertain family assignment, is known from a karstic cave hidden under a glacier in Switzerland (Mauriès 1986).

In such mountain systems, most species encountered in the nival orobiome also occur within the forest belts below, albeit some show higher population densities at higher elevations. This relative abundance can mask the real picture, providing the wrong impression of high-montane endemism. Thus, *Leptoiulus borisi* Verhoeff, 1926 (Julida: Julidae) is highly abundant on top of Vihren (2750 m a.s.l.), Pirin Mountains, one of Bulgaria's highest peaks, but it is rather typical of, yet never so numerically prolific in, the foothill to mid-montane woodlands of Bulgaria and Greece (Beron 2008).

All of the morphotypes except perhaps the polyxenidan and glomeroid ones appear to populate the orobiome.

Caves

Cavernicoles are common among Diplopoda. Not only numerous species of the juloid, glomeroid and polydesmoid morphotypes are troglobites representing the life form of troglobionts, but virtually all are local endemics of a particular cave or group of caves. Their distribution shows that most of them are restricted to limestone karst, being characteristic not only of caves but also of the so-called 'milieu souterrain superficiel', or MSS. Few diplopods are endemic to lava caves and none to ice, sea or salt caves (Vandel 1964).

Troglobites are lacking among cave-dwelling millipedes of Siberia and the Russian Far East (Mikhaljova 2004), and troglaphiles are scarce. The same holds true for Central Asia (Read & Golovatch 1994) and Canada (Shelley 2002b). Diplopod troglobites seem to be characteristic of the warm temperate and temperate belts, with many relict taxa present only in caves in the Spanish cordilleras, Pyrenees, Alps, Carpathians and Caucasus, as well as in Korea, Japan and China. Thus, the above monotypic relictual genera *Marboreuma* and *Niphatrogleuma*, from the Pyrenees and Alps, respectively, are of uncertain family placement, as is another monobasic genus, *Caucasodesmus* Golovatch, 1985 (Polydesmida), from the

northern Caucasus (Shear & Shelley 2007). *Cantabrodesmus* Mauriès, 1971, from Spain, is a monotypic genus, the only known representative of the basically tropical family Chelodesmidae (Polydesmida) in Europe (Mauriès 1974, Hoffman 1980).

Until recently, the caves of tropical countries, despite the rich faunas they had long been shown to contain, were believed to harbour only few troglobites if any (Vandel 1964). However, this viewpoint has since become refuted, with numerous examples of troglobitic arthropods, Diplopoda included, currently known from Southeast Asia, New Guinea and tropical Africa (Deharveng & Bedos 2000, Deharveng 2005), as well as from Brazil (Trajano et al. 2000) and Mexico (Bueno-Villegas et al. 2004).

Deeper soil

Geobites seem to be uncommon among millipedes. Furthermore, direct observations of their ecology are nearly absent. Some information is available for the minute, parthenogenetic, calcicolous species *Geoglomeris subterranea* Verhoeff, 1908 (Glomerida: Glomeridae) ranging from France, Britain and Ireland in the West to Austria in the East. This species occurs not only in the uppermost soil, usually between 10 and 20 cm deep, but also under boulders, in ant nests, and in old chalk and limestone quarries (Kime 2004, Lee 2006). Such examples link the life form of pedobionts to the MSS and caves. Even artificial MSS and caves are populated by several diplopod species reported as soil-dwelling elsewhere in Europe (Geoffroy 1991). Indeed, most if not all of the remaining *Geoglomeris* species are cavernicoles (Gruber 1984, Kime 2004).

In *Napocodesmus* Ceuca, 1974 (Polydesmida: Trichopolydesmidae), the type-species, *N. endogeus* Ceuca, 1974, is a troglobite from Romania, whereas its only other congener, *N. florentzae* Tabacaru, 1975, seems to be a pedobiont hitherto encountered in Romania and Moldova. In Moldova, this parthenogenetic species is highly common and abundant in the soils under apple orchards (L. Rybalov, in litt.). Similarly, one of the two species of *Tonodesmus* Silvestri, 1925, the single genus from the basically tropical family Pyrgodesmidae (Polydesmida) that occurs in Europe, has been found in soil at Malaga, Spain (Silvestri 1925).

In *Metaniulus pratensis* Blower & Rolfe, 1956 (Julida: Julidae) from Great Britain and France, one of the subspecies is epigeal, one more is cavernicolous, and still another one is a geobite (Mauriès 1965c). Another example of one and the same species showing both cavernicolous and endogean populations is the blind *Rodopiella beroni* (Strasser, 1966) (Julida: Julidae) in the Balkans (Stoev 2004).

The seldom seen *Galliobates gracilis* (Ribaut, 1909) (Julida: Galliobatidae) occurs at the interface between the soil and deeply embedded boulders and tree trunks in France. This is a species with a very slender body, as well as short legs and antennae. Like *Galliobates* Verhoeff, 1911, both monotypic *Occitaniulus* Mauriès, 1965 (Julida: Blaniulidae) from southern France and *Basoncopus* Enghoff, 1985 (Julida: Nemasomatidae) from eastern Kazakhstan, Central Asia are remarkable not only in showing very slender bodies and short legs, but also in being apparently restricted to the topsoil (Mauriès 1965a, Enghoff 1985).

In *Typhloglomeris* Verhoeff, 1898 (Glomerida: Glomeridellidae), a genus with about 15 species ranging from the Dinaric Alps through the Balkans to Anatolia, Caucasus and Middle East, most species are epigeal, with vivid colour patterns, a few are unpigmented troglobites,

and at least one, the unpigmented *T. fumarana* Verhoeff, 1899 from Croatia, seems to be a geobite (Golovatch 2003). In the Pyrenees, a few very small species of Chordeumatida, e.g. *Xystrosoma cassagnai* Mauriès, 1965 (Chordeumatidae) and *Cranogona dalensi* Mauriès, 1965 (Anthogonidae), which belong to large genera, seem to be the only congeners restricted to the topsoil, maybe also to the MSS (Mauriès 1965b). A similar example is represented by the Mediterranean genus *Metonomastus* Attems, 1937 (Polydesmida: Paradoxosomatidae), in which several of the currently known 11 species show clear inclinations to geo- and/or cavernicolity (Golovatch & Stoev 2004).

Species of the order Siphoniulida are particularly slender and tiny, superficially resembling nematodes. In Mexico and Guatemala, these presumed pedobionts have been taken using Berlese extraction both from topsoil (deep humus) and litter (Sierwald et al. 2003).

Beyond any life-form approach, deeper to topsoil are used by most Diplopoda as shelter for aestivation, oviposition and development. Special egg and moulting chambers are thereby usually constructed, differing from one order to another. Thus, soil properties are crucial for numerous millipedes, especially calcicoles, that can tolerate neither increased acidity nor waterlogged habitats. Not surprisingly, juvenile stadia in most species of diplopods can only be encountered in special chambers more or less deep in the soil, whereas adults and certain advanced juvenile stadia are the only truly active stages. Depending on conditions, sometimes these are observed swarming in great numbers (Hopkin & Read 1992). Sandy soils and friable loams are much more easily penetrated than heavy clay soils and tend to have higher populations of millipedes unless they are too dry (Kime & Wauthy 1984).

Other difficult to extreme habitats, periodomorphosis, parthenogenesis and anthro-pochorism

Some diplopods are encountered in suspended soil (mainly of epiphytes), on vegetation, in bird, ant and termite nests, under the bark of trees, as well as in dung and compost. As already noted above, a life-form of subcorticoles is rather well delimited, in contrast to that of epiphytobionts which is still questioned (Kime & Golovatch 2000).

Epiphytes, including even ground-dwelling bromeliads with their characteristic water tanks (= phytotelmata), are often populated by various, usually small-bodied to tiny diplopods. It still remains to evaluate the degree of diplopod-plant association, but in principle a life-form of epiphytobionts might only have become established in humid subtropical to tropical forests, where the debris and soil of the epiphytes could remain humid all the year round or nearly so. Such conditions are observed, e.g., in lowland hylaea and montane cloud forests in tropical parts of Africa, Indo-Australia and the Americas. Bromeliads are highly characteristic of the Amazonian and, especially, Atlantic forest biomes of Brazil (Por et al. 2005), whence several small species of *Apomus* Cook, 1911 (Polydesmida: Cryptodesmidae), *Catharosoma* Silvestri, 1897 (Polydesmida: Paradoxosomatidae) etc. have been reported from bromeliads alone (Schubart 1945, 1953). In contrast, in seasonal and dry tropical forests suspended soils usually remain dry too long to support any characteristic diplopod fauna (Vietnam, personal observations of the first author).

There is even less evidence of diplopod arboricoles (= dendrobionts) as a separate life-form, even though there are a few species that seem to live only or mainly in the canopy. Thus, *Epinannolene exilio* (Brölemann, 1904) (Spirostreptida: Pseudonannolenidae), from the

upland forests near Manaus, Brazil, is a true canopy-dweller (Hoffman et al. 2002). Several brightly coloured, apparently aposematic species of *Desmoxytes* Chamberlin, 1923 (Polydesmida: Paradoxosomatidae) are characteristic of arboreal vegetation in Southeast Asia (Enghoff et al. 2007). In southern Africa, the arboreal species of the large genus *Centrobolus* Cook, 1897 (Spirobolida: Pachybolidae) are often scarlet red while related stratobionts usually appear to be more drab coloured (R. L. Hoffman, in litt.). Similar observations concern numerous aposematic Xystodesmidae (Polydesmida) from the Appalachians (Whitehead & Shelley 1992), although xystodesmids, while surface active at night, never climb trees in places where Spirobolida do so in large numbers (R. L. Hoffman, in litt.).

Further examples of possibly arboreal millipedes can be found in Hoffman (1975), VandenSpiegel (2001) and Golovatch et al. (2003).

There are numerous subcorticoles among Diplopoda, e.g. the above-mentioned European *Proteroiulus fuscus*. Furthermore, many of them are so conspicuous morphologically (thin, small and/or flat-bodied) that they definitely warrant recognition of a separate life-form (see above). Only such millipedes appear to represent an unquestioned life form among the numerous species occurring on vegetation.

Although coprophagy is essential in some species for weight gain and even survival, there seem to be neither specialised dung- nor compost-dwellers among Diplopoda (Sierwald & Bond 2007).

Concerning diplopod symbionts, Rettenmeyer (1962) found seven species of Pyrgodesmidae (Polydesmida) as definitely being myrmecophiles of army ants (Dorylinae) in Panama. These millipedes have been observed both within the nests and at the periphery of army ant bivouacs and ant workers often carry symbiotic diplopods during colony emigrations. The ranges of the few myrmecophilous diplopod species tend to be vast, closely following the distribution of their hosts. However, although the small myrmecophile *Myrmecodesmus hastatus* (Schubart, 1945) (Pyrgodesmidae) occurs over most of South America, its long-distance distribution along the Amazon/Solimões River, ranging from Pucallpa, Loreto Dept., Peru to Belém, Brazil, could be accounted for by downstream transportation on floating debris as shown for other millipede species (Golovatch & Adis 2004, Bergholz et al. 2004).

Ants are far from always harmless to symbiotic Diplopoda. Thus, the Southeast Asian *Probolomyrmex* ants are specialised predators of Polyxenida (Ito 1998). Similarly, some ants in Brazil are specialised on eating certain Polyxenida and Spirobolida, sometimes with special care of millipede eggs or brood in the nest (Brandão et al. 1991, Diniz & Brandão 1993).

Several dozen species of Polyxenida, Glomerida, Julida, Spirostreptida, Spirobolida and Polydesmida commonly occur in ant nests all over the globe, but only a few, nearly all representing tropical Pyrgodesmidae, could be termed as obligate myrmecophiles (Schubart 1950, Stoev & Lapeva-Gjonova 2005). However, none of these is striking enough morphologically to warrant recognition of a separate life form.

Similar observations concern termitophily in diplopods. There seem to be only few millipedes more or less associated with termitaria. Such are, e.g., some of the few, small species of *Termitodesmus* Silvestri, 1911 (Glomeridesmida), an oligotypic genus from South and Southeast Asia representing a subfamily or family of its own (Hoffman 1980). In contrast, *Pelmatojulus tigrinus* Hoffman & Mahsberg, 1996 (Spirobolida: Pachybolidae) is a very large

juliform that abundantly uses large nests of Macrotermitinae termites in Ivory Coast, both as shelter and source of calcium-rich food (Mahsberg 1997).

Millipedes (Polyxenida, as well as small/juvenile Polydesmida and Julida) have also been reported from bird nests and plumage in southern Russia (D. Krivolutsky, in litt.), but none seems to be their obligate symbiont. A special survey of the millipedes extracted from 301 bird nests representing seven nest types and 40 bird species throughout Slovakia revealed 18 diplopod species from four orders (with the addition of one form of Chordeumatida). Likewise, none of them is an obligate nidicole, *Polyxenus lagurus* and *Proteroiulus fuscus* being the most common (Tajovský et al. 2001). On the other hand, as noted above, the presently highly sporadic distributions of *Aporodesminus wallacei* and *Cryptocorypha ornata* are best explained in terms of ornithochory (Adis et al. 1998).

Both parthenogenesis and periodomorphosis appear to be characteristic of the millipedes that occur in difficult to extreme environments. These are obvious adaptations to adverse survival conditions (Kime & Golovatch 2000). Unsurprisingly, both opportunist and obligate parthenogens tend to be widespread (Enghoff 1978, 1994). Examples where, within a single genus, the parthenogenetic species are much more widely distributed than their congeners are numerous, especially in the Holarctic. Such are, e.g., *Polyxenus* Latzel, 1884 (Polyxenida: Polyxenidae), *Proteroiulus* Silvestri, 1897 (Julida, Blaniulidae), *Okeanobates* Verhoeff, 1939, *Nemasoma* C. L. Koch, 1847 and *Orinisobates* Lohmander, 1933 (all three Julida: Nemasomatidae) (Fig. 5) (Enghoff 1978, 1979, 1985).

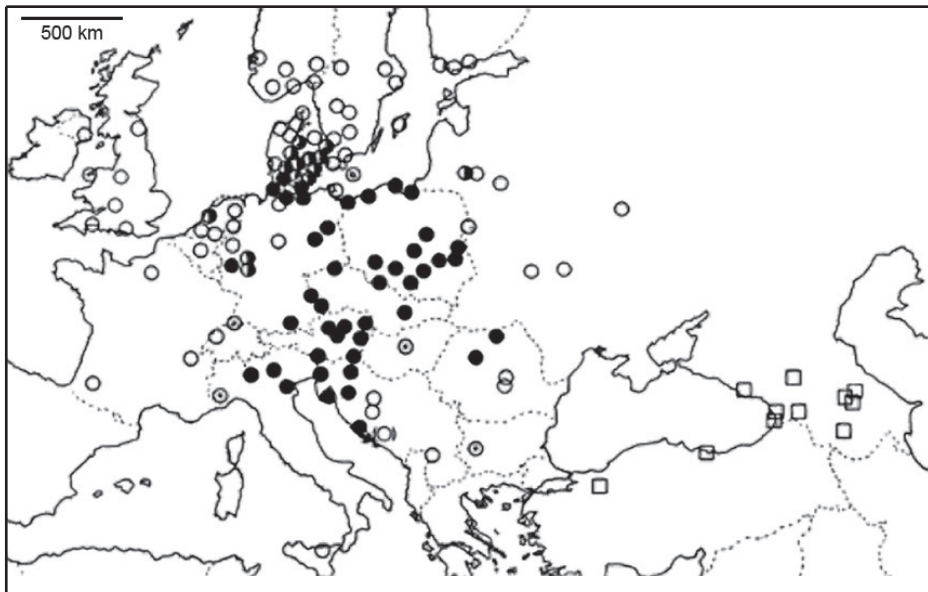


Fig. 5 Distribution of the genus *Nemasoma* C. L. Koch, 1847 (after Hoy Jensen et al. 2002, with modifications). Filled circles: bisexual form of *N. varicorne* C. L. Koch, 1847, open circles: parthenogenetic form of *N. varicorne*, half-filled circles: both forms, circles with dot: mode of reproduction unknown, open squares: *N. causicum* (Lohmander, 1932). Symbols in parentheses: exact locality unknown.

Anthropochorism only concerns a few dozen diplopod species, yet representing various families and orders. Among them, the few particularly small species of the order Polydesmida (less than 1 cm long, i.e., other than the family Paradoxosomatidae) appear to be parthenogenetic. None of these species, however, shows any remarkable morphological modifications that would allow for a separate life form to be distinguished (Minelli & Golovatch 2001). Man-made habitats or environments, such as agricultural fields, arable soil, parks etc., support few millipede species, but those that are present, whether introduced or not, often show high population densities (Hopkin & Read 1992). Needless to say, anthropochores are especially widely distributed, either pantropical, e.g. *Orthomorpha coarctata* (DeSaussure, 1860) (Polydesmida: Paradoxosomatidae), *Trigoniulus corallinus* (Gervais, 1847) (Spirobolida: Pachybolidae), *Glyphiulus granulatus* (Gervais, 1847) (Spirostreptida: Cambalopsidae), *Rhinotus purpureus* (Pocock, 1894) (Polyzoniida: Siphonotidae) etc., or subcosmopolitan, e.g. *Oxidus gracilis* (C. L. Koch, 1847) (Polydesmida: Paradoxosomatidae) (VandenSpiegel & Golovatch 2007). Naturally, most of the temperate introductions among Diplopoda are of European origins (Hopkin & Read 1992), most of the tropical ones seem to be of Southeast Asian stock.

It remains unclear why, often among numerous congeners, only one particular species shows inclination to anthropochorism. None of the above examples of widespread introductions has parthenogenetic populations, nor does any demonstrate periodomorphosis or peculiar morphism. Just like a hint to possible advantages, *Glyphiulus granulatus* is among the smallest congeners perhaps requiring fewer stadia/molts to attain maturity (Golovatch et al. 2007).

Sometimes the distribution of synanthropic species reflects their area of origin. Thus, in Middle America, *Oxidus gracilis* prefers higher, cooler elevations, as in Costa Rica, showing its north temperate ancestry in ?Japan, whereas *Orthomorpha coarctata* is clearly partial to hot, lowland places to colonise (Hoffman 1999).

The distribution of each species of diplopod is usually quite restricted, especially in the humid subtropical and tropical biomes, which are particularly rich in millipedes. This is rooted in the bulk of the millipedes showing only highly limited powers of dispersal. Regardless of the handful of anthropo- and possible zoochores, the largest distribution ranges belong to only very few boreal, mainly Palaearctic species, such as the nearly pan-European *Ommatoiulus sabulosus* (Linnaeus, 1758) and the Eastern European-Southwest Siberian *Megaphyllum sjaelandicum* (Meinert, 1868) (both Julida: Julidae), as well as the nearly pan-European *Polyzonium germanicum* Brandt, 1837 and the nearly trans-Siberian *Angarozonium amurense* (both Polyzoniida: Polyzoniidae) (Golovatch 1997a, 1997b, Mikhaljova 2004).

There are several similarly widespread Nearctic diplopods, e.g. *Oriulus venustus* (Wood, 1864) or *Aniulus garius* (Chamberlin, 1912) (both Julida: Parajulidae), of which the former species occurs across roughly 3/4 of the continent, from the Atlantic Ocean to about the western border of Utah (= the eastern border of the Great Basin Physiographic Province) (Shelley 2002a). In contrast, *A. garius* ranges roughly from the Atlantic Ocean to the Rocky Mountains (Shelley 2001), yet with only a few populations in the Southeast, never in large numbers. Basically, distributions of any group of organisms are rarely static and can be visualised in dynamics like hundreds of ‘ameboid’ patterns, superimposed in the same

geographical area, expanding or contracting at different rates. If the periphery of the range is richly endowed with populations, it is expanding. If there is no real distinct periphery, but a lot of isolated populations, then it is contracting. So the range of *A. garius* in the southeastern U.S.A. is apparently in decline (R. L. Hoffman, in litt.).

The vast distribution of *Ommatoiulus sabulosus*, ranging from Fennoscandia in the North to the Balkans in the South, and from Spain and Great Britain in the West to the Ural Mountains in the East, and its occasional mass outbreaks can be explained at least in part by periodomorphosis (Halkka 1958, Helb 1975). The even greater distribution of *Polyxenus lagurus* covering most of the Euro-Mediterranean region and much of North America seems to be accounted for not only by its numerous populations showing opportunist parthenogenesis (Enghoff 1994), but also by its myrmecophily (Stoev & Lapeva-Gjonova 2005) and even possible zoochory (often found in bird nests and plumage) (Tajovský et al. 2001).

The small, European, mostly subcorticolous species *Nemasoma varicorne* C. L. Koch, 1847 (Julida: Nemasomatidae) represents a classical example of geographic parthenogenesis (Fig. 5). Solely bisexual populations occur at the centre of the range, all peripheral ones are parthenogenetic, while the fewer mixed ones are only encountered within the contact zones (Enghoff 1976). Genetic evidence suggests that such a pattern is the result of direct competition between the bisexual and parthenogenetic populations (Hoy Jensen et al. 2002).

In the tropics, the tiny, apparently obligate parthenogenetic *Moojenodesmus pumilus* Schubart, 1944 (Polydesmida: Fuhrmannodesmidae) seems to be widespread in the Amazonian and Atlantic forest biomes of Brazil only because of parthenogenesis, since all the other species of this family in the Neotropics are bisexual and show highly local distributions (Golovatch 1992b, Enghoff 1994). On the other hand, *Poratia obliterated* is most widespread in Amazonia, with solely bisexual populations occurring all along the Amazon/Solimões River, but only parthenogenetic introductions are encountered sporadically, chiefly in hothouses, both in Europe and North America (Adis et al. 2000, Golovatch & Sierwald 2001). A similar case is represented by the nearly pantropical, also apparently anthropochorous species *Cylindrodesmus hirsutus* Pocock, 1889 (Polydesmida: Haplodesmidae), whose parthenogenetic and bisexual populations seem allopatric, while parthenogenetic populations occur not only in European hothouses, but also in some tropical environments (Golovatch et al. 2001, Golovatch & Sierwald 2001). Another obligate? parthenogenetic introduction, *Amphitomeus attemsi* (Schubart, 1934) (Polydesmida: Oniscodesmidae), has hitherto been reported only from a few European hothouses and in some man-made habitats in southeastern Brazil while its motherland is still unknown, only presumed to lie in Colombia or Venezuela (Golovatch et al. 2002).

At least the bulk of parthenogens in Diplopoda are believed to represent spanandry, i.e., no or non-functional males. Genetic studies of *Poratia obliterated* and *P. digitata* (Porat, 1889) showed that the agent inducing parthenogenesis in millipedes is different from *Wolbachia* bacteria, long known as endocyttoplasmic parasitoids commonly causing spanandry in filarial nematodes, insects, arachnids and crustaceans (Witzel et al. 2003).

4. Diversity patterns: local patterns, regional patterns, global patterns

There are few places on the globe, even in the especially species-rich tropics, where a local diplopod fauna, or faunule, exceeds two dozen species (Golovatch 1997a). Indeed, the remarkable overall diversity of Diplopoda, currently estimated as exceeding 80 000 species (Shelley 2007), appears to be extremely low per site/faunule. As mentioned above, very few diplopods show truly vast distributions, whereas local endemisms strongly prevail. There are countless examples of millipedes restricted to a single cave, mountain, forest patch, island etc.

Considering the landscape-zonal distribution of millipede faunules, they largely repeat that of life forms and of zonal or regional faunas, yet also far less diverse than the faunas. In Eurasia, diplopods are virtually absent from the polar deserts and tundra belt (Fig. 4), followed by an increase southwards from one to a few species in the boreal forest biome. The richest belts across the Eastern European, or Russian, Plain are broadleaved (= nemoral) forest and forested steppe biomes, supporting 47 and 33 millipede species or subspecies, respectively (Golovatch 1984, 1992a). However, even there the number of syntopically occurring species rarely reaches a dozen. Further to the south, in the steppe belt, the zonal fauna drops drastically to five species, the faunules to 0–3 per habitat. In semi-deserts and deserts, diplopods are either totally absent or barely thriving. The same trends apply to broader, up to global, scales as well (see below).

Even in one of the temperate belt's optima, the nemoral seaside forests of the Caucasus, one of the major 'Tertiary refugia' in the entire Palaearctic, the maximum millipede diversity so far recorded per site (Myussera Nature Reserve in Abkhazia) amounts to some 16 species (Golovatch, unpublished). On the island of Madeira, Portugal, as many as 15 species may be found per site, largely represented by members of the *Cylindroiulus madeirae* group (Julida: Julidae), which tends to be restricted to the laurisilva, a relict subtropical woodland type (Enghoff 1992). In the particularly rich tropical forests, the millipede faunule of a patch of upland rainforest at 'Reserva Florestal A. Ducke' near Manaus, Brazil currently holds the world record of 33 species (Adis et al. 2002, Hoffman et al. 2002). At Manaus, every few hundred square metres of woodland, be it flooded or not, support its own, basically original millipede faunule (Golovatch 1997a, Minelli & Golovatch 2001). Only a slightly poorer local fauna, about 30 species, has recently been revealed in a patch of seasonal tropical lowland forest at Nam Cat Tien National Park, South Vietnam (Golovatch, unpublished).

This shows that Diplopoda are remarkable in the distribution patterns of their faunules per habitat/site being highly patchy and mosaic-like. The lists of syntopically occurring species tend to be quite modest, apparently in response to the group's profound ecological integrity and monotony, seen against a background of poor vagility and active speciation characteristic of most of the modern diplopod orders (Golovatch 1997a). Niche segregation in syntopic millipedes usually implies more distant phylogenetic relations and often (but not always) marked size differences which tend to change also with age.

The intricate processes of speciation and habitat partitioning in Diplopoda have been best studied in several species swarms characteristic of the Canary Islands and Madeira (see review by Enghoff 1992). The large, subendemic Macaronesian genus *Dolichoïulus* comprises 46 and ten species restricted to the Canaries and Madeira, respectively. A few more congeners are known from the Cape Verde Islands and the western Mediterranean mainland. Similarly, *Acipes* Attems, 1937 (Julida: Blaniulidae) shows six species endemic to the

Canaries, one to Madeira, and two to the mainland of Spain, whereas the *Glomeris alluaudi* group (Glomerida: Glomeridae) (6–7 species) is strictly endemic to the Canaries (Golovatch & Enghoff 2003). In contrast, the *Cylindroiulus madeirae* group dominates the fauna of Madeira (29 endemic species versus two on the Canaries, nearly all confined to the laurisilva biome). The evolutionary scenario for the appearance of each of these species swarms seems to have followed roughly the same pathway (Enghoff 1992, Enghoff & Báez 1993). The founder species, more likely one single, could have arrived to this or that archipelago from the Iberian and/or North African mainland by rafting. These must have been relatively small species more or less well adapted to coastal environments. Even with further in-situ speciation on the first island, the colonisers within the same archipelago had to largely remain of similar ecology, since the dispersal of medium- to high-altitude species, especially forest-dwellers, from island to island was far less likely. Such a picture agrees quite well with the basics of island biogeography (Enghoff & Báez 1993).

As a result, on each island/archipelago, a single or at most only a few colonising species could have given rise to a variable number of descendent species. Smaller species swarms like *Acipes* or the *Glomeris alluaudi* group tend to show more or less strict allopatry, with one, rarely two, species per island. The larger swarms reveal an elaborate mosaic of allo-, para- or sympatric congeners differing in structure (size, colour, leg length etc.) and habitat (laurisilva, xeric biotopes, caves etc.). Species which have since moved to the forests tend to be larger, lighter in coloration and often log-dwellers (Enghoff 1992, Enghoff & Báez 1993).

On a regional scale, mosaic complexes and patterns are generally highly characteristic of Diplopoda (Shelley 1990, Hopkin & Read 1992). These complexes usually show large-scale generic or familial distributions, limited component ranges, tightly fitted parapatric and less common sympatric patterns, and only slight differences between some of the constituent species. Passive vicariance partitioning of mosaics with extinctions of intermediate forms is deemed to have been a prevailing pathway of evolution and speciation in this class.

Mesibov (1996, 1997, 2006), surveying the invertebrate fauna of Tasmania, including diplopods, delimited a number of lines of what he called ‘faunal breaks’, which, despite the lack of apparent zoogeographical barriers within a superficially monotonous and ‘pristine’ woodland, show abrupt regional changes in species assemblages. These lines and mosaics are seen not just as divides, or narrow zones of concentration of certain range limits, but rather as some congruence of climatic, geologic, edaphic and vegetational change in the past.

In southern Europe, mosaic patterns are often hard to discern because of the complex nature of the topography and east-west mountain barriers which are more disruptive than north-south mountain barriers in times of climate change (Kime & Golovatch 2000).

Sometimes the mosaic distributions of species in a complex seem to be due to morphism, which is most common in Diplopoda. Since the bulk of the millipedes are bisexual, males and females usually differ not only in genitalic, but also in a number of peripheral sex-linked features. Males are normally smaller, slenderer and longer-legged than females. Typical sexual dimorphism in certain instances can be accompanied by phenetic polymorphism of some usually stable structures. Thus, *Epanerchodus polymorphus* Mikhaljova & Golovatch, 1981 (Polydesmida: Polydesmidae), which is very common in the southern part of the Russian Far East and in North Korea, shows two distinct male morphs, but a continuous variation range in the females, all morphs always coexisting (Mikhaljova & Golovatch 1981,

Mikhaljova 2004). Similar observations concern a few more, apparently troglobitic congeners in Japan (Mikhaljova & Golovatch 1981). Generally, the large East Asian genus *Epanerchodus* Attems, 1901 represents a good example of a mosaic complex, being very large, comprising over 50 described species and difficult systematically.

Using enzyme electrophoresis techniques, phenetically expressed polymorphism of the colour pattern, i.e., a character not linked to sex, has been revealed in several European species of *Glomeris* Latreille, 1802/03 (Glomerida: Glomeridae). This has resulted in a number of species synonymies (Hoess 2000). In contrast, PCR analysis has allowed to discriminate cryptic genetic polymorphism and describe a new sibling species within a taxonomically difficult diplopod species group/swarm on Jamaica (Bond & Sierwald 2002, 2003), or else to reconfirm genetically the internal integrity of the trans-Amazonian species *Poratia obliterata* (see above and Bergholz 2007). In general, given the high number of mosaic complexes in Diplopoda, cryptic species therein may be quite common. Population structuring seems to start on a fine geographical scale, siblings first appearing as diverging sympatric lineages at the molecular level (Sierwald & Bond 2007).

Diplopoda show several most remarkable regional or global distribution patterns. These primarily concern a few relictual orders that are presumably in decline. Thus, the currently 2–3 known species of Siphoniulida are only known from Sumatra (1) and Mexico+Guatemala (1–2) (Sierwald et al. 2003). However, such a peculiar disjunction might also reflect our imperfect knowledge of the actual distribution of these minute, cryptic, likely geobitic millipedes.

The pattern demonstrated by Siphonocryptida is also quite peculiar. This small order contains one genus and species living on Madeira and the Canaries, where it is largely confined to the relict laurisilva biome, as well as one congener each in Malaya, Taiwan and Nepal, a different, monotypic genus occurs on Sumatra (Korsós et al. 2009).

Despite these few exceptions, the distribution patterns of Diplopoda at the regional and global levels largely agree with conventional wisdom. The overall geography of millipedes is consistent with the world's biogeographical regionalization known since the times of J. Hooker and A. Wallace. The traditional division of the globe's territory into the Holarctic (= Palaearctic + Nearctic), Afrotropical (including Madagascar and the Cape), Neotropical, Oriental (Indian + Malesian), and Australian (including New Guinea and the islands of the southern Pacific) realms is supported by the patterns demonstrated by diplopod higher taxa. Antarctica is the only continent devoid of myriapods (Minelli & Golovatch 2001). However, any attempts at deriving the recent patterns directly from ancient continental drift like Gondwanaland fragmentation must be cautioned (Eskov & Golovatch 1986).

Reviews of some high-level regional patterns are available for Europe (Kime & Golovatch 2000, Kime 2000), as well as the entire Holarctic (Enghoff 1993, 1995, Sanmartín et al. 2001), the whole of Eurasia (Golovatch 1997a, 1997b) and Australia (Black 1997). Most of these studies contain faunogenetic reconstructions or implications.

5. Conclusions

Despite the basic morphological and ecological similarity and conservatism expressed through only a small number of morphotypes and life forms in Diplopoda, among which the juloid morphotype and the stratobiont life-form are dominant, most of the recent orders constituting this class of terrestrial Arthropoda are in a highly active and dynamic stage of evolution. This has allowed the colonization by some millipedes of a number of derivative, often extreme and adverse environments more or less strongly differing from the basic habitat, i.e., the floor of temperate (especially nemoral), subtropical or tropical forests (in particular, humid ones). Such are the marine littoral, freshwater habitats, deserts, zonal tundra, high mountains, caves, deep soil, epiphytes, the bark of trees, tree canopies, ant, termite and bird nests etc. Most of such difficult environments are only marginally populated by diplopods, but caves and high altitudes are often full of them. To make the conquest of ecological deviations easier, and the distribution ranges greater, some millipedes show parthenogenesis, periodomorphosis or morphism.

Mosaic complexes are quite common in Diplopoda, as possibly are cryptic species therein. Siblings seem to appear as diverging sympatric lineages still at the molecular level.

Only very few millipede species demonstrate vast natural distributions. The majority have restricted ranges, with many local endemics in a single cave, mountain, valley or island. This contrasts with the remarkable overall diversity of the Diplopoda (currently estimated as exceeding 80 000 species, mostly confined to tropical countries), as there are few places on the globe where a local diplopod fauna, or faunule, exceeds two dozen species. The world record is apparently a patch of rainforest in central Amazonia where as many as 33 millipede species have been revealed (Adis et al. 2002).

Considering the landscape-zonal distribution of millipede faunules, they largely repeat that of life forms and of zonal or regional faunas. Diplopoda are entirely absent from the polar desert and tundra belts, apparently due to the presence of superficial permafrost. In the boreal forest belt, or taiga, zonal faunas barely total a few dozen in the entire Holarctic, the faunules from zero to just a few species per site. Within the temperate nemoral forest biome, especially in the mountains composing the so-called 'Tertiary refugia' and lying at the southern periphery of the Holarctic, the regional millipede faunas are far richer, often comprising several hundred species, nearly all life forms occur there, whereas the faunules often exceed a dozen species per site. After a rapid drop further to the south, in the more arid grassland/savannoid, semi-desert and desert belts and regions, where the millipede faunas, life forms and faunules are again relatively few, the strongly fragmented humid subtropical and, especially, tropical rainforest parts enjoy the richest diversities of millipedes at all levels (Kime & Golovatch 2000).

Such a highly patchy, mosaic distribution of diplopod diversity over the globe is rooted in the group's general structure (morphological conservatism and monotony, only few morphotypes, etc.), biology (anamorphosis, basically terrestrial, poor compensation and dispersal capacities, overall saprophagy etc.), ecology (few life forms, meso- to hygrophily, niche segregation patterns etc.) and phylogeny (geologically ancient age, certain fossil record, numerous higher taxa, speciation modes etc.). This particular combination has long made the Diplopoda a group most attractive for biogeographical reconstructions. We hope the present review will reinforce this opinion and promote further studies in analysing millipede distributions.

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