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## The Size of a Millipede

by

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**Abstract:** The factors influencing body size in millipedes are reviewed, and examples are given for correlations between body size and: ancestry, individual age, sex, food, latitude, altitude, habitat, and coexistence with other species. The body size of a cylindrical millipede, such as a species of *Juliformia*, has two main components: body diameter and number of segments. In groups where growth does not terminate at maturity, body diameter cannot straightforwardly be employed as a taxonomic character. In groups like the *Julida*, where new segments are often added after attainment of maturity, even segment number is an unreliable character. The best way to represent the size of such species is a scattergram showing number of segments and body diameter for each individual.

### 1. Introduction:

Size is of one of most basic characteristics of an organism and has immense implications for almost any aspect of its life. From the point of view of the diplopodologist (or any other student of organisms) size is one of the most conspicuous characters usable for identification. Size has been widely used as a taxonomic character, sometimes rightly, but sometimes wrongly, authors having not been aware of the factors influencing body size.

The present paper is about the size of millipedes, in particular about the factors that determine size. *Juliformian* millipedes are used as examples, these being "the millipedes" to most people. Much of what is said applies, however, to other millipedes as well (and in fact to numerous other animal groups).

*Juliformian* millipedes exhibit an impressive diversity of size: *Archispirostreptus gigas* (PETERS, 1855) (*Spirostreptidae*) may reach a length of 260 mm and a diameter of 20 mm (KRABBE 1982), whereas the smallest males of *Nemasoma varicorne* C.L. KOCH, 1847 (*Nemasomatidae*) are only 4 mm long and 0,33 mm in diameter (SCHUBART 1934). The volume ratio between these extreme examples exceeds 200,000, corresponding to the weight ratio between an elephant and a mouse. See also Fig. 1.

### 2. Measuring Size:

The body of a *juliformian* millipede can be likened to a cylinder. There are variations in height/width ratio, posterior and/or anterior attenuation etc. (e.g., ENGHOF 1982 a: Fig. 10), but still the cylinder is a good approximation. The size of a cylinder has two components: length and diameter; the same is true, roughly spoken, for a *juliformian* millipede.

When measuring the diameter of a millipede it is important to specify whether vertical or horizontal diameter has been measured, since although the difference between height and width is usually negligible it may sometimes amount to 35 % (ENGHOFF 1982 a: 100). It must also be specified at which place the measurement has been taken: at segment no. X, at midlength, or at the place with maximum diameter.

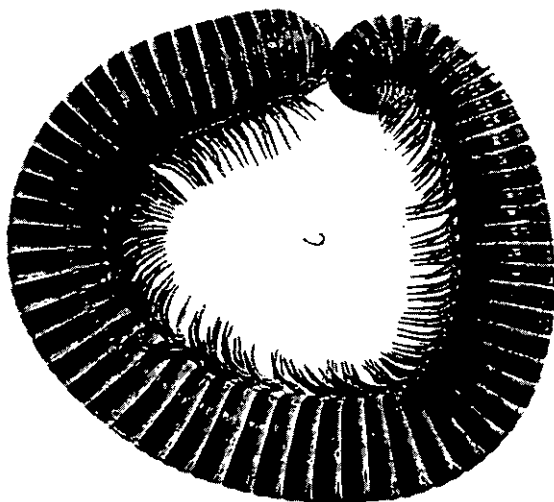


Fig. 1: Juliformian extremes: One of the World's largest millipedes, a female *Triaenostreptus triodus* (ATTEMS, 1909) (Spirostreptidae) from Namibia. In the center a male of the tiny European *Nemasoma varicorne* C.L. KOCH, 1847 (Nemasomatidae). Natural size. — G. Brovad phot.

Measuring the length of a millipede is hampered by the telescopic properties of the body. BLOWER & GABBUTT (1964) showed that the length of a maximally contracted millipede is a reliable measurement; however, the use of this concept puts considerable demands on the preservation of specimens. Anybody who has examined julids collected by means of formalin or  $\text{KCr}_2\text{O}_7$  traps will know that many specimens are not maximally contracted.

A more precise measurement of length is the length of a single segment combined with the number of segments. The length of a juliformian (diplo)-segment decreases from dorsal to ventral, therefore the length should consistently be measured at ozopore level. Certainly, segment length is not entirely constant along a millipede's body (ENGHOFF 1982a: Fig. 10) but (length of a mid-body segment)  $\times$  (number of segments) will still be a reliable measurement of body length. When indicating number of segments, it is important to state which segments have been considered. The formula (podous segments incl. collum) + (apodous segments) + (T = telson including preanal ring) is recommended (example: 43 + 2 + T).

Segment shape can be described as the diameter/length ratio. This ratio is a function of diameter and leg length: larger millipedes have relatively shorter segments (MANTON 1954, ENGHOFF 1982 a: Fig. 230), and the longer the legs, the longer the segments (ENGHOFF 1982a: Fig. 232).

For most purposes, however, length of individual segments needs not to be considered. A simpler way of measuring a millipede's size consists of counting the segments and measuring the body diameter. When many specimens are available these parameters, when plotted on a scattergram, describe an oblong and oblique point swarm for each sex, giving a good representation of a millipede species' size (e.g., Figs 2 - 3).

Even this simple method entails a lot of tedious counting and measuring work. A quicker way is just to consider minimum and maximum values of number of segments and body diameter for each sex. On a scattergram, these values delimit a rectangle with its sides parallel to the axes rather than an oblique ellipsoid — distinction between species of different size will thus be considerably less clear.

### 3. Determinants of Size:

#### 3.1. Ancestry:

Any organism's size is to a certain extent determined by its ancestry: closely related species usually are of roughly the same size: Spirostreptidae, Harpagophoridae, and Pachybolidae are thus generally large (up to 30 cm length); Odontopygidae, cambaloids, and Julidae are generally medium-sized (rarely under 1, rarely over 10 cm); Blaniulidae and Nemasomatidae are generally small and in particular slender. Among non-juliformian millipedes, Penicillata are all very small (< 1 cm), and the two orders of pill-millipedes (Glomerida: "ordinary" pill millipedes, and Sphaerotheriida: giant pill millipedes) show only marginal size overlap.

On a lower taxonomic level, within genera, one would expect to find size constancy more widespread, and certainly there are genera containing species of roughly the same size: thus species of *Archispirostreptus* and *Triaenostreptus* (Spirostreptidae), are all huge millipedes. *Hypocambala* (Cambalopsidae) are all very small. *Pachyiulus* are all very large for Julidae, whereas *Enantiulus* are all very small. But there are also julid genera containing species of widely different sizes, e.g. *Cylindroiulus* (ENGHOFF 1982 a), *Nepalmatoiulus* (ENGHOFF 1987), and *Dolichoiulus* (ENGHOFF in press).

Body size is therefore only a weak indicator of a millipede species' ancestry and should be used with great caution as a taxonomic character above specific level. In this connection it deserves mention that LØTRUP et al. (1974) presented data in favour of the idea that body size is a character capable of evolving "in large steps", more specifically that body volume or weight may evolve in steps which are powers of two.

#### 3.2. Age:

That size depends on age is trivial. In the numerous juliformian species where growth is not terminated at the attainment of adulthood, the age-size correlation does, however, become relevant also to taxonomists. In particular in the Julida (but also in the Colobognatha), many species continue with adding new segments, and increasing their diameter, after having become mature. In some species, both sexes exhibit prolonged growth; in others, only the females do so (see READ 1989 for a review). That large size-differences obtain in certain species has been recognized for a long time. Thus, VERHOEFF (1928/32: 62) recorded ranges of variation of 15 - 22 (diplo)segments in adult males of three species of Julids. In two of these, a number of varieties or forms were named, solely based on the number of segments.

This does not mean that size differences should be neglected by taxonomists. In groups like Spirostreptidae (and Callipodida, Chordeumatida, and Polydesmida), where growth terminates at maturity, the number of segments is a potentially good taxonomic character, as is the body diameter. In groups where addition of segments, but not moulting with size increment, terminates at maturity (hemianamorphosis, e.g. pill millipedes, possibly some Rhinocricidae), number of segments, but not body diameter, is a reliable character.

But where both number of segments and diameter continue to grow during maturity, neither is, by itself, of much taxonomic value. Consider for instance Figure 3: males of *Acipes atlanticus* ATTEMPS, 1937, and *A. serratus* ENGHOFF, 1983, overlap widely both in number of segments and in body diameter, but when segment number and diameter are combined, the overlap becomes almost negligible. ENGHOFF (1987) used size, expressed as "number of segments/diameter" relationships, as a taxonomic character in the *Nepalmatoiulus crassus*-group (Julidae).

In some Julida, a third dimension can be added to size scattergrams, namely the actual stadium number, determined by means of the ocular field method (e.g., SAHLI 1969) or by other means. In such cases the stadium number can be entered on a segment number/diameter diagram (Fig. 4) and species may be separated which show overlap on segment number/diameter scattergrams but where a given size is attained in different stadia.

Even though some millipedes seem to grow indefinitely, the correlation between number of segments and diameter is not a simple, linear one: specimens with very high segment numbers tend to be "too slender" (e.g., males of *A. atlanticus* with > 54 podous segments, Figs 2 - 3). This indicates a "maximum limit" to body diameter in a given species. Possible causes of such a limit are discussed below (habitat, coexistence).

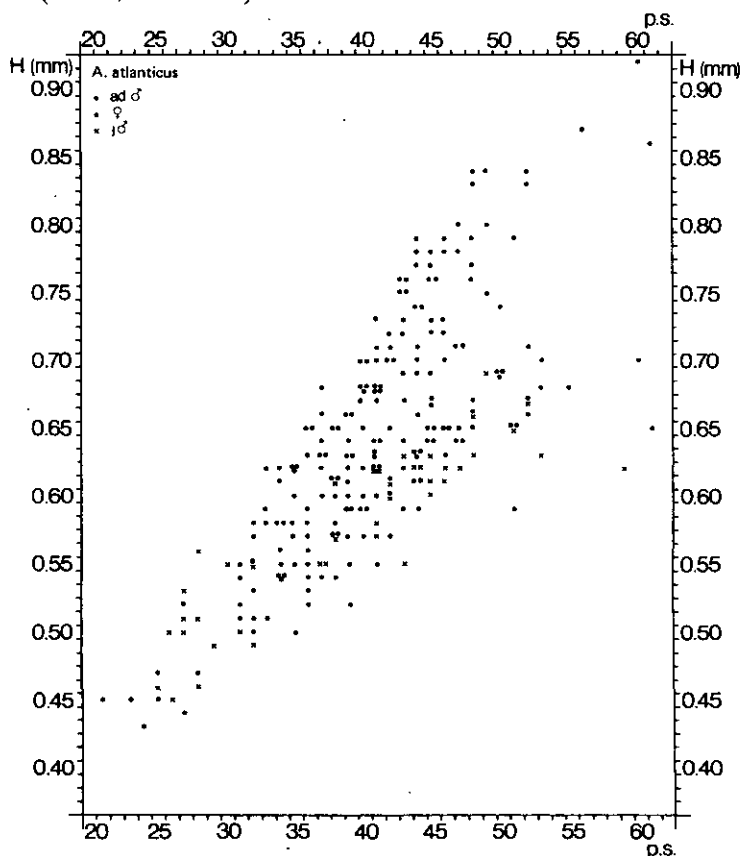


Fig. 2: Scattergram showing number of podous segments (p.s.) and vertical body diameter (H) in *Acipes atlanticus* ATTEMS, 1937 (Blaniulidae). From ENGHOFF (1983 b).

### 3.3. Sex:

Juliformian males are generally smaller than females. This difference has two components. First, in many species females live longer and undergo more moults, and hence attain more segments and a larger diameter (cf. READ 1989). Second, males are usually slenderer than females with the same number of segments. "Male slenderness" was studied in Maderian species of the julid genus *Cylindroiulus* by ENGHOFF (1982 a), who observed that immature males generally had larger diameters than mature males in the same stadium and with the same number of segments. Such a difference does not exist in females. This suggests that at the onset of maturity, males "suddenly" become thinner, which may help to explain why males usually have relatively longer legs, and relatively longer segments, than females.

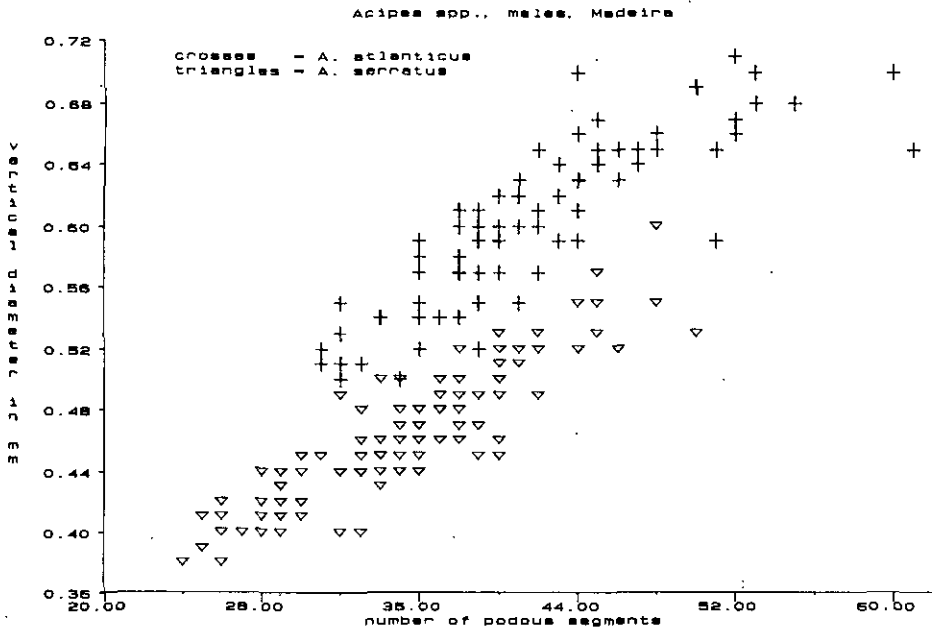


Fig. 3: Scattergram showing number of podous segments and vertical body diameter in males of two coexisting species of the blaniulid genus *Acipes* (*A. atlanticus* and *A. serratus* ENGHOFF, 1983) from Madeira. Based on ENGHOFF (1983 b).

### 3.4. Food:

That amount and quality of available food influences an animal's size is logical. BERNES & KEETON (1968 a, b) demonstrated this in an experiment with *Narceus annularis* (RAFIN-ESQUE, 1820) (Spirobolida): Semi-starved juveniles grow less than well-fed ones in terms of body length and diameter, and add fewer segments during anamorphosis. Concerning number of segments, *N. annularis* seems to possess a mechanism compensating for the lesser increment during early anamorphosis: later juvenile stadia of semi-starved *N. annularis* actually add more segments per moult than well-fed ones; also the semi-starved animals tend to extend their ontogenesis by adding one anamorphic stadium compared with their well-fed relatives.

BAKER (1985) studied distribution, abundance and size of the julid *Ommatoiulus moreleti* (LUCAS, 1860) in Australia. *O. moreleti* has been introduced in Australia where it is a considerable pest and is obviously in a stage of range-expansion. BAKER found correlations between the time elapsed since invasion and body size (both number of segments and diameter) in stadium 9 females and males: the more recently a site had been invaded, the larger the millipedes. The greatest abundances of *O. moreleti* were found in relatively recently invaded sites. These relationships were explained as possibly due to food shortage: when a site is invaded, population density is initially low, food is plentiful, and specimens grow large. When the population grows, food becomes limiting, specimens grow less, and the population density eventually declines. In accordance with this pattern, BAKER & BAEZ (1989) found an inverse relationship between population density and body size of *O. moreleti* in Australia, Portugal (natural distribution area of the species), and Madeira.

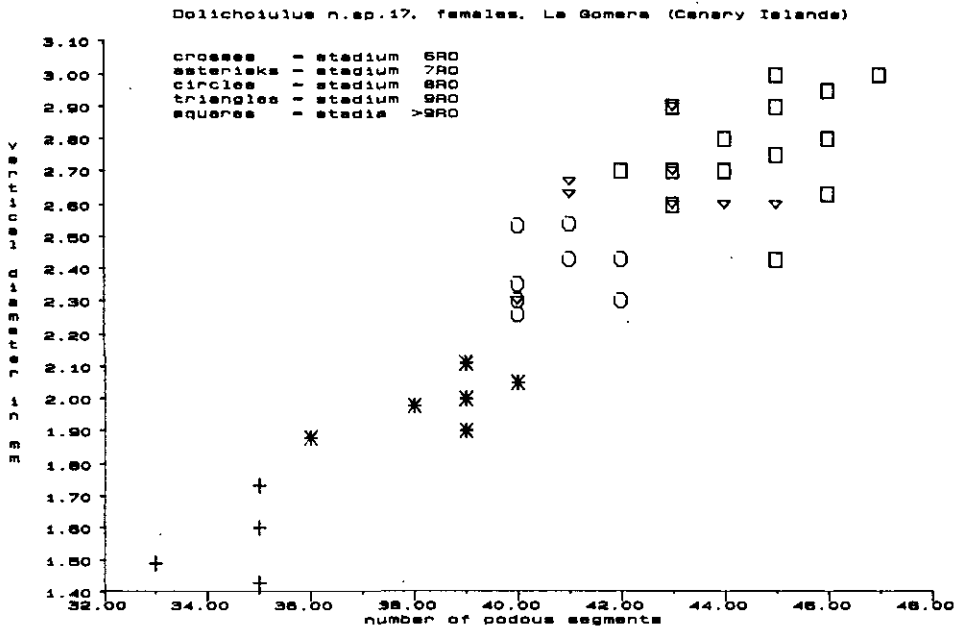


Fig. 4: Scattergram showing number of podous segments, vertical body diameter, and stadium number in females of an undescribed species of the julid genus *Dolichoium* from La Gomera (Canary Islands).

### 3.5. Latitude:

The general trend for terrestrial invertebrates to be larger in the tropics also holds for millipedes. Among Juliformia, the huge species of Spirostreptidae, Harpagophoridae, Rhinocricidae, and Pachybolidae, all occur at low latitudes. In Europe, the largest julids (*Pachyiulus* spp., up to 10 cm long) only occur in the south. Central and northern European species seldom exceed 3 cm. The northernmost European juliformian is the minute blaniulid *Proteroiulus fuscus* (AMSTEIN, 1857) (KIME 1990).

### 3.6. Altitude:

SAHLI (1969) showed that the julid *Tachypodoiulus niger* (LEACH, 1815) [= *albipes* (C.L. KOCH, 1838)] may grow through more stadia, and hence attain more segments, at high altitudes than at lower ones. Similarly, BAKER & BAEZ (1989) found that *Ommatoiulus moreleti* is larger at high altitudes than at lower ones on Tenerife (Canary Islands). They attributed this difference to the inverse relationship between population density and body size (see above), the millipedes being generally scarcer at high altitude.

The opposite correlation was recorded for the julid *Leptoiulus simplex* (VERHOEFF, 1894), by VERHOEFF (1926/32: 63): purely high alpine subspecies are shorter than the medium to high alpine ssp. *glacialis*.

### 3.7. Habitat:

Some correlations between millipedes' habitats and their sizes are evident. For example, juliformian millipedes found under relatively fresh bark are generally very small. In Central Europe, this habitat is occupied by the nemasomatid *Nemasoma varicorne* C.L. KOCH, 1847, and the blan-

iulid *Proteroiulus fuscus* (AM STEIN, 1857). In the forests of the United States of America, these are replaced by *Orinisobates* spp. (Nemasomatidae) and the blaniulid *Virgoiulus minutus* (BRANDT, 1841). In northern Thailand I have collected the cambalopsid *Hypocambala helleri* SILVESTRI, 1897, in a similar habitat and was firmly convinced that I had found a nemasomatid, until the specimens could be studied microscopically. All these millipedes are minute, not exceeding 1 mm in diameter.

In the other end of the spectrum, millipedes inhabiting deserts are usually large, which gives them an advantage over smaller-bodied forms in preventing water loss (CRAWFORD 1979).

Juvenile millipedes generally are more secretive than adults, probably because of the size/desiccation-resistance correlation.

Cave millipedes are often larger than related epigeal forms (CAUSEY 1960, SHEAR 1969). This is in particular typical of the family Blaniulidae, where the constellation large troglobionts/small epigeans recurs in several genera (BRÖLEMANN 1923). In the small family Zosteractinidae, the epigeal species is smaller than the two cave-dwellers (ENGHOFF 1982 b).

In order to test whether size-habitat correlations have any significance one may look for observations indicating that a given millipede species, when not subjected to the habitat factor hypothesized to influence its size, will attain a different size. The only available evidence of this kind concerns the spirostreptid *Archispirostreptus tumuliporus judaicus* (ATTEMPS, 1927) studied by CRAWFORD et al. (1987). In this species, specimens from an arid locality tend to have more segments and a larger diameter than specimens of the same sex and in the same stadium from a mesic locality: in CRAWFORD et al.'s Tables 4 - 7, there are 12 instances of a difference in segment number, all indicating more segments in specimens from the arid locality. And 10 out of 12 differences indicate a larger diameter at the arid site. This indicates that aridity is correlated with large size in *A. tumuliporus judaicus*.

Still, such data cannot alone answer the question whether *A. tumuliporus judaicus* is large because it can live in a desert, or whether it can do so because it is large. And analogously: Do *Nemasoma varicorne* and *Proteroiulus fuscus* live under bark because they are small, or are they small because they live under bark?

We can make educated guesses by looking at the ancestry of the species in question: *P. fuscus* is a member of a family (Blaniulidae) where all species are minute, except a few cavernicoles (BRÖLEMANN 1923), and where far from all species are bark-dwellers. It is thus reasonable to assume that small size preceded bark-dwelling in the course of evolution of the Blaniulidae. The same argument may apply to the Nemasomatidae, where all species are small as well (ENGHOFF 1985), but here the bark-dwelling habitat is relatively more widespread.

The case of the desert millipedes is more difficult. Desert millipedes mostly belong to the family Spirostreptidae which includes some of the World's largest millipedes, but also relatively minute forms of about 1 mm diameter (KRABBE 1982).

### 3.8. Size and Coexistence:

Whether animals' sizes are influenced by coexisting competitors or not is a hot topic in evolutionary ecology. In particular it has been discussed whether there is a constant size ratio between coexisting, otherwise similar competitors. See SIMBERLOFF & BOECKLEN (1981) for a critical review.

Many of the alleged size-coexistence relationships suffer from the lack of testability: one may have noticed that two or more coexisting species are of different sizes, but data on size of the same species in the absence of competitors is lacking. Such is the case with the few cases hitherto reported from millipedes.

The first author to notice a size-difference between coexisting, closely related millipede species was VERHOEFF (1928) who found that whenever two species of *Leptoiulus* (Julidae) were found together in the high Alps, there was always a marked size difference between the two.

Size-differences between coexisting juliformians were also found by ENGHOFF (1983 a, b) in endemic Madeiran species of the genera *Cylindroiulus* (Julidae) and *Acipes* (Blaniulidae). Especially in Madeiran *Cylindroiulus*, many species often occur in the same locality. They then tend to occupy different microhabitats, but sometimes two or more species share the same microhabitat, and then they are sometimes (but not always) of different sizes (diameter). On one locality (Faja da Nogueira), for instance the microhabitat "logs" was occupied by the species listed in Tab. 1. These five species show only marginal size overlap (although juveniles and the generally thicker females of course will blur the distinction) and thus appear to constitute a nice example of "coexisting species being of different sizes".

Table 1: Dominating endemic juliformian millipedes from logs in laurel forest at Faja de Nogueira, Madeira (data from ENGHOFF 1983 a, b).

Species	diameter of adult males
<i>Cylindroiulus gemellus</i> ENGHOFF, 1982	1,3 - 1,8 mm
<i>Cylindroiulus infernalis</i> LOHMANDER, 1955	0,9 - 1,3 mm
<i>Cylindroiulus kapp</i> ENGHOFF, 1982	0,8 mm
<i>Acipes atlanticus</i> ATTEMS, 1937	0,5 - 0,7 mm
<i>Acipes serratus</i> ENGHOFF, 1983	0,4 - 0,6 mm

It deserves notice that the size differentiation in Madeiran logs transcends taxonomic borderlines: the smallest *Cylindroiulus* is larger than the largest *Acipes* (*Acipes* belongs to the generally slender blaniulid stock, cf. above).

Some other microhabitats in the Madeiran laurel forest also contain *Cylindroiulus*-species of dissimilar size, viz., soil and soil/litter interface (Tables 2 and 3). Some microhabitats, however, are dominated by species of similar size, viz. "on living trees" and "under moss on stones", where the dominating species are *Cylindroiulus lundbladi* LOHMANDER, 1955 (diameter of adult males 1,6 - 1,9 mm) and *C. hirticauda* ENGHOFF, 1982 (1,6 - 2,0 mm).

Table 2: Dominating endemic juliformian millipedes from soil in laurel forest at Faja de Nogueira, Madeira (data from ENGHOFF 1983 a).

Species	diameter of adult males
<i>Cylindroiulus gemellus</i> ENGHOFF, 1982	1,3 - 1,8 mm
<i>Cylindroiulus pallidior</i> ENGHOFF, 1982	1,1 - 1,2 mm
<i>Cylindroiulus rabacalensis</i> LOHMANDER, 1955	0,8 - 1,0 mm

Table 3: Dominating endemic juliformian millipedes from the soil/litter interface in laurel forest at Faja da Nogueira, Madeira (data from ENGHOFF 1983 a, b).

Species	diameter of adult males
<i>Cylindroiulus laurissilvae</i> ENGHOFF, 1982	2,0 - 2,4 mm
<i>Cylindroiulus gemellus</i> ENGHOFF, 1982	1,3 - 1,8 mm
<i>Cylindroiulus rabacalensis</i> LOHMANDER, 1955	0,8 - 1,0 mm
<i>Acipes waldeni</i> ENGHOFF, 1983	0,5 - 0,6 mm



More generally KIME (1990) noted about European millipede communities: "Significant size differences exist between species in a community, and also between different stadia of a species. Perennial millipedes occupy at least two size niches at any one time since there are stadia born in two or more different years".

A unique size-sex-coexistence relationship was found by ENGHOFF (1987) in two strictly syntopic, litter-dwelling species of the julid genus *Nepalmatoiulus* living on the summit of the forest-clad mountain Doi Inthanon in N. Thailand: as in other julids, males are slenderer than females with the same number of segments (cf. above) but, whereas males of *N. brevipes* ENGHOFF, 1987, are slenderer than both sexes of *N. longipes* ENGHOFF, 1987, females of *N. brevipes* are thicker (Fig. 5).

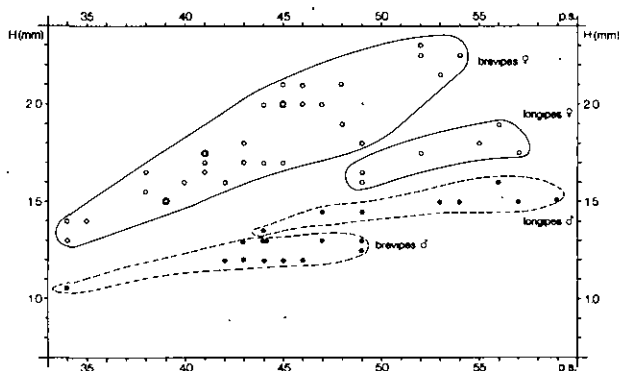


Fig. 5: Scattergram showing number of podous segments (p.s.) and vertical body diameter (H) in two coexisting species of the julid genus *Nepalmatoiulus* from Doi Inthanon, N. Thailand. Notice how both sexes of *N. longipes* ENGHOFF, 1987, are "squeezed" between males and females of *N. brevipes* ENGHOFF, 1987. From ENGHOFF (1987), modified.

Thus size differences between coexisting millipede species certainly exist, although not universally. But again, there is no directly comparative evidence (sizes of the species in the absence of competitors). In both *Cylindroiulus* and *Acipes* there is, however, the extra facet that the size differences observed probably have evolved in situ, since both species swarms probably have descended each from a single colonizing species.

#### 4. Conclusion:

The size of millipedes is governed by much the same factors that govern sizes of other organisms. It is important to stress that especially in groups like Julida and Colobognatha, where growth, including acquisition of new segments, often continues after the attainment of adulthood, size as a taxonomic character must be used with great caution. One aspect of millipede size: the slenderness of adult males, may at least in the Julidae be the result of a mechanism particular to this group.

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