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Abstract

Studying the diversification of body size in a taxon of parasites allows comparison of patterns of variation observed in the parasites with patterns found in free-living organisms. The distributions of body size of oxyurid nematodes (obligate parasites of vertebrates and invertebrates) are lognormally right-skewed, except for male oxyurids in invertebrates which show left-skewed distributions. In these parasitic forms, speciose genera do not have the smallest body sizes. Parasite body size is positively correlated with host body size, the largest hosts possessing the largest parasites. This trend is shown to occur within one monophyletic group of oxyurids, those of Old World primates. Comparative methods are used to take account of the effects of phylogeny. The use of multiple linear regression on distance matrices allows measurements of the contribution of phylogeny to the evolution of body size of parasites. Evolution of body size in female pinworms of Old World primates appears to be dependent only on the body size of their hosts. The tendency of parasite body size to increase with host body size is discussed in the light of the evolution of life-history traits.

Introduction

Variation in body size is one of the most biologically important and conspicuous traits of the metazoa, the size of an organism influencing almost all aspects of its biological and behavioural characteristics (Sibly and Calow 1986; Naganuma and Roughgarden 1990; Harvey and Pagel 1991; Kozłowski 1992; Stearns 1992; Charnov 1993). During phylogenesis, size traits of organisms show tremendous diversification, patterns of variation in size occurring both within and among related species. Understanding the processes and mechanisms which produce patterns of variation in body size in phylogenetically related species is one of the central questions in morphologically based studies of evolution (Hutchin-

son and MacArthur 1959; Lewin 1983; Maurer *et al.* 1992).

The apparent tendency of body size to increase over time in many taxonomic groups of organisms is known as Cope's rule (Stanley 1973). Different models have been proposed to explain this phenomenon and studies of natural or artificial selection indicate that microevolutionary processes operating through differential survival and reproduction could lead to an evolutionary change in the body size of a species. Larger individuals are often thought to accrue ecological advantages such as increased ability to compete for resources, or a selective advantage for larger body size in predator-prey relationships. Macroevolutionary explanations for variation in body size invoke differential extinction and speciation within and among lineages (Gould 1988). Stanley (1973) invokes a macroevolutionary hypothesis in testing Cope's rule, by arguing that the ancestor of a lineage may have a small body size and a simple increase of variance of the size through cladogenesis could explain the actual distribution of body sizes among phylogenetically related species.

May (1978) stated that small organisms are taxonomically more diverse than large organisms because small individuals are more capable of exploiting their environment in a fine-grained way. However, Dial and Marzluff (1988) showed that organisms with intermediate body sizes have greater taxonomic diversity. They failed to reject the hypothesis that "... through evolutionary time, extinction of taxa with extreme sizes and radiation of small taxa leads to a preponderance of small, but not the smallest, sized taxa."

Parasites provide an ideal model for testing ecological constraints, such as the size of the host, on the evolution of body size in a group of organisms (Harvey and Keymer 1991; Poulin 1995b). Changes in body size related to evolution towards parasitism follow diverse trends depending on the parasite group. For instance, increase in body size with switching towards parasitism is observed for nematodes (Kirchner *et al.* 1980) while decrease in body size occurs in isopods (Poulin 1995a).

Nematode parasites of the order Oxyurida have not

Key words: body size, host-parasite relationship, lognormally skewed distribution, nematodes, independent comparisons, Cope's rule.

yet been used in studies of evolution of body size. We consider this group of nematodes an excellent model for comparisons with free-living organisms because of the extremely intimate relationship that exists between the hosts and their parasites (Adamson 1989). Because of this, the body size of these parasitic nematodes may be strongly influenced by the body size of their hosts.

By analyzing the evolution of body size of parasites, we want to answer two primary questions: (1) What is the pattern of distribution of body sizes in a phylogenetic lineage? (*i.e.* what is the general pattern of morphological size-diversification, and are the smallest organisms the most diverse?) (2) Is the body size of parasites correlated with that of their hosts? To get a clear answer to this question, the influence of the phylogeny of the relation between body sizes of hosts and those of their parasites must be assessed.

Materials and methods

The data

A data base was assembled on 605 species of Oxyurida, from original descriptions of species and from the summary books of Skrjabin *et al.* (1960) and Leiber-sperger (1960). Information on egg size, female body size and male body size was complete for only 461 species (Table 1). Measurements of hosts (maximum length) were taken from Walker (1968), Pasteur and Bons (1959, 1960), and Dawling (1966), and also obtained from specialists of the Muséum d'Histoire Naturelle of Paris. Data on invertebrate hosts are often missing.

Table 1 Taxonomy of Oxyurida with numbers of genera and species in each family, host groups and mean body lengths of oxyuroid males and females. This taxonomy is based on Adamson (1989), Hugot (1988, 1990), Petter and Quentin (1975) and Poinar (1977)

Taxa of Oxyurida	Number of genera (number of species)	Host groups	Mean body length of female in (µm) (±SD and range)	Mean body length of male in (µm) (±SD and range)
Chitwoodliellidae	8 (14)	Insects, Diplopods	2917±1478 (1330-6980)	1087±382 (660-1790)
Hystriognathidae	9 (18)	Insects	2970±953 (1700-4790)	910±171 (720-1050)
Protrelloididae	4 (13)	Insects	5070±2143 (2620-10370)	759±506 (270-1730)
Pseudonymidae	4 (15)	Insects	3146±906 (1751-4675)	1226±201 (932-1500)
Thelastomatidae	28 (93)	Insects, Oligochaetes, Diplopods	3495±1759 (1335-14400)	1162±468 (410-2700)
Pharyngodonidae	23 (185)	Fishes, Amphibians, Reptiles, Aves, Rodents	4624±2120 (1900-23500)	2591±1138 (677-9600)
Oyuridae	4 (13)	Perissodactyls, Artiodactyls	13350±15516 (1500-90000)	6205±3667 (660-14200)
Heteroxynematidae	11 (50)	Aves, Rodents, Lagomorphs	6315-3650 (2220-21400)	2283±994 (1035-5700)
Citellinidae	5 (25)	Dermoptera, Marsupials	7276±2726 (3515-13400)	3731±1715 (1100-7000)
Trypanoxyuridae	5 (48)	Primates, Rodents	6315±3650 (2220-21400)	2283±994 (1035-5700)
Syphaciidae	16 (97)	Rodents, Lagomorphs	7594±6359 (1430-40000)	2864±2175 (880-13400)

Biology of the parasites

More than 600 species of the order Oxyurida have been described, representing 11 families parasitizing both invertebrates and vertebrates. Most are highly host-specific (Table 1).

Despite this great diversity in hosts, the life cycle remains identical in all oxyurid species. Adult worms inhabit the digestive tract of herbivorous or, more rarely, omnivorous hosts. In the generalised oxyurid life cycle, females produce eggs which exit the host with feces. In the external environment, embryonic development continues up to the second juvenile stage, the egg then becoming capable of infecting a new host. All oxyurids that have been studied have a direct life cycle; eggs hatch only after being ingested by a host and juveniles complete two more moults in the host digestive tract. These nematodes are characterised by a haplo-diploid mode of reproduction, as only recently discovered by Adamson (1989, 1990). Females are produced from fertilised eggs, while males develop from unfertilised ova. Males are smaller than females, and a correlation between haplo-diploidy and sexual dimorphism has been postulated by Adamson (1989).

Unfortunately, the biological characteristics and phylogenetic relationships of the oxyurids are not well known. Life cycles, with information on rate of maturation of females, have been described from fewer than ten species. Host-parasite coevolution using phylogenetic methods has been studied in only a handful of the Oxyurida (Brooks and Glen 1982; Hugot 1988, 1990). It is not possible to generalise about levels of cospeciation from these

few studies and more work in this area is needed. Cospeciation events may be frequent, as in the pinworm-primate (Brooks and Glen 1982; Brooks and McLennan 1993) and the pinworm-rodent assemblages (Hugot 1988, 1990).

Analysis

Because of the diversity of host taxa used by oxyurids, host length may be a poor comparative measure of host body size. Length may be related to mass in very different ways in different host groups (Peters 1983). However, body mass is very sensitive to environmental conditions in invertebrates (Hopkin and Read 1992; Kooijman 1993). It is also very difficult to obtain information on body mass of invertebrates, so we decided to use host length in our comparative analysis.

We used the methodology of Maurer *et al.* (1992) to address the question of selection favouring either small or large sizes in oxyurids. The lengths of male and female parasites were log-transformed (\ln) and the skewness of distributions was calculated. This coefficient is equal to zero for non-skewed (*i.e.* symmetrical) distributions. We tested for significant departures from zero using Student's *Mest* based upon the standard error of the coefficient of skewness (Sokal and Rohlf 1981). Skewness of (\ln body sizes) was calculated and tested for males and females among species and genera of oxyurids, from vertebrate and invertebrate hosts.

All data were \ln transformed (Harvey 1982). MA (major axis) regressions were performed. When neither dependent nor independent variables are controlled, model II regression (MA or RMA) should be applied to estimate the functional relationship between two variables, because the slope found by the ordinary least-squares method may be biased (Legendre and Legendre 1996). The MA method has no systematic bias according to Legendre and Legendre (1995). Since both variables in each regression are random (*i.e.* measured with error), both are in \ln scale, and we are interested in describing the functional relation between them, major axis regression (MA) was used (Pearson 1901; Jolicoeur and Mosimann 1968; Jolicoeur 1973; Sokal and Rohlf 1981). The regression line computed by this method is actually the first principal component of the scatter of points; 95% confidence intervals (CI) of the slope parameter were also computed, allowing testing of the null hypothesis that the slope of the relationship between the two variables is zero.

Evolution of body size in relation to host size was examined in the genus *Enterobius*, for which phylogenies are known (Brooks and Glen 1982; Brooks and McLennan 1993).

To address the question of whether the body size of parasites is correlated with the body size of their hosts, one has to take parasite phylogeny into account. An observed correlation between parasite and host sizes might be spurious, resulting from the fact that phylogenetically related species of parasites tend to infest hosts of about

the same size. In general, closely related species are more likely to exhibit similar development than distant species; this is a consequence of the "taxon-level effect" (Pagel and Harvey 1988). We are looking instead for a correlation between host and parasite body sizes that would result from a functional microevolutionary process by which parasites would have evolved larger body sizes in larger hosts. A number of "comparative methods" have recently been proposed to take this possibility into account, considering the phylogeny fixed and controlling for its effect in order to study the correlation among traits; they have been summarised by Harvey and Pagel (1991).

To take account of the effects of phylogeny we use the method of independent contrasts (Felsenstein 1985; see also Burt 1989). We use the CAIC program (Purvis and Rambaut 1994, 1995). Regressions performed on phylogenetically independent contrasts were forced through the origin.

In the present paper, we also use a multiple regression method on distance matrices. This method was recently proposed by Legendre *et al.* (1995) to "explain" matrices representing either plain distances, dendrograms or cladograms, using other matrices also representing plain distances, dendrograms or cladograms. The coefficient of determination of the multiple regression, as well as the partial regression coefficients, are tested for significance through permutation methods appropriate for each type of dependent matrix-variable. The regression method is thus naturally extended to the problem of controlling for the effect of a phylogeny in studying the correlation among traits.

1. The dependent variable, size of parasites, is transformed into a distance matrix Y by computing the "distance" among size values (absolute value of the difference, which is also equal to the Euclidean distance among values).
2. Similarly, the host size variable is turned into a "distance" matrix $X1$.
3. The parasite phylogeny is represented in the analysis by a matrix $X2$ of patristic distances among species; since no segment length estimations are available, patristic distances are computed as the number of segments along the evolutionary tree that separate two species.
4. A multiple regression is computed with Y as the dependent variable.
5. Regression coefficients are obtained for $X1$ and $X2$ and tested for significance using the method for simple dependent distance matrices of Legendre *et al.* (1995). Multiple regression coefficients are actually partial regression coefficients (Sokal and Rohlf 1981, p. 620). For instance, the regression coefficient of $X2$ in our equation describes the partial effect of parasite phylogeny on differences in parasite sizes, after controlling for the effect of differences in size of hosts.
6. Probabilities were computed after 999 random permutations of the distance matrix; the lowest attainable probability value is therefore 0.001. The values in both dis-

tance matrices were standardised before computing the regression, so that there is no intercept and the regression coefficients become standard regression coefficients.

A major advantage of this method over the comparative techniques is that the multiple regression on distance matrices provides an estimate of the contribution of the phylogeny to the structure of the dependent variable, as well as that of the independent variable to be tested. Other comparative techniques do not offer this benefit.

Results

Distribution of parasites among host groups

Representatives of five families of Oxyurida occur in invertebrates (insects, oligochaetes, and diplopods); our data represent 153 species and 53 genera (Table 1). Species of six families are parasites of vertebrates; 418 species of 64 genera are included in our data base.

Patterns of body size distribution of oxyurids

Small body sizes of parasitic nematodes are found in species occurring in invertebrates (Table 1). The largest body sizes occur in species of oxyurids found in the ungulates

(mammalian suborders Artiodactyla and Perissodactyla). The distribution of ln body size of female oxyurid species is statistically positively skewed, which means that there are more species with body size larger than the mode than expected in a symmetric distribution. An alternative but equally adequate description is that the mode is on the left of the mean body size value (Figure 1, Table 2). A similar pattern is found in males, except for those from invertebrate hosts, which have a negatively skewed distribution (mode larger than the mean). In the case of genera, the distribution of (log body size) is also positively skewed (Table 2); no difference was detected between host types.

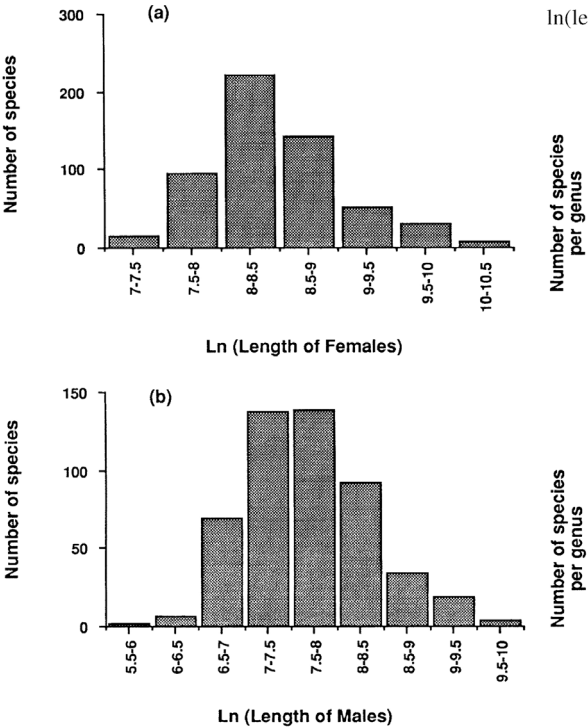
The most diverse genera of oxyurids, appreciated in terms of number of species, are not the smallest (Figure 2).

Importance of host body size

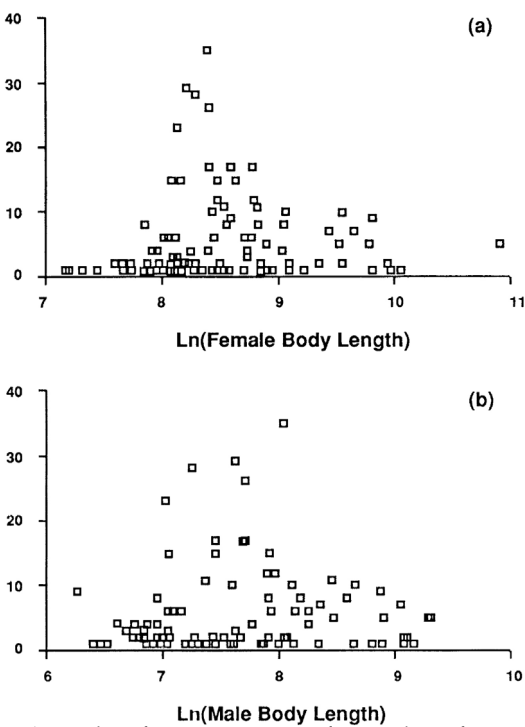
In this part of the analysis, we examine the relationship between the body sizes of the hosts and parasites. All data were logarithmically transformed (Figure 3).

Two MA regression equations were obtained. The first one links female parasite body size to host body size:

$$\ln(\text{length of female})=0.643 \ln(\text{length of host})+5.118$$



Figures 1a, b Ln body size (mm) distribution of oxyurid a females and b males. Both distributions are skewed towards species of large body size

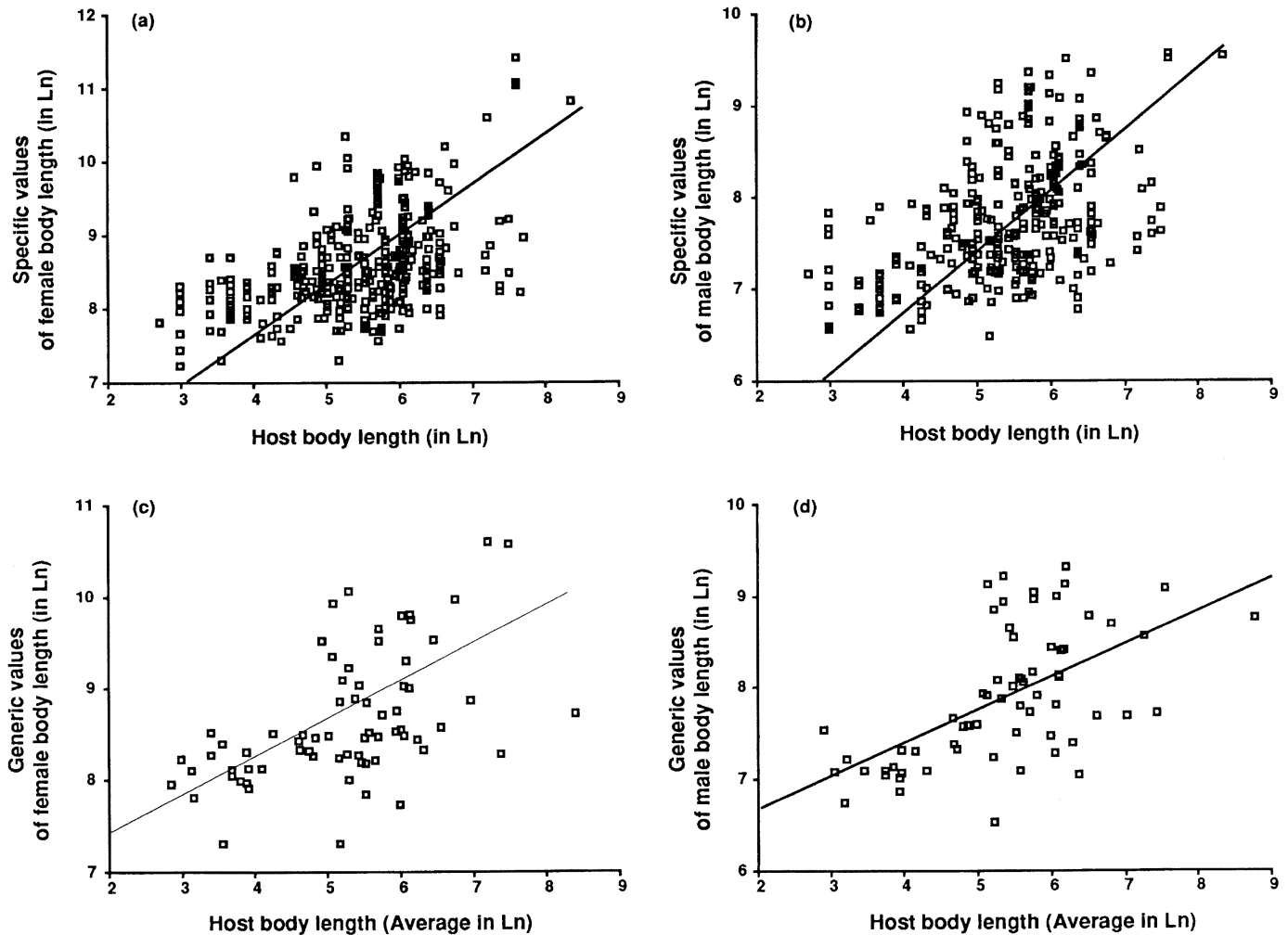


Figures 2a, b Number of species per genus of oxyurids as a function of average body size (ln size, mm) of species in each genus for a females, b males

Table 2 Skewness of ln length (size) of females and males among species and genera of oxyuroids

		<i>n</i>	Species skewness	SE	<i>n</i>	Genera skewness	SE
All hosts	Female	571	1.01*	0.10	114	0.85*	0.23
	Male	468	0.35*	0.11	97	0.57*	0.24
Invertebrate hosts	Female	153	0.46*	0.20	55	-0.15	0.32
	Male	107	-0.45*	0.23	42	0.12	0.37
Vertebrate hosts	Female	419	1.08*	0.12	38	0.05	0.38
	Male	364	0.57*	0.13	38	0.16	0.38

**P*>0.05, reject (H0: skewness not different from 0)



Figures 3a-d Relationships between \ln body length of hosts (mm) and specific values of **a** \ln body size of oxyurid females (mm) and **b** \ln body size of oxyurid males (mm). Relationships between generic values of **c** \ln body size of oxyurid females (mm) and **d** \ln body size of oxyurid males (mm), and average \ln body length of hosts (mm). The major axis (MA) regression lines are shown.

with 95% CI of slope=(0.584, 0.706). So, the slope differs significantly from zero. The second MA equation links male parasite body size to host body size:

$$\ln(\text{length of male}) = 0.684 \ln(\text{length of host}) + 4.072$$

with 95% CI of slope=(0.618, 0.756). The slope is significantly different from zero, but does not differ from the slope of the female-to-host body size relationship (0.643).

Similar relationships were found for values of parasite body size averaged per genus:

$$\ln(\text{average length of female}) = 0.406 \ln(\text{average length of host}) + 6.532$$

with 95% CI slope=(0.253, 0.578)

$$\ln(\text{average length of male}) = 0.462 \ln(\text{average length of host}) + 5.395$$

with 95% CI slope=(0.307, 0.638)

Thus, it appears that body size of parasites increases

significantly with host body size. Larger hosts have larger pinworm parasites. Similar trends found both in cross-species and cross-genus correlations to exclude a phylogenetic artefact.

Importance of host body size: the oxyurids of Old World primates

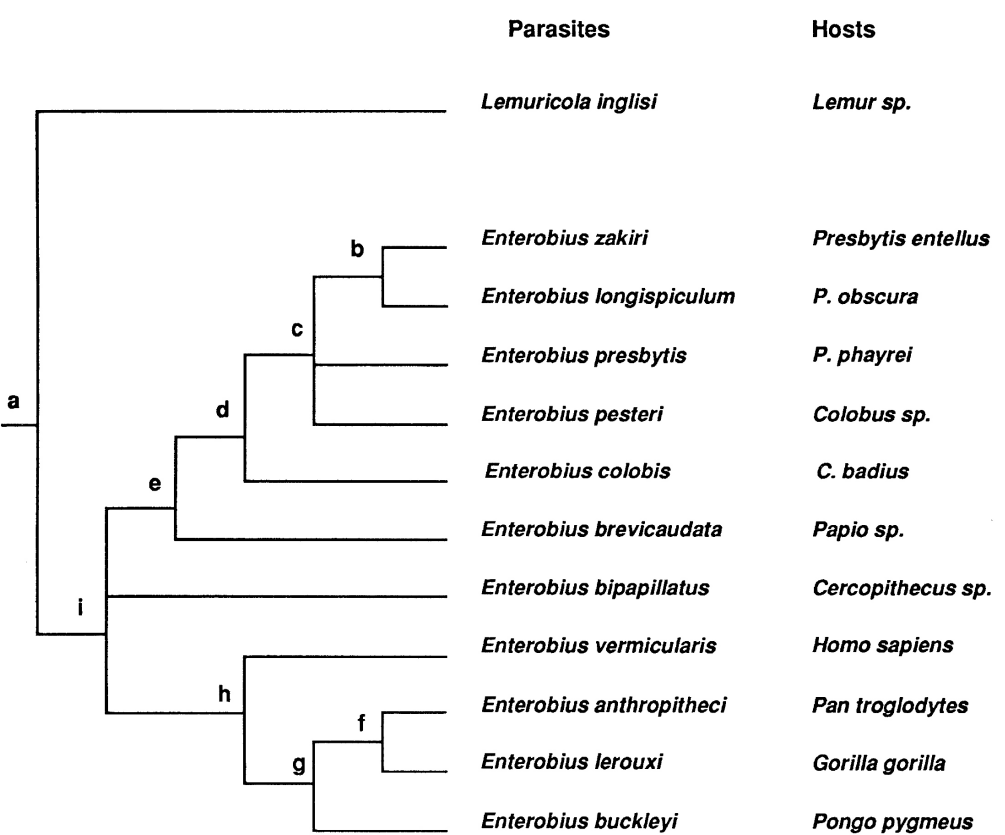
The hypothetical phylogeny of the oxyurids of Old World primates has been developed by Brooks and Glen (1982) and Brooks and McLennan (1993) (Figure 4).

The results of ordinary regressions performed on cross-species and independent contrasts of host and parasite body sizes are reported in Figure 5. Both regressions show significant increase of parasite body sizes with host body sizes.

We used the regression method on distance matrices to test the effect, on parasite body size, of both host body size (X_1) and parasite phylogeny () (Table 3). We found the following significant linear relation linking the matrix of distances among female parasite body sizes (Y) to the distance matrix among host body sizes (X_1):

distances among female parasite body sizes = 0.487 x distances among host body sizes.

Figure 4 Phylogeny of the oxyurids of Old World primates. Redrawn from Brooks and Glen (1982)



($R^2=0.238$, $P=0.031$). We are especially interested here in the significance of the relationship. The actual value of the regression parameter is of little interest; it would only be useful for prediction purposes. As for the functional relationship, the slope of the MA regression equation among distance matrices would be 1 since both matrix variables have been standardised prior to the calculations.

In the case of male parasites, we found the following multiple regression equation with all terms significant (Table 3):

$$\text{distances among male parasite body sizes} = 0.505 \times \text{distances among female parasite body sizes} - 0.317 \times \text{distances among host body sizes}$$

$$(R^2=0.203, P=0.024).$$

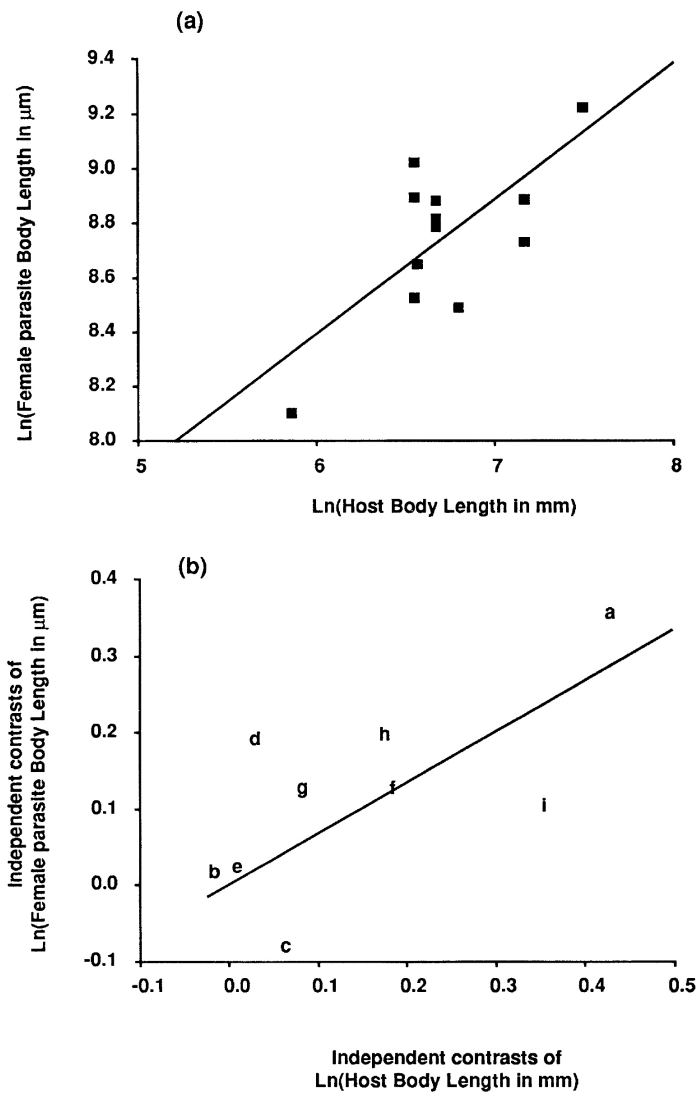
Discussion

Nematodes of the order Oxyurida include numerous species that infect a wide range of hosts, from invertebrates to vertebrates. No other groups of helminth parasites occur as sexually reproducing adults in such a wide diversity of hosts. The study of diversification of body size in this parasite group allows us to compare observed patterns in the parasites with patterns of variation in free-living organisms. Statistical bias is not completely excluded, because the nematode fauna of vertebrates is much better known than the fauna of invertebrates, but our large sample size (153 species of oxyurids in invertebrates) may strongly reduce it.

Body size distributions of oxyurid nematodes are log-normal and right-skewed. These distributions are observed both in vertebrate and invertebrate hosts, except for male oxyurids of invertebrates which show a left-skewed distribution (towards small body size). This pattern is similar to those exhibited by free-living nematodes which also show a lognormally right-skewed distribution of body sizes as pointed out by Kirchner *et al.* (1980).

Maurer *et al.* (1992) constructed a simulation model to test both micro- and macroevolutionary hypotheses about the evolution of body size. The first hypothesis explains the change of body size by differential adaptation of individuals to their environment. The macroevolutionary hypothesis deals with rapid body-size changes through phases of speciation. The simulation model of Maurer *et al.* (1992) clearly shows that lognormal right-skewed distributions of body size are not obtained only by macroevolutionary processes, *i.e.* by differential rates of extinction/survival of taxa within a lineage. The right-skewed distribution of body sizes of the Oxyurida, similar to those distributions found in mammals and birds, suggests that adaptive processes play a significant role.

Taxonomic diversity is appreciated by studying the distribution of species/genera relative to average body size. The distributions of species/genera observed both in vertebrate and invertebrate hosts are right-skewed. Parasite genera with the most species are not the smallest-sized taxa. Parasites which are believed to live in a relatively stable and predictable environment (according to Jennings and Calow 1975) show a pattern of body



Figures 5a, b The relationships between female parasite body sizes (ln) and host body size (ln). **a** The ordinary regression performed on cross-species comparisons gives: slope= 0.487 ± 0.155 ($df=11$, $P=0.009$) (shown in figure). **b** The regression performed on independent contrasts (OLS without intercept) gives: slope= 0.662 ± 0.159 ($df=8$, $P=0.003$) (shown in figure; letters refer to nodes of the phylogeny given in Figure 4)

size distribution comparable to that shown by free-living nematodes (Kirchner *et al.* 1980). This is interesting in itself because of the potential for testing hypothesis of body size of organisms correlated with habitat heterogeneity and the problems of scaling. This also highlights the fact that, contrary to Jennings and Calow's claim, parasites are exposed to a relatively large degree of environmental heterogeneity, both during their life cycles, and as populations living in discontinuous habitat (hosts).

We have shown a link between parasite and host body sizes. Parasite body size is positively correlated with host body size; larger hosts have larger parasites, and selection may be at work to maintain this pattern. This pattern was found by Harvey and Keymer (1991) in the case

Table 3 Backward elimination procedure of the distance matrix method for selecting an optimal subset of explanatory matrix-variables for the female and the male parasite body length (mm, ln) of Old World primates (Std. *b* the standard partial regression coefficient). All probabilities (*P*, one-tailed), are computed after 999 random matrix permutations of the dependent matrix-variable. At each step, the variable with the largest probability is eliminated if its probability is larger than the Bonferroni-corrected significance level ($\alpha'=0.05/\text{number of variables in the model at the given step}$)

Dependent matrix-variable	Step 1	Step 2
Independent matrix-variables	Std. <i>b</i> (<i>P</i>)	Std. <i>b</i> (<i>P</i>)
Female body size		
Host weight (g, ln)	0.442 (0.085)	0.487 (0.006)
Parasite phylogeny	0.094 (0.291)	
<i>R</i> ² (<i>P</i>)	0.244 (0.056)	0.238 (0.031)
Male body size		
Host weight (g, ln)	-0.317 (0.005)	-0.317 (0.005)
Parasite female body size	0.505 (0.006)	0.505 (0.006)
Phylogeny	0.047 (0.398)	
<i>R</i> ² (<i>P</i>)	0.204 (0.036)	0.203 (0.204)

of pocket gophers and their associated chewing lice and in the case of primates and their pinworms. In their study independent comparisons were obtained by assuming co-speciation between hosts and parasites. The method of Legendre *et al.* (1995) does not need this assumption.

We have found that if lateral transfers of a parasites occur from one host species to another, or parasites transfer vertically during speciation of hosts, any change in host body size has a correlated effect on parasite body size. A correlated increase of body size of female parasites with that of their hosts does not necessarily contradict Cope's rule. Indeed, we would emphasise here that nematode parasites of invertebrates started to diversify a long time before the evolution of parasites in vertebrates began (Adamson 1989).

Here we have also shown that slopes of MA regressions of parasite female body sizes on host body sizes are similar in a monophyletic group of oxyurids for which phylogeny is known, the oxyurids of Old World primates (0.913). These results are the same as those presented by Harvey and Keymer (1991) except that length is used here as a measure of host body size instead of mass. The phylogeny of parasites does not appear to play any role in female pinworms of Old World primates. The evolution of male body size is also independent of phylogeny.

The evolution of parasite life-history traits has not been widely investigated. Some studies have tried to explain the variation of life-history according to r-K theory (Esch *et al.* 1977) while others have emphasised the importance of trade-offs between fecundity and reproductive lifespan (Wharton 1986). The studies of Keymer *et al.* (1991) and Skorpung *et al.* (1991) investigate the selective pressures driving the evolution of life-history traits of parasitic nematodes. Morand (1996b) investigated the evolution of life-history traits in free-living, plant, insect and vertebrate parasite nematodes. The allometries of life-history traits with body size were calculated, in partic-

ular the allometry between size and fecundity (Morand 1996a, b). The prepatent period of parasites, or the maturation time in free-living nematodes, is correlated with body size (Morand 1996b). This indicates that delaying reproduction is associated with large body size. Because large body size is correlated with high fecundity, a fecundity advantage is thus associated with delaying maturity as pointed out by Skorping *et al.* (1991) and Keymer *et al.* (1991). A similar correlation between mortality rate and age at maturity (or prepatent period) is found in both free-living and parasitic nematodes (Morand 1996b). This suggests that the adult mortality rate might be the central factor that drives the evolution of parasite life-history traits. The maturation of the parasites within their hosts (prepatent period) occurs at the age that maximises lifetime reproductive success. Because larger hosts provide more energy and live longer, they can favour longer-lived parasites and thus can determine the parasites' adult body size, as pointed out by Harvey and Keymer (1991), and ultimately their lifetime reproductive output.

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