Evolutionary trends in body size of parasitic flatworms

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Evolutionary trends in body size have been identified within several lineages, but not all have followed Cope’s rule, which states that average body size within a taxon tends to increase over time. In organisms such as parasites, space constraints may have shaped the evolution of body sizes, favouring small-bodied taxa capable of exploiting new niches. Here, the average adult body sizes of families in three groups of parasitic flatworms, the Digenea and two clades of Monogenea (Monopisthocotylea and Polyopisthocotylea), are related to their clade rank. Clade rank reflects the number of branching events, and thus the total path length, between an extant family and the root of the phylogenetic tree. Among families of Digenea, all of which are endoparasites of vertebrates, there was no trend in body size evolution. In contrast, the Monopisthocotylea and Polyopisthocotylea, which are (with the exception of Polystomatidae and Sphyranuridae) ectoparasites of fish, revealed significant negative relationships between family body size and clade rank, suggesting an evolutionary trend of decreasing size. In addition, an analysis of body size distributions in monogenean families also provides support, albeit weak, for this trend. From an ancestor parasitic on the skin of fishes, monogeneans have diversified by colonizing other microhabitats on their hosts, including such space-limited sites as the gaps between secondary gill lamellae. Using a conservative likelihood ratio test, however, a random walk, or null model of evolution could not be discarded in favour of the directional trends mentioned above. Nevertheless, these results suggest that body size has taken different evolutionary paths in endo- and ectoparasitic flatworms. © 2005 The Linnean Society of London, Biological Journal of the Linnean Society, 2005, 85, 181–189.


INTRODUCTION

Body size is the single most important characteristic of an animal, as it relates strongly to life-history traits, metabolic rate, population density and geographical distribution (see Peters, 1983; Schmidt-Nielsen, 1984; Brown, 1995). Evolutionary trends in body size indicate that average sizes have increased over evolutionary time in several distinct animal taxa, a phenomenon known as Cope’s rule. Fossil evidence from taxa as diverse as foraminiferaans, molluscs and mammals generally supports Cope’s rule (Stanley, 1973; Bonner, 1988; Arnold, Kelly & Parker, 1995; Alroy, 1998). The rule is not universal, however, and sufficient exceptions exist to suggest that body size may follow different evolutionary trajectories in different groups of organisms (Jablonski, 1997; Knouft & Page, 2003). Not only is the direction of evolutionary trends variable among taxa, but the nature of the underlying factors can also vary from selection-driven to passive or random processes (McShea, 1994, 1998; Wagner, 1996; Alroy, 2000).

In certain groups of organisms, evolutionary decreases in body size are expected a priori. For instance, lineages making an evolutionary transition from a free-living to a parasitic mode of life are generally assumed to evolve smaller body sizes (Price, 1980; Hanken & Wake, 1993). The comparative evidence, however, is equivocal. Among extant members of groups ranging from nematodes to crustaceans, parasitic lineages are sometimes larger, sometimes smaller than their closest free-living relatives (Kirchner, Anderson & Ingham, 1980; Poulin & Hamilton, 1995; Poulin, 1995a, b).

What remains unclear is what happens after the transition to parasitism. Given that parasites living in or on other animals normally face more severe space constraints than most free-living animals, what have been the evolutionary trends in their body sizes following the adoption of a parasitic mode of life? If the
first parasites in a lineage exploited the most acces-
sible organs of their hosts (gastrointestinal tract for
endoparasites, skin for ectoparasites), what happened
to their body sizes when some groups colonized new
microhabitats where space constraints may have been
more intense (e.g. gill lamellae for fish ectoparasites)?

The frequency distribution of body sizes, even when
the latter are log-transformed, tends to be right-
skewed in most higher taxa (e.g. Van Valen, 1973; Dial & Marzluff, 1988; Blackburn & Gaston, 1994; Brown, 1995), and the same is true of all major parasitic taxa
(Poulin & Morand, 1997). This could be taken as evi-
dence that, in parasites and free-living animals in
general, small-bodied taxa proliferate at higher rates
than related but larger-bodied taxa. Proper compara-
tive tests of this idea, however, indicate that body size
is not a universal determinant of rates of diversifica-
tion in free-living animals (Gardezi & da Silva, 1999;
Orme et al., 2002b; Orme, Isaac & Purvis, 2002a) and
in certain parasite groups (Poulin, 2002).

In higher taxa experiencing directional evolutionary
trends in body size, one might expect that the skew-
ness of body sizes would differ between species issued
from basal phylogenetic branches and those from more
derived lineages, as evolution would need time to
shape the body size distributions of new lineages. To
test for evolutionary trends in body size within higher
taxa of parasites, one would need to determine
whether the size of recent taxa is consistently differ-
ent from that of ancestral taxa. Such a test can be
problematic because there is no adequate fossil record
of extinct parasite taxa; only extant taxa are available
for analyses of evolutionary trends.

Using phylogenetic information, however, it is pos-
sible to identify basal and derived taxa (i.e. taxa that
have originated at different distances from the base of
the tree; see Pagel, 1997, 1999, 2002; Knouft & Page,
2003). Although this still does not provide information
on the characteristics of extinct taxa, the body sizes of
extant taxa give an indication of how ancient and
recent branches in the same phylogenetic tree have
evolved since branching out.

In this paper, I examine evolutionary trends in body
size of basal and derived families in the Monogenea
and Digenea, groups of flatworms belonging to the
same phylum (Platyhelminthes). This also makes pos-
sible a contrast between monogeneans, which are, for
the most part, ectoparasites of aquatic vertebrates,
and digeneans, which are endoparasites of verte-
brates. A priori, I expected a tendency for body size to
decrease over evolutionary time as more derived
groups invaded smaller microhabitats (e.g. gill lamel-
lae for monogeneans, blood vessels for digeneans,
etc.).

I also examine how body size distributions vary
among families, expecting stronger right-skewed dis-
tributions (i.e. biased toward small body sizes) in the
more basal families (i.e. lineages that have had a
longer evolutionary history). The present analyses are
the first to make use of large data sets, combined with
recent and well-supported phylogenies, to uncover
phylogenetically informative statistical trends in the
evolution of body size in parasitic organisms.

METHODS

Data on monogenean body sizes used here are the
same as those previously compiled (Poulin, 2002) from
earlier monographs. Body size was taken as total body
length, as most monogenean taxa have slender bodies
that are much longer than they are wide. Average
body lengths were first obtained for each genus by
averaging species values, and family values by aver-
aging generic values. The phylogeny used here was the
complete tree of monogenean families proposed by
Boeger & Kritsky (1997, 2001). Although based on
morphological data, it is generally very well supported
by molecular evidence (Olson & Littlewood, 2002).
Several molecular analyses have recently cast doubt
on the monophyly of the Monogenea (Mollaret et al.,
1997; Justine, 1998; Littlewood, Rohde & Clough,
1999). Because of the strong possibility that they are
paraphyletic, I here treat the two major branches
of monogeneans, the Monopisthocotylea and the
Polyopisthocotylea, as separate clades.

Data on digenean body sizes have been taken from
the appendix in Poulin (1997); these were compiled
from extensive searches through the literature. Body
size is measured as the product of adult body length
and width; given the wide range of shapes among
digeneans, from long and thin to almost circular, this
proved a better index of body size than simple length.
Average family values were obtained as for mono-
ogeneans. The digenean phylogeny used here was the
comprehensive molecular phylogeny proposed by
Olson et al. (2003).

All data on body sizes were log-transformed prior to
analysis. Evolutionary trends were examined sepa-
rately within each of the three groups of parasites
(Monopisthocotylea, Polyopisthocotylea and Digenea)
using a generalized least squares regression (GLS).
This allows one to determine whether body size corre-
lates with clade rank among families within a group
rank is not equivalent to taxonomic rank; rather, it is
the number of branching or speciation events between
an extant family and the root of a phylogenetic tree,
the root being the bifurcation from which all taxa in
the group have descended (Norell & Novacek, 1992;
Knouft & Page, 2003). It quantifies the evolutionary
position of a family within a clade, or the total path
length from the root of the tree to a given family. Basal
families are taxa with the lowest rank, while derived families have the highest rank.

Although data on body size were not available for all families in the monogenean and digenean phylogenies, all families were included in the computations of clade ranks and in the GLS model in order to obtain accurate phylogenetic information. Average body size for each family is predicted from the GLS regression of body size on clade rank (i.e. the distance from the root of the phylogeny to the family; Pagel, 1997, 1999, 2002; Knouft & Page, 2003). In this directional model of evolution, the slope defines the phylogenetically correct slope of the line relating clade rank to log-transformed family body size (Pagel, 1997, 1999, 2002; Knouft & Page, 2003). Information on branch length was not available, and all branches within a clade were set equal; this places a constraint on the evolutionary model, where most of the divergence in body size between sister taxa must be assumed to take place at, and not between, speciation events.

A likelihood-ratio (LR) test statistic was used to assess the probability that the GLS model was a better predictor of body size evolution within a clade than a null, or random walk, model in which the slope equals zero. In the test, $LR = -2 \log (H_0/H_1)$, where $H_0$ is the likelihood associated with the null hypothesis and $H_1$ is the likelihood associated with the directional hypothesis (Pagel, 1997, 1999). The significance of the test is determined by comparing LR to a Chi-square distribution, the standard coefficient of skewness, $g_1$, was computed (Sokal & Rohlf, 1995). This coefficient is scaled to equal zero in symmetrical, non-skewed distributions; negative values indicate a left-skew and positive values a right-skew (i.e. a distribution mode shifted toward larger and smaller body sizes within the range, respectively). Because values of $g_1$ co-vary with mean body size ($P = 0.004$ in this analysis), they were corrected for body size by taking the residuals of the regression of $g_1$ against mean body size across all family values; these residuals were then correlated with clade rank.

**RESULTS**

Data on body sizes were available for 13 families of Monopisthocotylea, 26 families of Polyopisthocotylea, and 53 families of Digenea. These numbers represent, respectively, 65, 81 and 69% of the families in the comprehensive phylogenies of these higher taxa used in this study. There was no difference between the clade ranks of families included in the analysis and those of families for which no body size data were available, in any of the three higher taxa (Mann–Whitney U-tests, all $P > 0.21$).

Among monogeneans, the body sizes of Monopisthocotylea were smaller on average than those of Polyopisthocotylea (Fig. 1). At the level of mean family body sizes, a right-skew is not clearly evident in these two taxa, because the influence of a few species-rich families with small body sizes is negated. Among digeneans, however, the right-skew is apparent among family mean body sizes (Fig. 1).

In all three parasitic taxa, many families with relatively large average body sizes tend to be basal (i.e. they have a low clade rank), whereas many families with relatively small sizes tend to be more derived (Fig. 2). This resulted in negative slopes in the GLS regressions (Table 1). In the Monopisthocotylea, the regression is actually significant ($r^2 = 0.531$, $P = 0.0047$; see Fig. 2). However, using the more conservative LR test, the trend between body size and clade rank is not significant in any of the three higher taxa (Table 1).

If two families that do not exploit fish hosts (Polystomatidae and Sphyranuridae, two points in the bottom left corner of the figure; see Discussion) are excluded from the analysis of the Polyopisthocotylea, the regression becomes significantly negative ($\beta = -0.777$, $r^2 = 0.264$, $P = 0.0102$; see Fig. 2), and the LR test also comes close ($P = 0.066$) to indicating that there has been a significant evolutionary decrease in body size among the families that exploit fish hosts. Still, the random walk model cannot be rejected in any of the three groups, due to the fact that the directional model of evolution is not explaining significantly more of the variance in average family body sizes.

Except for significantly right-skewed body size distributions in the families Dactylogyridae and Gyrodactylidae (two-tailed t-tests, both $P < 0.001$), there were few strong skew values for other monogenean families (Table 2). There was a weak general tendency for skewness of body sizes within a family to go from right to left (i.e. from positive to negative values) with increasing clade rank (Fig. 3). This was true for both Monopisthocotylea ($r = -0.753$, $N = 5$, $P = 0.142$) and Polyopisthocotylea ($r = -0.613$, $N = 8$, $P = 0.106$), as well as for all monogenean families pooled together ($r = -0.677$, $N = 13$, $P = 0.011$), although the fact that few families could be included limited the power of the analyses. Still, the more derived families tend not to show the typical right-skewed body size distributions commonly found in most taxa.
DISCUSSION

Every lineage of parasites has diversified from a single ancestor, with different taxa within the same lineage colonizing and adapting to slightly different micro-habitats within the host. The hosts themselves have changed over evolutionary time, with extinction and speciation causing several turnovers of available host species. It is likely, however, that the internal and external structures that provide habitats for parasites have remain more or less constant within any higher host taxa.

Adult monogeneans and digeneans live in or on vertebrates. While host species come and go, their
internal anatomy probably remains broadly the same, at least on the scale that matters to parasites. The same is probably true of the external structures of fish (skin, fins, gills) to which monogeneans attach themselves. The digestive system and external surfaces of extant fishes are probably not much different from those of fish that lived several million years ago. From the parasites’ perspective, the host landscape has probably remained roughly constant during much of their evolution. It is the colonization of new microhabitats within the host paralleling the diversification of parasites that must have shaped the evolution of body sizes, since nutrient and space availability may be key determinants of optimal size.

The present analyses suggest that there has been no trend in the evolution of body sizes in digenean parasites. In the two clades of monogeneans, mean family body size covaried significantly and negatively with clade rank, but this trend could not be distinguished from a random walk process. The cautious conclusion is therefore that the most derived taxa are not necessarily smaller-bodied than the more basal ones.

Inferring evolutionary trends based solely on data from extant species is not without problems. Most phylogenetic methods used to reconstruct ancestral phenotypes make assumptions that are likely to be violated in many cases (see Cunningham, Omland & Oakley, 1998; Oakley & Cunningham, 2000). Only fossil evidence from a direct ancestor can allow unambiguous interpretation of evolutionary trends. The methods used here, based on the identification of basal and derived taxa in a phylogeny, provide one way of obtaining a rough idea of the evolutionary direction taken by these lineages since branching out (Pagel, 1997, 1999, 2002; Knouft & Page, 2003).

### Table 1. Results of the analyses of the relationship between mean family body size (log-transformed) and clade rank within three higher taxa of parasitic Platyhelminthes

<table>
<thead>
<tr>
<th>Taxon</th>
<th>No. families</th>
<th>Mean no. species per familyσ</th>
<th>α (SE)</th>
<th>β (SE)</th>
<th>P†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monogenea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monopisthocotylea</td>
<td>13</td>
<td>67.9</td>
<td>0.755 (0.273)</td>
<td>-0.101 (0.063)</td>
<td>0.1422</td>
</tr>
<tr>
<td>Polyopisthocotylea</td>
<td>26</td>
<td>16.2</td>
<td>0.980 (0.198)</td>
<td>-0.055 (0.048)</td>
<td>0.2460</td>
</tr>
<tr>
<td>Digenea</td>
<td>53</td>
<td>14.3</td>
<td>0.780 (0.235)</td>
<td>-0.017 (0.019)</td>
<td>0.3593</td>
</tr>
</tbody>
</table>

σNumber of species used to measure body size, not actual species diversity.
†α is the Y-axis intercept and β the phylogenetically correct slope of the regression of log family body size on clade rank from the directional model of evolution; P is from the likelihood ratio test based on the difference between the likelihoods of the directional and random walk models.

### Table 2. Skewness of species body size distributions in 13 monogenean families

<table>
<thead>
<tr>
<th>Family</th>
<th>No. species</th>
<th>Size range (mm)</th>
<th>Clade rank</th>
<th>Skewness (g1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monopisthocotylea</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capsalidae</td>
<td>51</td>
<td>0.90–22.50</td>
<td>3</td>
<td>-0.072</td>
</tr>
<tr>
<td>Dactylogyridae</td>
<td>462</td>
<td>0.13–4.97</td>
<td>9</td>
<td>0.792</td>
</tr>
<tr>
<td>Diplectanidae</td>
<td>51</td>
<td>0.32–1.66</td>
<td>10</td>
<td>0.187</td>
</tr>
<tr>
<td>Gyrodactylidae</td>
<td>132</td>
<td>0.20–3.30</td>
<td>6</td>
<td>1.110</td>
</tr>
<tr>
<td>Monocotylidae</td>
<td>34</td>
<td>0.48–12.00</td>
<td>2</td>
<td>0.385</td>
</tr>
<tr>
<td>Polyopisthocotylea</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Axinidae</td>
<td>29</td>
<td>1.60–8.10</td>
<td>8</td>
<td>-0.535</td>
</tr>
<tr>
<td>Diclidophoridae</td>
<td>20</td>
<td>0.99–10.00</td>
<td>8</td>
<td>-0.800</td>
</tr>
<tr>
<td>Discocotylidae</td>
<td>20</td>
<td>1.36–19.00</td>
<td>6</td>
<td>0.046</td>
</tr>
<tr>
<td>Gastrocotylidae</td>
<td>25</td>
<td>1.40–12.00</td>
<td>9</td>
<td>-0.084</td>
</tr>
<tr>
<td>Hexabothriidae</td>
<td>27</td>
<td>1.62–22.50</td>
<td>4</td>
<td>-0.440</td>
</tr>
<tr>
<td>Mazocraeidae</td>
<td>31</td>
<td>0.51–12.50</td>
<td>6</td>
<td>-0.023</td>
</tr>
<tr>
<td>Microcotylidae</td>
<td>75</td>
<td>1.15–15.00</td>
<td>9</td>
<td>-0.269</td>
</tr>
<tr>
<td>Polystomatidae</td>
<td>31</td>
<td>1.50–10.00</td>
<td>2</td>
<td>0.413</td>
</tr>
</tbody>
</table>
Two potentially confounding factors can probably be eliminated as sources of artefacts in the analyses. First, taxon sampling was relatively good, with between 65 and 81% of families in each of the three higher taxa being included. Their positions were evenly distributed among the branches of the phylogenetic trees when compared to missing families, and there was no difference in clade rank (i.e. path length from the root to the family) between the included and excluded families. Thus the analyses covered representative samples of existing families.

Second, the lack of information on branch length meant that a speciational model of evolution was adopted instead of a model of gradual change. This probably did not matter. Using the imperfect information on branch lengths for some of the families derived from recent molecular analyses (Olson & Littlewood, 2002; Olson et al., 2003) I carried out partial analyses that suggested that including estimates of branch lengths in the model has no effect on the results other than altering intercept or slope values (unpubl. data). Therefore, the speciational model used here is unlikely to have led to erroneous results. When the evolution of a trait is associated with niche shifts, as with body size being linked to the colonization of new microhabitats within hosts, a speciational model of evolutionary change often provides an accurate representation of evolutionary trends (e.g. Mooers, Vamosi & Schluter, 1999).

The first monogeneans, whether Monopisthocotylea or Polyopisthocotylea, were probably opportunistic browsers on the skin of early fishes (Llewellyn, 1965; Kearn, 1970; Kearn, 1998). Most extant Monopisthocotylea still live on the skin of fish hosts, feeding on epidermal cells. These range from the basal family Capsalidae (largest-bodied Monopisthocotylea family in Fig. 2) to the more derived Gyrodactyliidae (third smallest-bodied Monopisthocotylea family in Fig. 2). Physical factors and the risk of detachment, as well as potential predation by cleaner organisms feeding on fish external surfaces (Grutter, 2002), may have constrained any increases in body size and their associated increases in reproductive output.

Colonization of the buccal and branchial cavities has taken place more than once among the Monopisthocotylea (Kearn, 1998), perhaps favoured because of the protection this offered from cleaners. Some members of the Gyrodactyliidae live in the gill cavity, but the most specialized gill inhabitants are some of the most derived Monopisthocotylea families, as well as some of the smallest-bodied, such as the Dactylogyriidae, Tetraonchidae and Diplectanidae (the three points in the bottom right corner in Fig. 2). These monogeneans live between the secondary gill lamellae of fish, in spaces where other Monopisthocotylea would not fit. The pattern in Figure 2 suggests that invasion of these space-limited microhabitats by derived families may have been associated with a general decrease in body size. The fact that the trend is not supported by the statistical analysis may simply be due to the lack of sufficient families in this taxon and therefore to the low power of the test.

In contrast to Monopisthocotylea, most Polyopisthocotylea are blood feeders living in the gill cavity, or on the gills themselves, of their fish hosts (Kearn, 1998). The two exceptions are the Polystomatidae and Sphyranuridae (the two points in the bottom left corner of Fig. 2), which are endoparasites of non-fish aquatic vertebrates (i.e. amphibians and turtles), though one polystomatid species lives on the skin below the eyes of the hippopotamus (Kearn, 1998).

Excluding these two families, a trend appears, similar to that in the Monopisthocotylea. Among the fish parasites, the largest-bodied and most basal family, the Chimaericolidae, infect holocephalan fishes; the more recently derived families all tend toward smaller sizes, as smaller spaces within the gill cavity were colonized. Mode of attachment may also have played a role in body size evolution in these parasites. The Chimaericolidae penetrate the soft gill tissue and clamp into the cartilage, whereas more derived families attach to the surfaces of the gill lamellae; this difference may well have influenced the sizes they could attain.

Once again, a weak trend in body size evolution may exist, although there are not enough families in the analysis to reject the random walk model using the conservative LR test. The fact that the earliest mono-
Monogeneans appear to have been large worms may also provide an ecological clue as to the identity of the sister-group of the Neodermata, the clade to which monogeneans and digeneans belong. Phylogenetic studies have yet to resolve which flatworms are the closest free-living relatives of the Neodermata (Littlewood et al., 1999).

In both Monopisthocotylea and Polypisthocotylea, the analyses of body size distributions within families also reveal a possible similar trend. The more derived families tend not to show the typical right-skewed body size distributions commonly found in most higher taxa (Van Valen, 1973; Dial & Marzluff, 1988; Blackburn & Gaston, 1994; Brown, 1995). If small-bodied species are favoured and diversify at a higher rate than larger species, it would take time for the body size distribution of species in a new lineage to adopt the characteristic right-skewed shape, with the mode shifting toward smaller sizes. Again, it may only be a lack of statistical power that kept the trend non-significant within each of the two taxa (it is significant when all 13 monogenean families are pooled).

Digeneans have complex life-cycles, in which larval development almost always begins in a mollusc, and adult worms almost always live in vertebrate hosts. One scenario postulates that the ancestor of all living digeneans was a ciliated flatworm that developed a symbiotic association with a mollusc (Llewellyn, 1965; Pearson, 1972; Kearn, 1998). As fish became dominant predators in aquatic habitats, frequent predation on the free-living stages of these early digeneans may have led to the addition of fish hosts to the life-cycle.

In an alternative scenario, supported by recent phylogenetic evidence, the vertebrate host came first, and the molluscan intermediate host was adopted subsequently (Cribb et al., 2003). In any event, the first digenean with a complex life-cycle matured and lived as an adult in the gastrointestinal tract of fish. From there, digeneans colonized other organs in their vertebrate definitive host. These include: the circulatory system, now used by three relatively basal and small-bodied families (Sanguinicolidae, Spirorchidae and Schistosomatidae); the liver, inhabited by the large Fascioliidae (second largest digenean family in Fig. 2) of intermediate clade rank; and the connective tissue and muscle, where the Didymozoidae, the largest digenean family in the analysis (and in Fig. 2) is found.

Several extant families still inhabit the gastrointestinal tract of their vertebrate host, but these include both basal and derived families, as well as small-bodied and large-bodied ones (i.e. the Microphallidae and Gorgoderidae, which differ in size by more than two orders of magnitude). Some very small-bodied digenean lineages may have never used the host gut as an infection site: adults of the Transversotrema family, for instance, live beneath the scales of teleost fish (smallest-bodied family in the bottom-left corner of Fig. 2).

It appears that the evolutionary history of body size in digeneans has been less constrained by opportunities than that of monogeneans. A comparative analysis has shown that digenean body size does not correlate with host body size (Poulin, 1997), and the site of infection itself seems to be a more important determinant. From an ancestral site of infection in the gut of the vertebrate host, digeneans have repeatedly invaded sites where space constraints were either more relaxed or more severe. This is unlikely to have led to a directional change in body size within the group.

Trends in body size evolution have been reported for a range of free-living taxa (Stanley, 1973; Bonner, 1988; Arnold et al., 1995; Jablonski, 1997; Alroy, 1998; Knouft & Page, 2003). The present analysis is the first to investigate body size evolution in parasitic taxa. Based on the available evidence, it is impossible to reject the null, or random walk, model of evolution, and therefore there may have been no directional trend in the evolution of monogenean and digenean body sizes.

However, the appearance of similar tendencies for mean family body size to decrease as a function of distance from the root of the phylogeny in both groups of monogeneans suggests that the power of the analyses may be solely responsible for the null model not being rejected. From an ancestor parasitic on the skin of fish, the only options open for monogeneans, in terms of unexploited microhabitats on the outside of the host, were sites requiring small body size. This may have placed constraints on body size evolution in monogeneans, and on the evolutionary success and diversification rates of new lineages.

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REFERENCES


