*Biological Journal of the Linnean Society*, 2009, **96**, 533–540. With 3 figures

# Interspecific allometry of morphological traits among trematode parasites: selection and constraints

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*Received 21 May 2008; accepted for publication 11 August 2008*

Developmental constraints and selective pressures interact to determine the strength of allometric scaling relationships between body size and the size of morphological traits among related species. Different traits are expected to relate to body size with different scaling exponents, depending on how their function changes disproportionately with increasing body size. For trematodes parasitic in vertebrate guts, the risk of being dislodged should increase disproportionately with body size, whereas basic physiological functions are more likely to increase in proportion to changes in body size. Allometric scaling exponents for attachment structures should thus be higher than those for other structures and should be higher for trematode families using endothermic hosts than for those using ectotherms, given the feeding and digestive characteristics of these hosts. These predictions are tested with data on 363 species from 13 trematode families. Sizes of four morphological structures were investigated, two associated with attachment (oral and ventral suckers) and the other two with feeding and reproduction (pharynx and cirrus sac). The scaling exponents obtained were generally low, the majority falling between 0.2 and 0.5. There were no consistent differences within families between the magnitude of scaling exponents for different structures. Also, there was no difference in the values of scaling exponents between families exploiting endothermic hosts and those using ectotherms. There were strong correlations across families between the values of the scaling exponents for the oral sucker, the ventral sucker and the pharynx: in families where the size of one trait increases relatively steeply as a function of body size, the same is generally true of the other traits. These results suggest either that developmental constraints link several morphological features independently of their specific roles or that similar selection pressures operate on different structures, leading to covariation of scaling exponents. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **96**, 533–540.

ADDITIONAL KEYWORDS: body size – flatworms – interspecific variation – morphology – parasitism – scaling relationships.

## INTRODUCTION

Organisms that differ in body size also tend to differ in the relative size of various organs or body structures (Gould, 1966; Huxley, 1972). Within species, the allometric relationships between the size of anatomical structures and body size are not necessarily constant for all populations of the same species; there is growing evidence that both selection and environmental conditions, such as food quality or quantity, can modulate these allometries (e.g. Emlen, 1997; Moczek, 2002; Frankino *et al.*, 2005). The interplay between weak developmental constraints and strong selective forces can result in departures from the usual allometric relationship between body size and the size of specific structures, thus allowing distinct populations to rapidly diverge morphologically. In comparisons between species, different allometric relationships can therefore reflect different selective regimes and shed light on prior evolutionary trends.

In practice, the interspecific relationship between body size and the size of specific organs is best described by a power function of the form

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$$Y = aW^b$$

where $Y$ is a dependent variable representing the size of a specific organ or structure, $W$ is body size, $a$ is a normalization constant and $b$ is a scaling exponent. Except for the cases where $b = 0$ or $b = 1$, this power equation does not describe a straight line when $Y$ is plotted against $W$. However, it does yield a straight line if we use a logarithmic transformation to express it instead as

$$\log Y = \log a + b \log W$$

where $\log a$ becomes the intercept and the scaling exponent $b$ becomes the slope of the linear equation, thus making it easy to calculate (Harvey, 1982). For many non-morphological traits, using body mass as the measure of body size, the value of $b$ is typically $< 1$ and often approximately 0.75; thus, for instance, basal metabolic rate is proportional to $W^{0.75}$ across most animal taxa (Brown *et al.*, 2004; Savage *et al.*, 2004). Such allometric relations, in which the value of the trait $Y$ and body size increase at different rates, are common for many physiological and life history traits (Peters, 1983; Schmidt-Nielsen, 1984; Brown *et al.*, 2004; Savage *et al.*, 2004). For morphological traits, in contrast, $b$ usually indicates an isometric relationship, such that body structures increase in size in roughly direct proportion to increases in body size (Gould, 1966; Huxley, 1972). Therefore, across different but related species that exploit similar niches but vary in body size, resources tend to be allocated in roughly equal proportions to different organs and structures. There are many exceptions to this rule, however. In insects, for instance, an apparent lack of strong developmental constraints allows selective departures from the usual allometric relationship for particular structures (Weber, 1990; Emlen, 1996; Frankino *et al.*, 2005; but see Kunte, 2007). For example, secondary sexual ornaments such as horns in stag beetles and forceps in earwigs scale with body length with $b$ values almost always substantially $> 1$ (Kodric-Brown, Sibly & Brown, 2006). Because these structures play an important role in mating success and are key determinants of fitness, they are allocated a disproportionate amount of resources.

Parasitic organisms may also allocate disproportionately more resources to the growth of structures whose importance scales allometrically with size. For example, among intestinal parasites, the sizes of attachment organs may increase at rates disproportionate to body size, because the probability of dislodgement should increase non-linearly with body size. Very small parasites can easily blend into the epithelial lining of the gut, whereas larger ones become increasingly likely of being ripped loose by peristaltic movements and passing food. There may also be different selective pressures on parasites of endothermic (birds and mammals) and ectothermic (fish, amphibians and reptiles) hosts, as peristalsis and the amounts of food passing through the gastrointestinal tract of the former are generally greater than in the latter. In contrast, organs associated with feeding, excretion or reproduction are more likely to be directly proportional with body size, showing a roughly constant size relative to body size.

Here, I quantify allometric relationships for several structures in different trematode families. Trematodes are parasitic flatworms using vertebrates as definitive hosts. All taxa considered in the present analyses live either within the host's gastrointestinal tract or within associated organs (e.g. pyloric appendages, pancreas duct, gall bladder, liver); there, they attach using mainly suckers and feed either on host gut contents or on host blood and mucus. The dimensions of internal and external structures of trematodes, as in other organisms, are important taxonomic features, allowing one to distinguish between closely related species. For instance, the relative sizes of the oral and ventral suckers, of the oesophagus and pharynx, or of the cirrus sac, as well as the ratios between these measurements, are routinely used in trematode species descriptions to differentiate between species (Gibson, Jones & Bray, 2002; Jones, Bray & Gibson, 2005). However, little attention has been paid to the evolution of these structures, in particular to the evolution of their relative sizes and how these vary among related species. In addition to providing the first quantitative estimates of interspecific allometric relationships in trematodes, this study tests the predictions that: (1) scaling exponents for attachment structures should be higher than those for structures with basic physiological functions, with the latter predicted to show isometric scaling with body size; (2) scaling exponents for attachment structures should be higher for trematode families using endothermic hosts than for those using ectotherms; and (3) scaling exponents for different structures within the same family should covary; i.e. certain families will have generally high scaling exponents for all structures, whereas others will show generally low exponent values, a phenomenon expected if developmental constraints have measurable impacts on allometry. The latter two predictions were also tested using the intercepts of the scaling relationships, instead of the scaling exponents, as the intercepts also provide a measure of relative structure size when the scaling exponents are similar for two or more families.

## MATERIAL AND METHODS

Data were compiled from original species descriptions published in all issues of the *Journal of Parasitology* (volumes 44–93) and *Systematic Parasitology* (volumes 36–69), available electronically at the University of Otago (http://www.library.otago.ac.nz/index.php). While these do not cover the whole range of trematode species in existence, they nevertheless provide a representative sample of the existing variation in body morphometrics within the group. The taxonomy proposed in the original sources was generally accepted, although several taxa were cross-checked with the recent classification proposed by Gibson *et al.* (2002) and Jones *et al.* (2005). Only data on adult worms were included. Measurements used here are either the means or the mid-point of ranges based on the examination of several specimens per species. Although trematodes are not necessary flattened, only two dimensions are reported in species descriptions (body length and width); thus, the surface area of a two-dimensional projection was used as the best estimate one can get of trematode body size. Their surface area was estimated using the formula for an ellipsoid, $(\pi LW)/4$, where $L$ and $W$ are the length and width of the worm, respectively.

In addition to body size, the lengths (or widths, in cases where width exceeded length) of four other structures were also recorded for each species: (1) the oral sucker; (2) the ventral sucker or acetabulum; (3) the pharynx, a muscular structure serving to pump food in through the mouth; and (4) the cirrus (sinus) sac, the terminal portion of the reproductive system which typically houses either an intromittent organ or the terminal male genitalia (Galaktionov & Dobrovolskij, 2003). These are four morphological features possessed by most trematode species and for which data are routinely provided in species descriptions. Species in the family Bucephalidae lack an oral sucker and instead possess an anterior organ known as the rhynchus; although the homology of this structure with the oral sucker is debatable, its dimensions are here used in place of those of a true sucker.

Thus, surface area is used as a measure of body surface, whereas only linear measurements were available for the four structures. Because surface increases with the second power of linear measurements, the expected scaling coefficient for an isometric relationship between structure sizes (linear) and body size (surface area) is 0.5 in log–log space. Any slope not different from 0.5 would indicate isometry, i.e. that body structures increase in length in direct proportion to increases in body size.

For each trematode family, the scaling exponent and the intercept of the relationship against body size were estimated separately for each of the four morphological structures using linear regressions across species values. Using log-transformed data, the scaling exponent corresponds to the slope of the ordinary least-squares regression; their values were compared (using $t$-tests) with the expected isometric value of 0.5 to detect significant departures from isometry.

One-way ANOVAs were used to compare the values of scaling exponents and intercepts between families exploiting endothermic definitive hosts and those using ectotherms, separately for each of the four morphological structures. Scaling exponents for different structures were also compared with each other, in a pair-wise manner taking family identity into account, using two-tailed paired $t$-tests. Finally, possible pair-wise relationships between the values of scaling exponents or intercepts for different structures across families were tested using Pearson's product-moment correlation coefficients.

## RESULTS

Sufficient data were obtained for 13 different trematode families, including a total of 363 species and 216 genera (Table 1); the complete dataset is available online (Appendix S1). Four of these families use endothermic vertebrates as definitive hosts, whereas the rest use ectotherms. The species within the dataset show considerable variation in all recorded dimensions; for instance, there is a more than 300-fold difference in body surface area between the smallest and largest species. Although variation within families is less extensive, it is always sufficient to estimate scaling exponents. Note that no scaling exponents are available for the ventral sucker or cirrus sac in some families (Table 1), because these families lack these particular structures.

Not surprisingly, most scaling exponents are associated with highly significant regressions (43 of the 48 regressions in Table 1 are significantly positive at $P < 0.05$). However, their values range mostly between 0.200 and 0.500 (Fig. 1); the majority (33 out of 48) are not statistically different from the expected value of 0.5 representing an isometric scaling relationship and those that differ from 0.5 are all significantly lower (Table 1). Although some families tend to have lower scaling exponents for all four morphological structures (e.g. Macroderoididae), there is no difference in the values of scaling exponents between families exploiting endothermic definitive hosts and those using ectotherms (one-way ANOVAs, $P > 0.33$ for all four structures). There is also no difference in the intercept values of scaling relationships between families exploiting endotherms and those in ectotherms ($P > 0.28$ for all structures).

Scaling exponents are also generally comparable when contrasting values obtained for different

**Table 1.** Allometric scaling exponents (measured as the slope of log–log regressions against body surface area) for four morphological traits within 13 trematode families

| Family | Normal definitive host | Number of species (genera) | Oral sucker | Ventral sucker | Pharynx | Cirrus sac |
|---|---|---|---|---|---|---|
| Allocreadiidae | Ectotherm | 13 (11) | 0.345 | 0.217* | 0.428 | 0.481 |
| Bucephalidae | Ectotherm | 32 (11) | 0.279* | – | 0.402 | 0.403 |
| Cryptogonimidae | Ectotherm | 28 (17) | 0.298 | 0.372 | 0.380 | – |
| Dicrocoeliidae | Endotherm | 22 (11) | 0.381 | 0.420 | 0.437 | 0.424 |
| Echinostomatidae | Endotherm | 29 (18) | 0.298* | 0.355 | 0.351* | 0.191* |
| Fellodistomidae | Ectotherm | 24 (17) | 0.373 | 0.325 | 0.414 | 0.237* |
| Hemiuridae | Ectotherm | 27 (19) | 0.414 | 0.486 | 0.360 | – |
| Heterophyidae | Endotherm | 15 (7) | 0.317 | 0.144* | 0.325 | – |
| Lecithodendriidae | Endotherm | 16 (13) | 0.476 | 0.480 | 0.528 | 0.275 |
| Lepocreadiidae | Ectotherm | 73 (44) | 0.363 | 0.337* | 0.266* | 0.328* |
| Macroderoididae | Ectotherm | 18 (9) | 0.177* | 0.086* | 0.249* | 0.226* |
| Opecoelidae | Ectotherm | 45 (25) | 0.422 | 0.433 | 0.393 | 0.499 |
| Plagiorchiidae | Ectotherm | 21 (14) | 0.344 | 0.159* | 0.397 | 0.432 |

*$P < 0.05$; comparison with expected isometric scaling value of 0.5 (*t*-test).

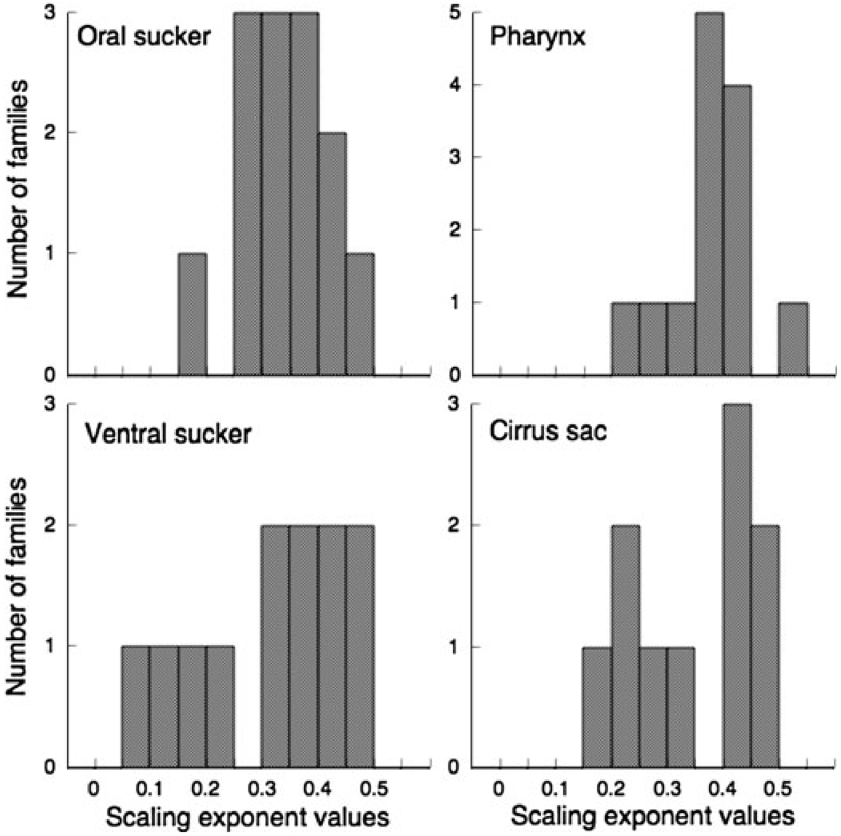

**Figure 1.** Frequency distributions of allometric scaling exponents characterizing the interspecific relationships of four morphological traits with body size among trematode families.

**Table 2.** Pair-wise comparisons between the values of allometric scaling exponents for four morphological traits (two-tailed paired *t*-tests; above the diagonal) and pair-wise relationships among these scaling exponents (Pearson product–moment correlation coefficients; below the diagonal)

| | Oral sucker | Ventral sucker | Pharynx | Cirrus sac |
|---|---|---|---|---|
| Oral sucker | – | $t_{11} = 1.223$ | $t_{12} = 2.002$* | $t_9 = 0.103$ |
| Ventral sucker | 0.757‡ | – | $t_{11} = 1.758$ | $t_8 = 0.545$ |
| Pharynx | 0.658† | 0.506* | – | $t_9 = 0.982$ |
| Cirrus sac | 0.307 | 0.061 | 0.283 | – |

*$P < 0.10$; †$P < 0.05$; ‡$P < 0.005$.

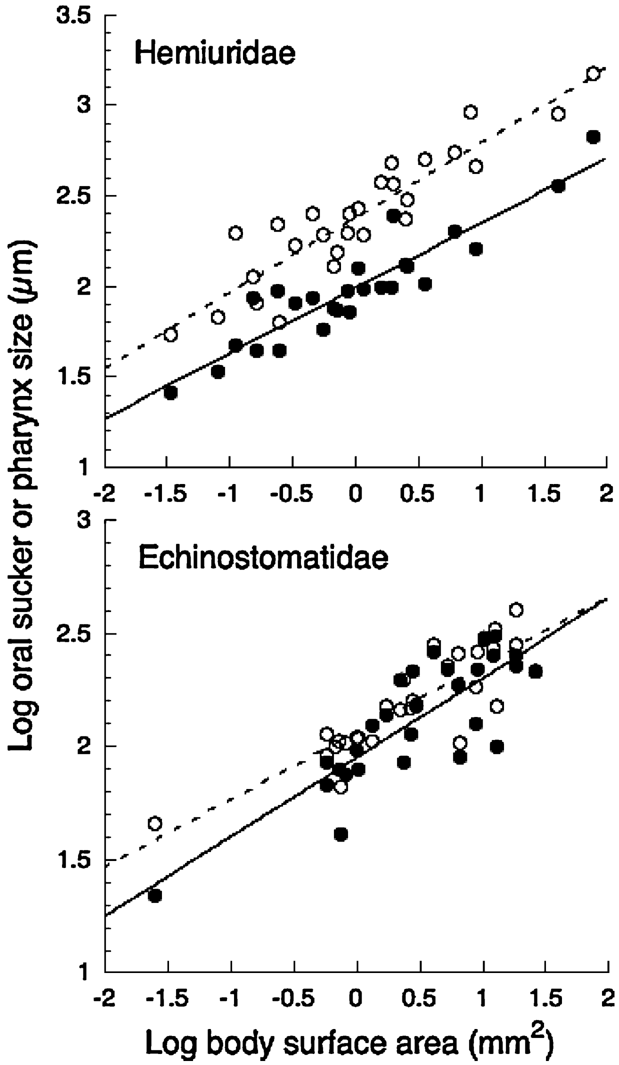

**Figure 2.** Allometric scaling relationship of oral sucker size (open circles, dashed lines) and pharynx size (black circles, solid lines) across trematode species in two trematode families.

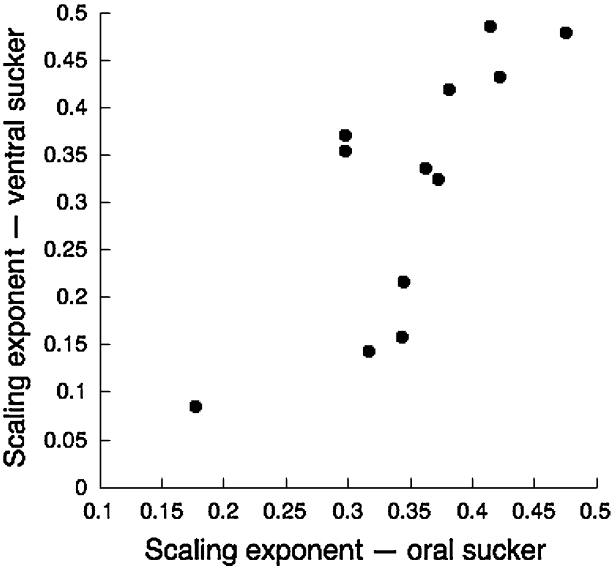

**Figure 3.** Relationship between the values of the allometric scaling exponents for two morphological traits, oral sucker size and ventral sucker size across trematode families.

morphological structures (Fig. 1; Table 2). Scaling exponents for pharynx size show a weak tendency to be higher than those for the oral sucker in most families (Table 2). However, regardless of which of these two structures displays the highest scaling exponent in a particular family, they are generally still very close to each other (see Fig. 2 as an example). Therefore, there are no consistent differences within families in the magnitude of scaling exponents for different structures.

Across trematode families, there is a strong correlation between the value of the scaling exponent for the oral sucker and that for the ventral sucker (Table 2). Thus, in families where the size of the oral sucker increases relatively steeply as a function of body size, the same is generally true of the ventral sucker (Fig. 3). Also, the scaling exponents for the sizes of both suckers tend to covary with that for the size of the pharynx (Table 2). In contrast, the scaling exponents for the size of the cirrus sac are independent of those for the other three structures investigated here. When the same correlation analyses were repeated using intercept values instead of scaling exponents, no significant relationships were found between any pair of structures (all $P > 0.17$).

## DISCUSSION

Parasites in general, and trematodes in particular, display a wide range of body sizes and shapes and substantial variation in the relative dimensions of anatomical structures (Gibson *et al.*, 2002; Jones *et al.*, 2005). Yet the roles of various selective forces in shaping the evolution of these features remain mostly unexplored. There have been a few investigations of allometry within species of parasitic flatworms (e.g. Fischthal, 1978; Fischthal, Carson & Vaught, 1982; Swarnakumari & Madhavi, 1992; Kostadinova *et al.*, 2000; Pappas, 2000), but no comprehensive look at interspecific patterns. The present study provides an analysis of allometric scaling exponents for various body structures in 13 different trematode families. As these families are scattered throughout the phylogeny of trematodes (Olson *et al.*, 2003), they represent more or less independent lineages and thus they provide information on distinct evolutionary trajectories that have been followed by these parasites. It was expected that the function of a particular structure (i.e. attachment versus ingestion) or the nature of the definitive host (endotherm vs. ectotherm) would influence the value of the allometric scaling exponent or the rate of change in the structure's size as a function of increasing body size. Although these predictions were not verified, the present study revealed several intriguing patterns.

First, the values observed for the scaling exponents of all structures considered here were generally low, the majority falling between 0.2 and 0.5; most did not depart significantly from 0.5 (isometry) and those that did were all inferior to 0.5 (hypoallometry). This may have something to do with the roughly flattened shape of trematode bodies. As many (although not all) trematodes are almost two-dimensional, as opposed to most other organisms that are generally three-dimensional, their mass and volume do not increase with body length and width at the same rate as they do in other taxa. Thus, lesser investments in attachment and other functions as a function of body size may be the norm in these parasites because of their flat bodies. Interestingly, however, in round-bodied acanthocephalan parasites, which use rows of hooks around their proboscis for attachment to the intestinal wall of their host, total combined hook length scales with parasite body size with a low exponent (0.146), so that larger species have fewer or shorter hooks relative to their body size than small species (Poulin, 2007). Therefore, the flattened shape of trematodes may not be the reason for the (generally hypoallometric) scaling exponent values found in this study. In the case of attachment structures, perhaps a minimum sucker size is necessary to allow even a small trematode to maintain its position; for worms of larger sizes, relatively slight increases in sucker sizes might suffice for secure attachment. This would be true if sucker efficiency does not increase proportionately with sucker size. It must also be noted that other structures contribute to attachment in trematodes, sometimes more so than suckers. For instance, minute tegumental spines are important attachment structures for small trematodes and tentacles serve as attachment organs in the family Bucephalidae (Galaktionov & Dobrovolskij, 2003). In one trematode family, Echinostomatidae, a row of anterior spines is also believed to help in attachment (Galaktionov & Dobrovolskij, 2003). Among the 25 echinostome species in the dataset used here for which spine numbers were available, the allometric scaling exponent for numbers of spines was very low (0.066) and the relationship was only marginally significant, again suggesting that increments in body size need not be associated with much greater investments in attachment structures than those already made by small species. Of course, the above arguments assume that the functional performance of an attachment structure and its size are linearly correlated; studies on other organisms suggest that low scaling exponents between the size of holdfast structures and body size do not mean that holdfast performance also scales with body size with the same low exponent (see Irschick *et al.*, 1996). There is currently no data on the relationship between sucker size and sucker performance in trematodes.

A second important finding of this study, related to the previous one, is that there are no consistent differences between the scaling exponents for the various types of structure examined. Attachment structures, i.e. the ventral and oral suckers, do not scale more steeply with body size than structures associated with ingestion and reproduction. The contrast between structures involved in attachment and those involved in other functions is not clear-cut. As seen above, structures other than suckers can serve to attach the worm to host tissue and the oral sucker can play a role in feeding (Smyth & Halton, 1983). Nevertheless, whatever their function, the same proportional increase in size is seen in all structures following a given increment in body size. There were also no differences between the scaling exponents of families exploiting endothermic hosts and those exploiting ectotherms, whatever the structure concerned. This finding contrasts with results obtained for acanthocephalan parasites, where investments in hook production were higher in species exploiting endothermic hosts, especially birds, than in those living in ectotherms (Poulin, 2007). One would expect that passage of greater amounts of food and more intense peristaltic movements in the gastrointestinal tract of endotherms, associated with their higher metabolic rate, would lead to a higher probability of parasites being dislodged and thus to selection for more secure attachment. Endothermic vertebrates also harbour more parasites than ectotherms, both in terms of numbers of species and individuals (Bush, Aho & Kennedy, 1990; Poulin & Morand, 2004), and the resulting intense competition should also select for greater investments in attachment structures. However, intestinal trematodes are generally much smaller than acanthocephalans or other intestinal worms like cestodes and nematodes. It is possible that within this restricted size range they can use villi and folds on the gut wall to escape detachment without investing proportionately more in sucker development as a function of body size, even when living inside an endotherm.

The third pattern observed here is quite intriguing: the scaling exponents for different structures are not independent of each other. There is an association between scaling exponent values for the oral and ventral sucker and, to a lesser extent, between values for both suckers and for the pharynx. In families where one of these structures shows a relatively high scaling exponent, the exponents for the other two structures also tend to be high. This could hint at some developmental constraints linking several morphological features independently of their specific roles, with different species maintaining the family body plan independently of size. Alternatively, similar selection pressures could act on different structures; for instance, we might expect that, if selection pressures operating on the oral suckers are strong, they might be equally strong for the ventral sucker, leading to covariation of scaling exponents.

In addition to the morphological structures investigated here, several other features of trematodes are correlated with body size, such as gonad size, fecundity, egg volume and other life history traits (Poulin, 1997; Trouvé *et al.*, 1998; Thomas & Poulin, 2003). What is remarkable about the present results is the consistency in the values of scaling exponents obtained for vastly different structures. The cost of producing a morphological structure and the functional performance of that structure both increase with its size, but probably at different rates, setting up a trade-off that should select for an optimal size for that structure. The similar scaling exponents describing the allometric relationships of all four structures investigated here suggest that the body size-dependent selective pressures acting on them are not strong enough to modify that trade-off significantly. Developmental constraints are therefore apparently severe and difficult to overcome. Phylogenetic constraints may also act to restrict the values of scaling exponents within families, possibly explaining, for instance, why exponents for the Macroderoididae are the lowest for all structures considered here. Experimental studies that either manipulate selective pressures on specific traits or use artificial selection protocols have succeeded at elucidating the forces shaping or constraining allometric relationships in particular insect species (Weber, 1990; Emlen, 1996; Frankino *et al.*, 2005). One possibility for future studies on trematodes would be to adopt a similar approach with model species as a way to disentangle the roles of developmental constraints and selective forces.

## ACKNOWLDEGEMENTS

I thank Kim Bryan-Walker for assistance with the compilation of the dataset and Haseeb Randhawa for useful comments on an earlier version.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Trematode allometry data.