THE ROYAL SOCIETY

Received 21 December 2001
Accepted 1 March 2002
Published online 24 May 2002

Are most species small? Not within species-level phylogenies

C. David L. Orme*, Nick J. B. Isaac† and Andy Purvis

Department of Biological Sciences, Imperial College, Silwood Park, Ascot SL5 7PY, UK

The robust macro-ecological observation that there are more small-bodied species implies that small-bodied organisms have experienced elevated net rates of diversification. We investigate the role of body size in creating non-random differences in rates of cladogenesis using a set of 38 species-level phylogenies drawn from a range of animal groups. We use independent contrasts to explore the relationship between body size and species richness within individual phylogenies and across related sets of phylogenies. We also carry out a meta-analysis looking for associations between body size and species richness across the taxa. We find little evidence for increased cladogenesis among small-bodied organisms within taxa, and no evidence for any consistent differences between taxa. We explore possible explanations for the inconsistency of our findings with macro-ecological patterns.

Keywords: diversity; speciation; phylogeny; body size

1. INTRODUCTION

Body size is one of the most fundamental ecological parameters for animal taxa, correlating with many other life-history traits (Peters 1983). Understanding the distribution of body sizes among related species in an ecological community is, therefore, a key question in macro-ecology. Interspecific distributions of body size commonly exhibit a high degree of positive (or right) skew and often retain significant skew after log transformation (e.g. Gaston & Blackburn 2000). This macro-ecological pattern has prompted the development of models providing functional explanations for the abundance of small-bodied species. Models of body-size evolution are reviewed elsewhere (e.g. Gardezi & da Silva 1999; Gaston & Blackburn 2000) but fall into four broad categories based on: (i) the finer subdivision of the environment or resources by small-bodied organisms (Hutchinson & MacArthur 1959); (ii) interspecific body-size optima resulting from energetics (e.g. Brown *et al.* 1993); (iii) intraspecific optimization of body size, with consequent predictions about interspecific distributions of body size (Kozlowski & Weiner 1997); and (iv) passive diffusion of body size with constrained minumum size (Stanley 1973). Whilst such models have been successful in generating body-size distributions that match those found empirically, there has been less success in demonstrating evolutionary correlations between body size and increased species richness.

Early studies comparing body sizes across lineages did find correlations between smaller body size and increased species richness (e.g. Dial & Marzluff 1988; Kochmer & Wagner 1988; Van Valen 1973). In the absence of well-resolved phylogenies, however, such studies employed statistics based on taxonomic rank, an approach that is subject to the confounding effects of non-equivalence within a taxonomic rank and differing degrees of shared evolutionary history below that rank (Harvey & Pagel 1991; Avise & Johns 1999). The use of phylogenies to identify sister taxa ensures that comparisons are made between equivalent taxa (i.e. those of equal age); using the differences in a biological trait between sister taxa, rather than the absolute values of that trait, accounts for the shared evolutionary history of those taxa before they diverged (Felsenstein 1985). This method has recently been used to study patterns of species richness and body size within a number of taxa: for example, carnivores and primates (Gittleman & Purvis 1998); all mammals (Gardezi & da Silva 1999); birds (Nee *et al.* 1992); hoverflies (Katzourakis *et al.* 2001); and a broad-scale study of the metazoan phyla (Orme *et al.* 2002). Although some such studies have looked for differences in pattern within subclades (Nee *et al.* 1992; Gittleman & Purvis 1998; Gardezi & da Silva 1999), we are unaware of any study looking at differences in the relationship between species richness and body size across a broad range of taxa.

We present the results of a meta-analysis of the results from 38 new and directly comparable analyses of the relationship between body size and species richness. We examine the distribution and evolutionary pattern of body size across a range of species-level phylogenies from vertebrate and invertebrate groups, and look for common trends across and within taxa.

2. DATA

We collected a set of 38 complete species-level phylogenies from the recent literature. All are constructed using an optimality criterion: the majority use maximum parsimony but maximum likelihood, neighbour joining and matrix representation using parsimony phylogenies are also included. In all cases, we used the single most parsimonious or most likely phylogeny found, or the strict consensus of all equally most parsimonious trees. Phylogenies were selected that contained at least six species and where body-size data were available for at least 75% of those species. Whilst not selected randomly, the phylogenies are otherwise unbiased with respect to species richness and body size.

*Author for correspondence (d.orme@ic.ac.uk).
† Present address: Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK.

We collected body-size data for as many species as possible, using a consistent linear measurement within each taxon. Linear measurements were used throughout to facilitate direct comparison of the results of analyses among clades. Where data were only readily available as body mass, we converted mass to linear dimensions using a power function. Parameters for the power function were taken from Peters (1983) for the avian taxa, and calculated for the mammalian taxa from the following datasets: marsupials (Seal 1997), carnivores and primates (Gittleman & Purvis 1998). Within each phylogeny, we collected data from a single sex where possible but have accepted mixed sex datasets where sources did not record the sex of individuals. Where neither sex provided a complete dataset, we have filled the gaps in the more complete set using data for the other sex. Within mammals and birds, the mean body size of species was used; for all other taxa we recorded the maximum body size for each species, since mean size data were not available for the majority of species. Body-size data were log transformed before further analysis.

The phylogenies and data sources, and details of the body-size measurement used, are given in table 1 and the full datasets are available on request from the senior author and from the following URL: http://www.bio.ic.ac.uk/evolve/index.html. Table 1 also records the number of species in each phylogeny and the number of species for which body-size data were available. Many of the phylogenies are too small to produce powerful tests on their own, but our main intention was a meta-analysis to assess any general tendency.

We also constructed a phylogeny (figure 1) linking the taxa comprising the 38 studies, in order to identify valid comparisons between groups of our study taxa at higher taxonomic levels. Resolution of the three phyla studied (Chordata, Mollusca, Arthropoda) is non-controversial (e.g. Nielsen 1995; Zrzavy *et al.* 1998), as is the division between Osteichthyes and the amniotes (e.g. Hedges 2001). The amniotes are left as a polytomy due to uncertainty over the position of the turtles (Gauthier *et al.* 1988). Resolution of the mammalian and avian groups follows, respectively, Liu *et al.* (2001) and Sibley & Ahlquist (1990), whilst the osteichthyean taxa under study are resolved using phylogenies in Springer & Williams (1994) and Vari (1989*a*). Resolution of the clade of chelicerates, hexapods and crustaceans follows Giribet *et al.* (2001) and Hwang *et al.* (2001). The relationships of the orders of the hexapods are taken from Wheeler *et al.* (2001). Within the hexapod orders, we used information presented in the Tree of Life Web site (http://tolweb.org/tree/phylogeny.html).

3. ANALYSIS

(a) *Species richness and body size*

For each phylogeny, we calculated standardized phylogenetically independent contrasts of body size at each bifurcating node according to the methods described by Felsenstein (1985) and Pagel (1992). We also calculated the species-richness contrasts as the relative rate difference (RRD): $\ln(n_i/n_j)$, where n_i and n_j are the number of species in the larger and smaller bodied clade; no species-richness contrast can be calculated where both clades are single species (Agapow & Isaac 2002; Isaac *et al.* 2002). Calculation of both sets of contrasts was performed using the computer program MacroCaic (Agapow & Isaac 2002). Although branch lengths are available for some of the phylogenies, we assumed all branch lengths were equal to ensure that all 38 phylogenies are comparable. We analysed the calculated contrasts as follows.

First, we used least-squares linear regression through the origin (Garland *et al.* 1992) to examine the relationship between body-size and species-richness contrasts within each phylogeny. The p-values from these regressions were assessed using a sequential Bonferroni test (Rice 1989) to correct the bias in significance levels resulting from multiple tests. In order to evaluate whether the probability of finding a significant correlation increases with the phylogeny size, we calculated a least-squares linear regression of the individual test p-values against the number of contrasts (n_c). We used a logit ($\log(p/(1-p))$) transformation of p and log transformation of n_c to remove non-normality in these variables. We used a Wilcoxon signed-ranks test to establish whether the central tendency of the set of regression coefficients (b) across phylogenies differs from zero. In order to account for the uncertainty in the calculated regression coefficients, we also performed a Wilcoxon signed-ranks test on b weighted by the inverse of the standard errors of b. The choice between Wilcoxon's signed-rank test and t-tests of location throughout these analyses was made on the basis of unreported Shapiro Wilks' tests for normality.

Second, analysis of the central tendency of the set of values of regression coefficients does not reveal whether there are significant differences between individual values of b. We therefore used figure 1 to identify sets of our 38 studies for which it is phylogenetically meaningful to look for differences in b. At each node in figure 1, we used analysis of covariance (ANCOVA) to compare regression coefficients calculated for the sister taxa descending from that node. To enable comparisons at higher taxonomic levels (i.e. internal nodes), we created sets of contrasts for the sister taxa at a node, by pooling the contrasts from the studies within each sister taxon. For example, the ANCOVA at node 1 incorporates a pooled analysis of all 38 datasets, and compares the slopes of the vertebrate and invertebrate taxa. ANCOVA also enabled us to assess whether any clade delimited by a node in figure 1 showed an overall relationship between RRD and body-size contrasts.

Last, the calculation of phylogenetically independent contrasts includes the calculation of an estimate of the mean log body size at each node. We used linear regression of nodal mean body size as a predictor of RRD to assess whether the relationship between body size and species richness changes with the actual sizes of the organisms, following Gittleman & Purvis (1998). The sign of RRD values for any body-size contrast indicates whether the smaller or larger bodied clade is more speciose. A significant negative regression, therefore, indicates the existence of a global intermediate optimum size: at small body size, the larger bodied clade is more speciose (positive RRD), but at large body size the smaller bodied clade is more speciose (negative RRD).

Table 1. Phylogenies and body-size data sources used in this study.
(The phylogeny source for each taxon is identified along with the higher taxonomy and the number of species (n_{spp}). The body-size metric is given for each taxon along with an indication of whether the data are taken from males (M), females (F), individuals of both sexes (B) or whether the sex is unknown (U) and the number of species for which body-size data were available ($n_{body\ sizes}$). The body-size data source is also identified; where the source is the same as the phylogeny source this is indicated by a dash.)

clade	higher	phylogeny source	n_{spp}	body-size metric	sex	body-size source	$n_{body\ sizes}$
Mallos and *Mexitlia*	Arenoidea	Bond & Opell (1997)	17	body length	F	—	17
Pimoidae	Arenoidea	Hormiga (1994)	20	cephalothorax length	B	—	20
Chimarrita	Trichoptera	Blahnik (1997)	18	forewing length	M	—	18
Contulma	Trichoptera	Holzenthal & Flint (1995)	21	body length	M	—	21
Greya	Lepidoptera	Davis *et al.* (1992)	15	wingspan	F	—	15
Xylomia	Lepidoptera	Mikkola (1998)	7	wingspan	U	—	6
Rekoa	Lepidoptera	Robbins (1991)	7	forewing length	M	—	7
Pnyxiopalpus	Diptera	Vilkamaa & Hippa (1999)	16	forewing length	B	—	16
Thinempis	Diptera	Bickel (1996)	6	body length	U	—	6
Bonjeania	Diptera	Winterton *et al.* (2000)	10	body length	B	—	10
Bitheca	Diptera	Marshall (1987)	14	body length	U	—	14
Mosillus	Diptera	Mathis *et al.* (1993)	6	body length	U	—	6
Hecamede	Diptera	Mathis (1993)	12	body length	U	—	12
Microdonacia	Coleoptera	Reid (1992)	10	body length	M	—	10
Hister servus group	Coleoptera	Caterino (1999)	6	body length	U	—	6
Neoclypeodytes	Coleoptera	Miller (2001)	25	body length	U	—	25
Platynus degallieri group	Coleoptera	Liebherr (1992)	36	body length	U	—	36
Anchomenus clade	Coleoptera	Liebherr (1991)	29	body length	U	—	29
Ortheziola	Hemiptera	Kozar & Miller (2000)	16	body length	F	—	16
Atractotomus	Hemiptera	Stonedahl (1990)	37	body length	M	—	37
Amicotermes	Isoptera	Sands (1999)	12	head width	U	—	12
Astacoides	Decapoda	Horton (1987)	6	body length	M	—	6
Cardiolucina	Mollusca	Taylor & Glover (1997)	11	shell height	U	—	11
Pyrgulopsis	Mollusca	Hershler (1994)	60	shell height	U	—	60
Istiblennius	Osteichthyes	Springer & Williams (1994)	14	body length	M	—	14
Blenniella	Osteichthyes	Springer & Williams (1994)	9	body length	M	—	9
Curimata	Osteichthyes	Vari (1989*b*)	12	body length	U	—	12
Steindachnerina	Osteichthyes	Vari (1991)	21	body length	U	—	21
Psectrogaster	Osteichthyes	Vari (1989*a*)	8	body length	U	—	8
Ctenoluciidae	Osteichthyes	Vari (1995)	7	body length	U	—	7
Gruidae	Aves	Krajewski & King (1996)	15	body mass	B	Soden (2001)	15
Sulidae	Aves	Friesen *et al.* (1996)	9	body mass	F	Soden (2001)	9
Tetraoninae	Aves	Lucchini *et al.* (2001)	17	body mass	B	Soden (2001)	17
Alectoris	Aves	Randi (1996)	7	body mass	B	Soden (2001)	7
Kinosterninae	Chelonia	Iverson (1991)	20	body length	U	Ernst *et al.* (1998)	20
Marsupialia	Mammalia	Seal (1997)	273	body mass	B	Silva & Downing (1995)	215
Primates	Mammalia	Purvis *et al.* (2000)	233	body mass	B	Gittleman & Purvis (1998)	194
Carnivora	Mammalia	Bininda-Emonds *et al.* (1999)	271	body mass	B	Gittleman & Purvis (1998)	240

(b) *Body-size distribution*

We explored the distribution of body sizes within our dataset in two further ways. First, we calculated the skew (g_1) of the log-transformed body sizes within each phylogeny and tested for significant skew (Sokal & Rohlf 1995). We used a *t*-test to assess whether the mean skew across phylogenies differed significantly from zero. We also used a χ^2 contingency table to reveal whether the signs of the values of g_1 and b are independent, or whether an excess of large or small body sizes produces, respect-

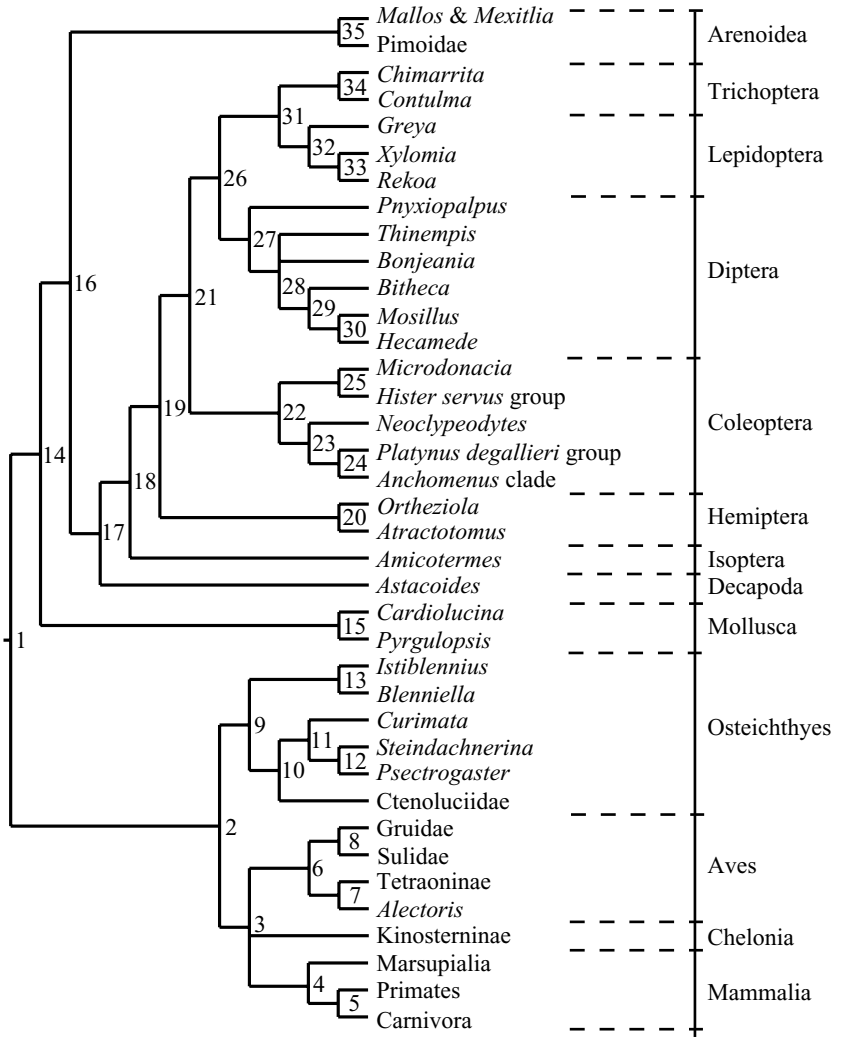

Figure 1. A cladogram of the relationships between the 38 study taxa.

ively, a positive or negative regression coefficient. Second, we examined the distribution of body-size values on each phylogeny to reveal whether there is any consistent pattern in the direction of body-size evolution. We used the number of nodes between each tip on the phylogeny and the root as a simple measure of whether species are placed distally or basally, and used Spearman's rank correlation (r_S) to test for any relationship between body size and node count within phylogenies. Node count and body size show non-independence within phylogenies and hence the significance levels of within phylogeny tests are unreliable. We therefore only assess, using a *t*-test, whether the mean r_S across phylogenies is significantly different from zero.

(c) *Tree imbalance*

Questions concerning differing rates of diversification between taxa are only meaningful if one can demonstrate that such rates do, in fact, differ. Tree imbalance statistics provide a way of assessing the likelihood of the distribution of taxa on a test phylogeny under a null model of equal net speciation rates across all lineages: the Equal Rates Markov (ERM) model (Raup *et al.* 1973). Many such statistics have been described, and their behaviour is well understood (see a review by Mooers & Heard 1997). We have used a modification of Fusco & Cronk's (1995) *I*, proposed by Purvis *et al.* (2002) and implemented in the computer program Mesa (Agapow & Purvis 2002). The weighted mean *I* has an expected mean of 0.5 under an ERM model (Purvis *et al.* 2002). We calculated the weighted mean *I* for each phylogeny, and used a Wilcoxon's signed-ranks test to establish whether the weighted mean *I* across phylogenies varies significantly from the expectation of 0.5. It should be noted that it is only sensible to calculate an imbalance for bifurcating nodes with four or more daughter taxa, since smaller nodes do not vary in their topology.

MacroCaic and Mesa both run under Mac OS and are freely available from http://www.bio.ic.ac.uk/evolve/software/index.html. Regression through the origin within studies is performed automatically by MacroCaic (Agapow & Isaac 2002): all other statistical analyses, including diagnostic plots for assessing the suitability of statistical models, were performed using R v.1.3.1 for Macintosh (Ihaka & Gentleman 1996).

4. RESULTS

Table 2 presents the results of the analyses of independent contrasts of body size against RRD, giving, for each phylogeny: the number of contrasts and the results of regression through the origin. Only one regresssion, for *Bitheca*, is significant at a table-wide level after sequential

Table 2. Results of within phylogeny analyses.
(The table shows the number of nodes for which I could be calculated for each phylogeny and the weighted mean of those I-values within phylogenies. The number of independent contrasts (n_c) calculated from each phylogeny is given along with the following details of regression through the origin of RRD against body-size contrasts for individual taxa: the regression coefficient (b), the standard error of b (s.e.$_b$), and the p-value (calculated from an F-ratio with 1 and $n_c - 1$ degrees of freedom). The sequential Bonferroni correction, assuming independence between the individual tests, has been used to calculate critical individual values of p for table-wide significance ($\alpha = 0.05$) (Rice 1989). The skew in the distribution of $\log_e$ body size and the Spearman's rank correlation coefficient (r_S) of node height against $\log_e$ body size are also given. Significant tests are indicated as follows: $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.)

	tree imbalance		independent contrasts				size distribution	
taxon	n_{nodes}	mean I_w	n_c	b	s.e.$_b$	p	skew	r_s
Mallos and *Mexitlia*	9	0.87	10	1.85	5.51	0.744	−0.21	−0.03
Pimoidae	4	0.39	6	4.79	3.09	0.182	−0.34	0.25
Chimaritta	6	0.26	8	−3.77	2.25	0.138	0.01	−0.77***
Contulma	3	0.64	7	3.90	4.32	0.402	0.57	0.11
Greya	6	0.74	8	5.95	5.14	0.285	−0.74	0.33
Xylomia	3	0.65	4	−9.18	15.37	0.592	0.35	−0.14
Rekoa	3	0.43	3	4.45	18.07	0.829	0.66	0.28
Pnyxiopalpus	6	0.29	7	−4.39	5.44	0.451	−0.5	−0.07
Thinempis	2	0.45	3	3.36	3.05	0.386	−0.39	0.64
Bonjeania	6	0.94	7	3.30	4.87	0.523	−0.25	0.04
Bitheca	7	0.33	7	−8.95	1.57	0.001*	−0.62	−0.76**
Mosillus	1	0	3	−3.48	3.91	0.467	0.25	−0.41
Hecamede	3	0.76	4	−8.85	18.10	0.658	0.01	−0.34
Microdonacia	5	0.56	6	−6.30	9.13	0.521	−0.55	0.06
Hister servus group	2	0.74	3	−3.46	4.05	0.483	0.98	−0.49
Neoclypeodytes	5	0.68	6	25.57	30.58	0.441	−0.68	0.02
Platynus degallieri group	16	0.79	22	−8.09	6.91	0.255	−0.33	−0.35*
Anchomenus clade	14	0.78	18	−0.98	4.48	0.830	0.21	−0.17
Ortheziola	8	0.95	9	−0.69	5.83	0.909	−0.69	−0.48
Atractotomus	21	0.88	26	−3.36	4.79	0.489	0.51	−0.29
Amicotermes	7	0.91	9	0.68	21.37	0.976	0	0.09
Astacoides	2	0.74	3	6.49	4.05	0.250	−0.1	0.74
Cardiolucina	3	0.36	5	−1.55	1.60	0.388	0.05	−0.65*
Pyrgulopsis	16	0.85	20	−1.89	2.31	0.425	−0.05	0.04
Istiblennius	2	0.79	4	1.02	12.74	0.941	−0.73	0.30
Blenniella	2	0	2	−1.34	0.43	0.198	−0.3	0.00
Curimata	2	0.35	4	−4.29	4.67	0.427	−0.25	−0.27
Steindachnerina	7	0.86	8	4.57	5.55	0.437	0.25	0.08
Psectrogaster	3	0.71	3	4.07	7.98	0.661	−0.95	0.28
Ctenoluciidae	2	0.25	3	4.37	1.80	0.136	0.61	0.75
Gruidae	7	0.72	10	−1.94	5.08	0.711	−0.14	0.06
Sulidae	4	0.71	6	8.31	6.11	0.232	0.05	0.25
Tetraoninae	7	0.48	10	1.05	3.13	0.745	0.35	0.53*
Alectoris	4	1	5	2.59	24.96	0.922	−0.68	0.27
Kinosterninae	12	0.81	15	−1.86	4.65	0.695	−0.1	−0.02
Marsupialia	69	0.61	75	−0.25	1.12	0.826	0.04	0.20**
Primates	71	0.55	98	0.32	1.34	0.810	−0.32	0.25***
Carnivora	105	0.61	117	−1.78	0.96	0.066	0.64***	−0.18**

Bonferroni correction (indicated by an asterisk in table 2). There is no tendency for the logit significance level of these regressions to increase with the log number of contrasts ($a = -0.20$, $b = -0.10$, $F_{1,36} = 0.108$, $p = 0.74$). The regression coefficients across phylogenies do not differ significantly from zero, as assessed by a Wilcoxon signed-ranks test ($V = 365$, $n = 38$, $p = 0.94$). A Wilcoxon test of b weighted by the inverse of the standard error of b is also non-significant ($V = 327$, $n = 38$, $p = 0.54$).

The results of the analyses of covariance using higher taxonomic relationships shown in figure 1 are summarized by node in table 3. Our model for the root node (node 1) shows no overall significant correlation for all pooled contrasts ($b = -0.77$, $F_{1,563} = 2.322$, $p = 0.13$). Linear regression, using all pooled contrasts, shows that RRD does not change with the mean body size at a node ($a = 0.02$, $b = -0.025$, $F_{1,562} = 0.988$, $p = 0.32$).

The mean skew in body sizes across phylogenies is not significantly different from zero (mean skew = −0.090, s.e. = 0.076, $t_{37} = -1.182$, $p = 0.25$) and the signs of g_1 and b are independent ($\chi^2_1 = 1.08$, $p = 0.30$). There is no consistent phylogenetic pattern of body size with respect to

Table 3. Analyses of covariance for higher taxonomic comparisons between our study taxa.
(For each node in figure 1, the contrasts are pooled for all the studies in the clade defined by that node, and also identified as subsets by daughter clade at the node. This table lists the *F*- and *p*-values for the overall relationship between RRD and body-size contrasts for the pooled contrasts and the *F*- and *p*-values for a difference between regression coefficients calculated for each daughter clade. The number of contrasts (n_c) pooled at each node is shown: the degrees of freedom for all *F*-tests are 1 and $n_c - 2$, except for the two polytomous nodes (3 and 28) where the degrees of freedom are 1 and $n_c - 3$ for the overall relationship and 2 and $n_c - 3$ for the subset differences. Significant tests are indicated as follows: $^*p < 0.1$, $^{**}p < 0.05$.)

node	n_c	F_{pooled}	p_{pooled}	$F_{subsets}$	$p_{subsets}$
1	564	2.32	0.13	0.07	0.79
2	360	1.34	0.25	0.63	0.43
3	336	1.69	0.19	0.19	0.83
4	290	1.70	0.19	0.43	0.51
5	215	2.14	0.15	1.58	0.21
6	31	0.18	0.67	< 0.01	0.99
7	15	0.09	0.77	0.01	0.94
8	16	0.09	0.77	1.43	0.25
9	24	0.27	0.61	0.08	0.78
10	18	0.33	0.57	0.30	0.59
11	15	0.05	0.82	1.71	0.21
12	11	0.91	0.37	< 0.01	0.97
13	6	< 0.01	0.96	0.03	0.88
14	204	1.05	0.31	0.48	0.49
15	25	0.95	0.34	0.01	0.94
16	179	0.13	0.72	1.42	0.24
17	163	0.63	0.43	0.96	0.33
18	160	0.88	0.35	0.01	0.91
19	151	0.93	0.34	0.08	0.78
20	35	0.30	0.59	0.14	0.71
21	116	0.62	0.43	0.45	0.50
22	55	0.80	0.38	0.13	0.72
23	46	0.29	0.59	0.85	0.36
24	40	0.41	0.53	0.61	0.44
25	9	0.99	0.35	0.08	0.78
26	61	0.11	0.74	0.01	0.93
27	31	0.04	0.85	0.44	0.51
28	24	< 0.01	0.98	3.11	0.07*
29	14	7.40	0.02**	0.50	0.49
30	7	0.44	0.53	0.10	0.76
31	30	0.09	0.76	1.11	0.30
32	15	0.48	0.50	0.84	0.38
33	7	0.15	0.71	0.30	0.61
34	15	0.88	0.37	2.60	0.13
35	16	0.75	0.40	0.17	0.69

distal and basal nodes (mean $r_s = 0.005$, s.e. $= 0.061$, $t_{37} = 0.082$, $p = 0.94$).

Table 2 also summarizes the calculation of imbalance statistics for each phylogeny, giving the number of nodes with more than three descendants, and the weighted mean imbalance of those nodes. The values of weighted mean *I* across phylogenies show negative skew ($g_1 = -0.70$), with a median value of 0.697. A Wilcoxon signed-ranks test shows the weighted mean *I* across phylogenies to be significantly different from 0.5; the expectation under an ERM null model ($V = 558.8$, $n = 38$, $p = 0.007$).

5. DISCUSSION

Although the weighted mean *I* shows that the phylogenies used in this study range from perfectly balanced (*Mosillus*, *Bleniella*) to perfectly unbalanced (*Alectoris*), the set of phylogenies is significantly unbalanced as a whole, rejecting an ERM null model of clade growth. Despite this evidence that rates of cladogenesis vary within phylogenies, we find little support for the hypothesis that this variation depends on body size. Within our 38 test phylogenies, only *Bitheca* (Diptera: Sphaeroceridae) shows a significant relationship, showing increased species richness at small body size. The sequential Bonferroni correction shows that the result for *Bitheca* ($p = 0.001$, $r^2 = 0.84$) is still significant with a table-wide α of 0.048, when the increased type I error rate from multiple tests is taken into account. Counter-intuitively, *Bitheca* is one of the 12 test phylogenies that have a weighted mean *I* of less than 0.5. The phylogeny of *Bitheca* contains seven nodes for which *I* can be calculated, of which three are maximally unbalanced and four are highly balanced, with a weighted mean *I* of 0.33. Contrasts can be calculated at the same seven nodes: all four balanced nodes (i.e. low RRD) show only small differences in body size between the sister taxa, whereas all three unbalanced nodes (i.e. higher RRD) compare a single larger bodied species with a more spe-

ciose sister clade with markedly smaller body size. The result for *Bitheca*, therefore, does appear to reveal a consistent pattern in the evolution of the clade, despite the small number of contrasts. The regression coefficients (b) across phylogenies, however, show no overall trend towards higher species richness at small body size, even when uncertainty in estimates of b is taken into account.

Investigation of the differences between clades at nodes identified from figure 1, and overall relationships at each node using ANCOVA, reveals no taxonomic pattern in the relationship between species richness and body size. Node 29 shows an overall significant relationship ($p = 0.02$) for the clade (*Bitheca*, (*Mosillus*, *Hecamede*)), with no differences between those genera, but this is unsurprising, given the strength of the relationship within *Bitheca*. It is also, perhaps, unsurprising that the closest to a significant difference between groups at a node is the comparison among (*Bitheca*, (*Mosillus*, *Hecamede*)), *Bonjeania* and *Thinempis* (node 28, $p = 0.07$).

This lack of any convincing evolutionary pattern is inconsistent with the macro-ecological pattern of body-size distributions. There are a number of possible methodological explanations for this inconsistency within this study. Our set of phylogenies comprises a taxonomically restricted subset of metazoan taxa, reflecting unevenness in the distribution of taxonomic effort across the Metazoa. The taxa used are also a biotically restricted subset, with marine taxa noticeably underrepresented. The failure to find any differences at higher taxonomic levels, particularly at the deepest nodes in figure 1, may reflect failings in the coverage of the data. Additionally, the power of independent contrasts of species richness to detect correlates of net rates of diversification is not, as yet, fully explored (Isaac *et al.* 2002). The use of real branch lengths is known to increase the power of independent contrasts to reveal significant correlations: Gittleman & Purvis (1998) found a significant ($p = 0.03$) negative relationship between body size and species richness for the carnivores, using real branch lengths; this study substitutes equal branch lengths and finds a non-significant ($p = 0.07$) relationship. Simulations have shown that, while inaccurate branch length information does increase type I error rates for independent contrast analyses (e.g. Martins & Garland 1991; Purvis *et al.* 1994; Díaz-Uriarte & Garland 1998), such analyses are no more unreliable than employing 'non-phylogenetic' analyses (Martins & Garland 1991).

Whilst we accept the reality of these concerns, we think it unlikely that they invalidate our findings. Not only do we find little evidence within phylogenies for a relationship between body size and species richness, we find no support whatsoever for any consistent pattern across a large set of independent studies. Our results also broadly agree with previous studies looking within clades using independent contrasts: of the studies mentioned in the introduction, Katzourakis *et al.* (2001), Orme *et al.* (2002) and Nee *et al.* (1992) found no evidence, Gittleman & Purvis (1998) found a significant relationship only within the caniform carnivores, and Gardezi & da Silva (1999) found that small size is not a general correlate of species diversity, but that radiations among mammalian clades tend to be small bodied. Independent contrasts have been successfully used to support several other hypotheses of correlates of species richness. Such supported correlates include latitude (Cardillo 1999), diet breadth (Owens *et al.* 1999; Katzourakis *et al.* 2001), sexual dimorphism (Owens *et al.* 1999), sexual selection (Barraclough *et al.* 1995), rates of genetic change (Barraclough *et al.* 1996) and dispersal ability (Owens *et al.* 1999).

Another possible explanation is that the body-size distributions of our studies do not show any general pattern towards positive skew, with only the Carnivora showing a significant level of skew. Since we are testing for the increased speciation rates among small-bodied taxa implied by positive skew in size distributions, such an explanation seems persuasive, but there are two possible confounding factors. The first is that assessing the significance and, to a lesser degree, the extent of skew of small samples is statistically unreliable (Sokal & Rohlf 1995). Second, it is known that the spatial scale at which size distributions are assessed changes the resulting distribution, with small spatial scales giving approximately uniform body-size distributions (Brown & Nicoletto 1991), and the taxa used here span a range of spatial scales. It is also unclear whether the body-size distribution of an evolutionarily defined group is always equivalent to a body-size distribution for an ecologically defined group, such as those typically used in macro-ecological studies. Higher rates of cladogenesis at large body size, in conjunction with strong upper constraints on body size, could lead to larger numbers of smaller bodied species in the absence of selection for small size, but such a pattern would be revealed as a positive regression coefficient in analysis of species-richness contrasts against body-size contrasts.

It is possible that organisms compared at a species level may be too constrained by ecological similarities for differences in body size to drive speciation rate. If this argument is correct then significant correlations may only emerge when considering nodes with large body-size differences. We have investigated this possibility by using the unstandardized body-size contrasts (Felsenstein 1985) to identify subsets within our pooled body-size and species-richness contrasts. We have fitted sequential regressions through the origin of the standardized body-size contrasts as predictors of RRD, removing individual data points by increasing value of the unstandardized body-size contrasts. None of these sequential models shows a significant relationship between RRD and body size: the magnitude of the body-size differences considered is not important in our dataset.

This study therefore serves to emphasize the lack of any strong support for evolutionary trends towards increased cladogenesis in smaller bodied clades. We also present evidence that there are no consistent differences in the body-size–species-richness relationship across a wide range of animal taxa. Reconciliation of the macro-ecological pattern of increased species richness associated with small body size, with the absence of any consistent evidence of the evolution of that pattern, represents a major challenge for the future.

We thank David Soden and Ian Owens for use of avian body-size data, Paul-Michael Agapow for his help with MESA and access to unpublished work and Robert Belshaw, Rich Grenyer and one anonymous referee for comments on the manuscript. We particularly thank Steve Heard for his thoughtful and detailed review of the manuscript. This work was supported

by NERC grants to A.P. (GR3/11526) and C.D.L.O. (GT04/98/MS/154).

REFERENCES

Agapow, P.-M. & Isaac, N. J. B. 2002 MacroCaic: revealing correlates of species richness by comparative analysis. *Diversity Distrib.* **8**, 41–43.

Agapow, P.-M. & Purvis, A. 2002 Mesa: a framework for macroevolutionary simulation and analysis. *Syst. Biol.* (Submitted.)

Avise, J. C. & Johns, G. C. 1999 Proposal for a standardized temporal scheme of biological classification for extant species. *Proc. Natl Acad. Sci. USA* **96**, 7358–7363.

Barraclough, T. G., Harvey, P. H. & Nee, S. 1995 Sexual selection and taxonomic diversity in passerine birds. *Proc. R. Soc. Lond.* B **259**, 211–215.

Barraclough, T. G., Harvey, P. H. & Nee, S. 1996 Rate of *rbc*L gene sequence evolution and species diversification in flowering plants (angiosperms). *Proc. R. Soc. Lond.* B **263**, 589–591.

Bickel, D. J. 1996 *Thinempis*, a new genus from Australia and New Zealand (Diptera: Empididae), with notes on the tribal classification of the Empidinae. *Syst. Entomol.* **21**, 115–128.

Bininda-Emonds, O. R. P., Gittleman, J. L. & Purvis, A. 1999 Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biol. Rev.* **74**, 143–175.

Blahnik, R. J. 1997 Systematics of *Chimarrita*, a new subgenus of *Chimarra* (Trichoptera: Philopotamidae). *Syst. Entomol.* **22**, 199–243.

Bond, J. E. & Opell, B. D. 1997 Systematics of the spider genera *Mallos* and *Mexitlia* (Araneae, Dictynidae). *Zool. J. Linn. Soc.* **119**, 389–445.

Brown, J. H. & Nicoletto, P. F. 1991 Spatial scaling of species composition: body masses of North American land mammals. *Am. Nat.* **138**, 1478–1512.

Brown, J. H., Marquet, P. A. & Taper, M. L. 1993 Evolution of body-size—consequences of an energetic definition of fitness. *Am. Nat.* **142**, 573–584.

Cardillo, M. 1999 Latitude and rates of diversification in birds and butterflies. *Proc. R. Soc. Lond.* B **266**, 1221–1225. (DOI 10.1098/rspb.1999.0766.)

Caterino, M. S. 1999 Taxonomy and phylogeny of the *Hister servus* group (Coleoptera: Histeridae): a neotropical radiation. *Syst. Entomol.* **24**, 351–376.

Davis, D. R., Pellmyr, O. & Thompson, J. N. 1992 Biology and systematics of *Greya* Busck and *Tetragma*, new genus (Lepidoptera: Prodoxidae). *Smithson. Cont. Zool.* **524**, 1–88.

Dial, K. P. & Marzluff, J. M. 1988 Are the smallest organisms the most diverse? *Ecology* **69**, 1620–1624.

Díaz-Uriarte, R. & Garland, T. 1998 Effects of branch length errors on the performance of phylogenetically independent contrasts. *Syst. Biol.* **47**, 654–672.

Ernst, C. H., Altenburg, R. G. M. & Balbour, R. W. 1998 *Turtles of the world 1.0 CD-ROM*. France: UNESCO Publishing.

Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.

Friesen, V. L., Baker, A. J. & Piatt, J. F. 1996 Phylogenetic relationships within the Alcidae (Charadriiformes: Aves) inferred from total molecular evidence. *Mol. Biol. Evol.* **13**, 359–367.

Fusco, G. & Cronk, Q. C. B. 1995 A new method for evaluating the shape of large phylogenies. *J. Theor. Biol.* **175**, 235–243.

Gardezi, T. & da Silva, J. 1999 Diversity in relation to body size in mammals: a comparative study. *Am. Nat.* **153**, 110–123.

Garland, T., Harvey, P. H. & Ives, A. R. 1992 Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–32.

Gaston, K. J. & Blackburn, T. M. 2000 *Pattern and process in macroecology*. Oxford: Blackwell Science.

Gauthier, J., Kluge, A. G. & Rowe, T. 1988 Amniote phylogeny and the importance of fossils. *Cladistics* **4**, 105–209.

Giribet, G., Edgecombe, G. D. & Wheeler, W. C. 2001 Arthropod phylogeny based on eight molecular loci and morphology. *Nature* **413**, 157–161.

Gittleman, J. & Purvis, A. 1998 Body size and species-richness in carnivores and primates. *Proc. R. Soc. Lond.* B **265**, 113–119. (DOI 10.1098/rspb.1998.0271.)

Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford Series in Ecology and Evolution. Oxford University Press.

Hedges, S. B. 2001 Molecular evidence for the early history of living vertebrates. In *Major events in early vertebrate evolution: paleontology, phylogeny, genetics and development* (ed. P. E. Ahlberg), pp. 119–134. London: Taylor & Francis.

Hershler, R. 1994 A review of the North American freshwater snail genus *Pyrgulopsis* (Hydrobiidae). *Smithson. Cont. Zool.* **554**, 1–115.

Holzenthal, R. W. & Flint, O. S. J. 1995 Studies of neotropical caddisflies, LI: systematics of the neotropical caddisfly genus *Contulma* (Trichoptera: Anomalopsychidae). *Smithson. Cont. Zool.* **575**, 1–59.

Hormiga, G. 1994 A revision and cladistic analysis of the spider family Pimoidae (Araneoidea: Aranae). *Smithson. Cont. Zool.* **549**, 1–104.

Horton, H. H. J. 1987 A review of the crayfish genus *Astacoides* (Decapoda: Parasiticidae). *Smithson. Cont. Zool.* **443**, 1–50.

Hutchinson, G. E. & MacArthur, R. H. 1959 A theoretical ecological model of size distributions among species of animals. *Am. Nat.* **93**, 117–125.

Hwang, U. W., Friedrich, M., Tautz, D., Park, C. J. & Kim, W. 2001 Mitochondrial protein phylogeny joins myriapods with chelicerates. *Nature* **413**, 154–157.

Ihaka, R. & Gentleman, R. 1996 R: a language for data analysis and graphics. *J. Comp. Graph. Stat.* **5**, 299–314.

Isaac, N. J. B., Agapow, P.-M. & Purvis, A. 2002 The effect of analysis techniques on the broad-sense validity of a new method for testing macroevolutionary hypotheses. *Evolution.* (Submitted.)

Iverson, J. B. 1991 Phylogenetic hypotheses for the evolution of modern kinosternine turtles. *Herpetol. Monogr.* **5**, 1–27.

Katzourakis, A., Purvis, A., Azmeh, S., Rotheray, G. & Gilbert, F. 2001 Macroevolution of hoverflies (Diptera: Syrphidae): the effect of using higher-level taxa in studies of biodiversity, and correlates of species richness. *J. Evol. Biol.* **14**, 219–227.

Kochmer, J. P. & Wagner, R. H. 1988 Why are there so many kinds of passerine birds? Because they are small. A reply to Raikow. *Syst. Zool.* **37**, 68–69.

Kozar, F. & Miller, D. R. 2000 World revision of *Ortheziola* Sulc (Homoptera: Coccoidea: Ortheziidae) with descriptions of eleven new species. *Syst. Entomol.* **25**, 15–45.

Kozlowski, J. & Weiner, J. 1997 Interspecific allometries are by-products of body size optimization. *Am. Nat.* **149**, 352–380.

Krajewski, C. & King, D. G. 1996 Molecular divergence and phylogeny: rates and patterns of cytochrome *b* evolution in cranes. *Mol. Biol. Evol.* **13**, 21–30.

Liebherr, J. K. 1991 Phylogeny and revision of the *Anchomenus* clade: the genera *Tetraleucus*, *Anchomenus*, *Sericoda*, and *Elliptoleus* (Coleoptera: Carabidae). *Bull. Am. Mus. Nat. Hist.* **202**, 1–163.

Liebherr, J. K. 1992 Phylogeny and revision of the *Platynus*

degallieri species group (Coleoptera: Carabidae: Platynini). *Bull. Am. Mus. Nat. Hist.* **214**, 1–115.

Liu, F. G. R., Miyamoto, M. M., Freire, N. P., Ong, P. Q., Tennant, M. R., Young, T. S. & Gugel, K. F. 2001 Molecular and morphological supertrees for eutherian (placental) mammals. *Science* **291**, 1786–1789.

Lucchini, V., Höglund, J., Klaus, S., Swenson, J. & Randi, E. 2001 Historical biogeography and a mitochondrial DNA phylogeny of grouse and ptarmigan. *Mol. Phyl. Evol.* **20**, 149–162.

Marshall, S. A. 1987 Systematics of *Bitheca*, a new genus of New World Sphaeroceridae (Diptera). *Syst. Entomol.* **12**, 355–380.

Martins, E. P. & Garland, T. 1991 Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* **45**, 534–557.

Mathis, W. N. 1993 Studies of Gymnomyzinae (Diptera: Ephydridae). IV. A revision of the shore-fly genus *Hecamede* Haliday. *Smithson. Cont. Zool.* **541**, 1–46.

Mathis, W. N., Zatwarnicki, T. & Krivosheina, M. G. 1993 Studies of Gymnomyzinae (Diptera: Ephydridae). V. A revision of the shore-fly genus *Mosillus* Latreille. *Smithson. Cont. Zool.* **548**, 1–38.

Mikkola, K. 1998 Revision of the genus *Xylomoia* Staudinger (Lepidoptera: Noctuidae), with descriptions of two new species. *Syst. Entomol.* **23**, 173–186.

Miller, K. B. 2001 Revision and phylogenetic analysis of the New World genus *Neoclypeodytes* Young (Coleoptera: Dytiscidae: Hydroporinae: Bidessini). *Syst. Entomol.* **26**, 87–123.

Mooers, A. Ø. & Heard, S. B. 1997 Inferring evolutionary processes from phylogenetic tree shape. *Q. Rev. Biol.* **72**, 31–54.

Nee, S., Mooers, A. & Harvey, P. 1992 Tempo and mode of evolution revealed from molecular phylogenies. *Proc. Natl Acad. Sci. USA* **89**, 8322–8326.

Nielsen, C. 1995 *Animal evolution: interrelationships of the living phyla*. Oxford University Press.

Orme, C. D. L., Quicke, D. L. J., Cook, J. M. & Purvis, A. 2002 Body size does not predict species richness among metazoan phyla. *J. Evol. Biol.* **15**, 235–247.

Owens, I. P. F., Bennett, P. M. & Harvey, P. H. 1999 Species richness among birds: body size, life history, sexual selection or ecology? *Proc. R. Soc. Lond.* B **266**, 933–939. (DOI 10.1098/rspb.1999.0726.)

Pagel, M. D. 1992 A method for the analysis of comparative data. *J. Theor. Biol.* **156**, 431–442.

Peters, R. H. 1983 *The ecological implications of body size*. Cambridge Studies in Ecology. Cambridge University Press.

Purvis, A., Gittleman, J. L. & Luh, H.-K. 1994 Truth or consequences: effects of phylogenetic accuracy on two comparative methods. *J. Theor. Biol.* **167**, 293–300.

Purvis, A., Agapow, P.-M., Gittleman, J. L. & Mace, G. M. 2000 Nonrandom extinction and the loss of evolutionary history. *Science* **288**, 328–330.

Purvis, A., Katzourakis, A. & Agapow, P.-M. 2002 Evaluating phylogenetic tree shape: two modifications to Fusco & Cronk's method. *J. Theor. Biol.* **214**, 99–103.

Randi, E. 1996 A mitochondrial cytochrome *b* phylogeny of the *Alectoris* partridges. *Mol. Phyl. Evol.* **6**, 214–227.

Raup, D. M., Gould, S. J., Schopf, T. J. & Simberloff, D. 1973 Stochastic models of phylogeny and the evolution of diversity. *J. Geol.* **81**, 525–542.

Reid, C. A. M. 1992 The leaf-beetle genus *Microdonacia* Blackburn (Coleoptera, Chrysomelidae, Galerucinae)—revision and systematic placement. *Syst. Entomol.* **17**, 359–387.

Rice, W. R. 1989 Analyzing tables of statistical tests. *Evolution* **43**, 223–225.

Robbins, R. K. 1991 Evolution, comparative morphology and identification of the eumaeine butterfly genus *Rekoa* Kaye (Lycaenidae: Theclinae). *Smithson. Cont. Zool.* **498**, 1–64.

Sands, W. A. 1999 A review of the soldierless African termite genus *Amicotermes* Sands 1972 (Isoptera, Termitidae, Apicotermitinae). *Bull. Nat. Hist. Mus. Lond.* (*Entomol.*) **68**, 145–193.

Seal, G. 1997 Phylogeny and macroevolution of marsupials. MSc thesis, Natural History Museum & Imperial College, UK.

Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and the classification of the birds: a study in molecular evolution*. New Haven, CT: Yale University Press.

Silva, M. & Downing, J. A. 1995 *CRC handbook of mammalian body masses*. Boca Raton, FL: CRC Press.

Soden, D. 2001 Size, dichromatism and cladogenesis of birds. MSc thesis, Natural History Museum & Imperial College, UK.

Sokal, R. R. & Rohlf, F. J. 1995 *Biometry*. New York: Freeman.

Springer, V. G. & Williams, J. T. 1994 The Indo-West Pacific blenniid fish genus *Istiblennius* reappraised: a revision of *Istiblennius*, *Blenniella*, and *Paralticus*, new genus. *Smithson. Cont. Zool.* **565**, 1–193.

Stanley, S. M. 1973 An explanation for Cope's rule. *Evolution* **27**, 1–26.

Stonedahl, G. M. 1990 Revision and cladistic analysis of the Holarctic genus *Atractotomus* Fieber (Heteroptera: Miridae: Phylinae). *Bull. Am. Mus. Nat. Hist.* **198**, 1–88.

Taylor, J. D. & Glover, E. A. 1997 The lucinid bivalve genus *Cardiolucina* (Mollusca, Bivalvia, Lucinidae): systematics, anatomy and relationships. *Bull. Nat. Hist. Mus. Lond.* (*Zool.*) **63**, 93–122.

Van Valen, L. 1973 Body size and numbers of plants and animals. *Evolution* **27**, 27–35.

Vari, R. P. 1989*a* A phylogenetic study of the neotropical characiform family Curimatidae (Pisces: Ostariophysi). *Smithson. Cont. Zool.* **471**, 1–71.

Vari, R. P. 1989*b* Systematics of the neotropical characiform genus *Curimata* Bosc (Pisces: Characiformes). *Smithson. Cont. Zool.* **474**, 1–42.

Vari, R. P. 1991 Systematics of the neotropical characiform genus *Steindachnerina* Fowler (Pisces: Ostariophysi). *Smithson. Cont. Zool.* **507**, 1–118.

Vari, R. P. 1995 The neotropical fish family Ctenoluciidae (Teleostei: Otariophysi: Characiformes): supra and intrafamilial phylogenetic relationships, with a revisionary study. *Smithson. Cont. Zool.* **564**, 1–97.

Vilkamaa, P. & Hippa, H. 1999 The genus *Pnyxiopalpus* gen.n. (Diptera: Sciaridae). *Syst. Entomol.* **24**, 209–241.

Wheeler, W. C., Whiting, M., Wheeler, Q. D. & Carpenter, J. M. 2001 The phylogeny of the extant hexapod orders. *Cladistics* **17**, 113–169.

Winterton, S. L., Skevington, J. H., Irwin, M. E. & Yeates, D. K. 2000 Phylogenetic revision of *Bonjeania* Irwin & Lyneborg (Diptera: Therevidae). *Syst. Entomol.* **25**, 295–324.

Zrzavy, J., Mihulka, S., Kepka, P., Bezdek, A. & Tietz, D. 1998 Phylogeny of the Metazoa based on morphological and 18S ribosomal DNA evidence. *Cladistics* **14**, 249–285.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.