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A morphometrics-based phylogeny of the temperate Gondwanan mite harvestmen (Opiliones, Cyphophthalmi, Pettalidae)

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Abstract

A phylogenetic estimation of the temperate Gondwanan mite harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi) was conducted using 143 morphological variables (59 raw and 84 scaled measurements) from 37 ingroup and 15 outgroup terminals. We used custom algorithms to do pairwise comparisons between characters and identify sets of dependent characters, which were collapsed using principal components analysis. We analysed the resulting data without discretization under the parsimony criterion. Monophyly or paraphyly of most groups suspected from previous molecular and morphological phylogenetic studies were recovered. Trees were optimized for monophyly of 20 different focus clades by varying character phylogenetic independence. This yielded a final tree with monophyly of 15 out of 20 focus clades, including the South African pettalids, which contains the troglomorphic species *Speleosiro argasiformis* Lawrence, 1931. Two of the remaining five clades were found paraphyletic, with the genera *Aoraki*, *Rakaia*, and *Siro* always being found polyphyletic.

Key words: Continuous data – morphometrics – character independence – Cyphophthalmi – Pettalidae – character coding – homology – troglomorphism

Introduction

The phylogenetic placement of a species or supraspecific taxon entails considerable data collection, including morphoanatomical descriptors and molecular data. Morphological data begin with descriptions rich in size and shape information, continue through codifications of characters for phylogenetic analysis and, in some cases, return to morphometrics. For example, Pelser et al.'s (2004) first combined molecular and morphological analysis of ragworts, which is also the first to include ragwort characters derived from morphological measurements and ratios, begins with a history of the genus from its original description in the early 19th century and subsequent reinterpretations of its features, to more detailed inspections and attempts to discretize characters and finally to molecular analyses from the previous year. In addition, recent analyses of rodent skulls in search of phylogenetic information (Gunduz et al. 2007; Macholan 2008) are an interesting return to morphology in a group that has helped mark the milestones in systematics, from the phenetic analysis of morphological data (Lidicker 1973; Levenson et al. 1985) and cladistic analysis of electrophoretic (Levenson et al. 1985) and discrete morphological data (Novacek 1992), to some of the more illuminating discussions on the analysis of DNA sequence data (Allard et al. 1991; Graur et al. 1991; Luckett and Hartenberger 1993; Sullivan and Swofford 1997; DeBry 2003). Other researchers have looked to measurements and shape descriptors for new characters (Fink and Zelditch 1995; Zelditch et al. 1995; Chu 1998; Budd and Klaus 2001; Bookstein 2002; Buijsen et al. 2003; Datwyler and Wolfe 2004; Pelser et al. 2004; Dessein et al. 2005; Abdala 2007; Lens et al. 2007; Lycett 2007; Asher et al. 2008; Dominguez and Roig-Junent 2008; Hardy et al. 2008; Moon et al. 2008) and we join their efforts here.

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Cyphophthalmi are small (1–8 mm) arthropods that have a single adult molt and adult sizes and proportions conserved enough to be useful in species descriptions. Species ranges are often just the forests around their type localities, and they have been shown to be extremely poor dispersers and thus excellent biogeographic models of vicariance (Giribet 2000). A number of cyphophthalmid molecular phylogenies exist (Giribet and Boyer 2002; Giribet 2003; Boyer et al. 2005; Schwendinger and Giribet 2005; Boyer and Giribet 2007; Boyer et al. 2007a; b; Clouse and Giribet 2007; Boyer and Giribet 2009), which, combined with their tendency to form monophyletic groups that correlate with historical landmasses (Boyer et al. 2007b), give us multiple opportunities to evaluate the reasonableness of the phylogenies produced here. We were especially interested in the placement of the troglomorphic South African species *Speleosiro argasiformis* Lawrence, 1931 (Fig. 1). It shares clear synapomorphies with the Pettalidae, but without molecular data, we have not been able to explore its relationship with other species in the family. We wondered if it is a derived or relictual member of one of the two other South African genera (*Purcellia* and *Parapurcellia*), or whether it represents a lineage more closely aligned with genera outside the region. In addition, we wondered if measurements of morphological features of this species would contain a phylogenetic signal strong enough to overcome its clear adaptations to a cave habitat.

One of our main concerns in this study was the phylogenetic independence of the measurements being optimized during tree searches. Phylogenetic independence of characters means that each changes state due to genetic events isolated from those causing state changes in other characters. It has been called 'the fundamental attribute of a useful character' (Doyle 1997), and the interplay of coding methods and character independence has been the subject of some discussion with discretized data (Kluge and Farris 1969; Pimentel and Riggins 1987; Pleijel 1995; Lee and Bryant 1999; Fitzhugh 2006; Vieira et al. 2007). Combining suspected non-independent characters to

create multistate discrete characters mitigates the probability of counting dependent events multiple times in phylogenetic reconstruction, although this can also eliminate important information (Lee and Bryant 1999; Strong and Lipscomb 1999). Two other options besides combining all suspected non-independent characters are (1) an *a priori* assumption that all characters are independent pending *a posteriori* evidence to the contrary (Felsenstein 1973; Fink and Zelditch 1995; Wagner 2000; Strait and Grine 2004); and (2) tests for independence before tree searching.

For the latter, a common method has been to eliminate or combine correlated characters (Poe and Wiens 2000; Poe 2004; Molina et al. 2008; Dell'Ampio et al. 2009; Naczi 2009) or at least test which characters are providing the most signal and should be examined more closely for correlations (DeGusta 2004). This follows from a definition of independence that 'the state of one character does not predict the state of another' (Doyle 1997). However, eliminating correlated characters completely may not be desirable, for they could trend together simply because they are actual synapomorphies of the same clade or because of biological constraints such as pleiotropy, allometry, biomechanics and adaptation (Emerson and Hastings 1998; Kluge 2007). Indeed, phylogenetic independence cannot be entirely known beforehand (Zelditch et al. 2000) and correlated characters have not necessarily both changed state due to a single mutation. For this reason, O'Keefe and Wagner (2001) introduced a pre-tree–searching ('tree-free') test of independence that relies on recursive vector analysis, which has been used by Sadleir and Makovicky (2008) on a data set of crocodilian cranial features. Moreover, confusion between phylogenetic independence and the independence of ecological hypotheses being tested by character correlation has warranted a clarification by Luckow and Bruneau (1997).

The need to focus on character independence has been raised in various discussions of systematic methods (Wilkinson 1995; Wiens and Hillis 1996; Grant and Kluge 2004; Goloboff et al. 2006; Assis and Brigandt 2009), with perhaps the most urgency coming from vertebrate morphologists (Emerson and Hastings 1998), especially anthropologists (Pope 1992). Strait and Grine (2004) downweighted hominid cranial characters that were parts of a single functional complex, but other characters that evolved in unison and were perhaps integrated in some way were left as independent, since they previously demonstrated that hypotheses of dependence tended to be overstated and remove too much phylogenetic information (Strait 2001). Other studies have specifically examined skulls of certain taxa *vis-à-vis* a phylogeny for the independence and thus phylogenetic usefulness of their features (Macholan 2008; Tückmantel et al. 2009). González-José et al. (2008) identified character complexes that had been determined previously to be part of certain 'modules' on the hominid skull and they then collapsed each complex into a single character using principal components analysis.

Material and Methods

Using the applications Adobe Photoshop CS Version 8.0 and ImageJ available at http://rsb.info.nih.gov/nih-image, we measured 59 features from 37 ingroup and 15 outgroup terminals (Table 1) (Appendix S1) in our collection of specimen photographs [captured using electron and light microscopy, as described in Clouse and Giribet (2007)]. We measured males, which are the standard sex used in cyphophthalmid taxonomy and when possible, type specimens. From the 59 raw measurements, an additional 84 scaled

measurements were calculated (such as the ratio of the chelicer to the dorsal scutum length) (Fig. 2) (Table 1). The use of simple ratios has been the subject of debate, since they can both fail to eliminate size information and introduce new relationships (Atchley et al. 1976; Corruccini 1977; Albrecht 1978; Atchley 1978; Atchley and Anderson 1978; Dodson 1978; Hills 1978; Albrecht et al. 1993; Rae 2002), but we used them as a first pass to see if our independence analysis would sufficiently collapse those that still correlated with size. All the data were normalized by conversion into z-scores and they were made positive by subtracting the minimum value of the whole data set (continuous data in TNT must be positive, as discussed below).

In the application MatLab (The Mathworks, Inc., Natick, MA, USA) independence analysis (IA) and subsequent character collapses were done using custom scripts (Appendix S2). We recognized dependence by a correlation between characters with an absence of outliers; thus, we developed a cutoff value parameterizing the area around the unity line of the scatter plots between characters, which created a zone in which we would find dependent characters (Fig. 3). Zones determined by the cutoff parameter should, by design, reflect nested confidence intervals and their shape should be determined empirically by the distributions of pairwise character scatter plots. In our dataset, character pairs had scatter plots with confidence intervals ranging in shape from linear (highly correlated characters) to elliptical (partially correlated) to circular (uncorrelated). Thus, we used linear confidence intervals at distances from the linear trendline determined by the cutoff value. This value, which had units of standard deviations in our normalized data sets, could be changed, allowing us to optimize the definition of an outlier in character correlations. [Our minimum requirement of only a single exception to character state correlation to establish independence is reminiscent of Patterson's (1988) use of a single example of character co-occurrence to determine a lack of homology.] Alternative methods to detect non-linear dependence would require non-linear confidence intervals and corresponding cutoff values.

Character comparisons in which all data were within the cutoff parameter were considered dependent and characters could be sequentially or simultaneously dependent on more than one other character at the same cutoff value. That is, character A could be dependent on both B and C or A could be dependent on B, which in turn was dependent on C. We called these groups of connected characters 'dependence networks' and each network was collapsed using PCA. Establishing character independence required having terminals with outlier values for each character pairing. Thus, independence was highly terminal-dependent, and consequently so was the nature of each terminal's dependence networks and their resulting PCAs. The various rotations of the multivariate space representing each dependence network would be affected by the inclusion or exclusion of certain characters (Adams and Rosenberg 1998; Rohlf 1998; Monteiro 2000), which, in turn, would be affected by the terminal set. Terminal-dependent effects in phylogenetics are not desirable but neither are they new, and given our broad selection of terminals from across different families, sizes and shapes, we felt the effects here would be minimal.

We did tree-searches on five alternate data sets to test the efficacy of IA and PCA, as well as explore alternate views of the appropriate handing of raw and scaled data. For example, the collapse of raw and scaled measurements in the same PCA is arguably mathematically dubious (as their original units are not comparable), but to have separate independence analyses of raw and scaled measurements opens the door to dependent characters entering the phylogenetic searches. The methods were as follows:

(1) all data, with no IA or PCA;

(2) only the scaled data, with no IA or PCA;

(3) all raw measurements were reduced by PCA to two PCs (encompassing >90% of the variance in the data), then IA was performed on the scaled measurements, with networks of dependent scaled measurements determined by the cutoff value and collapsed using separate PCAs;

(4) IAs were done on raw and scaled measurements separately (using a single cutoff value) and sets of dependent characters from each category were collapsed using distinct PCAs for each set; and

Table 1. Characters for the Pettalidae data set, grouped into dependent networks at the optimal cutoff value. The left column contains raw size measures, and the right column contains scaled measures denoted by the ratio of raw measure characters (or by specific measurements taken for the sole purpose of local scaling). Alternating shaded blocks (gray and white) indicate groups of characters that were identified as mutually dependent and collapsed in the data set used to generate the optimal tree

1 Dorsal scutum max length	70 Width between two most posterior points (11/3)
2 Prosomal max width	71 Width between ozophore lateral margins (8/2)
3 Opisthosomal max width	72 Width between ozophore distal tips (9/2)
4 Scutum max thickness	73 Ozophore height above lateral margin $(10/73_D)$
5 Tergite max thickness	87 Anal plate midline depression width $(87_N/20)$
6 Sternite max thickness	88 Anal plate midline depression length $(88_N/21)$
7 Tergite I min width	91 Anal plate unornamented region width $(91_N/20)$
8 Width between ozophore lateral margins	93 Fraction of anal plate modified max $(87 \times 88, 89 \times 90, 91 \times 92)$
9 Width between ozophore distal tips	96 Tergite IX length (23/1)
10 Ozophore height above lateral margin	102 Sternite 9 concavity (24/1)
12 Tergite VIII width	103 Sternite 8 concavity (25/1)
14 Tergite VII length	104 Sternite 7 concavity (26/1)
15 Tergite VI length	112 Gonostome distance from anterior margin (36/1)
20 Anal plate width	114 Sternal plate length (37/1)
21 Anal plate length	118 Coxae IV midline meeting length (38/1)
23 Tergite IX length	61 Prosomal max width position $(61_N/1)$
24 Sternite 9 length	62 Opisthosomal max width position $(62_N/1)$
25 Sternite 8 length	121 Coxae I radial length (40/2)
26 Sternite 7 length	122 Coxae II radial length (41/2)
27 Sternite 6 length	123 Coxae III radial length (43/2)
28 Sternite 9 concavity	124 Coxae IV radial length (44/2)
29 Sternite 8 concavity	133 Chelicer mobile digit length (52/1)
30 Sternite 7 concavity	134 Chelicer mobile digit local length (52/51)
32 Spiracle width	137 Chelicer segment 1 thickness (55/4)
33 Width between spiracles	138 Chelicer segment 1 proximal narrowness (56/4)
34 Gonostome width	60 Length to width ratio (1/max(2,3))
35 Gonostome length	63 Max thickness position $(63_N/1)$
36 Gonostome distance from anterior margin	64 Tergite max thickness position $(64_N/1)$
37 Sternal plate length	65 Sternite max thickness position $(65_N/1)$
38 Coxae IV midline meeting length	66 Sternal thickness (6/4)
39 Sternal plate width	67 Tergite thickness (5/4)
40 Coxae I radial length	68 Prosomal to opisthosomal width ratio (2/3)
41 Coxae II radial length	69 Tergite I minimum width (7/3)
42 Coxae III radial length	74 Ozophore longitudinal position $(74_N/1)$
43 Coxae IV radial length	75 Tergite VIII width (12/3)
44 Distance between coxae I and II tips	76 Tergite VIII length (13/1)
45 Distance between coxae II and III tips	77 Tergite VII length (14/1)
46 Distance between coxae III and IV tips	78 Tergite VI length (15/1)
47 Coxae IV thickness	79 Tergite VIII concavity (16/1)
48 Width across coxae IV	80 Tergite VII concavity (17/1)
50 Chelicer segment 1 length	81 Tergite VI concavity (18/1)
51 Chelicer segment 2 length	82 Anal plate tergite overlap (19/4)
52 Chelicer mobile digit length	83 Anal plate width (20/3)
53 Chelicer segment 1 width	84 Anal plate length (21/1)
54 Chelicer segment 2 width	85 Anal plate thickness (22/4)
55 Chelicer segment 1 thickness	86 Anal plate length to width ratio (21/20)
56 Chelicer segment 1 proximal narrowness	89 Anal plate carina width $(89_N/20)$
57 Distance to chelicer segment 1 dorsal crest	90 Anal plate carina length $(90_N/21)$
58 Distance to chelicer segment 2 max width	92 Anal plate unornamented region length $(92_N/21)$
13 Tergite VIII length	94 Anal plate setae length $(94_N/1)$
16 Tergite VIII concavity	95 Tergite IX setae length $(95_N/1)$
11 Width between two most posterior points	97 Sternite 9 length (24/1)
17 Tergite VII concavity	98 Sternite 8 length (25/1)
18 Tergite VI concavity	99 Sternite 7 length (26/1)
19 Anal plate tergite overlap	100 Sternite 6 length (27/1)
22 Anal plate thickness	101 Fusion of sternite 8 and 9 width $(101_N/3)$
31 Sternite 6 concavity	105 Sternite 6 concavity (31/1)
49 Anterior scutum margin concavity	106 Spiracle width (32/3)
59 Chelicer segment 1 articulation distance	107 Width between spiracles (33/3)
	108 Spiracle opening angle $(108_N/360)$
	109 Gonostome width (34/max(2,3))
	110 Gonostome length (35/1)
	111 Gonostome length to width ratio (35/34)
	113 Gonostome distance from sternite 1 $(113_N/1)$
	115 Coxae I midline meeting length $(115_N/1)$
	116 Coxae II midline meeting length $(116_N/1)$

Table 1. (Continued).

	117 Coxae III midline meeting length (117_N/1)
	119 Coxae II-III endite margin distance (118_N/1)
	120 Sternal plate width (39/2)
	125 Distance between coxae I and II tips (44/1)
	126 Distance between coxae II and III tips (45/1)
	127 Distance between coxae III and IV tips (46/1)
	128 Coxae IV thickness (47/4)
	129 Width across coxae IV (48/2)
	130 Anterior scutum margin concavity (49/1)
	131 Chelicer segment 1 length (50/1)
	132 Chelicer segment 2 length (51/1)
	135 Chelicer segment 1 width (53/2)
	136 Chelicer segment 2 width (54/2)
	139 Chelicer segment 1 dorsal crest height (139_N/55)
	140 Distance to chelicer segment 1 dorsal crest (57/50)
	141 Distance to chelicer segment 2 max width (58/51)
	142 Chelicer segment 1 articulation distance (59/1)
	143 Chelicer segment 2 fraction ornamented (143_N/51)

(5) raw and scaled measurements were combined for a single IA and all dependent networks were collapsed using PCA.

We also explored a method for downweighting (instead of collapsing) dependent networks, and we developed a non-parametric version of each method. These methods were comparably successful or inferior to the methods we present and we do not detail them here.

Character matrices were made at a variety of cutoff values for each method and imported into the phylogenetic program TNT (Goloboff et al. 2008). TNT can import continuous data that range between 0 and 65 000, and it treats them as additive characters where each character change of 0.001 is counted as one step (Goloboff et al. 2006). Once imported, we conducted heuristic searches under the parsimony criterion; each search consisted of 100 random addition replicates with SPR and TBR branch swapping followed by ratcheting (Nixon 1999), sectorial searches, drifting and tree fusing (Goloboff 1999).

The number and identity of collapsed characters, the shortest tree and bootstrap supports were recorded for each cutoff. The monophyly of the following taxonomic and biogeographic groups were assessed for each tree: Stylocellidae, Sironidae, Pettalidae, Neogoveidae, Troglosironidae, (Neogoveidae + Troglosironidae), *Fangensis*, *Stylocellus*, *Purcellia*, *Parapurcellia*, (*Purcellia* + *Parapurcellia*), *Karripurcellia*, *Pettalus*, *Chileogovea*, *Austropurcellia*, *Aoraki*, *Rakaia*, *Siro*, the European Sironidae, and the South African Pettalidae. Most of these clades – the exceptions being Sironidae, *Stylocellus*, (*Purcellia* + *Parapurcellia*), *Siro*, and the latter two biogeographic groups – have consistently been found with strong support in previous morphological and molecular phylogenies (Giribet and Boyer 2002; de Bivort and Giribet 2004; Schwendinger and Giribet 2005; Boyer and Giribet 2007; Boyer et al. 2007b; Clouse and Giribet 2007). The genus *Fangensis* was set as the outgroup in all tree searches following the findings of Boyer et al. (2007b). Bootstrap supports greater than 50% were summed across each tree for all nodes and for the subset of clades with strong support in previous phylogenetic analyses.

Because mophometric data have been associated with phenetics and distance methods (MacLeod 2002), we also constructed trees from our data using the distance algorithms Neighbor Joining (NJ) (Saitou and
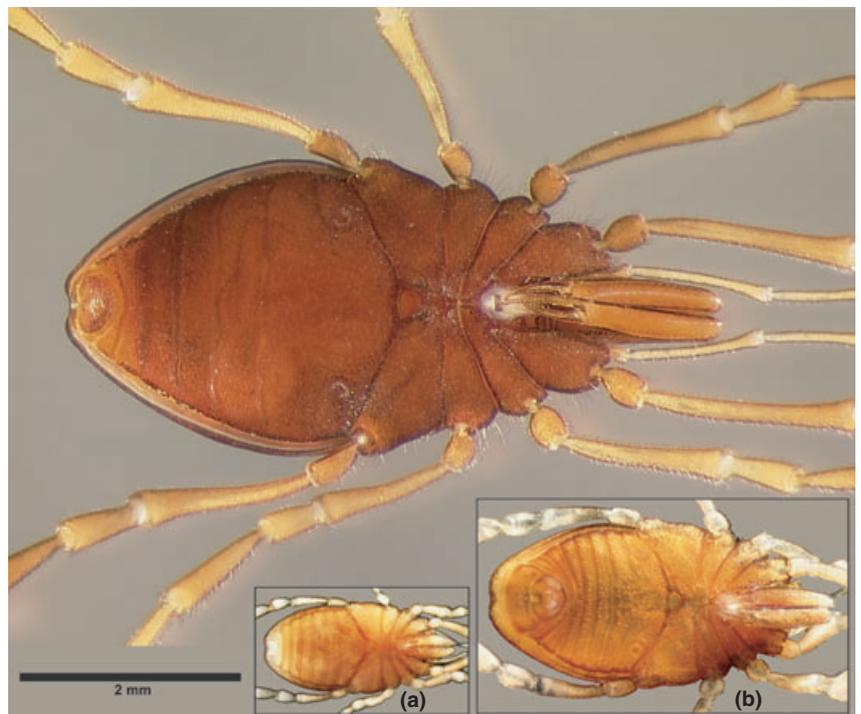

Fig. 1. The South African Pettalidae: *Speleosiro argasiformis* Lawrence, 1931 (main image), *Parapurcellia* n. sp. 4 (inset a), and *Purcellia illustrans* Hansen and Sørensen, 1904 (inset b)
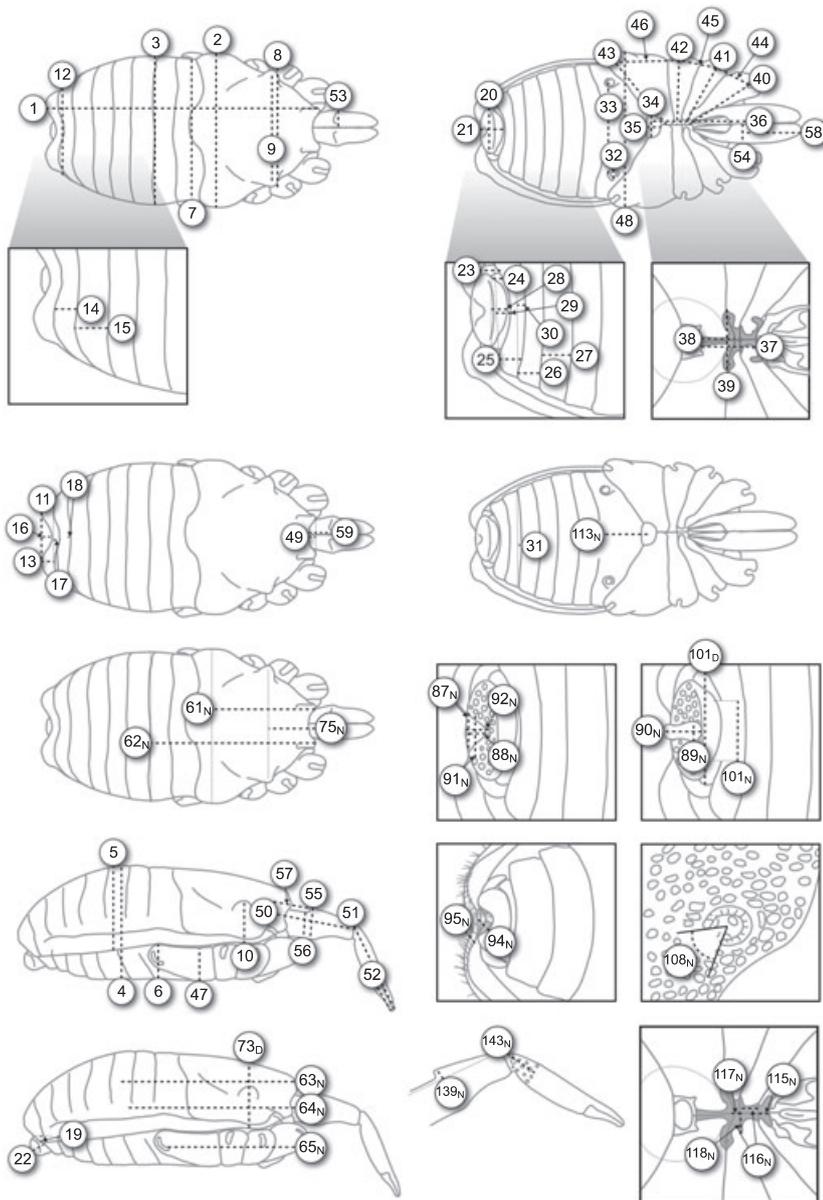
Fig. 2. Measurements listed in Table 1 indicated by dotted lines and their respective numbers

Nei 1987) and UPGMA (Sokal and Michener 1958). Distance methods are based upon a very different theoretical framework of phylogenetics than parsimony, but we wanted to see if there was evidence for the assertion that using morphometric data, even in a cladistic framework, differs little from practising phenetics. For different combinations of raw, scaled and collapsed characters, a matrix of uncorrected distances was constructed in Mesquite 2.6 (Maddison and Maddison 2009). Data were imported into Mesquite either as z-scores without IA or after IA and PCA around the cutoff values that yielded the best trees under parsimony. In addition to the five combinations of characters detailed above, here we also performed IA and PCA on just the scaled data and used a wide variety of cutoff values. Distance matrices were then input into PAUP* (Swofford 2001) for tree-building, with branch lengths constrained to be non-negative.

Results

The 20 focus clades were mostly recovered in TNT using the various combinations of raw measurements, scaled data, IA at various cutoffs, and PCA (Fig. 4). The New Zealand genera *Aoraki* and *Rakaia* and the Laurasian genus *Siro* were never

recovered as monophyletic or even paraphyletic. The lowest recovery rates were when all data were searched as-is (without IA or PCA) and at extreme cutoff values in IA. The most robust and complete recovery of focus clades was when IA and PCA were done on raw and scaled measures separately, a method that resulted in all the focus clades (except the genera noted above and the biogeographic groups) to usually be recovered as monophyletic. This improved at the cutoff of 1.31 (collapsing 143 characters down to 78), where *Speleosiro argasiformis* was found as sister to *Purcellia*. The clade (*Speleosiro* + *Purcellia*) rendered the clade (*Purcellia* + *Parapurcellia*) paraphyletic, but it also resulted in the South African Pettalidae being found monophyletic (Fig. 5). Down-weighting and non-parametric methods did not perform as well as using parametric methods with PCA, although they did recover most of the focus clades.

When analysed by doing IA and PCA on raw and scaled data separately, the optimal cutoff point (1.31) was a value right below cutoffs where the characters quickly collapsed.
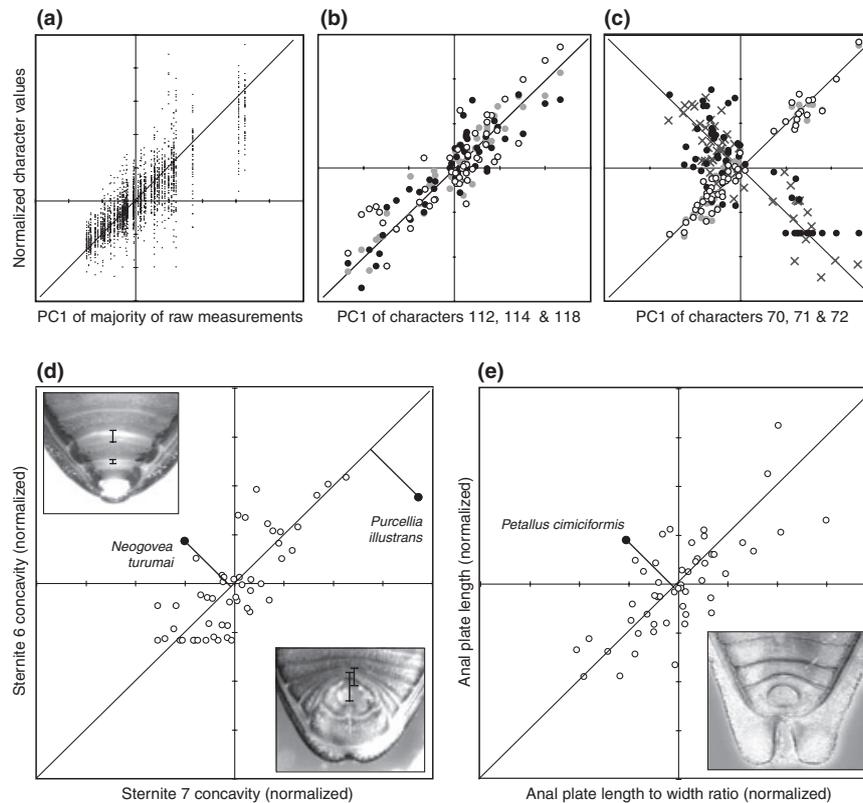
Fig. 3. Independence analysis, illustrated for select characters. (a) Normalized unscaled character values versus PC1 of the PCA done with these dependent values. Each vertical column of points represents one species in the analysis. (b) Character values versus PC1 for the network comprised of characters 112 (black), 114 (white) and 118 (grey) (scaled gonostome distance from anterior margin, scaled sternal plate length and scaled coxae IV midline meeting length, respectively). (c) Character values versus PC1 for the network comprised of characters 70 (black), 71 (white), 72 (grey) and 73 (exes) (scaled width between two most posterior points, scaled width between ozophore lateral margins, scaled width between ozophore distal tips and scaled ozophore height above lateral margin, respectively). (d and e) Correlations between the two pairs of pettalid characters exhibiting the least independence for the cutoff of 1.31. Black points are species farther from the trend line than 1.31 standard deviations, thus establishing independence. Insets illustrate the corresponding character pairs from those species

Raw measurements formed dependent networks quite readily, and the optimal cutoff was at a point where most of them were combined into one principal component but before many of the scaled data had started to collapse. Summed bootstrap values for all clades and just those found in previous studies, as well as the total number of supported clades, all tended to rise at the optimal cutoff (Fig. 6).

The trees resulting from NJ and UPGMA were different from those found under parsimony using the same characters (Fig. 7) and were best improved by the removal of all raw measurements. Neither distance method found a close relationship between *Speleosiro argasiformis* and the other South African pettalids.

Discussion

It would be highly anomalous taxonomically and biogeographically, given our knowledge of cyphophthalmid history, for *Speleosiro* to be anything but a close relative of the other South African pettalids, but its extremely modified morphology (large size, elongate appendages, discoid opisthosoma) made the recovery of such a relationship highly doubtful in a morphometric analysis. Its recovery as such, without the disruption of other groups (except, understandably, *Purcellia* + *Parapurcellia*, which was a likely tradeoff to the three genera forming a clade) is made all the more compelling by the

location of the IA cutoff at a point where characters are close to a large collapse and bootstrap values rise. Remarkably, we recovered almost half our focus clades by doing neither independence analysis nor collapsing dependent networks by principal components analysis, i.e. by putting our large collection of measurements and related ratios into tree searches unexamined. Still, doing independence analysis and collapsing characters that were highly correlated without outliers, especially among the raw measurements, reduced the number of misleading characters in the data, and optimizing the outlier cutoff further improved phylogenetic resolution.

Evaluating our methodology requires independent knowledge of the correct clades. Since these data are not from a simulated phylogeny, as with Naylor's 'imaginary fishes' (1996), the actual historical events leading to our data set cannot be known and the correctness of our clades depends on the reliability of previous analyses from other data. We have included certain weakly supported groups, like Sironidae and *Siro*, mostly for completeness. The two biogeographic clades, European Sironidae and South African Pettalidae are scrutinized here more for the potential of this study to inform other analyses than the reverse. But the remaining clades have withstood multiple morphological and molecular investigations and jibe with our understanding of geologic history. We are not alone in evaluating trees from new data and methods by comparing them with previous phylogenies
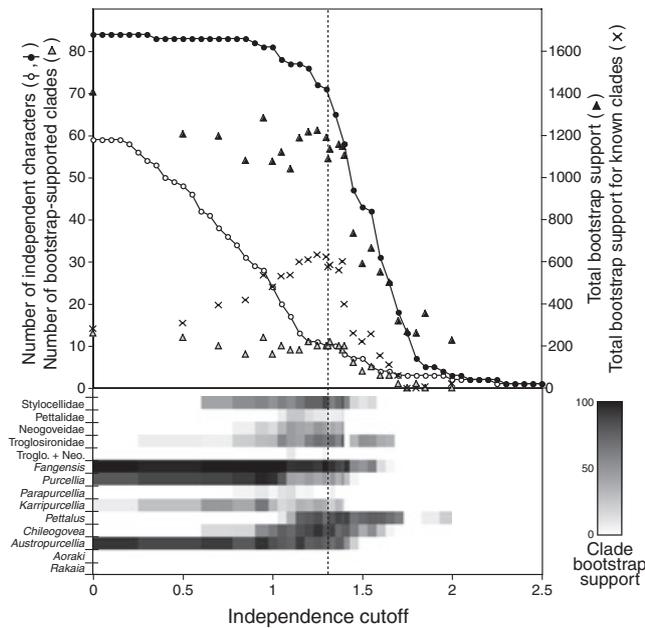
Fig. 4. Sensitivity of clades in the pettalid analysis to variations in independence analysis and cutoff values, analysed under parsimony in TNT. Table headers indicate independence analysis method (including none, in the first two columns), cutoff value and the resulting number of characters. Data rows show the recovery of focus clades. Black cells indicate monophyly, grey paraphyly and white polyphyly

Fig. 5. Phylogeny found doing independence analysis on raw and scaled measurements separately at cutoff value 1.31

Fig. 6. Analysis of independence cutoff values for Pettalidae where IA and PCA is done on raw and scaled measurements separately. Top: the number of independent characters after collapse by PCA are shown separately for scaled and raw measurements (black and white circles, respectively) and plotted versus the left y-axis. The number of clades receiving bootstrap support over 50% (grey triangles) and the total amount of bootstrap support in resulting trees (versus the right axis) across all the trees (black triangles), and just across clades well supported in previous literature (exes), for each cutoff value. Bottom: bootstrap support for those well supported clades scaled from 0% (white) to 100% (black). Dashed line indicates the independence cutoff value used to generate the optimal tree

(MacLeod 2002; Guerrero et al. 2003; Macholan 2008), nor are we unique in using summaries of resampling support to judge tree quality (Guerrero et al. 2003). On the latter point, we found it interesting that not only was the optimal cutoff value found where bootstrap support appeared to locally peak, but also that support increased at all as characters collapsed; we would have predicted that the removal of redundant characters, even if misleading, would generally lead to a steady decrease in support as more dependent characters collapsed, but this was the case only at the beginning and after the optimal cutoff.

The role of size information

We expected the collapse of many of the raw measures into a single PC, since their values were mostly determined by species sizes. Additionally, our use of simple ratios, unadjusted for possible curvilinear relationships or non-zero y-intercepts (Atchley et al. 1976; Albrecht et al. 1993), meant many of them, too, still contained size information. The independence of our characters could be undercut if many of them were simply various manifestations of body size (Rae 2002), but our IA and subsequent character collapses apparently mitigated this problem. In fact, in line with Bookstein et al. (1985), who argued that size is a 'perfectly meaningful' covariable (p. 27), we left the raw measurements in the data set, ensuring at least one character (the first PC from their collapse) would bring size information into the analysis. Still, we were surprised to see that not so much size information was carried in the data set so as to separate the large *Fangensis* from the co-familial *Stylocellus ramblae* Giribet, 2002, one of the smallest Stylocellidae known. The distance methods, NJ and UPGMA, were more sensitive to size information, clustering together the larger species [*S. tambusisi*, Shear 1993, both species of *Fangensis*, *Pettalus cimiciformis* (Pickard-Cambridge, 1875), and *Speleosiro argasiformis*] in the trees built from all 143 characters. When raw measurements were completely removed, the distance trees improved significantly, with NJ in fact outperforming parsimony (Fig. 7). However, IA and PCA, even on just the scaled measurements, did not improve distance trees as much as they did parsimony trees or as much as just removing raw measurments did for distance trees. For all NJ trees, *Speleosiro* and *Pettalus* never separated, and among UPGMA trees, *Speleosiro* was found as sister to either *Pettalus* or *Chileogovea* or as unresolved within Pettalidae.

Another size effect for which we made no adjustment was among differently sized (in other taxa equivalent to differently aged) individuals of the same species. Cyphophthalmi species have highly conserved adult body sizes and proportions, and upon their final molt into adulthood, individuals stop growth.
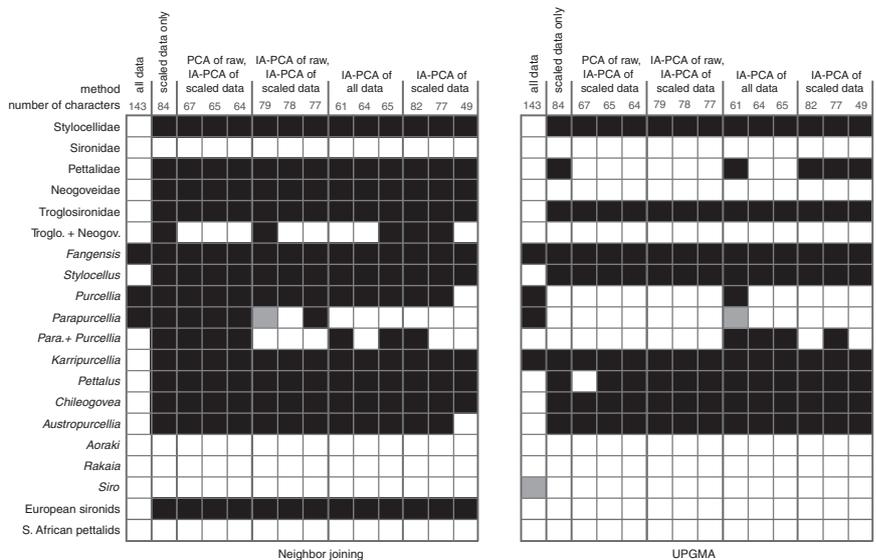
Fig. 7. Recovery of focus clades from trees built using Neighbor Joining (left) and UPGMA (right)

This relieved us of having to standardize measurements across individuals at different ontogenetic stages (Rohlf and Bookstein 2003). Farris (1966) has argued that characters should be inversely discounted by their variance, and Farris and Kluge (1969) applied this idea in a phylogenetic analysis where families were terminals and characters were downweighted by intrafamilial variation. Conversely, it has been argued that intrataxon character variance positively correlates with intertaxa variance and thus character usefulness [the Kluge-Kerfoot phenomenon, Kluge and Kerfoot (1973)], although this may be a statistical artefact (Archie 1985). The phylogenetic effects of character variation have often been discussed in the context of ontogeny (Zelditch and Fink 1995; Adams and Rosenberg 1998; Macrini et al. 2007), intraspecific variation and polymorphism (Seiffert and Kappelman 2001; Rae 2002) and even theoretical examinations of how continuous characters evolve (Kirkpatrick 1982). The program we used, TNT, can handle data input as ranges, so a confidence interval or range for each character for each species could have been used in our analysis. However, some of our most interesting species are known from very few specimens (we only have two male specimens of *Speleosiro argasiformis*), and the total intraspecific ranges for Cyphophthalmi body and appendage measurements are quite small. In the descriptions of *Stylocellus lydekkeri* Clouse and Giribet (2007) and *S. novaguinea* Clouse and Giribet (2007), the normalized range for all measurements averaged only 10.3%, which is akin to the tallest and smallest women in the USA differing by only 16.7 cm or 6.6 in.

Measurements as characters

Our use of measurements, ratios and (especially) principal components as characters places this study in the middle of a long debate on the role of morphometrics in phylogenetics. A primary challenge with measurement data has been that they can take on any value – i.e. they can vary continuously – and thus they have traditionally required a discretization step to code them for use in cladistic analyses. General discussions of coding include the use of multistate characters to avoid problems of independence (Pleijel 1995; Fitzhugh 2006), subjectivity and arbitrariness (Stevens 1991; Gift and Stevens 1997) and comparisons of commonly used methods (Thorpe 1984; Archie 1985; Chappill 1989). One of the most extensive reviews of coding methods was done by Thiele (1993), who introduced a method of 'gap-coding' that included information on the magnitude of the relative differences between character states. Thiele's method has been popular, either used in its original form, with minor variations or in combination with other methods (Table 2). One of the most important modifications of Thiele's gap coding was Wiens's (2001) addition of a step matrix to weight different state changes. Thiele's method required that the range of states be reduced to the number of states allowed by the phylogenetic program, but Wiens's (2001) method eliminated the need for this standardization and it has been used in several studies (Table 2).

Despite the popularity of Thiele's (1993) and Wiens's (2001) methods, there is still a wide variety of coding methods from which to choose: relying on a visual inspection of graphed or clustered data, doing it just informally, developing custom methods or using one of the less popular methods, like Bininda-Emonds and Bryant's (1998) matrix representation with parsimony or Smith and Gutberlet's (2001) generalized frequency coding (Table 2). This abundance of options

underlines the contentiousness of continuous data and although many have decided that the gain of information was worth their possible theoretical costs (Linder and Mann 1998), others concluded early-on that continuous data, however coded, should not be used in cladistic analyses (Pimentel and Riggins 1987; Cranston and Humphries 1988; Stevens 1991; Pennington 1996). The distinction between the two kinds of characters may be a matter of degree, and 'qualitative' characters (like feather colour or larva type) have been argued to be informally discretized continuous characters (Gift and Stevens 1997; MacLeod 2002; Haas 2003). Also, Thiele (1993) has argued that 'quantitative' and 'continuous' (as opposed to 'qualitative' and 'discrete') were being interchanged with 'overlapping', which was the real issue with coding characters. Thiele (1993) went on to distinguish the general feature of a taxon from its histogram of individual values, the latter of which could overlap between taxa to a degree determined by the investigator; ultimately, Thiele argued, the rejection of a character should rest on its phylogenetic content, not its degree of overlap.

In addition to choosing a coding method or discarding continuous data altogether, a third option exists, which is to use them undiscretized, as we did here. There have been two methods available for phylogenetic analyses of undiscretized data, one in a maximum likelihood framework (CONTML in PHYLIP, Felsenstein 2008) and the other using parsimony (TNT, Goloboff et al. 2008). The former was designed mostly for allelic-frequency data, and various studies have used the program for both those (Glaubitz et al. 2003; Kim et al. 2007; Matsui et al. 2008) and other kinds of data (Athreya and Glantz 2003; Caumul and Polly 2005). Athreya and Glantz (2003) stated that CONTML, like distance methods, was sensitive to the order that taxa were input, but this appears to be in error; the program uses heuristic methods to find trees with better scores than the starting tree. Still, the program has not been wholly embraced, likely due to its underlying evolutionary model, which assumes states change in a random, Brownian-motion path through time (Cavalli-Sforza and Edwards 1967; Wiens 1999). In fact, its developer has stated (Felsenstein 2002) that because all the correlations of continuous data cannot be known, a probabilistic model of their evolution cannot be built, and they are useful in retrospect only (mapped on to trees built from other data). TNT, the parsimony program, has received similar attention (Abdala 2007; Dominguez and Roig-Junent 2008), also being rejected by some for its underlying assumptions about the evolution of characters (Legendre et al. 2008).

The question of homology

Morphometric data add another layer of controversy. They rely on landmarks, like eyes or gland openings, with the relative positions of landmarks in different species constituting shape differences (Rohlf 2002). Bookstein et al. (1985) pointed out that although landmarks could be homologues, the non-landmark spaces between them were something else, what he called 'computed-homologues'. Pimentel and Riggins (1987) argued for the non-homology of quantitative data in general and Bookstein (1994) argued for the exclusion of shape descriptors from systematics (since equivalent deformations could arise from different operations and changes in the order of operations could give rise to different final shapes). Likewise, Zelditch et al. (1995) argued that morphometric

Table 2. A selection of methods used to discretize continuous characters, including examples of their employment by others

Method name	Method reference	Additional applications
Gap-coding	Thiele (1993)	Chandler and Crisp (1998)
		Ghebrehiwet et al. (2000)
		Lee et al. (2001)
		Ezcurra (2002)
		Prat (2002)
		van de Wouw et al. (2003)
		Archangelsky (2004)
		D'Hondt et al. (2004)
		Pelser et al. (2004)
		Bogdanowicz et al. (2005)
		Caetano-Anolles (2005)
		Schols et al. (2005)
		Brown et al. (2006)
		Coppard and Campbell (2006)
		De-Nova et al. (2006)
		Giugliano et al. (2007)
		Lens et al. (2007)
		Macrini et al. (2007)
		Zhang et al. (2007)
		Lycett (2007)
		Druckenmiller and Russell (2008)
		Lens et al. (2008)
		Moon et al. (2008)
		Pessacq (2008)
		Nagels et al. (2009)
	Thiele's gap-coding (1993), modified	Ryding (1998)
		Alvarez et al. (2000)
		Christiansen (2008)
	Thiele's gap-coding (1993), combined with other methods	Simonovic (1999)
		Pelser et al. (2004)
		Rican and Kullander (2006)
Step-matrix gap-weighting	Wiens 2001	Etheridge (2000)
		Wiens and Etheridge (2003)
		Marek and Kavanaugh (2005)
		Rican and Kullander (2006)
		Torres-Carvajal (2007)
		Vieira et al. (2007)
		Rican et al. (2008)
		Werneck et al. (2009)
Visually inspecting graphed or clustered data		Almeida and Bisby (1984)
		Naylor (1996)
		Linder and Mann (1998)
		O'Grady and May (2003)
		Pelser et al. (2004)
		Scharaschkin and Doyle (2006)
Informally		Livezey (1997)
		Cotton (2001)
		Eklund et al. (2004)
		Bergmann and Russell (2007)
Custom methods	Kluge and Farris (1969)	
	Smith and Gutberlet (2001)	
	Gilbert and Rossie (2007)	
	Wortley et al. (2007)	
	Molina et al. (2008)	
	Naczi (2009)	
Matrix representation with parsimony	Bininda-Emonds and Bryant (1998)	Cannon and Manos (2001)
Segment coding	Chappill's (1989)	Chappill and Ladiges (1996)
Generalized additive coding	Goldman's (1988)	Cranston and Humphries (1988)
Gap coding	Mickevich and Johnson's (1976)	Singleton (2000)
		Garcia-Cruz and Sosa (2006)
C-coding	Pleijel's (1995)	Schulze (2003)
Polymorphism overlap coding	Unpublished dissertation by MJ Sanderson	Heenan (1998)
Homogenous subset coding	Simon's (1983)	Van Velzen et al. (1998)
		Strait and Grine (2004)
Generalized frequency coding	Smith and Gutberlet's (2001)	Meland (2004)
Finite mixture coding	Strait et al.'s (1996)	Liu et al. (2007), with modifications

Table 2. (Continued).

Method name	Method reference	Additional applications
Divergence coding	Thorpe's (1984)	Davis et al. (2001)
		Lycett and Collard (2005)
		Collard and Wood (2007)
		Lycett (2007)
Gap coding	Thorpe's (1984)	Hibbitts and Fitzgerald (2005)
Frequency coding	Wiens (1995, 1999)	Chu (2002)
		Stephens and Wiens (2003)
		Poe (2004)
		Datwyler and Wolfe (2004)

data could not pass the similarity test (Patterson 1988) of homology, but she did posit that partial warps could work. With Fink, Zelditch used partial warps to describe shape changes in fish (Fink and Zelditch 1995; Zelditch and Fink 1995), but the following year Lynch et al. (1996) cautioned against using partial warps in phylogenetics without doing simulations first, which were then done (with debatable results) by Naylor (1996). Rohlf (1998) criticized partial warps as non-homologous and biologically arbitrary and Adams and Rosenberg (1998) similarly felt that the ontogenetic shape transformations constructed from partial warps by Fink and Zelditch (1995) were not suitable for cladistics. These criticisms brought rebuttals (Zelditch and Fink 1998; Zelditch et al. 1998, 2000), and the debate has continued. Partial warps continue to be used (Bogdanowicz et al. 2005), relative warps have been argued to be more useful than partial warps (MacLeod 2002) and some hold that shapes are useful only as a first step in searching for phylogenetic characters (Rohlf 2002). Meanwhile, David and Laurin (1996) objected to shape data in cladistics because of shape's epigenetic quality, Swiderski et al.'s (1998) argument that morphometrics should be coded for cladistic analysis like any other data was answered with an argument that morphometrics can in fact create arbitrary characters (Monteiro 2000), Roth and Mercer (2000) rejected morphometric data as 'intrinsically unsuitable' for phylogenetics based on non-homology, and Petersen and Seberg (2003) also disagreed with making homology statements on continuous data.

Still, positions on these issues have been dynamic and proposed moratoriums on certain methods softened. The rejection of outline-based methods by Zelditch et al. (1995) (famously illustrated with a scapula, potato chip and choco-late-chip cookie) has been called 'too broad' more recently by the same authors (Swiderski et al. 2002), and Bookstein (2002) has advocated creases as a possible morphometric source of phylogenetic characters. Some of the flexibility may have actually started with Bookstein's (1994) original discourage-ment of shape descriptors in systematics, for there he allowed that incorrect shape descriptions could be inconsequential when differences were small, like using a flat map to take a short hike. Indeed, flat maps are useful even when driving across continents, in spite of the Earth's spherical shape creating a non-Euclidian geometry on its surface. In response to Bookstein's (1994) assertion that homology cannot be approximated, Naylor (1996) argued that there had been and continues to be an allowable level of imprecision in homology statements. In fact, an early study demonstrated a certain tolerance of phylogenetic studies to homology errors (Fisher and Rohlf 1969). Accordingly, quantitative data have been argued to be most useful when species are closely related

(Chappill 1989; Polly 2002), although here we had more trouble resolving two genera on the same landmass than families separated by hundreds of millions of years (Boyer et al. 2007b).

Morphometrics and phenetics

The increased use of morphometrics in phylogenetics has partially resulted from a general acceptance of the means when considering the ends (Crowe 1994), a problematic trend for those who consider morphometrics a variant of phenetics. Arguments have been made for the inclusion of morphometric data in cladistics because they can produce superior trees (Linder and Mann 1998; Guerrero et al. 2003) and it has been concurrently asserted that continuous data are perhaps no more problematic than other types (Rae 1998; Zelditch et al. 2000; Wiens 2004). Moreover, studies have had success using not just continuous data but shape descriptors in phylogenetic analyses (Singleton 2000; Cannon and Manos 2001), including, like us, principal components [Van Velzen et al. 1998; Athreya and Glantz 2003; Caumul and Polly 2005; Gunduz et al. 2007; González-José et al. 2008; Macholan 2008 (multiple-group PCA)]. PCA has another attractive trait, which is that it insures the independence of characters; this was recognized early by Pimentel and Riggins (1987) (who nonetheless rejected PCs because of a broader aversion to continuous data in cladistics). Such successes, however, do not directly address the associations many systematists make between morphometrics and phenetics and indeed, phenetics has fallen out of favour despite making good approximations for cladistic phylogenies in many instances. Distance data come with a number of assumptions, analytic limitations and philosophical problems (Farris 1981; Farris et al. 1996), and it would be difficult to recommend their use, even if they resulted in the best recovery of our focus clades. However, the connection between morphometrics and phenetics persists as more of a historical association than one demonstrated theoretically. PCA has commonly been used to generate ordination plots revealing taxonomic clusters from measurement data (Chandler and Crisp 1998; Myers 2007; Saunders et al. 2008), and such plots have been compared with the results of clustering methods like UPGMA (Powers and Rohlf 1972; Cole et al. 2002; Saitoh et al. 2008). This has led to the argument that morphometrics and phenetics are essentially the same (Crowe 1994; Zelditch et al. 1995; Cole et al. 2002), an idea that has been rebutted by MacLeod (2002). In fact, not only does TNT treat measure-ments and PCs as additive (Farris) characters (Goloboff et al. 2006), but our trees from distance matrices were distinctly different from those found using the same data under parsimony. Parsimony was less sensitive to spurious size

information and we were able to improve parsimony trees through the mitigation of dependent characters.

Given our results, we echo recent calls by others that continuous data and morphometrics do contain phylogenetic information (Bogdanowicz et al. 2005; Garcia-Cruz and Sosa 2006; Lehtonen 2006; Abdala 2007; Buchanan and Collard 2007; Gilbert and Rossie 2007; Lycett 2007; Asher et al. 2008; González-José et al. 2008; Hardy et al. 2008). Recent advances in the conceptualization of homology (Humphries 2002; Assis and Brigandt 2009) may prove useful with this thorny problem in morphometrics, and the use of programs that can handle continuous data as-is offer a new option for those who are caught between discarding continuous data and applying distasteful discretization methods (Reid and Sidwell 2002). We recommend further research on our method of independence analysis *vis-à-vis* its effectiveness with data based on landmark-coordinate methods, since our underlying data here are simple linear distances. Inasmuch as single morphological evolutionary events can change the positions of many landmarks, it seems reasonable to consider the phylogenetic independence of landmark-coordinate characters; indeed, we have already used the method to recover the correct tree from Naylor's (1996) partial warp scores (authors's unpublished results). Perhaps most promising of all are new options for including continuous characters in combination with other types of data. In our investigations of Cyphophthalmi systematics, we look forward to using continuous, discrete and molecular data in concert to deepen our understanding of this group's history.

Acknowledgements

Résumen

Una filogenia de los cifoftalmos (Opiliones, Cyphophthalmi, Pettalidae) de la Gondwana templada basada en análisis morfométricos

Se investiga la filogenia de los cifoftalmos gondwánicos de la familia Pettalidae (Arachnida, Opiliones, Cyphophthalmi) mediante la utilización de 143 variables morfológicas (59 variables sin transformar y 84 medidas transformadas) de 37 taxones terminales internos y 15 grupos externos. Para ello, se utilizan algoritmos diseñados especialmente para hacer comparaciones dos a dos entre caracteres e identificar los conjuntos de caracteres dependientes, los cuales son colapsados mediante un análisis de componentes principales. Los datos resultantes fueron analizados sin necesidad de discretización, utilizando parsimonia como criterio de optimalidad. De este modo se obtuvo la monofilia o parafilia de varios grupos, como ya se había obtenido en otros análisis con otros datos morfológicos o molecul-

ares. Los árboles obtenidos en los análisis morfométricos fueron optimizados para la monofilia de 20 clados postulados en estudios anteriores mediante la variación de los parámetros de independencia de caracteres. Esto produjo un cladograma final donde 15 de los 20 grupos postulados eran monofiléticos, incluyendo los petálidos sudafricanos, que incluyen la especie troglomorfa *Speleosiro argasiformis* Lawrence, 1931. Dos de los otros grupos aparecen como parafiléticos, mientras que los géneros *Aoraki*, *Rakaia* y *Siro* siempre son polifiléticos.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. List of species studied, including author names and localities.

Appendix S2. Custom scripts used in Independence Analysis, with annotation.

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