A molecular phylogeny of the temperate Gondwanan family Pettalidae (Arachnida, Opiliones, Cyphophthalmi) and the limits of taxonomic sampling

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We evaluate the phylogenetic and biogeographical relationships of the members of the family Pettalidae (Opiliones, Cyphophthalmi), a textbook example of an ancient temperate Gondwanan taxon, by means of DNA sequence data from four markers. Taxon sampling is optimized to cover more than 70% of the described species in the family, with 117 ingroup specimens included in the analyses. The data were submitted to diverse analytical treatments, including static and dynamic homology, untrimmed and trimmed alignments, and a variety of optimality criteria including parsimony and maximum-likelihood (traditional search and Bayesian). All analyses found strong support for the monophyly of the family Pettalidae and of all its genera, with the exception of Speleosiro, which is nested within Purcellia. However, the relationships among genera are poorly resolved, with the exceptions of a first split between the South African genus Parapurcellia and the remaining species, and, less supported, a possible relationship between Chileogovea and the other South African genus Purcellia. The diversification of most genera is Mesozoic, and of the three New Zealand genera, two show evidence of constant diversification through time, contradicting scenarios of total submersion of New Zealand during the Oligocene drowning episode. The genera Karripurcellia from Western Australia and Neopurcellia from the Australian plate of New Zealand show a pattern typical of relicts, with ancient origin, depauperate extant diversity and recent diversification. The following taxonomic actions are taken: Milipurcellia Karaman, 2012 is synonymized with Karripurcellia Giribet, 2003 syn. nov.; Speleosiro Lawrence, 1931 is synonymised with Purcellia Hansen & Sørensen, 1904 syn. nov. The following new combinations are proposed: Parapurcellia transvaalica (Lawrence, 1963) comb. nov.; Purcellia argasiformis (Lawrence, 1931) comb. nov.

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ADDITIONAL KEYWORDS: biogeography – diversification – mite harvestmen.

INTRODUCTION

The mite harvestman family Pettalidae Shear, 1980 (the ‘lignée gondwanienne’ or Gondwanan lineage of...
Juberthie, 1971) has become an iconic invertebrate group for the study of Gondwanan biogeography (e.g. Boyer & Giribet, 2007; Wallis & Trewick, 2009; Heads, 2014). Distinguished by the dorsal position of the ozo-phores – the unique structure bearing the odoriferous glands of Cyphophthalmi – and dual cheliceral dentic-
Juberthie & Muñoz-Cuevas, 1970; Shear, 1993), Three genera, *Parapurcellia* Rosas Costa, 1950 (ten spp.), *Purcellia* Hansen & Sørensen, 1904 (five spp.) and *Speleosiro* Lawrence, 1931 (one sp.) are found in South Africa (Hansen & Sørensen, 1904; Lawrence, 1931, 1933, 1939, 1963; Starega, 2008; de Bivot & Giribet, 2010) – no other continental African country has yet yielded a specimen of Pettalidae. Two species of Cyphophthalmi are known from Madagascar (Shear & Gruber, 1996): while the monotypic *Manangotria* Shear & Gruber, 1996 most probably belongs to Pettalidae, the monotypic *Ankaratra* Shear & Gruber, 1996 does not (Giribet et al., 2012). No molecular data are available for either Malagasy species. The type genus of the family, *Pettalus* Thorell, 1876, is endemic to Sri Lanka, and comprises four described species (and a large number of undescribed ones) (Cambridge, 1875; Pocock, 1897; Sharma & Giribet, 2006; Giribet, 2008; Sharma, Karunathana & Giribet, 2009). Australia is home to two genera, *Karripurcellia* Giribet, 2003 (three spp.) in the south-west (Giribet, 2003a), and *Austropurcellia* Juberthie, 1988 (19 spp.) in Queensland (Davies, 1977; Juberthie, 1988, 2000; Boyer & Giribet, 2007; Boyer & Reuter, 2012; Popkin-Hall & Boyer, 2014; Boyer et al., 2015). In a revision of *Karripurcellia*, Karaman (2012) erected the new genus *Milipurcellia* Karaman, 2012 for one of the *Karripurcellia* species. Here we consider *Milipurcellia* a junior synonym of *Karripurcellia*.

Interestingly, Tasmania, home to many other temperate Gondwanan taxa (the velvet worm Peripatidae, the harvestmen Triarachyidae and Neopilionidae, the pseudoscorpion Pseudotyrannochthoniidae, the centipede Paralaymeetes, the spider families Austrochilidae, Migidae and Orsolobiidae, etc.), has no known cyphophthalmid. Finally, the pinnacle of described pettalid biodiversity is New Zealand, with three genera, *Aoraki* Boyer & Giribet, 2007 (11 spp. and subspp.), the monotypic *Neopurcellia* Forster, 1948; and *Rakaia* Hirst, 1925 (18 spp. and subspp.) (Hirst, 1925; Roewer, 1942; Forster, 1948, 1952; Boyer & Giribet, 2003, 2007, 2009; Giribet, Fernández & Boyer, 2014a). Some authors, especially R. Forster, named several subspecies of *Aoraki*. Without a thorough revision of those groups we use the existing taxonomy, although understanding that Forster’s subspecies are most likely species. This adds up to a total of 76 named species and subspecies in the family.

While several morphological cladistic analyses have contributed to understanding the phylogeny of Pettalidae (Giribet & Boyer, 2002; Giribet, 2003a; de Bivot, Clouse & Giribet, 2010; de Bivot & Giribet, 2010; Giribet et al., 2012), at least for some of the genera, the overall molecular phylogeny of the family is limited to relatively few taxa, particularly those from outside New Zealand and Sri Lanka (Boyer & Giribet, 2007, 2009; Boyer et al., 2007b, 2015; Giribet et al., 2012). The most comprehensive analysis published to date, in the broader context of Cyphophthalmi phylogeny, included molecular sequence data from two species of *Parapurcellia*, one *Purcellia*, two *Chileogovea*, one *Karripurcellia*, seven *Pettalus*, ten *Aoraki*, one *Neopurcellia*, four *Austropurcellia* and 19 *Rakaia* (Giribet et al., 2012). The ingroup taxa in that study asymmetrically sampled New Zealand and Sri Lanka; the remaining taxa constituted merely ten specimens, far from optimal sampling for most genera, and did not include the South African genus *Speleosiro* or the Malagasy genera.

It was therefore our goal to generate a comprehensive molecular analysis of the family Pettalidae thoroughly sampling every pettalid genus – with the exception of the to-date inaccessible Malagasy specimens. We here present new analyses including molecular data from *Aoraki* (24 specimens), *Austropurcellia* (14 specimens), *Chileogovea* (seven specimens), *Karripurcellia* (six specimens), *Neopurcellia* (four specimens), *Parapurcellia* (14 specimens), *Pettalus* (eight specimens), *Purcellia* (11 specimens), *Speleosiro argasiformis* (two specimens) and *Rakaia* (27 specimens), totalling 127 specimens, comprising 70% of the accepted pettalid species, in addition to several undescribed ones. With this comprehensive phylogeny we could further test particular aspects of the diversification of this temperate Gondwanan family, such as the origin of the New Zealand fauna and their relation to the Oligocene drowning.

MATERIAL AND METHODS

**TAXON SAMPLING**

Pettalid specimens (Table 1) were collected during multiple field seasons between 2001 and 2014, by the authors but also by several colleagues. Additional collecting details are provided in the online database MCZbase (http://mczbase.mcz.harvard.edu). Specimens were mostly collected by sifting leaf litter or by direct search under stones and logs. While litter sifting has been a preferred collecting method yielded large numbers of specimens, direct search worked better in most South African localities; direct collecting was also used for the cave species *Speleosiro argasiformis* (see Giribet et al., 2013).

**MOLECULAR MARKERS**

Four legacy markers were used for this study, building upon a dataset over 10 years in the making. Two nuclear ribosomal RNA genes (the nearly complete...
Table 1. Ingroup taxon sampling with MCZ catalogue number (except when indicated), major geographical region and sequenced fragments. For New Zealand, NI and SI refer to North Island and South Island, respectively

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</table>

18S rRNA and a c. 2200-bp fragment of 28S rRNA and two mitochondrial genes, one ribosomal RNA (16S rRNA) and the protein-encoding gene cytochrome c oxidase subunit I (hereafter COI), were amplified. Although we also used the nuclear protein-encoding gene histone H3 in previous analyses of Cyphophthalmi phylogeny, we left it out of this study, as most sequences for pettalids were of low quality. All protocols for DNA extraction, amplification and sequencing are thoroughly described elsewhere (e.g. Boyer & Giribet, 2007; Boyer et al., 2007b; Giribet et al., 2010), and we direct the reader to these studies for further details. Additional 16S rRNA primers were published by Fernández & Giribet (2014). All new sequences have been deposited in GenBank under accession numbers KU207229–KU207428, KU214865–KU214866 (Table 1, Fig. 2).

**PHYLOGENETIC ANALYSES**

To evaluate the sensitivity of our results to multiple factors determining phylogenetic hypotheses, we explored alternative methods based on (a) dynamic homology and (b) static homology approaches (Wheeler, 2001; Wheeler et al., 2005). The analyses therefore consisted of:

**Dynamic homology with POY**

We conducted a dynamic homology analysis analysing the individual markers as follows: 16S rRNA (94 sequences included) was divided into three fragments [the first fragment was not amplified in the pettalid-specific primer pair developed by Fernández & Giribet (2014)]; 18S rRNA (121 sequences included) was divided into six fragments; 28S rRNA (122 sequences included) was divided into ten fragments; and COI (113 sequences included), despite the length variation in some outgroups, was analysed as a single fragment. Although some studies provide pre-aligned COI data sets for direct optimization, the existence of amino acid indels within Cyphophthalmi (see, for example, Murienne, Karman & Giribet, 2010; Young & Hebert, 2015) prevented us from using pre-aligned data. This may have resulted in an exaggerated number of indels in the direct optimization analysis, when compared to the other methods.

Direct optimization analyses were conducted under the parsimony criterion in POY v.5.1.1 (Wheeler et al., 2015) under a selection of six parameter sets, as in earlier studies (e.g. Giribet et al., 2014b). For the individual partitions, timed searches of 1 h were run on six processors. For the combined analysis of the four markers we started with the same search strategy, and the resulting trees were given as input for a second round of analyses (sensitivity analysis tree fusing; SATF), as described by Giribet (2007), and continued until the tree lengths stabilized (Giribet et al., 2012) (Table 2). The optimal parameter set was estimated using modified WILD metrics (Wheeler, 1995; Sharma et al., 2011) as a proxy for the parameter set that minimizes overall incongruence among data partitions (Table 3). Nodal support for the tree obtained with the optimal parameter set was estimated via jackknifing (250 replicates) with a probability of deletion of e−1 (Farris et al., 1996) using auto_sequence_partition, as discussed in earlier work (Giribet et al., 2012).

<table>
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<th>Species</th>
<th>Catalogue no</th>
<th>Country</th>
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<th>16S rRNA</th>
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<td>DQ518117</td>
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Static homology analyses
For the static homology analyses, the same raw data given to POY were submitted to multiple sequence alignments using MAFFT-FFT-NS-I (Katoh et al., 2005; Katoh & Standley, 2014). The alignments were subsequently concatenated using SequenceMatrix (Vaidya, Lohman & Meier, 2011), or trimmed with Gblocks (Castresana, 2000; Talavera & Castresana, 2014).

Figure 2. Generic sampling in the different former temperate Gondwanan landmasses: Sri Lankan Pettalus (cyan), Western Australian Karripurcellia (orange), South African Purcellia (blue) and Parapurcellia (crimson), New Zealand Aoraki (yellow), Neopurcellia (black) and Rakaia (grey), Chilean Chileogovea (red) and eastern Australian Austropurcellia (white).

Table 2. Result of the POY timed searches and stabilization of the number of weighted steps after each round of SATF for the six explored parameter sets

<table>
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</table>

To represent all extant Opiliones suborders (Eupnoi: Protolophus singularis; Dyspnoi: Hesperonemastoma modestum; Laniatores: Equitius doriae) and constrained the age of Opiliones with a lognormal distribution (mean of 425 Ma in real space and offset of 411 Ma), reflecting the age of Eophalangium sheari, based upon the placements of Palaeozoic harvestman fossils in the total evidence dating approach of Sharma & Giribet (2014). A uniform prior of 465–495 Ma was applied to the root of the tree to constrain the split of Arachnida (Opiliones) from Limulus polyphemus.

Tests of diversification rate constancy were conducted using the R package LASER (Rabosky, 2006a) after removing the outgroups from the ultrametric tree generated in BEAST. In addition, we calculated the gamma statistic to detect evolutionary radiations with the function ‘gamstat’ from that same R package. We also used the function ‘medusa’ (a stepwise approach based on AIC) in the R package GEIGER (Harmon et al., 2008) to test for lineage-specific shifts in diversification rates on an incompletely resolved phylogeny, which fits a series of birth–death models with an increasing number of breakpoints (rate shifts), and estimates the ML values for each set of birth and death parameters (Alfaro et al., 2009). Finally, we conducted a relative cladogenesis test for all slices through the tree using GEIGER.

ML was used to compare models of lineage diversification and the best model was selected based on AIC. Using functions in the LASER library, we fitted the following models of diversification: pure birth, birth–death, Yule models with two to five birth rates, and uncorrelated lognormal relaxed clock were selected. Two parallel runs were specified, each including 50 million generations, sampling every 5000th generation. Tree and log files were combined in LogCombiner v.1.7 (Drummond & Rambaut, 2007) by resampling at lower frequency (15 000) and the results were visualized in Tracer v.1.5 (Rambaut & Drummond, 2007). Convergence of the chains was assessed by effective sample size (ESS) values higher than 200 in all the parameters. The final tree was generated by TreeAnnotator v.1.7 (part of the BEAST package) with a burnin of 2000. To provide a coarse time framework for Pettalidae (given that no pettalid fossil is known), we included three more outgroups in order to represent all extant Opiliones suborders (Eupnoi: Protolophus singularis; Dyspnoi: Hesperonemastoma modestum; Laniatores: Equitius doriae).

### Table 3. Number of weighted steps for each data partition, the combination of them (MOL) and wILD values

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<td>8353</td>
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</table>

The optimal parameter set is indicated in italics.

#### Diversification analyses

An ultrametric tree was generated in BEAST v.2.3.2 (Drummond et al., 2012) as implemented in the CIPRES Science Gateway (Miller et al., 2009; Miller, Pfeiffer & Schwartz, 2010). A unique general time reversible (GTR) model of sequence evolution with corrections for a discrete gamma distribution (GTR + Γ) was specified for each data partition (each gene), and 100 independent searches were conducted. Nodal support was estimated via the rapid bootstrap algorithm (1000 replicates) using the GTR-CAT model (Stamatakis, 2008). The amount of data utilized by each analysis is given in Table 4.

#### Table 4. The amount of data for each marker and the total used in each analysis, including the implied alignment obtained from POY (POY IA, parameter set 111), the resulting number of columns in the untrimmed MAFFT alignment (MAFFT) and after trimming with Gblocks (MAFFT-Gb)

<table>
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<td>386</td>
<td>657</td>
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</table>

that are largely congruent with respect to the genera and their composition. For example, all analyses recognize the monophyly of Pettalidae with 100% resampling support (bootstrap or jackknife), inclusion of Speleosiro within Purecellia, monophyly of all other genera, and a sister group relationship between Parapurcellia and a clade including all other pettalids. Major differences, however, exist among the relationships of the genera in the latter clade, which vary from analysis to analysis or among parameter sets (see below). The specifics and implications of these results are discussed below.

**DIRECT OPTIMIZATION ANALYSES**

Analyses of the combined data under six parameter sets stabilized after one to five rounds of SATF (Table 2). Parameter set 111 was selected as the preferred one for the parameter sets explored in the sensitivity analysis, with a qILD = 0.02446, closely followed by parameter set 211 (Table 3). The 111 tree, of 12 022 steps, was found after four rounds of SATF, and remained stable thereafter (six rounds conducted) (Fig. 3; see summary of the relationships under other parameter sets in Fig. 6).

The tree obtained under the optimal parameter set (111; Fig. 3) found strong jackknife support (hereafter JS) for the monophyly of Pettalidae (JS = 100%) and many of its genera (JS ≥ 98% for Parapurcellia, Neopurcellia, Pettalus, Karripurcellia and Chileogovea), but support for some of the most diverse genera (Aoraki, Austropurcellia and Rakaia) was lower (JS = 81, 64 and 61%, respectively). Finally, Purecellia was paraphyletic with respect to Speleosiro; the inclusion of Speleosiro in Purecellia has a JS of 89%, and the clade was found under every parameter set examined. Although relationships among genera received no support above 50%, all parameter sets agreed in finding Parapurcellia to be the sister group to all other genera, which form a clade under every examined parameter set. A few other generic relationships are stable to parameter set variation, especially the clade including Chileogovea + Purecellia (five out of six parameter sets), and the clade including all genera except Parapurcellia and Austropurcellia (four out of five parameter sets) (see Figs 3, 6). The internal relationships within each genus are discussed below.

**PROBABILISTIC ANALYSES OF ALIGNED DATA**

The ML analysis of the trimmed and untrimmed data sets yielded identical relationships of the pettalid genera, but few of these generic relationships found strong support (Fig. 4). As in the direct optimization analyses, the exception is the basal division between Parapurcellia and the remaining genera, which formed a clade with 91% bootstrap support (hereafter BS) (Fig. 4). Chileogovea and Purecellia formed a clade with 57% BS. The remaining genera formed a clade with 70% BS. As in the direct optimization analyses, Speleosiro renders Purecellia paraphyletic – a clade with 100% BS. All other genera were monophyletic with BS ≥ 98%.

Results of the Bayesian analysis coincide with the ML analysis in the split between Parapurcellia and the remaining genera [with a posterior probability value (hereafter pp) of 1.00], but little else (Fig. 5). As in several of the parsimony direct optimization analyses, Austropurcellia is supported as the sister group of all the remaining genera, the latter clade receiving significant support (pp = 0.99). Pettalus is then sister group to two clades, one comprising Aoraki, Neopurcellia and Karripurcellia, and another one comprising Rakaia, Chileogovea and Purecellia.

**DIVERSIFICATION ANALYSES**

Analysis of competing diversification models identified the logistic density dependence model (DDL) as the best rate variable model and best model overall and the pure birth model as the best constant rate model (Table 5). This result is congruent with the value recovered for the gamma statistics, which rejected the decrease of rates over time (γ = −4.900, P = 0.4772). When testing for lineage-specific instead of overall diversification shifts, the ‘medusa’ analysis did not detect any shifts. The test for recent cladogenesis indicated a shift in two clades: one within the genus Aoraki (including Aoraki denticulata, A. denticulata major, A. longitarsa, A. tumidata, A. granulosa, A. cf. tumidata and A. calcareobtusa westlandica), and one within Austropurcellia (including A. daviesae, A. tholei, A. despectata and A. cadens).

**GENERIC RELATIONSHIPS**

All analyses conducted, including all parameter sets under direct optimization and the probabilistic analyses, find a sister group relationship between Parapurcellia and all the other pettalid genera (Figs 3–6), the latter clade receiving 95% BS in the ML analyses and a pp = 1.00. A relationship of Chileogovea and Purecellia is found under ML (BS = 57%) and Bayesian phylogenetics (pp = 1.00), as well as under all parameter sets, with the exception of 211, which finds Purecellia as the sister group to a clade composed of Chileogovea and Karripurcellia. A clade composed of these three genera is also found under parameter sets 111 and 3221 (Figs 3, 6). The ML analysis furthermore sup-
Limulus polyphemus

Figure 3. Best (12 022 steps) direct optimization tree found under the optimal parameter set, 111; this tree was found after four rounds of SATF. Numbers on nodes indicate jackknife support values >50%. Branch lengths are proportional to the amount of changes (indels and nucleotide transformations). Navajo rugs for selected deep nodes indicate stability after four rounds of SATF. Numbers on nodes indicate jackknife support values. 

A pattern of two ancient South African lineages not being sister taxa, and one being sister group to a Chilean clade, is also found in Peripatopsidae (Onychophora) (Murienna et al., 2014), where the South African genus Peripatopsis is closest to the Chilean Metaperipatus, while the other South African genus, Opisthopatus, is sister group to the previous clade, and thought to be related to another Chilean genus, Paropisthopatus (Reid, 1996). Also interesting is the early split between South Africa and the rest of the southern Gondwanan landmasses in the family Neopilionidae (Arachnida, Opiliones) (Vélez, Fernández & Giribet, 2014), although in this case sampling in South America and South Africa was not optimal and no molecular dating was performed to test the temporal correspondence in tree topology with landmass history. The early split between Africa and other parts of Gondwana is seen also in midig trap-door spiders (Griswold & Ledford, 2001) and was probably first demonstrated by Brundin (1966) in his phylogeny of austral chironomid midges.

An interesting biogeographical pattern related to the South African lineages is remarkably coincident with the deepest division in the area cladogram of Griswold (1991), where Purcellia corresponds to the Table Mountain–Knysna Forest area cladogram and Parapurcellia mostly follows its sister clade, although Parapurcellia is not known from the Eastern Arc Mountains, the East African Volcanoes or Madagascar. Nonetheless, two cyphophthalmid species occur in Madagascar (Shear & Gruber, 1996) and one in a cave system in Kenya (Shear, 1985), and although their phylogenetic affinities are poorly known (Giribet et al., 2012) and no specimens are available for molecular study, it is plausible that they may help refine the biogeographical tale of the southern African Cyphophthalmi.

The relationship of the Australian genera is poorly understood. The ML analysis finds a clade of Austropurcellia and Karripurcellia, albeit without support, and no parameter set under direct optimization favours this topology. Instead, direct optimization favours a relationship of the Western Australian Karripurcellia to the above-mentioned clade of Purcellia and Chileogovea, and the BEAST analysis places Austropurcellia in a much more basal position, while it places Karripurcellia with the New Zealand genera Neopurcellia and Aoraki.

With respect to the New Zealand genera, Aoraki and Rakaia form an unsupported clade of New Zealand taxa in the ML analyses (Fig. 4), but Neopurcellia diverges earlier (Fig. 4). No parameter set under direct optimization finds any New Zealand clade...
Figure 4. Optimal phylogenetic hypothesis based on the ML partitioned analysis of the untrimmed data set aligned with MAFFT (logL = −56 209.799040). Numbers at nodes indicate bootstrap support values >50%; asterisks indicate 100% bootstrap support. Colours as in Figure 3.
other than parameter set 3221, which finds a clade of *Neopurcellia* and *Aoraki* (Fig. 6), also recovered in the Bayesian tree, but including *Karripurcellia* (Fig. 5). While little can thus be concluded about the relationships among the three New Zealand genera, all tree topologies from this study support the gen-

Resolution of this conundrum may require different amounts of data, such as those generated for recent studies of Opiliones relationships (Hedin et al., 2012; Sharma & Giribet, 2014; Sharma et al., 2014).

Table 5. Fit of models to the pettalid log-lineages through time curve ordered by increasing Akaike information criterion (AIC).

<table>
<thead>
<tr>
<th>Model</th>
<th>lnL</th>
<th>AIC</th>
<th>Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>DDL</td>
<td>-165.5326</td>
<td>335.0652</td>
<td>r1 = 0.0214628, kparam = 89.79096</td>
</tr>
<tr>
<td>DDX</td>
<td>-172.0945</td>
<td>348.1890</td>
<td>r1 = 0.0456129, xparam = 0.455107</td>
</tr>
<tr>
<td>Yule-2-rate</td>
<td>-176.9459</td>
<td>359.8918</td>
<td>st1 = 8.983151, r1 = 0.009181212, r2 = 0.0028064</td>
</tr>
<tr>
<td>Pure birth</td>
<td>-178.9910</td>
<td>359.9821</td>
<td>r1 = 0.0086758</td>
</tr>
<tr>
<td>Birth-death</td>
<td>-178.9914</td>
<td>361.9821</td>
<td>a = 359.9821</td>
</tr>
<tr>
<td>Yule-3-rate</td>
<td>-176.7257</td>
<td>363.4514</td>
<td>st1 = 6.445763, st2 = 0.000000, r1 = 0.0091812, r2 = 0.0050526, r3 = 0.0019427</td>
</tr>
</tbody>
</table>

DDL and DDX refer to density-dependent logistic and exponential models, respectively. Selected model is shown in bold type.

Figure 6. Summary of the generic relationships for the different analyses conducted. Colours as in Figures 3–5.

eric designations emended by Boyer & Giribet (2007). Resolution of this conundrum may require different amounts of data, such as those generated for recent studies of Opiliones relationships (Hedin et al., 2012; Sharma & Giribet, 2014; Sharma et al., 2014).
The relationships of the Sri Lankan genus Pettalus also remain largely unresolved; Pettalus is found as the sister group of the non-Parapurcellia, non-Austropurcellia genera in the BEAST analysis (Fig. 5), included with the Australian/New Zealand genera in the ML analysis (Fig. 4), or it groups with Karripurcellia, from Western Australia, under several parameter sets in the direct optimization analyses. It also appears related to some New Zealand taxa under other parameter sets (Fig. 6), or under parameter set 3221 it appears as sister group to all other pettalids except Parapurcellia.

**Parapurcellia Rosas Costa, 1950**

The South African genus Parapurcellia appears as the sister group to all other pettalid genera in all our analyses, but its internal resolution shows little stability. Diversification of Parapurcellia started around the Jurassic (see 95% confidence interval in Fig. 5). This is consistent with interpretations about Eastern South Africa becoming geologically quiet around the end of the Cretaceous, with geological activity resuming with uplift near the end of the Palaeogene (King, 1982). This has been cited as significant in the evolution of microstigmatid spiders and cannibal snails (Herbert & Moussalli, 2010).

Previous molecular analyses included only two species of Parapurcellia (Boyer & Giribet, 2007; Giribet et al., 2012), although the relationships of the genus were later addressed based on morphological characters (de Bivort & Giribet, 2010; de Bivort et al., 2010). Our topologies contradict some of the previous clades based on morphology, but find little support for most clades. A clade of the Eastern Cape and KwaZulu-Natal species *P. convexa*, *P. fissa* and *P. rumpiana* is supported in ML (100% BS) and direct optimization, but the position of *P. monticola* appears unsupported. Another putative clade includes *P. staregai*, *P. minuta*, *P. amatola*, *P. peregrinator*, *P. silvicola* and an undescribed species from Limpopo, most similar to ‘Purcellia’ transvaalica, and therefore constituting a clade of species from KwaZulu-Natal, Mpumalanga and Limpopo.

**Parapurcellia** extends into Griswold’s Natal–Zulu-land Coast, Transkei–Natal Midlands and Natal Drakensberg areas of endemism (Griswold, 1991), a result consistent with our phylogenetic position of the close relative of ‘Purcellia’ transvaalica, but contradicted by the species morphology (see de Bivort & Giribet, 2010). The combination *Parapurcellia transvaalica* (Lawrence, 1963) comb. nov. is thus provided.

**Purcellia Hansen & Sørensen, 1904**

Purcellia constitutes the other South African clade, of relatively uncertain affinities, but it never constitutes the sister group of Parapurcellia (see discussion above). Diversification of this clade initiated in the Cretaceous (Fig. 5). All analyses include Speleosiro argasiformis, and a new species (MCZ IZ-129494), originally assigned to ‘Speleosiro’, nested within Purcellia. We thus synonymize Speleosiro Lawrence, 1931 with Purcellia Hansen & Sørensen, 1904 syn. nov. and transfer Speleosiro argasiformis to Purcellia, as Purcellia argasiformis (Lawrence, 1931) comb. nov. Purcellia argasiformis is the only troglobitic pettalid species (Rambla & Jubertie, 1994). The origin of the troglobitic fauna of the Cape Peninsula has been discussed by Sharratt, Picker & Samways (2000), who interpret this species as a relict in light of the Pleistocene-effect theory. However, the divergence of Purcellia argasiformis from its sister species, *P. cf. leleupi*, dates back to the Cretaceous. Pre-Pleistocene diversification has also been suggested for different clades of spiders (Griswold, 1991; Wood et al., 2013).

Our analyses include all of the previously described species of Purcellia, including *P. argasiformis*, except for *P. lawrencei* de Bivort & Giribet, 2010; plus at least three additional undescribed species. Purcellia is restricted to the coastal forests of the Western Cape province and to the westernmost coastal forests of the Eastern Cape province, showing no overlap with the distribution of Parapurcellia (Fig. 2). The pattern of a distinct south-western vs. a southern and tropical African clade is seen in many forest spiders including Phyxelididae (Griswold, 1990) and Cyatholipidae (Griswold, 2001); in some cases the south-western clade (‘Table mountain’ and ‘Knysna forest’ of Griswold, 1991) may be sister group to clades extending through tropical Africa and including Madagascar (Griswold, 2000; Griswold, Wood & Carmichael, 2012).

**Purcellia griswoldi** de Bivort & Giribet, 2010 is sympatric with *P. lawrencei*, and here we sequenced a female from Knysna (MCZ IZ-134756), which is sister group to *P. griswoldi*, and thus may correspond to *P. lawrencei* (Figs 3, 4). Few other clades within Purcellia are worth discussing, given the low support and/or stability. However, it is worth noting the existence of at least two undescribed species in Helderberg Mountain, one, MCZ IZ-129493, related to Purcellia illustrans, and another with a ‘Speleosiro’ morphology (MCZ IZ-129494), unrelated to MCZ IZ-129493.

Finally, our tentative assignment of specimens MCZ IZ-129098 to *P. leleupi* is due to the poor,
inaccurate description of the species (Starega, 2008) and lack of available type material to contrast our specimens from Jonkershoek Nature Reserve, in the Hottentots–Holland Mountain Range (Western Cape Province). The type locality of _P. leleupi_ is listed as ‘Prov. du Cap, Caledon distr., Sonder End Berg, Olifant rivier ...’, which is difficult to reconcile with modern localities. There is an Olifants River (_Olifantsrivier_ in Afrikaans) in the south-western area of the Western Cape Province, but this is far from Caledon. We interpret the type locality as possibly Riviersonderrand Mountains, near Riviersonderrand, a town in Western Cape Province, c. 45 km from Caledon. The mention of Olifant River is anomalous and possibly an error, as this lies well to the north of this area. Morphologically, our specimens could correspond to this species, but this is currently difficult to ascertain with the published description and lack of deposited type material.

**Austropurcellia Juberthie, 1988**

_Austropurcellia_ has been recently revised using both morphological and molecular data (Popkin-Hall & Boyer, 2014; Boyer et al., 2015). The clade initiated its diversification around the Triassic, but subsequent diversification of its main clades was somehow halted. However, this could be a consequence of missed sampling in Central and South Queensland, where several species exist but were not included in this study (Popkin-Hall & Boyer, 2014; Boyer et al., 2015).

Our trees show a deep split between two clades within _Austropurcellia_. One of those lineages includes only species from the Wet Tropics in far north Queensland and corresponds to the ‘Wet Tropics endemic clade’ of Boyer et al. (2015). The Australian Wet Tropics represent the largest remnant of rainforests that were once widespread across the Australian continent, and are distributed in a linear fashion parallel to the coast across a span only ~500 km in length. The sister clade to the Wet Tropics endemic clade is composed of _A. acuta_, the southernmost species of _Austropurcellia_ included in this analysis, and _A. clousei_, found in the southernmost Wet Tropics some 6.5° of latitude further north. Thus, _A. clousei_, located in the southern Wet Tropics and only 1.6° south of the closest of the Wet Tropics endemic clade species, is 6.5° apart from its sister species (Boyer et al., 2015). _Austropurcellia clousei_, _A. acuta_, and other species from central and southern Queensland share morphological characteristics, such as the shape of the adenostyle, that may warrant the elevation of this lineage to the status of genus (Popkin-Hall & Boyer, 2014). Such taxonomic revision awaits phylogenetic work with increased taxon sampling from central and south Queensland.

Within the Wet Tropics endemic clade, we find _A. sharmai_ from the northernmost range of the genus to be the sister group of the remaining species under direct optimization, although with low support. It appears as the sister group to _A. culminis, A. scoparia_ and _A. vicina_ in the ML and BEAST analyses. We find support for a clade of central Wet Tropics species including _A. tholei, A. despectata, A. cadens_ and _A. daviesae_, and of a north-central clade with _A. culminis, A. scoparia_ and _A. vicina_, as in Boyer et al. (2015). However, _A. arcticosa_, from the northernmost Wet Tropics, constitutes the sister group to the central clade, with _A. giribeti_, also from the north, branching earlier.

With its earliest diversification dating to the Cretaceous, _Austropurcellia_ has persisted throughout events of major climatic change that have no doubt shaped its evolutionary history. Studies of dispersal-limited assassin spiders indicate that the onset of Australian aridification during the Miocene may have been a major driver of diversification (Rix & Harvey, 2012). Much later, the glacial cycles of the Pleistocene also shaped the diversity of forest-restricted animals, especially those such as Cyphophthalmi that are dispersal-limited and thus susceptible to extinction due to local habitat shifts (Graham, Moritz & Williams, 2006). The nature and effect of forest contraction and fragmentation in the Australian Wet Tropics have been well studied using the tools of palaeoclimatology (e.g. VanDerWal, Shoo & Williams, 2009) and phylogeography (e.g. Bell et al., 2012), although most studies have been performed on vertebrate systems. Boyer et al. (2016) found that species richness and phylogenetic diversity of _Austropurcellia_ across sub-regions of the Wet Tropics are better predicted by climatic suitability during the Last Glacial Maximum than by present-day climatic suitability, affirming the role of historical refugia in determining present-day biogeographic patterns.

**Karripurcellia Giribet, 2003**

The Western Australian _Karripurcellia_ appears as a molecularly homogeneous genus, as also evidenced morphologically (Giribet, 2003a), restricted to the forests of south-west Australia. The genus originated during the Mesozoic, but the recent species only diversified during the last 8 Myr, its current diversity probably resulting from recent Miocene/Pliocene climatic changes (Rix et al., 2015). Giribet (2003a) described three species in the genus, one of which was later synonymized by Karaman (2012), who also erected the new genus _Milipurcellia_ Karaman, 2012.
for Karripurcellia sierwaldae Giribet, 2003, although this was based on characters not tested phylogenetically. This taxonomic action is not accepted here and therefore we synonymize Milipurcellia with Karripurcellia Giribet, 2003 syn. nov. However, morphological variation within the genus may reflect some level of plasticity, according to the molecular data presented here, which includes specimens from across the known range of the genus (Fig. 2), covering a linear distance of less than 70 km. Phylogeographical work within this isolated clade must be attempted in the future for testing molecular species delimitation.

**CHILEOGOVEA ROEWER, 1961**

The Chilean genus Chileogovea remains poorly known, with many recent samples of unstudied material. Here we included specimens from its two described species (Roewer, 1961; Juberthie & Muñoz-Cuevas, 1970; Shear, 1993) spanning the known range of the genus, although these samples may hide some cryptic diversity. We find a deep split between Chileogovea jocasta Shear, 1993 and Chileogovea oedipus Roewer, 1961, during the Cretaceous. Future work including many available specimens (Chileogovea can be extremely abundant in some localities, and both species have broader ranges than most other known pettalids) should clarify whether the group includes two widespread species or a larger number of species more restricted geographically.

**AORAKI BOYER & GIRIBET, 2007**

The genus Aoraki received considerable attention by Boyer & Giribet (2007, 2009). Its original diversification can be traced back to around the Jurassic, diversifying in New Zealand steadily for c. 160 Myr, a result that is inconsistent with the purported total submersion of New Zealand during the Oligocene (Trewick, Paterson & Campbell, 2007; Landis et al., 2008; Trewick & Bland, 2012). This has been argued in earlier work using members of this clade (Boyer, Baker & Giribet, 2007a; Fernández & Giribet, 2014), other organisms (Allwood et al., 2010; Giribet & Boyer, 2010; Murienne et al., 2014) and simulations (Sharma & Wheeler, 2013) – ‘Drowned New Zealand’ seems to be subsiding scientifically.

A few discrete clades are found within Aoraki, including one with the three species A. healyi, A. innerma and A. crypta, from the North Island and Marlborough Sounds. Another clade includes species from the northern South Island (A. calcarohtusa westlandica) and the North Island (A. tumidata and A. granulosa). The third clade includes the divergent A. denticulata denticulata, and the other two taxa within the clade, A. denticulata major and A. longitarsa, from the northern South Island. The taxonomic and evolutionary problems of the A. denticulata complex have been addressed in depth by Boyer et al. (2007a) and Fernández & Giribet (2014). These three clades, although with an unsupported relationship among them, were also found by Boyer & Giribet (2009). Finally, the phylogenetic position of an undescribed species from Mount Stokes (in Marlborough Sounds; northern South Island) remains unresolved.

**NEOPURCELLIA FORSTER, 1948**

After the revisionary work of Boyer & Giribet (2007), Neopurcellia remains monotypic, and as in the case of Karripurcellia, it constitutes an old lineage (probably of Mesozoic origin) that has remained stable in the Australian plate of New Zealand for a long period of time, and the Recent fauna probably represents a relicual clade of a once much more diverse group. We included specimens from four localities in Southland, for a maximum linear distance of 90 km, one specimen diverging from the other three c. 4 Mya, during the Pliocene (data not shown), a time of intense orogeny in New Zealand (Sutherland, 1994; Trewick, Wallis & Morgan-Richards, 2000). However, specimens of N. salmoni are difficult to access and future work will require intense sampling in Fiordland to address the phylogeographical and systematic status of this genus.

**RAKAIA HIRST, 1925**

Rakaia is the largest genus of Pettalidae, with 18 named taxa mostly on the South Island and southern North island of New Zealand. As with Aoraki, the genus started diversifying around the Jurassic, and has continued diversifying steadily, adding further refutation to the total drowning of New Zealand (see above citations). Relationships within Rakaia receive higher support than for most other genera, perhaps owing to the large taxon sampling – although taxon sampling has been optimized for most genera, there is no guarantee that the current diversity is a good sample of the historical one. Our tree is therefore very similar to that of Boyer & Giribet (2009), with four main clades. Clade a includes species from Stewart Island, in the southern tip of the South Island, the northern part of the South Island and the North Island, probably indicating an ancestral widespread distribution of this clade (R. stewartiensis, R. lindsayi, R. florensis and R. minutissima). Clades b, c and d from Boyer & Giribet (2009) form a stable well-supported group (BS = 95% in ML), but their
internal configuration differs. Clades b (from the south coast of the South Island: *R. sorenseni sorenseni* and *R. sorenseni digitata*, plus two undescribed species) and c (from Otago and Canterbury: *R. antipodiana*, *R. collaris*, *R. macra*, *R. pauli* and an undescribed species) are sister groups, and occupy adjacent geographical areas. Finally, this latter clade is sister group to a clade occupying the northern portion of the South Island (Lewis Pass and Marlborough Sound) and the North Island, including a large diversity of described (*R. dorothea*, *R. magna australis*, *R. media*, *R. solitaria*, *R. uniloca*) and undescribed species. Taxonomic work within this diverse genus is sorely needed (Boyer & Giribet, 2003; Giribet et al., 2014a).

**PETTALUS THORELL, 1876**

*Pettalus*, despite being the type genus of the family, remains one of the least understood pettalid genera, with four named but many undescribed species, all endemic to Sri Lanka (Cambridge, 1875; Pocock, 1897; Sharma & Giribet, 2006; Giribet, 2008; Sharma et al., 2009). Our analyses included representatives of one named species and seven undescribed species from a group that has been diversifying at least since the Jurassic, long before the Indian subcontinent collided with Southeast Asia (Ali & Aitchison, 2008).

Two of the sampled localities had more than one species occurring sympatrically, Hakgala (MCZ IZ-132353, IZ-132354) and Knuckles Range (MCZ IZ-132356, IZ-132357), but neither pair form sister clades, a phenomenon not uncommon in Cyphophthalmi, where sympatric species are usually not each other’s sister groups (see, for example, *Porcellia illustrans* and *P. argasiformis*; the two undescribed *Porcellia* from Helderberg Mountain, or several sympatric New Zealand species). While this could be interpreted as recent dispersal, the old divergences between these species pairs probably imply an old biogeographical history. Some of the stable and well-supported clades within *Pettalus* include the two species from Sabaragamuwa Province (MCZ IZ-132360 and IZ-134967), or a clade of species from the Province of Uva (MCZ IZ-132359), Hakgala Botanical Gardens (MCZ IZ-132354) and the Knuckles Range (MCZ IZ-132357). The relationships of *P. thewaitesi* differ among analyses, with support for a clade with the other Hakgala undescribed species (MCZ IZ-132353). Copious amounts of taxonomic work remain to be done for this genus of pettalids, the oldest (Cambridge, 1875; Pocock, 1897), yet the most enigmatic, with at least 13 species remaining to be described (Sharma et al., 2009).

**FINAL REMARKS**

The particular geographical distribution and phylogenetic relationships of Cyphophthalmi have attracted attention for more than four decades (Juberthie, 1970, 1971; Juberthie & Massoud, 1976; Shear, 1980; Giribet, 2000), with an early recognition of a temperate southern hemisphere clade (Juberthie, 1970) – currently the family Pettalidae – originally thought to be related to the temperate northern hemisphere species – currently the family Sironidae. It is now clear that Pettalidae and Sironidae are not sister clades, and that instead Pettalidae constitutes the sister group to all other Cyphophthalmi (Giribet et al., 2012; Sharma & Giribet, 2014), a result that corroborates hypotheses of ancient continental biogeography of both Cyphophthalmi and Pettalidae (Juberthie & Massoud, 1976; Boyer & Giribet, 2007; Boyer et al., 2007b), even at much smaller geographical scales (Forster, 1954). As Forster (1954) already recognized when studying the New Zealand fauna:

> the nocturnal and cryptozoic habit of the groups under consideration [e.g. Cyphophthalmi] does not lend itself to distribution by chance methods, and it is improbable that drift on floating logs or debris has played any great part in establishing the distribution patterns which are characteristic for the present fauna. It may therefore be inferred with reasonable assurance that continuous land or closely spaced islands are necessary for dispersal and that topographic features, such as water barriers and mountain ranges have played, and are still playing, an important part in the segregation of populations and their subsequent speciation... It may therefore be implied that distribution patterns exhibited by present day fauna will reflect recent geological change undergone by the area under consideration.

Pettalids are indeed remarkable for elucidating the breakup of Gondwana, with their only main biogeographical gap occurring in Tasmania. However, the results shown here, with a nearly complete extant taxon sampling, and using the markers that have provided resolution at the genus level in all other non-monogeneric Cyphophthalmi families (Boyer & Giribet, 2007; Clouse & Giribet, 2010; Giribet et al., 2012; Benavides & Giribet, 2013; Dreszer, Rada & Giribet, 2015), show a striking lack of support for most generic relationships, especially within eastern Gondwana. This lack of support or resolution using markers that work for several other comparable taxa may be due to lack of data from Madagascar and to large extinction events in putative intermediate lineages that once lived in large landmasses such as Antarctica or most of the now arid Australia (Rix...
et al., 2015) – as probably evidenced by the lack of Cyphophthalmi in Tasmania, or the two ‘relict’ lineages of Australia (Karripurcellia) and New Zealand (Neopurcellia). Future work will thus test whether the lack of resolution is due to deficient molecular sampling or to extinction by providing phylogenomic-level data for this family.

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