

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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INTRODUCTION

The mite harvestman family Pettalidae Shear, 1980 (the 'lignée gondwanienne' or Gondwanan lineage of

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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 ozopores – the unique structure bearing the odoriferous glands of Cyphophthalmi – and dual cheliceral denti-

tion, pettalids (Fig. 1) are distributed in virtually all the former temperate Gondwanan landmasses (Juberthie & Massoud, 1976; Shear, 1980; Boyer *et al.*, 2007b; Giribet *et al.*, 2012). In South America, the family is represented by two Chilean species in the genus *Chileogovea* Roewer, 1961 (Roewer, 1961;



Figure 1. Habitus of live specimens: A, *Pettalus thwaitesi*, Sri Lanka, 18.vi.2004 [MCZ IZ-132349]; B, *Chileogovea oedipus*, Chile, 15.xi.2014 [MCZ IZ-138106]; C, *Purcellia* sp. nov., South Africa, 16.xii.2014 [MCZ IZ-49518]; D, *Parapurcellia monticola*, South Africa, 15.xi.2011 [MCZ IZ-134571]; E, *Purcellia argasiformis*, South Africa, 5.xi.2011 [Photo MCZ IZ-134759]; F, *Purcellia argasiformis*, South Africa, 5.xi.2011 [MCZ IZ-134759]; G, *Aoraki longitarsa*, New Zealand, 20.i.2014 [MCZ IZ-29554]; H, *Aoraki inerma*, New Zealand, 12.i.2014 [MCZ IZ-29572]; I, *Neopurcellia salmoni*, New Zealand, 18.i.2014 [MCZ IZ-25981]; J, *Rakaia magna australis*, New Zealand, 17.i.2014 [MCZ IZ-29212]; K, *Austropurcellia* sp., Australia, v.2011 [Photo DSC_2946]; L, *Karripurcellia peckorum*, Australia, 12.x.2011 [MCZ IZ-134720].

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 Bivort & 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, Karunaratna & 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 Peripatopsidae, the harvestmen Triaenonychidae and Neopilionidae, the pseudoscorpion Pseudotyranochthoniidae, the centipede *Paralamyctes*, the spider families Austrochilidae, Migidae and Orsolobidae, 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 Bivort, Clouse & Giribet, 2010; de Bivort & 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 yielding 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

Species	Catalogue no	Country	18S rRNA	28S rRNA	16S rRNA	COI
<i>Aoraki calcarobtusa westlandica</i>	IZ-134653	New Zealand, SI	EU673626	DQ518038	DQ518070	EU673667
<i>Aoraki cf. tumidata</i>	–	New Zealand, NI	EU673614	–	–	DQ992318
<i>Aoraki crypta</i>	IZ-134654	New Zealand, NI	DQ518000	DQ518043	DQ518068	DQ518120
<i>Aoraki denticulata denticulata</i>	IZ-134642	New Zealand, SI	EU673618	EU673654	EU673584	DQ992309
<i>Aoraki denticulata denticulata</i>	IZ-134647	New Zealand, SI	EU673616	KU207278	KF822850	–
<i>Aoraki denticulata denticulata</i>	IZ-134639	New Zealand, SI	EU673615	EU673653	KF822798	–
<i>Aoraki denticulata denticulata</i>	IZ-134646	New Zealand, SI	DQ518001	DQ518040	KF822778	–
<i>Aoraki denticulata denticulata</i>	IZ-134659	New Zealand, SI	–	KU207279	KF822746	KU207376
<i>Aoraki denticulata major</i>	IZ-134644	New Zealand, SI	EU673620	EU673656	EU673585	DQ992203
<i>Aoraki denticulata major</i>	IZ-133836	New Zealand, SI	–	KU207280	KF822858	KU207377
<i>Aoraki denticulata major</i>	IZ-35669	New Zealand, SI	KU207229	KU207281	KU207333	KU207378
<i>Aoraki granulosa</i>	IZ-134675	New Zealand, NI	DQ517999	DQ518039	DQ518071	–
<i>Aoraki granulosa</i>	IZ-134684	New Zealand, NI	KU214865	KU207282	KU207334	KU207379
<i>Aoraki healyi</i>	IZ-134638	New Zealand, SI	DQ518002	DQ518042	DQ518067	DQ518122
<i>Aoraki inerma</i>	IZ-134648	New Zealand, NI	EU673622	EU673658	–	–
<i>Aoraki longitarsa</i>	IZ-134656	New Zealand, SI	EU673613	EU673652	–	DQ992313
<i>Aoraki longitarsa</i>	IZ-134656	New Zealand, SI	EU673613	EU673652	–	DQ992313
<i>Aoraki longitarsa</i>	IZ-134656	New Zealand, SI	KU207230	KU207283	–	KU207380
<i>Aoraki longitarsa</i>	–	New Zealand, SI	KU207231	KU207284	–	KU207381
<i>Aoraki longitarsa</i>	IZ-35659	New Zealand, SI	–	KU207285	KU207335	KU207382
<i>Aoraki longitarsa</i>	IZ-35660	New Zealand, SI	–	KU207286	–	KU207383
<i>Aoraki sp. nov.</i> Mount Stokes	IZ-134652	New Zealand, SI	EU673624	EU673659	–	–
<i>Aoraki tumidata</i>	IZ-133838	New Zealand, NI	KU207232	KU207287	KU207336	KU207384
<i>Austropurcellia acuta</i>	IZ-134701	Australia, QLD	KU207233	KU207288	KU207337	KU207385
<i>Austropurcellia arctica</i>	IZ-132325	Australia, QLD	KJ767458	KJ796908	KU214866	KJ796942
<i>Austropurcellia cadens</i>	–	Australia, QLD	KJ767465	KJ767411	–	KJ796951
<i>Austropurcellia clousei</i>	IZ-132339	Australia, QLD	KJ767459	KJ767415	KU207338	KU207386
<i>Austropurcellia culminis</i>	IZ-132322	Australia, QLD	KJ767469	KJ796919	KU207339	KJ796957
<i>Austropurcellia daviesae</i>	IZ-132323	Australia, QLD	KJ767470	KJ796920	–	KU207387
<i>Austropurcellia despectata</i>	IZ-132324	Australia, QLD	KJ767474	KJ796924	KU207340	KJ796973
<i>Austropurcellia giribeti</i>	IZ-134696	Australia, QLD	DQ517984	DQ518023	–	DQ518111
<i>Austropurcellia giribeti</i>	IZ-132337	Australia, QLD	KJ767474	KJ796925	KU207341	KJ796975
<i>Austropurcellia scoparia</i>	IZ-134700	Australia, QLD	DQ517982	DQ518021	DQ518065	DQ518108
<i>Austropurcellia sharmai</i>	IZ-134698	Australia, QLD	DQ517983	DQ518022	DQ518064	DQ518110
<i>Austropurcellia tholei</i>	IZ-134697	Australia, QLD	DQ517985	DQ518024	–	DQ518112
<i>Austropurcellia vicina</i>	IZ-132334	Australia, QLD	KJ767483	KJ796933	–	KJ767447
<i>Austropurcellia vicina</i>	IZ-132318	Australia, QLD	KJ767484	KJ796934	KU207342	KJ797000
<i>Chileogovea jocasta</i>	IZ-134715	Chile	DQ133722	DQ133734	DQ518054	DQ133746
<i>Chileogovea jocasta</i>	IZ-134714	Chile	KU207234	KU207292	KU207346	KU207391
<i>Chileogovea jocasta</i>	IZ-134713	Chile	KU207235	KU207293	KU207347	KU207392
<i>Chileogovea oedipus</i>	IZ-134709	Chile	DQ133721	DQ133733	DQ518055	DQ133745
<i>Chileogovea oedipus</i>	IZ-134711	Chile	KU207236	KU207289	KU207343	KU207388
<i>Chileogovea oedipus</i>	IZ-134710	Chile	KU207237	KU207290	KU207344	KU207389
<i>Chileogovea oedipus</i>	IZ-134712	Chile	KU207238	KU207291	KU207345	KU207390
<i>Karripurcellia peckorum</i>	IZ-132345	Australia, WA	DQ517980	DQ518019	DQ518062	DQ518106
<i>Karripurcellia peckorum</i>	IZ-134719	Australia, WA	KU207239	KU207294	KU207348	KU207393
<i>Karripurcellia peckorum</i>	IZ-134720	Australia, WA	KU207240	KU207295	KU207349	KU207394
<i>Karripurcellia peckorum</i>	IZ-134721	Australia, WA	KU207241	KU207296	KU207350	KU207395
<i>Karripurcellia peckorum</i>	IZ-134725	Australia, WA	KU207242	KU207297	–	KU207396
<i>Karripurcellia sp.</i>	IZ-134726	Australia, WA	KU207243	KU207298	–	KU207397

Table 1. Continued

Species	Catalogue no	Country	18S rRNA	28S rRNA	16S rRNA	COI
<i>Neopurcellia salmoni</i>	IZ-134739	New Zealand, SI	DQ517998	EU673650	DQ518066	DQ825638
<i>Neopurcellia salmoni</i>	IZ-133839	New Zealand, SI	–	DQ518037	–	DQ518109
<i>Neopurcellia salmoni</i>	IZ-134741	New Zealand, SI	KU207244	KU207299	KU207351	KU207398
<i>Neopurcellia salmoni</i>	IZ-29317	New Zealand, SI	KU207245	KU207300	KU207352	KU207399
<i>Parapurcellia amatola</i>	IZ-133841	South Africa	KU207246	KU207301	KU207353	–
<i>Parapurcellia</i> cf. <i>rumpiana</i>	IZ-134748	South Africa	KU207255	KU207310	KU207360	KU207407
<i>Parapurcellia</i> cf. <i>staregai</i>	IZ-134746	South Africa	KU207254	KU207309	KU207359	KU207406
<i>Parapurcellia convexa</i>	IZ-134744	South Africa	KU207247	KU207302	KU207354	KU207400
<i>Parapurcellia convexa</i>	IZ-128902	South Africa	KU207248	KU207303	KU207355	KU207401
<i>Parapurcellia fissa</i>	IZ-134745	South Africa	KU207249	KU207304	KU207356	KU207402
<i>Parapurcellia minuta</i>	IZ-134747	South Africa	KU207250	KU207305	KU207357	KU207402
<i>Parapurcellia monticola</i>	IZ-60357	South Africa	DQ518973	DQ518009	–	DQ518098
<i>Parapurcellia monticola</i>	IZ-60357	South Africa	KU207251	KU207306	–	KU207404
<i>Parapurcellia monticola</i>	IZ-134571	South Africa	KU207252	KU207307	–	–
<i>Parapurcellia</i> sp. nov. Limpopo	IZ-128900	South Africa	KU207257	KU207312	–	KU207409
<i>Parapurcellia peregrinator</i>	IZ-128901	South Africa	KU207256	KU207311	–	KU207408
<i>Parapurcellia silvicola</i>	IZ-134742	South Africa	AY639494	DQ518008	DQ518053	AY639582
<i>Parapurcellia silvicola</i>	IZ-134742	South Africa	KU207253	KU207308	KU207358	KU207405
<i>Pettalus</i> sp. nov.	IZ-132357	Sri Lanka	DQ517974	DQ518016	DQ518056	DQ518100
<i>Pettalus</i> sp. nov.	IZ-132353	Sri Lanka	DQ517976	DQ518017	DQ518058	DQ518102
<i>Pettalus</i> sp. nov.	IZ-132354	Sri Lanka	DQ517977	DQ518013	DQ518059	DQ518103
<i>Pettalus</i> sp. nov.	IZ-132359	Sri Lanka	DQ517978	DQ518014	DQ518060	DQ518104
<i>Pettalus</i> sp. nov.	IZ-132360	Sri Lanka	DQ517979	DQ518015	DQ518061	DQ518105
<i>Pettalus</i> sp. nov.	IZ-134967	Sri Lanka	DQ825538	DQ825577	DQ825614	DQ825637
<i>Pettalus</i> sp. nov.	IZ-132356	Sri Lanka	DQ825537	EU673632	–	DQ825636
<i>Pettalus thwaitesi</i>	IZ-132348	Sri Lanka	EU673592	EU673633	EU673569	EU673666
<i>Purcellia argasiformis</i>	IZ-134759	South Africa	KU207266	KU207321	KU207365	KU207418
<i>Purcellia argasiformis</i>	IZ-134762	South Africa	KU207267	KU207322	KU207366	KU207419
<i>Purcellia</i> cf. <i>leleupi</i>	IZ-129098	South Africa	KU207264	KU207319	KU207363	KU207416
<i>Purcellia griswoldi</i>	IZ-128898	South Africa	KU207262	KU207317	–	KU207414
<i>Purcellia illustrans</i>	IZ-134752	South Africa	EU673589	EU673629	DQ518052	EU673665
<i>Purcellia illustrans</i>	IZ-134753	South Africa	KU207258	KU207313	–	KU207410
<i>Purcellia illustrans</i>	IZ-134754	South Africa	KU207259	KU207314	–	KU207411
<i>Purcellia illustrans</i>	IZ-128896	South Africa	KU207260	KU207315	–	KU207412
<i>Purcellia</i> sp. nov.	IZ-129494	South Africa	KU207268	KU207323	KU207367	KU207420
<i>Purcellia</i> sp. nov.	IZ-129493	South Africa	KU207261	KU207316	KU207361	KU207413
<i>Purcellia</i> sp.	IZ-128897	South Africa	KU207265	KU207320	KU207364	KU207417
<i>Purcellia</i> sp.	IZ-134756	South Africa	KU207263	KU207318	KU207362	KU207415
<i>Rakaia antipodiana</i>	IZ-134580	New Zealand, SI	DQ517988	DQ518031	DQ518072	DQ518115
<i>Rakaia collaris</i>	IZ-134574	New Zealand, SI	EU673597	EU673637	EU673573	DQ992349
<i>Rakaia dorothea</i>	IZ-134577	New Zealand, NI	DQ517990	DQ518033	DQ518077	DQ992331
<i>Rakaia florensis</i>	IZ-134588	New Zealand, SI	DQ517986	DQ518025	DQ518083	DQ518113
<i>Rakaia lindsayi</i>	IZ-134598	New Zealand, SI	DQ517995	DQ518027	DQ518081	–
<i>Rakaia macra</i>	IZ-134582	New Zealand, SI	EU673596	EU673636	EU673571	EU673668
<i>Rakaia magna australis</i>	IZ-134592	New Zealand, SI	EU673601	EU673640	EU673575	DQ992333
<i>Rakaia media</i>	IZ-134581	New Zealand, NI	DQ517996	DQ518030	DQ518074	DQ518125
<i>Rakaia minutissima</i>	IZ-134591	New Zealand, NI	DQ517987	DQ518026	DQ518082	DQ518114
<i>Rakaia minutissima</i>	IZ-29280	New Zealand, SI	KU207272	–	KU207371	KU207424
<i>Rakaia</i> sp. nov. Akatarawa Divide	IZ-133847	New Zealand, NI	EU673608	EU673647	EU673579	DQ992344
<i>Rakaia</i> sp. nov. Beaumont Forest	IZ-134568	New Zealand, SI	EU673606	EU673645	–	–

Table 1. *Continued*

Species	Catalogue no	Country	18S rRNA	28S rRNA	16S rRNA	COI
<i>Rakaia</i> sp. nov. Kapiti Island	IZ-134575	New Zealand, NI	EU673610	EU673649	EU673581	DQ992322
<i>Rakaia</i> sp. nov. Wi Toko	IZ-134584	New Zealand, NI	EU673603	EU673642	EU673576	DQ992348
<i>Rakaia</i> sp. nov.	IZ-100753	New Zealand, NI	KU207270	KU207325	KU207369	KU207422
<i>Rakaia</i> sp. nov.	IZ-133849	New Zealand, NI	KU207271	KU207326	KU207370	KU207423
<i>Rakaia pauli</i>	IZ-134576	New Zealand, SI	DQ517992	DQ518032	DQ518073	EU673670
<i>Rakaia solitaria</i>	IZ-134585	New Zealand, NI	DQ517997	DQ518029	DQ518075	DQ518119
<i>Rakaia sorenseni digitata</i>	IZ-134571	New Zealand, SI	DQ517989	DQ518035	DQ518078	DQ518123
<i>Rakaia sorenseni sorenseni</i>	IZ-134567	New Zealand, SI	DQ517993	DQ518036	DQ518079	DQ518116
<i>Rakaia</i> sp.	IZ-134600	New Zealand, SI	KU207275	KU207330	–	–
<i>Rakaia</i> sp.	IZ-35668	New Zealand, SI	KU207276	KU207331	KU207374	KU207427
<i>Rakaia</i> sp.	IZ-129612	New Zealand, NI	KU207273	KU207328	KU207372	KU207425
<i>Rakaia</i> sp.	IZ-129614	New Zealand, NI	KU207274	KU207329	KU207373	KU207426
<i>Rakaia</i> sp. (cf. <i>media</i>)	IZ-134605	New Zealand, NI	KU207269	KU207324	KU207368	KU207421
<i>Rakaia</i> sp. nov.	IZ-35662	New Zealand, SI	KU207277	KU207332	KU207375	KU207428
<i>Rakaia stewartiensis</i>	IZ-134599	New Zealand, SI	DQ517994	DQ518028	DQ518080	DQ518117
<i>Rakaia uniloca</i>	IZ-134583	New Zealand, SI	EU673599	EU673638	–	EU673671

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, Karaman & 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).



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

	SATF1	SATF2	SATF3	SATF4	SATF5	SATF6
111	12 027	12 027	12 027	12 022	12 022	12 022
211	12 889	12 886	12 886	12 886	12 886	12 886
121	19 087	19 087	19 087	19 087	19 087	19 087
221	20 673	20 673	20 656	20 656	20 656	20 656
3211	19 704	19 704	19 704	19 704	19 697	19 697
3221	24 821	24 821	24 821	24 821	24 821	24 821

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,

Table 3. Number of weighted steps for each data partition, the combination of them (MOL) and w_{ILD} values

	18S	28S	COI	16S	MOL	w_{ILD}
<i>111</i>	<i>270</i>	<i>1273</i>	<i>6200</i>	<i>3985</i>	<i>12 022</i>	<i>0.02446</i>
211	279	1503	6248	4517	12 886	0.02631
121	379	1944	9459	6761	19 087	0.02850
221	391	2374	9522	7771	20 656	0.02895
3211	385	2035	9546	7141	19 697	0.02995
3221	551	2650	12 577	8353	24 821	0.02780

The optimal parameter set is indicated in italics.

2007) prior to concatenation, resulting in two matrices, one untrimmed (same data as analysed in POY) and one trimmed. Both sets of data were then analysed under the maximum-likelihood (ML) optimality criterion in RAxML v.7.2.7 (Stamatakis, 2006) 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, Hoover & Rougemont, 2008). The amount of data utilized by each analysis is given in Table 4.

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, 2010). GTR + I + Γ was specified as the best-fit evolutionary model, as selected by jModelTest v.2.1.3 (Darriba *et al.*, 2012) using the Akaike information criterion (AIC; Akaike, 1973). The analysis was conducted with a reduced dataset including only one individual per species. A Yule speciation model and an 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

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)

	18S rRNA	28S rRNA	16S rRNA	COI	Total
POY IA	1768	2273	1211	850	6102
MAFFT	1763	2158	560	657	5138
MAFFT-Gb	1762	2076	386	657	4861

(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, linear (DDL) and exponential (DDX) diversity-dependent diversification, and two models that varied either speciation (SPVAR) or extinction (EXVAR) through time (Rabosky, 2006b; Rabosky & Lovette, 2008; Derryberry *et al.*, 2011).

RESULTS AND DISCUSSION

Analysis of the molecular data under the different approaches and optimality criteria yielded results

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 *Purcellia*, 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 $wILD = 0.02446$, 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 \geq 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, *Purcellia* was paraphyletic with respect to *Speleosiro*; the inclusion of *Speleosiro* in *Purcellia* 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* + *Purcellia* (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 opti-

mization 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 *Purcellia* formed a clade with 57% BS. The remaining genera formed a clade with 70% BS. As in the direct optimization analyses, *Speleosiro* renders *Purcellia* paraphyletic – a clade with 100% BS. All other genera were monophyletic with BS \geq 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 *Purcellia*.

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 ($\gamma = -4.900$, $P = 0.4772$). 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. calcarobtusa 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 *Purcellia* 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 *Purcellia* 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-

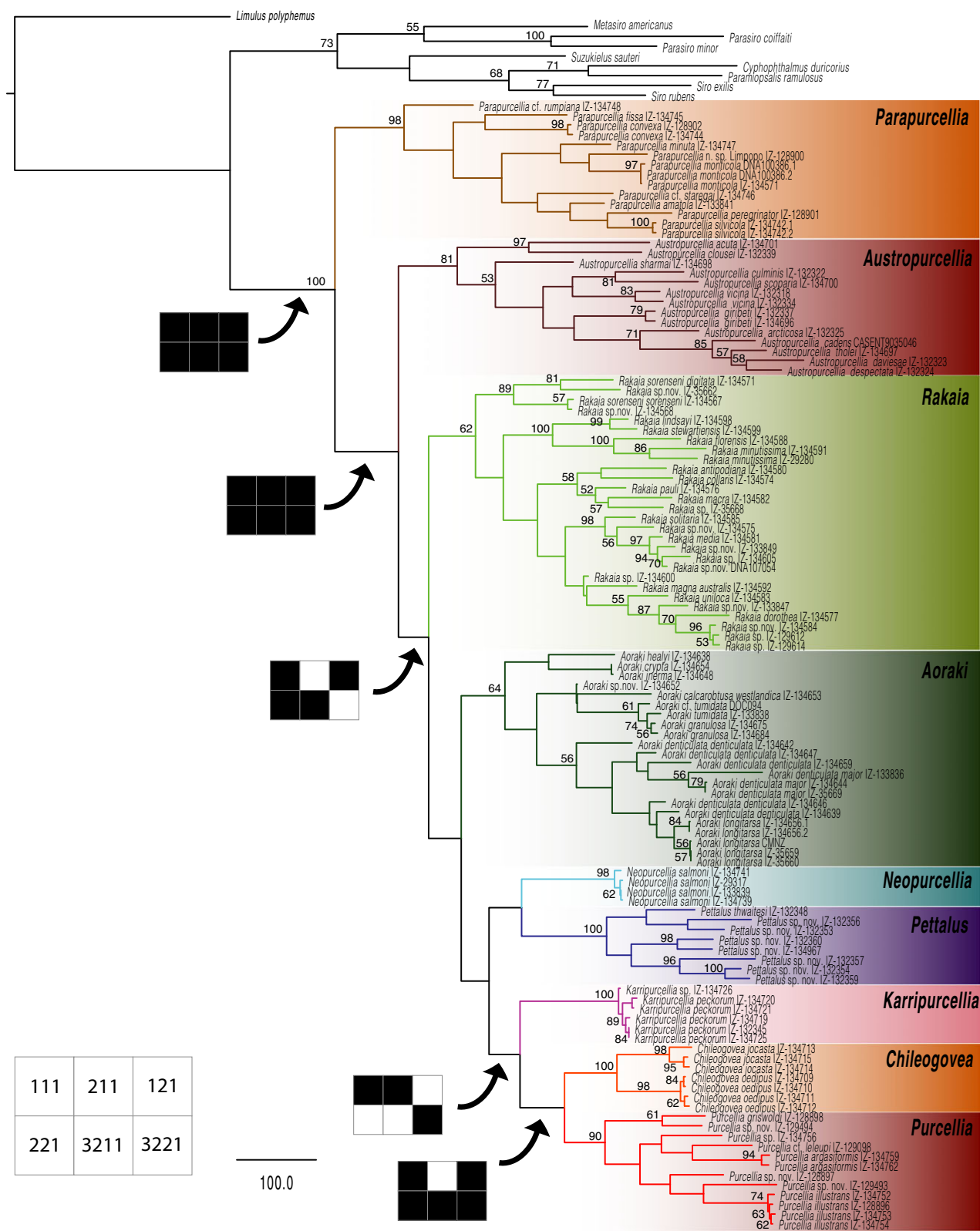


Figure 3. Best (12 022 steps) direct optimization tree found under the optimal parameter set, 111; this tree was found after four rounds of SATF. Numbers on nodes indicate jackknife support values >50%. Branch lengths are proportional to the amount of changes (indels and nucleotide transformations). Navajo rugs for selected deep nodes indicate stability under the six parameter sets examined (see legend for specific parameter sets represented by each square); black indicates monophyly and white non-monophyly. Only nodes supported by more than one parameter set are indicated; see Figure 6 for all specific generic relationships. Different colours are assigned to each genus.

ports a clade of Eastern Gondwanan genera, including the species from Sri Lanka (*Pettalus*), Australia (*Austropurcellia*, *Karripurcellia*) and New Zealand (*Aoraki*, *Neopurcellia*, *Rakaia*) (BS = 70%), but this clade is never found under direct optimization, which often places *Chileogovea* and *Purcellia* higher up in the tree (Fig. 6). This clade is also not found in the Bayesian analysis.

A consistent aspect of generic relationships is that the two genera from South Africa never form a clade; this is well supported in the ML analyses (BS for the non-*Parapurcellia* clade is 95%), and found under all parameter sets in the direct optimization analyses (albeit with low jackknife support). This result is therefore stable (*sensu* Giribet, 2003b) both to data (untrimmed and trimmed data sets), homology statements (dynamic versus static homology; multiple parameter sets in dynamic homology) and optimality criterion (parsimony and ML); it is also found in the Bayesian analysis (Fig. 5). It is thus clear that *Parapurcellia* constitutes the first divergence from the remaining pettalids, and this divergence probably took place late in the Palaeozoic or early in the Mesozoic (Fig. 5). It also seems likely that the other South African genus, *Purcellia*, from the western region of southern Africa, may be closest to the South American *Chileogovea*, both diverging during the Mesozoic, more or less during the period of opening of the South Atlantic ocean. In the South Atlantic, ocean floor extension began within continental South America at 150 Ma, inducing a rift zone between South America and Africa. Spreading extended southward along the South Atlantic ridge with a northward propagation leading to seafloor spreading in the 'Central' segment by 120 Ma (Seton *et al.*, 2012; Müller *et al.*, 2013). These dates are thus roughly concordant with our phylogenetic dating.

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) (Muriene *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 migid 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

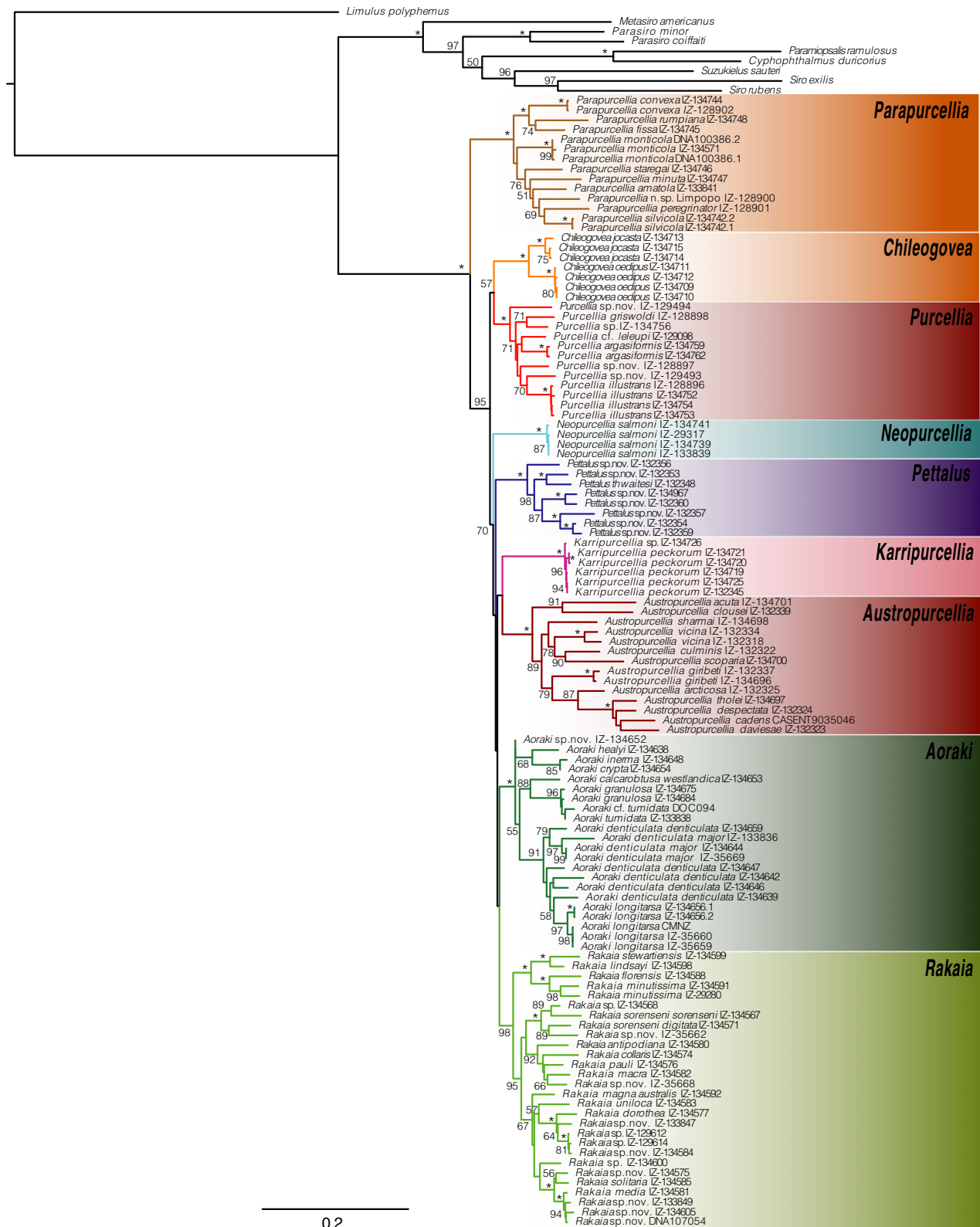


Figure 4. Optimal phylogenetic hypothesis based on the ML partitioned analysis of the untrimmed data set aligned with MAFFT (logL = -56 209.799040). Numbers at nodes indicate bootstrap support values >50%; asterisks indicate 100% bootstrap support. Colours as in Figure 3.

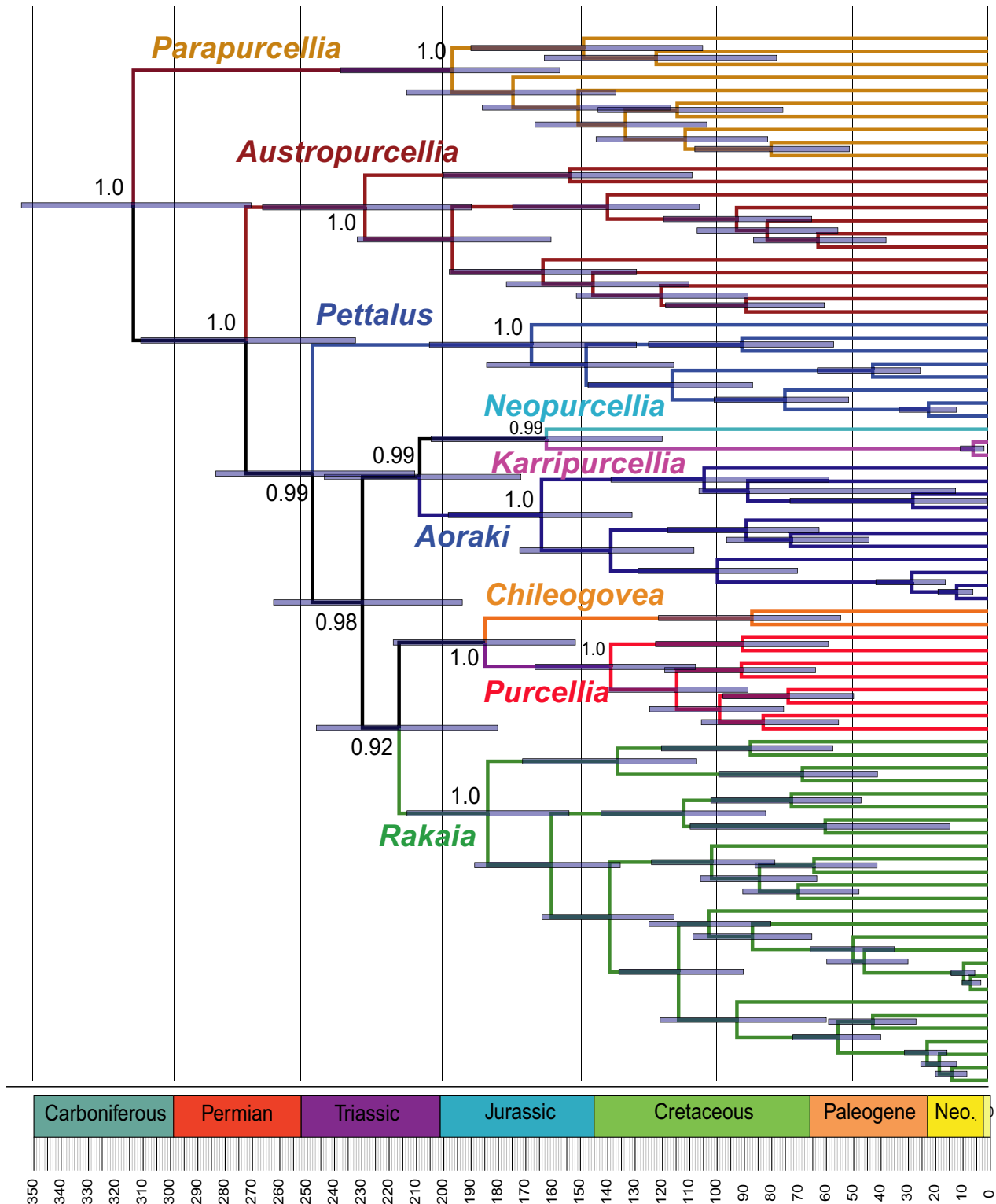


Figure 5. Chronogram generated in BEAST, with the root calibrated at 445 Ma. Colours as in Figures 3 and 4.

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-

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

Model	lnL	AIC	Parameters					
DDL	−165.5326	335.0652	r1 = 0.0214628	kparam = 89.79096				
DDX	−172.0945	348.1890	r1 = 0.0456129	xparam = 0.455107				
Yule- 2-rate	−176.9459	359.8918	st1 = 8.983151	r1 = 0.009181212	r2 = 0.0028064			
Pure birth	−178.9910	359.9821	r1 = 0.0086758					
Birth- death	−178.9914	361.9821	r1 = 0.0086842	a = 359.9821				
Yule- 3-rate	−176.7257	363.4514	st1 = 6.445763	st2 = 0.000000	r1 = 0.0091812	r2 = 0.0050526	r3 = 0.0019427	

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

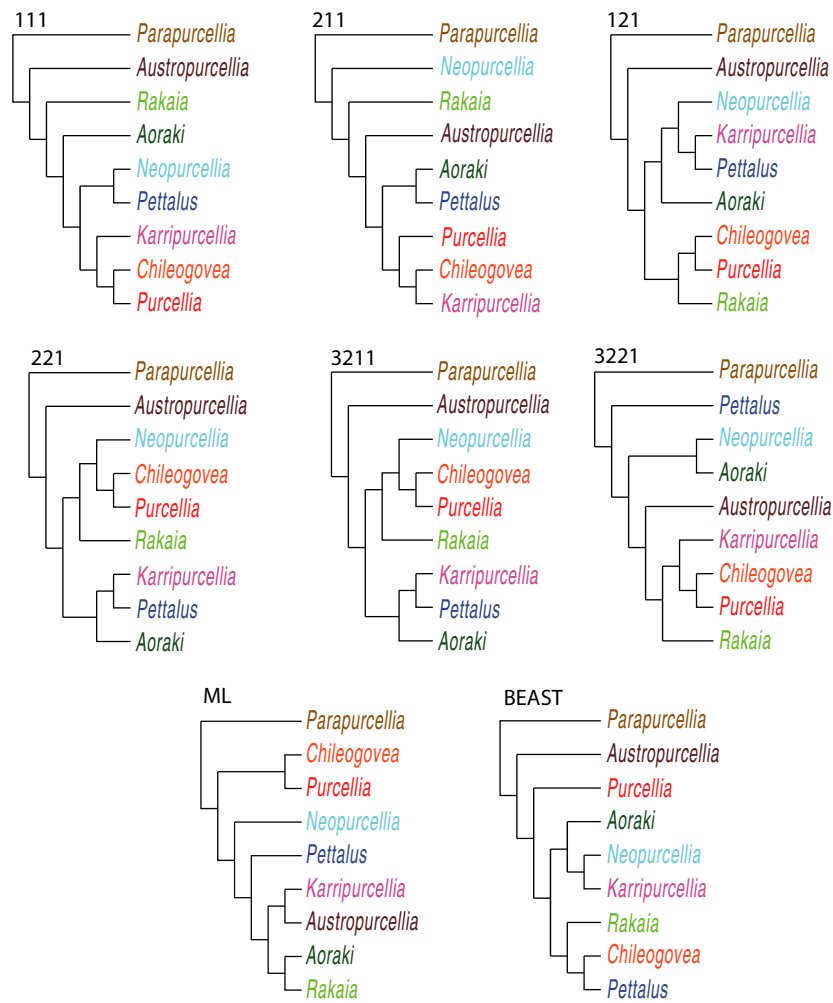


Figure 6. Summary of the generic relationships for the different analyses conducted. Colours as in Figures 3–5.

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 (Griswold, 1985) and pelican (Wood *et al.*, 2013) 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-Zululand 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 & Juberthie, 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 Riviersonderend Mountains, near Riviersonderend, 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 phylo-

genetic 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 subregions 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; Muriénne *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. inerma* and *A. crypta*, from the North Island and Marlborough Sounds. Another clade includes species from the northern South Island (*A. calcarobtusa 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 relictual 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).

PET TALUS 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, *Purcellia illustrans* and *P. argasiformis*; the two undescribed *Purcellia* 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. thwaitesi* 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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