Blackwell Publishing

Cladistics 23 (2007) 337–361

Cladistics

10.1111/j.1096-0031.2007.00149.x

A new model Gondwanan taxon: systematics and biogeography of the harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi), with a taxonomic revision of genera from Australia and New Zealand

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Accepted 26 December 2006

Abstract

The phylogeny of the temperate Gondwanan harvestman family Pettalidae is investigated by means of a new morphological matrix of 45 characters, and DNA sequence data from five markers, including two nuclear ribosomal genes (18S rRNA and 28S rRNA), one nuclear protein coding gene (histone H3), and two mitochondrial genes–one protein coding (cytochrome *c* oxidase subunit I) and one ribosomal (16S rRNA). Phylogenetic analyses using an array of homology schemes (dynamic and static), criteria (parsimony and maximum likelihood), and sampling strategies (optimal trees versus Bayesian phylogenetics) all agree on the monophyly of Pettalidae as well as several of its subclades, each of which is restricted to a modern landmass. While most genera as traditionally defined are monophyletic, *Rakaia* and *Neopurcellia*, distributed across Queensland (Australia) and New Zealand, are not. Instead, the species from Queensland, previously described under three genera, constitute a well-supported clade, suggesting that in this case biogeography prevails over traditional taxonomy. A taxonomic emendation of the genera from Queensland and New Zealand is presented, and the new genus *Aoraki* is erected to include the species of the New Zealand *denticulata* group. A biogeographical hypothesis of the relationships of the former temperate Gondwana landmasses (with the exception of Madagascar) is presented, although ambiguity in the deep nodes of the pettalid tree renders such inference provisional. The data suggest that neither the South African fauna, the New Zealand fauna nor the Australian fauna is monophyletic but instead monophyly is found at smaller geographic scales (e.g., Western Australia, Queensland, NE South Africa).

Geological and ecological context: the breakup of Gondwana

The breakup of the former supercontinent Gondwana is one of the most compelling subjects in historical biogeography. Gondwana formed the southern part of Pangaea during the Triassic, and broke into continental fragments starting in the Late Jurassic and continuing through the Cretaceous. During this time the organisms living on Gondwana drifted with the continental fragments, resulting in a disjunct distribution across those landmasses in many extant taxa, including such textbook examples as the chironomid midges (Brundin, 1965) and *Nothofagus*, the Southern Beech (Linder and Crisp, 1995). However, the biogeographical history of many Gondwanan groups is not a simple story of vicariance, as *trans*-oceanic dispersal has often played an important role in achieving present-day distributions. In *Nothofagus*, for example, palynological data, phylogenetic studies, and molecular dating all indicate that vicariance alone cannot explain the present distribution of these trees (Swenson et al., 2001a; Cook and Crisp, 2005). In other cases, the lack of compelling phylogenetic data for Gondwanan-distributed taxa has impeded more detailed biogeographical interpretations.

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Only recently have researchers analyzed Gondwanan taxa using explicit numerical techniques to test alternative hypotheses of diversification during the breakup of continental landmasses (e.g., Sanmartín and Ronquist, 2004; Giribet and Edgecombe, 2006).

The harvestman family Pettalidae (Arachnida, Opiliones, Cyphophthalmi) presents a classical Gondwanan distribution (e.g., Juberthie, 1988a; Giribet, 2003a), with its members inhabiting all the major former Gondwanan landmasses (except Antarctica): Chile, South Africa, Madagascar, the Indian subcontinent (Sri Lanka), Australia and New Zealand (Fig. 1). Pettalids are small (2–5 mm long), morphologically conserved harvestmen that spend their entire life cycle in leaf litter habitats, with the exception of one cave-dwelling species (Juberthie, 1971). The distribution range within each species is typically smaller than 100 km in diameter, with the majority known from fewer than five localities, suggesting little dispersal during individuals' lifetimes. In addition, no Cyphophthalmi are known from any Darwinian islands (*sensu* Gillespie and Roderick, 2002), such as islands formed *de novo* by volcanoes in the mid-ocean, suggesting that they are unable to disperse across oceanic barriers. This limited ability to disperse makes these organisms outstanding candidates for studying the process of vicariance.

Systematics of Pettalidae

The family Pettalidae currently includes 52 described species and subspecies in 10 genera: *Austropurcellia*, *Chileogovea*, *Karripurcellia*, *Manangotria*, *Neopurcellia*,

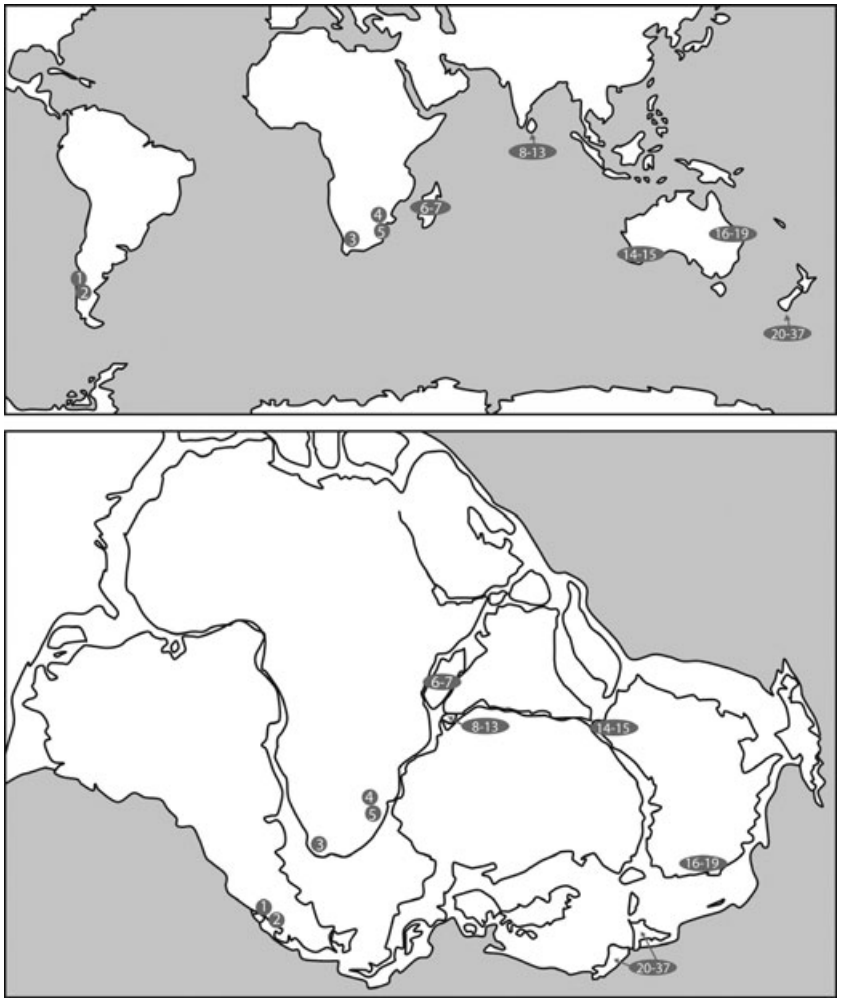

Fig. 1. Distribution of the members of the family Pettalidae, mapped on to a modern world map and a reconstruction from 150 Ma. Taxa represented: 1. *Chileogovea oedipus*; 2. *Chileogovea* sp.; 3. *Purcellia illustrans*; 4. *Parapurcellia silvicola*; 5. *P. monticola*; 6. *Ankaratra franzi*, 7. *Speleosiro argasiformis*; 8. *Pettalus* cf *brevicauda*; 9. *Pettalus* n.sp. DNA101283; 10. *Pettalus* n.sp. DNA101285; 11 *Pettalus* n.sp. DNA101286; 12. *Pettalus* n.sp. DNA101287; 13. *Pettalus* n.sp. DNA101288; 14. *Karripurcellia harveyi*; 15. *K. harveyi*; 16. *Austropurcellia scoparia*; 17. *Neopurcellia forsteri*; 18. *Rakaia arcticosa*; 19. *R. daviesae*; 20. *N. florensis*; 21. *N. minutissima*; 22. *N. salmoni*; 23. *R. antipodiana*; 24. *R. calcarobtusa westlandica*; 25. *R. crypta*; 26. *R. denticulata*; 27. *R. dorothea*; 28. *R. granulosa*; 29. *R. healyi*; 30; *R. inerma*; 31. *R. lindsayi*; 32. *R. magna australis*; 33. *R. media*; 34. *R. solitaria*; 35. *R. sorenseni sorenseni*; 36. *R. sorenseni digitata*; 37. *R. stewartiensis*.

Parapurcellia, *Pettalus*, *Purcellia*, *Rakaia* and *Speleosiro* (Giribet, 2003a; Sharma and Giribet, 2006). Most of these genera are restricted to a single continental landmass (e.g., *Pettalus* in Sri Lanka, *Parapurcellia* in Southern Africa; see Fig. 1), consistent with the hypothesis that vicariance has driven diversification within this group.

Two notable anomalies are the genera *Rakaia* and *Neopurcellia*, each of which includes species from both New Zealand and Queensland, Australia. *Rakaia* was described by Hirst in 1925 with the type species *R. antipodiana* from Rakaia Gorge in New Zealand. He predicted that "it is probable that the same genus or some allied form belonging to this suborder will also be found in Australia" (Hirst, 1925). Subsequently, additional *Rakaia* from both New Zealand and Queensland were described by Phillipps and Grimmett (1932), Forster (1948, 1952), Cantrell (1980), Juberthie (1989) and Boyer and Giribet (2003). *Neopurcellia* was erected by Forster in 1948 based on material from the type species *N. salmoni* from the west coast of the South Island of New Zealand, and additional species have been described from both New Zealand and Queensland by Forster (1948), Davies (1977) and Juberthie (2000). *Neopurcellia* is distinguished from *Rakaia* based on the condition of the fourth tarsus in males, which consists of a single segment in *Rakaia* (Fig. 7D) but two segments in *Neopurcellia* (as in Fig. 7E). Forster argued that this was an extremely important taxonomic character, and proposed a close relationship of *Neopurcellia* to the South African genera *Purcellia* and *Speleosiro* based on this feature (Forster, 1948). However, *Rakaia daviesae* from Queensland (Juberthie, 1989) has an intermediate condition in which the fourth tarsus of the male is bisegmented dorsally but unisegmented ventrally (Fig. 7F), indicating that this character is more variable than originally believed. As a result, we have previously questioned the validity of the genera *Neopurcellia* and *Rakaia* (Giribet and Boyer, 2002; Giribet, 2003a).

Although the relationships among most of the pettalid genera have been studied in detail in two cladistic analyses of morphological data (Giribet and Boyer, 2002; Giribet, 2003a), resolution based solely on morphology is poor and does not go beyond recognizing the monophyly of the family and a clade composed of the South African genera together with the species from Queensland and New Zealand. The present study is thus the first comprehensive work to incorporate molecular data to test the monophyly of the family, the pettalid genera, and species groups from the different geographic areas inhabited by these animals. The molecular data are also analyzed in combination with a morphological matrix that expands upon our previous studies of pettalid relationships (Giribet and Boyer, 2002; Giribet, 2003a). We are particularly interested in testing the monophyly of the New Zealand-Queensland genera *Rakaia* and *Neopurcellia* from both taxonomic and biogeographical points of view.

Methods

Taxon sampling

A total of 54 individuals from the suborder Cyphophthalmi were included in this study. These represent Pettalidae from Chile (genus *Chileogovea*), South Africa (*Purcellia* and *Parapurcellia*; the troglobiont *Speleosiro* was not available), Sri Lanka (*Pettalus*), Australia (*Austropurcellia*, *Karripurcellia*, *Neopurcellia* and *Rakaia*), and New Zealand (*Neopurcellia* and *Rakaia*). We were not able to obtain material for DNA sequencing from Madagascar despite checking the large litter samples obtained by B. Fisher and deposited at the California Academy of Sciences (C. Griswold and D. Ubick, pers. comm.). Members of the families Sironidae, Stylocellidae, Neogoveidae and Troglosironidae were included as outgroups (Table 1). All material was collected alive and fixed in 96% EtOH and all specimens are deposited as vouchers at the Museum of Comparative Zoology (MCZ), Department of Invertebrate Zoology DNA collection (see voucher numbers in Table 1).

A total of 45 morphological characters were scored for each species used in the molecular data set (Table 5, Appendix 1). Most characters are based on our previous morphological studies of Cyphophthalmi (Giribet and Boyer, 2002; Giribet, 2003a; de Bivort and Giribet, 2004), with further refinement in some cases. When appropriate specimens were available, they were mounted for SEM and examined using an FEI Quanta 200 microscope. Characters were also coded from specimens examined using light microscopy, including holotype material where available. The Harvard Museum of Comparative Zoology online database of photographs of Cyphophthalmi types is available at http://collections.oeb.harvard.edu/Invertebrate/Cyphophthalmi/species.cfm.

The morphological characters were optimized on to the strict consensus of the combined analysis of all data (total evidence tree) in Winclada (Nixon, 2002). Character state reconstructions were mapped according to whether the given state was homoplastic and showing unambiguous reconstructions only.

DNA extraction

Total DNA was extracted from whole animals using a DNeasy® Tissue Kit (Qiagen, Valencia, CA), either by crushing the individual or one appendage in the lysis buffer or by incubating an intact animal or appendage in lysis buffer overnight, then removing the

Table 1
MCZ voucher codes, general locality information, and GenBank accession numbers for taxa used in this study. Detailed locality information is available from the authors upon request

	MCZ voucher	Locality	18S	28S	16S	COI	H3
FAMILY PETTALIDAE							
Chileogovea oedipus	DNA100413	Chile	DQ133721	DA133733	DQ518055	DQ133745	
Chileogovea sp.	DNA100490	Chile	DA133722	DA133734	DQ518054	DQ133746	DQ518133
Parapurcellia monticola	DNA100386	South Africa	DQ518973	DA518009		DQ518098	DQ518135
Parapurcellia silvicola	DNA100385	South Africa	AY639494	DQ518008	DQ518053	AY639582	DQ518136
Purcellia illustrans	DNA100387	South Africa	AY639495	DQ518010	DQ518052	DQ518099	DQ518134
Pettalus cf *brevicauda*	DNA101227	Sri Lanka	DQ517975	DA518018	DQ518057	DQ518101	DQ518138
Pettalus n. sp.	DNA101283	Sri Lanka	DQ517974	DA518016	DQ518056	DQ518100	DQ518137
Pettalus n. sp.	DNA101285	Sri Lanka	DQ517976	DQ518017	DQ518058	DQ518102	DQ518139
Pettalus n. sp.	DNA101286	Sri Lanka	DQ517977	DQ518013	DQ518059	DQ518103	DQ318140
Pettalus n. sp.	DNA101287	Sri Lanka	DQ517978	DQ518014	DQ518060	DQ518104	DQ518141
Pettalus n. sp.	DNA101288	Sri Lanka	DQ517979	DQ518015	DQ518061	DQ518105	DQ518142
Karripurcellia harveyi	DNA101303	Western Australia	DA417980	DQ518019	DQ518062	DQ518106	DQ518143
Karripurcellia harveyi	DNA101304	Western Australia	DQ517981	DQ518020	DQ518063	DQ518107	DQ185144
Austropurcellia scoparia	DNA100946	Queensland/Australia	DQ517982	DQ518021	DQ518065	DQ518108	
Neopurcellia forsteri	DNA100945	Queensland/Australia	DQ517983	DQ518022	DQ518064	DQ518110	DQ518146
Rakaia arcticosa	DNA100951	Queensland/Australia	DQ517984	DQ518023		DQ518111	DQ518147
Rakaia daviesae	DNA100947	Queensland/Australia	DQ517985	DQ518024		DQ518112	DQ518148
Neopurcellia florensis	DNA101295	New Zealand	DQ517986	DQ518025	DQ518083	DQ518113	DQ518149
Neopurcellia minutissima	DNA101291	New Zealand	DQ517987	DQ518026	DQ518082	DQ518114	DQ518150
Neopurcellia salmoni	DNA100939	New Zealand	DQ517998		DQ518066		DQ518145
Neopurcellia salmoni	DNA100949	New Zealand		DQ518037		DQ518019	
Rakaia antipodiana	DNA100957	New Zealand	DQ517988	DQ518031	DQ518072	DQ518115	DA518151
R. calcarobtusa westlandica	DNA101125	New Zealand	DQ518004	DQ518038	DQ518070	DQ518121	DQ518163
Rakaia crypta	DNA101289	New Zealand	DA518000	DQ518043	DQ518068	DQ518120	DQ518156
Rakaia denticulata	DNA100961	New Zealand	DQ518001	DQ518040	DQ518069	DQ518126	DQ518158
Rakaia dorothea	DNA100943	New Zealand	DQ517990	DQ518033	DQ518077		
Rakaia granulosa	DNA101841	New Zealand	DQ517999	DQ518039	DQ517071		
Rakaia inerma	DNA100967	New Zealand	DQ518003	DQ518041			DQ518159
Rakaia healyi	DNA100940	New Zealand	DQ519002	DQ518042	DQ518067	DQ518122	DQ518160
Rakaia lindsayi	DNA101128	New Zealand	DQ517995	DQ518027	DQ518081	DQ518118	DQ518154
Rakaia magna australis	DNA101965	New Zealand	DQ517991	DQ518034		DQ518124	DQ518152
Rakaia magna australis	DNA100963	New Zealand			DQ518076		
Rakaia media	DNA101292	New Zealand	DQ517996	DQ518030	DQ518074	DQ518125	DQ518157
Rakaia pauli	DNA100968	New Zealand	DQ517992	DQ518032	DQ518073		DQ518161
Rakaia solitaria	DNA101294	New Zealand	DQ517997	DQ518029	DQ518075	DQ518119	DQ518155
Rakaia sorenseni sorenseni	DNA100969	New Zealand	DQ517993	DQ518036	DQ518079	DQ518116	DQ518153
Rakaia sorenseni digitata	DNA100970	New Zealand	DQ517989	DQ518035	DQ518078	DQ518123	DQ518162
Rakaia stewartiensis	DNA100944	New Zealand	DQ517994	DQ518028	DQ518080	DQ518117	
FAMILY SIRONIDAE							
Cyphophthalmustrebinjanum	DNA101038	Bosnia/Herzegov.	AY639483	DQ513119		AY639572	
Parasiro coiffaiti	DNA101383	Spain	AY918872	DQ513122	AY198877	DQ513110	AY918882
Siro rubens	DNA100457	France	AY428818	AY859602		DQ513111	
Siro valleorum	DNA100461	Italy	AY639492	DQ513123	AY639552	AY639580	AY639458
Suzukielus sauteri	DNA101543	Japan	DQ513138	DQ513116	DQ518086	DQ513108	DQ519166
FAMILY TROGLOSIRONIDAE							
Troglosiro cf *aelleni*	DNA100345	New Caledonia	AY639497	DQ518044	AY639555	AY639584	DQ518164
Troglosiro longifossa	DNA100867	New Caledonia	DQ518089	DQ518045	DQ518084	DQ518127	DQ518165
Troglosiro ninqua	DNA101577	New Caledonia	DQ518088	DQ518046	DQ518085	DQ518128	
FAMILY NEOGOVEIDAE							
Huitaca n. sp.	DNA101407	Colombia	DQ518090	DQ518047	DQ518050	DQ518129	DQ518167
Metagovea n. sp.	DNA101410	Colombia	DQ518091	DQ518048			DQ518168
Paragovia sironoides	DNA101059	Equatorial Guinea	DQ518092	DQ518049	DQ518051	DQ518131	DQ518169
FAMILY STYLOCELLIDAE							
Fangensis cavernarus	DNA101460	Thailand	DQ133714	DQ133726		DQ133740	DQ518132
Fangensis spelaeus	DNA100669	Thailand	AY639486	DQ133736		AY639583	AY639460
Stylocellus n. sp.	DNA101474	Sumatra	DQ518093	DQ518005			
Stylocellus n. sp.	DNA101478	Sumatra	DQ518094	DQ518006		DQ518096	
Stylocellus n. sp.	DNA101489	Thailand	DQ518095	DQ518007	DQ518087	DQ518097	

specimen before proceeding with the rest of the manufacturer's extraction protocol, as described by Boyer et al. (2005).

Polymerase chain reaction (PCR) and sequencing

Purified genomic DNA was used as a template for PCR amplification of the genes for 18S rRNA, 28S rRNA, 16S rRNA, cytochrome *c* oxidase subunit I (COI hereafter), and histone H3. The complete 18S rRNA (≈ 1.8 Kb) was amplified in three overlapping fragments of ≈900 bp each, using primer pairs 1F-5R, 3F-18Sbi and 18Sa2.0-9R (Giribet et al., 1996; Whiting et al., 1997). An additional primer internal to 1F-5R was used for sequencing, 4R (Giribet et al., 1996). The first ≈2200 bp of 28S rRNA were amplified using the primer sets 28SD1F/28Srd1a-28Sb (Whiting et al., 1997; Park and Ó Foighil, 2000; Edgecombe and Giribet, 2006), 28Sa-28Srd5b (Whiting et al., 1997; Schwendinger and Giribet, 2005) and 28S4.8a-28S7bi (Schwendinger and Giribet, 2005). Sequencing of the 28S rRNA gene was performed with those primers and some additional internal primers: 28Sa (Whiting et al., 1997) and 28Srd4b (Edgecombe and Giribet, 2006). 16S rRNA was amplified and sequenced using the primer pair 16Sar-16Sb (Xiong and Kocher, 1991; Edgecombe et al., 2002). COI was amplified and sequenced using the primer pair LCO1490-HCO2198 (Folmer et al., 1994). The complete coding region of histone H3 was amplified and sequenced using primer pair H3aF–H3aR (Colgan et al., 1998). Primer sequences are indicated in Table 2.

PCR reactions (50 μL) included 4 μL of template DNA, 1 μM of each primer, 200 μM of dNTPs (Invitrogen, Invitrogen, Carlsbad, CA), 1 × PCR buffer containing 1.5 mM $MgCl_2$, and 1.25 units of AmpliTaq DNA polymerase (Perkin Elmer). The PCR reactions were carried out using a GeneAmp PCR System 9700 thermal cycler, and involved an initial denaturation step (5 min at 95 °C) following by 35 cycles including denaturation at 95 °C for 30 s, annealing (ranging from 42 to 49 °C) for 30 s, and extension at 72 °C for 1 min, with a final extension step at 72 °C for 10 min.

The double-stranded PCR products were visualized by agarose gel electrophoresis (1% agarose), and purified using Qiagen QIAQuick spin columns. The purified PCR products were sequenced directly; each sequence reaction contained a total volume of 10 μL including 2 μL of the PCR product, irrespective of PCR yield, 1 μM of one of the PCR primer pairs, 1 μL of ABI BigDye™ 5 × sequencing buffer and 0.5 μL of Big Dye™ Terminator v3.0 (Applied Biosystems, Foster City, CA). The sequence reactions, performed using the thermal cycler described above, involved an initial denaturation step for 3 min at 95 °C, and 25 cycles (95 °C for 10 s, 50 °C for 5 s, 60 °C for 4 min). The BigDye-labeled PCR products were cleaned with AGTC® Gel Filtration Cartridges or Plates by Edge Biosystems. The sequence reaction products were then analyzed using an ABI Prism 3100 or 3730 Genetic Analyzer.

Table 2
List of primer sequences used for amplification and sequencing with original references of the primer sequences. Ribosomal genes were amplified at annealing temperatures ranging between 46 and 49 °C. Protein-coding genes were amplified at annealing temperatures between 42 and 45 °C

18S rRNA		
1F	5′-TAC CTG GTT GAT CCT GCC AGT AG-3′	Giribet et al. (1996)
3F	5′-GTT CGA TTC CGG AGA GGG A-3′	Giribet et al. (1996)
4R	5′-GAA TTA CCG CGG CTG CTG G-3′	Giribet et al. (1996)
9R	5′-GAT CCT TCC GCA GGT TCA CCT AC-3′	Giribet et al. (1996)
18Sa2.0	5′-ATG GTT GCA AAG CTG AAA C-3′	Whiting et al., 1997)
18Sbi	5′-GAG TCT CGT TCG TTA TCG GA-3′	Whiting et al. (1997)
28S rRNA		
28Sa	5′-GAC CCG TCT TGA AAC ACG GA-3′	Whiting et al. (1997)
28Sb	5′-TCG GAA GGA ACC AGC TAC-3′	Whiting et al. (1997)
28SD1F	5′-GGG ACT ACC CCC TGA ATT TAA GCAT-3′	Park and Ó Foighil (2000)
28S rd1a	5′-CCC SCG TAA YTT AGG CAT AT-3′	Edgecombe and Giribet (2006))
28S rd4b	5′-CCT TGG TCC GTG TTT CAA GAC-3′	Edgecombe and Giribet (2006)
28S rd5b	5′-CCA CAG CGC CAG TTC TGC TTA C-3′	Schwendinger and Giribet (2005)
28S rd4.8a	5′-ACC TAT TCT CAA ACT TTA AAT GG-3′	Schwendinger and Giribet (2005)
28S rd7b1	5′-GAC TTC CCT TAC CTA CAT-3′	Schwendinger and Giribet (2005)
16S rRNA		
16Sar	5′-CGC CTG TTT ATC AAA AAC AT-3′	Xiong and Kocher (1991)
16Sb	5′-CTC CGG TTT GAA CTC AGA TCA-3′	Edgecombe et al. (2002)
COI		
LCO1490	5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′	Folmer et al. (1994)
HCOoutout	5′-GTA AAT ATA TGR TGD GCT C-3′	Schwendinger and Giribet (2005)
Histone H3		
H3a F	5′-ATG GCT CGT ACC AAG CAG AC(ACG) GC-3′	Colgan et al. (1998)
H3a R	5′-ATA TCC TT(AG) GGC AT(AG) AT(AG) GTG AC-3′	Colgan et al. (1998)

Sequence editing

Chromatograms obtained from the automatic sequencer were read and both strands for each overlapping fragment were assembled using the sequence editing software Sequencher™ 4.0 (Gene Codes Corporation, Ann Arbor, MI, USA). Sequence data were edited in MacGDE 2.2 (Linton, 2005). All new sequences have been deposited in GenBank under accession numbers DQ517969–DQ518169 (Table 1).

Phylogenetic analysis

Direct optimization

Sequences from ribosomal genes were compared against secondary structure models, and then split into accordant fragments using internal primers and some visualized secondary structure features (see Giribet and Wheeler, 2001; Giribet, 2002). COI was split into four arbitrary fragments using areas where the amino acid sequences allowed us to do so unambiguously. The protein coding gene histone H3 showed no length variation and was treated as prealigned.

Data from each gene were analyzed in POY versus 3.0 (Wheeler et al., 2004) using the direct optimization method with parsimony as the optimality criterion (Wheeler, 1996). The direct optimization method allows analysis of sequences of unequal length without a predetermined static alignment. POY uses a dynamic optimization process that generates phylogenetic trees by searching for topologies that minimize total transformation cost under specified parameters (e.g., indels, transversions and transitions). Rather than performing sequence alignment and tree construction under different criteria and/or models, the same criterion and model is used consistently throughout the entire phylogenetic analysis.

The data for all genes were analyzed simultaneously. In addition, the data for each gene were analyzed independently and 18S and 28S rRNA were combined in an analysis of nuclear ribosomal genes. Tree searches were conducted on a cluster of 30 dual-processor nodes assembled at Harvard University (darwin.oeb.harvard.edu). Commands for load balancing of spawned jobs were in effect to optimize parallelization procedures (–parallel –dpm –dpmacceptratio 1.5 –jobspernode 2). Trees were built through a random addition sequence procedure followed by a combination of branch-swapping steps (SPR "subtree pruning and regrafting" and TBR "tree bisection and reconnection").

POY facilitates efficient sensitivity analysis (*sensu* Wheeler, 1995). All data sets (individual genes and combinations) were analyzed under 12 parameter sets for a range of indel-to-transversion ratios and transversion-to-transition ratios (see Tables 3 and 4). Implied

Table 3
Symmetrical step matrices used in the sensitivity analysis. Each weighting scheme is named by a three-digit code corresponding to the ratio of indel/transversion, transverion/transition, and transition values.

110

	A	C	G	T	–
A	0	1	0	1	1
C	1	0	1	0	1
G	0	1	0	1	1
T	1	0	1	0	1
–	1	1	1	1	0

111

	A	C	G	T	–
A	0	1	1	1	1
C	1	0	1	1	1
G	1	1	0	1	1
T	1	1	1	0	1
–	1	1	1	1	0

121

	A	C	G	T	–
A	0	2	1	2	2
C	2	0	2	1	2
G	1	2	0	2	2
T	2	1	1	0	2
–	2	2	2	2	0

141

	A	C	G	T	–
A	0	4	1	4	4
C	4	0	4	1	4
G	1	4	0	4	4
T	4	1	4	0	4
–	4	4	4	4	0

210

	A	C	G	T	–
A	0	1	0	1	2
C	1	0	1	0	2
G	0	1	0	1	2
T	1	0	1	0	2
–	2	2	2	2	0

211

	A	C	G	T	–
A	0	1	1	1	2
C	1	0	1	1	2
G	1	1	0	1	2
T	1	1	1	0	2
–	2	2	2	2	0

221

	A	C	G	T	–
A	0	2	1	2	4
C	2	0	2	1	4
G	1	2	0	2	4
T	2	1	2	0	4
–	4	4	4	4	0

241

	A	C	G	T	–
A	0	4	1	4	8
C	4	0	4	1	8
G	1	4	0	4	8
T	4	1	4	0	8
–	8	8	8	8	0

410

	A	C	G	T	–
A	0	1	0	1	4
C	1	0	1	0	4
G	0	1	0	1	4
T	1	0	1	0	4
–	4	4	4	4	0

411

	A	C	G	T	–
A	0	1	1	1	4
C	1	0	1	1	4
G	1	1	0	1	4
T	1	1	1	0	4
–	4	4	4	4	0

421

	A	C	G	T	–
A	0	2	1	2	8
C	2	0	2	1	8
G	1	2	0	2	8
T	2	1	2	0	8
–	8	8	8	8	0

441

	A	C	G	T	–
A	0	4	1	4	16
C	4	0	4	1	16
G	1	4	0	4	16
T	4	1	4	0	16
–	16	16	16	16	0

alignments (Wheeler, 2003) can easily be generated for each tree (see Giribet, 2005).

To identify the optimal parameter set or "model" we employed a character-congruence technique that is a modification of the ILD metric developed by Mickevich and Farris (1981). The value is calculated for each parameter set by subtracting the sum of the scores of all partitions from the score of the combined analysis of all partitions, and normalizing it for the score of the combined length. This has been interpreted as a meta-optimality criterion for choosing the parameter set that best explains all partitions in combination, maximizing overall congruence and minimizing character conflict among all the data. This parameter set was given special consideration in the analysis of data from each individual gene and is referred to throughout the paper as the "optimal parameter set." Although Wheeler (1995) proposed the use of such a measure as an option for choosing among multiple hypotheses, the measure has been modified subsequently (e.g., Wheeler and Hayashi, 1998). The ILD has been compared with other measures by Aagesen et al. (2005), and subsequently criticized for being partition-dependent (Wheeler et al., 2006). In both these studies, the ILD results in similar (but not necessary identical) parameter choice. We use the ILD test as a rough way to choose a tree, but still consider the remainder parameter sets as part of our hypothesis by evaluating the alternative trees obtained under the different parameter sets and by considering the strict consensus of all trees obtained under the different analytical parameter sets (interpretive functions of Wheeler et al., 2006), as discussed by Giribet (2003b). Nodal support for all topologies was measured using parsimony jackknifing (Farris et al., 1996).

Once the optimal parameter set was determined based on congruence among the molecular partitions, we performed an analysis combining the molecular and morphological data under that parameter set, with morphological character transitions weighted identically with the maximum weight allowed for any molecular transition.

Static alignments

Even though direct optimization approaches such as the one employed here are compelling philosophically (e.g., De Laet, 2005; Fleissner et al., 2005; Redelings and Suchard, 2005; Wheeler, 2005), they are not wanting for detractors (e.g., Kjer, 2004; Simmons, 2004). In order to further evaluate the hypotheses derived under direct optimization we performed a more traditional two-step phylogenetic analysis of the data by submitting the sequence loci with length variation to a static alignment procedure. We generated manual alignments for 18S rRNA, 28S rRNA and COI, excluding areas that were difficult to align visually. For ribosomal data, alignments were generated by initially splitting the sequences into fragments as described for direct optimization, and then modifying the alignments by eye. Alignment of COI was based on translation of the DNA sequences into amino acids. For the static alignment of each data set, as well as for the entire concatenated data set, we determined the best choice of model using ModelTest 3.7 (Posada and Crandall, 1998) under the Akaike Information Criterion (AIC), as recommended by Posada and Buckley (2004). The model chosen was GTR + I + Γ in each case except for the 18S rRNA data partition, for which TrN + I + Γ was selected where "I" stands for the invariant sites correction and "Γ" for the discrete gamma correction (Tavaré, 1986; Tamura and Nei, 1993). We then analyzed the data under the recommended model using MrBayes 3.1.1 (Huelsenbeck and Ronquist, 2001), running sufficient generations such that the average deviation of split frequencies reached < 0.01. In each case, four chains were employed and the number of generations was 5 000 000 except in the case of the 18S rRNA, 28S rRNA, and histone H3 partitions in which 1 000 000 generations were sufficient to bring the average deviation of split frequencies to a value < 0.01. For the combined (concatenated) data set, each partition was allowed a separate model. We also analyzed the combined molecular data using PAUP* portable version 4.0b10 (Swofford, 2002) for Unix on the Harvard University Center for Genomic Research supercomputing cluster (portal.cgr.harvard.edu) under the single model chosen using the AIC criterion as implemented in ModelTest 3.7, GTR + I + Γ. We calculated bootstrap support with 100 replicates.

Results

The analyses of the different data sets resulted in several clades found in all or most cases. The family

Table 4
Tree length and calculated ILD (incongruence length difference) values for the partitions including total combined data (Molecular), 18S rRNA (18S), 28S rRNA (28S), 16S rRNA (16S), cytochrome *c* oxidase subunit I (COI), and histone H3 (H3) at the different parameter set values listed in Table 3 (110, 111, 121, 141, 210, 211, 221, 241, 410, 411, 421 and 441)

	Molecular	18S	28S	16S	COI	H3	ILD
110	9018	152	1106	3312	3898	304	0.027279
111	16276	390	2352	4470	7462	978	0.038339
121	12832	273	1750	4098	5797	655	0.020184
141	21915	425	2853	7469	9730	970	0.021356
210	5008	80	693	1959	1994	152	0.025959
211	8705	200	1342	2704	3799	489	0.019644
221	13877	281	2049	4727	5877	655	0.020754
241	23971	441	3426	8667	9887	970	0.024200
410	5775	88	958	2342	2046	152	0.032730
411	9528	208	1623	3132	3845	489	0.024245
421	15442	297	2607	5521	5966	655	0.025645
441	27028	473	4521	10232	10068	970	0.028270

Pettalidae was consistently found to be monophyletic with high support in every analysis of the combined molecular and molecular and morphological data sets. The genus *Pettalus* from Sri Lanka almost always formed a clade with high support, as did *Parapurcellia* from eastern South Africa, *Chileogovea* from Chile, and the two specimens of *Karripurcellia harveyi* from Western Australia. The species from Queensland (*Austropurcellia scoparia*, *Neopurcellia forsteri*, *Rakaia arcticosa* and *R. daviesae*) appeared as a monophyletic group in most analyses and will be referred to as the Queensland group. A clade including some of the New Zealand species was likewise retrieved, which will be referred to as the *denticulata* group: *Rakaia calcarobtusa westlandica*, *R. crypta*, *R. denticulata*, *R. granulosa*, *R. healyi* and *R. inerma*. The remaining New Zealand *Rakaia* species plus *Neopurcellia florensis* and *N. minutissima* also formed a clade in most analyses, and this will be referred to as the *antipodiana* group. The autapomorphic New Zealand species *Neopurcellia salmoni* almost never grouped with other *Neopurcellia* or *Rakaia*. In this section we present the results from analyses of all of the different data partitions, although only selected trees are included as figures.

Direct optimization sensitivity analysis

Of the 12 parameter sets under which we analyzed our data, the one that minimized overall incongruence is that for a indel/transversion ratio of 2 : 1 and a transversion/transition ratio of 1 : 1 (parameter set 211, ILD = 0.0196; Tables 3 and 4) (tree shown in Fig. 2).

Combined molecular data

When analyzed under direct optimization, the strict consensus of all shortest trees from all parameter sets retrieved a monophyletic Pettalidae, and the following clades within Pettalidae: *Chileogovea*, *Parapurcellia*, *Karripurcellia harveyi*, *Pettalus*, the Queensland group, the New Zealand *denticulata* group, and the New Zealand *antipodiana* group. When analyzed under the 211 parameter set each of those groups receives high support from jackknife frequencies (JF hereafter): Pettalidae (100% JF), *Chileogovea* (100% JF), *Parapurcellia* (100% JF), *Karripurcellia harvey* (100% JF), *Pettalus* (100%), the Queensland group (93% JF), the New Zealand *denticulata* group (87% JF), and the New Zealand *antipodiana* group (89% JF) (Fig. 2). The biogeographical hypotheses supported by the results of analysis under each parameter set are summarized in Fig. 3.

Bayesian analysis of the manually aligned combined molecular data using unlinked mixed models retrieved a topology very similar to that found in the direct optimization analysis, differing only in the relationship of the *denticulata* and *antipodiana* groups to one another and the relationship between *Chileogovea* + *Purcellia* to *Karripurcellia* (Fig. 4). None of these groupings received significant jackknife support in the parsimony direct optimization analysis.

Likelihood analysis of combined data under static homology in PAUP using a single GTR + I + Γ model retrieved a monophyletic Pettalidae (100% bootstrap support), as well as the same monophyletic continent-specific clades found in other analyses: *Parapurcellia* (100% bootstrap support; BS hereafter), *Chileogovea* (100% BS), *Pettalus* (100% BS), the Queensland group (100% BS), the *antipodiana* group (97% BS), and the *denticulata* group (96% BS). The most likely tree found *Pettalus* as sister to all other Pettalidae, but BS was below 50%. Bootstrap values are shown in Fig. 2; however, because the topology concurs with results from parsimony direct optimization and Bayesian analyses, this tree is not shown.

Combined molecular and morphological data

Four equally parsimonious trees were found when the molecular and morphological data were combined and analyzed in POY under the optimal parameter set as determined by sensitivity analysis of molecular data alone. The strict consensus from the analysis of combined data is shown in Fig. 5 with all morphological characters (described in Appendix 1) optimized on the tree.

Nuclear ribosomal data

When the 18S rRNA data set was analyzed alone under direct optimization, the family Pettalidae was found to be monophyletic in the strict consensus of all shortest trees from all parameter sets. Within Pettalidae, *Chileogovea* and *Parapurcellia* were found as a paraphyletic grade sister to the rest of Pettalidae. The genus *Pettalus* (from Sri Lanka) was found to be monophyletic, as was the Queensland group.

When the 18S rRNA data were analyzed under the parameter set 211, 49 shortest trees were retained (at 200 weighted steps). In addition to the clades retrieved in the strict consensus from all parameter sets, the *denticulata* group was retrieved as monophyletic. Each of these clades received JF higher than 50%, but very few nodes within Pettalidae received support higher than 70% JF. The static alignments for 18S rRNA were analyzed with MrBayes under the model TN + I + Γ as the best-fit model. The same clades that were found in the jackknife analysis in POY were found in the Bayesian analysis, and posterior probabilities followed the same trends as jackknife proportions.

When 28S rRNA data were analyzed alone under direct optimization, the family Pettalidae was again found to be monophyletic in the strict consensus of all

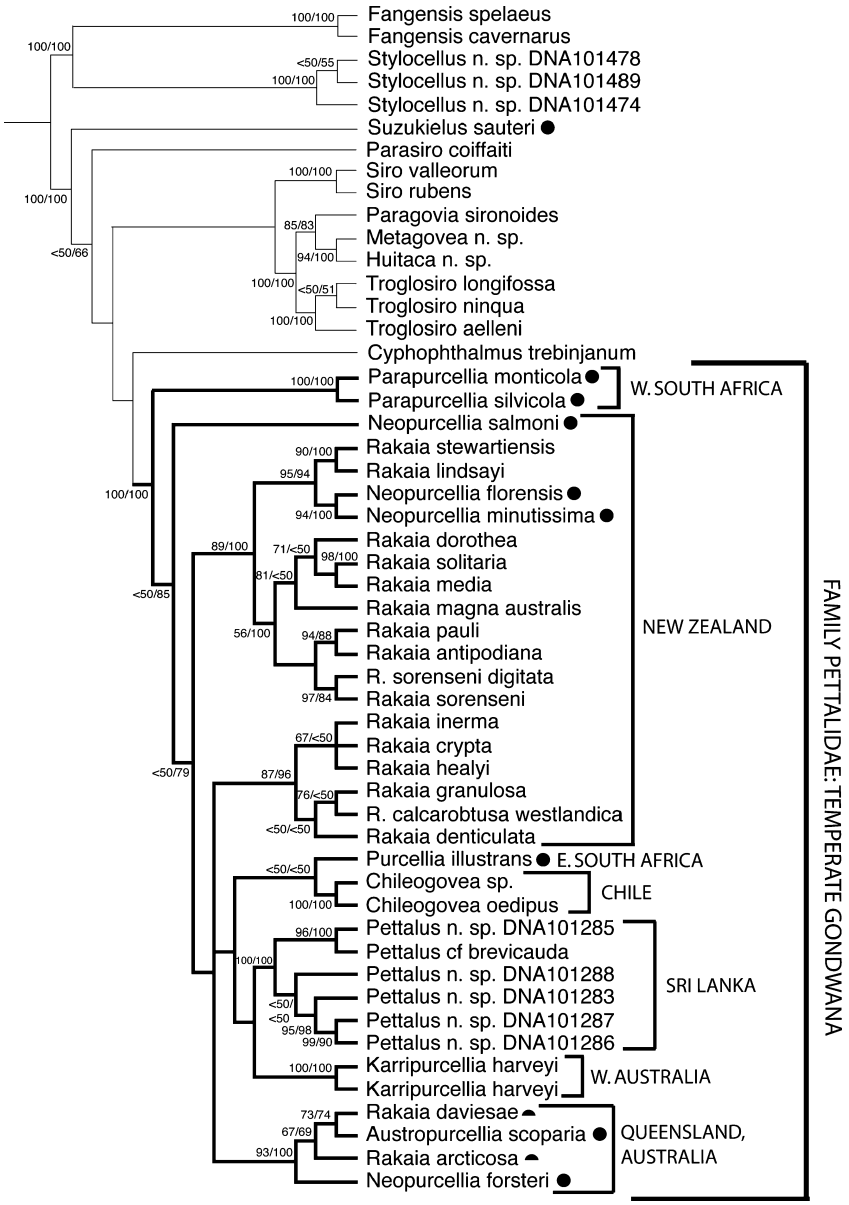

Fig. 2. Phylogeny of Pettalidae based on direct optimization analysis of 18S rRNA, 28S rRNA, 16S rRNA, histone H3 and COI data sets under the parameter set which minimized incongruence. Support values on branches indicate jackknife frequency values from direct optimization analysis followed by support values from ML analyses of manually aligned 18S rRNA, 28S rRNA, histone H3 and COI data sets. The circle symbol indicates taxa with bisegmented male tarsus IV, and the half circle indicates taxa with male tarsus IV bisegmented dorsally only.

shortest trees from all parameter sets. *Pettalus* was retrieved as monophyletic, as were *Chileogovea*, *Parapurcellia*, and the *denticulata* group. In the jackknife analysis under the 211 parameter set, Pettalidae was retrieved as monophyletic with 100% JF. *Pettalus* was found as the sister to all other pettalids, although JF for the clade containing the genera outside of *Pettalus* occurred with only 62% JF. In the Bayesian analysis of the 28S rRNA data, very little structure was found within Pettalidae, with only *Parapurcellia*, *Pettalus*, and some subgroups of New Zealand species found with > 95% posterior probability; in addition, *Chileogovea*, *Parapurcellia* and *Pettalus* were monophyletic, although with low posterior probabilities.

When 18S and 28S rRNA were analyzed together under direct optimization, the family Pettalidae was again found to be monophyletic in the strict consensus of all shortest trees from all parameter sets. Under the 211 parameter set, *Pettalus* was found to be sister to all other pettalids, but with only 67% JF. Monophyletic groups within Pettalidae included *Pettalus* (100% JF), *Karripurcellia harveyi* (100% JF), *Parapurcellia* (100%

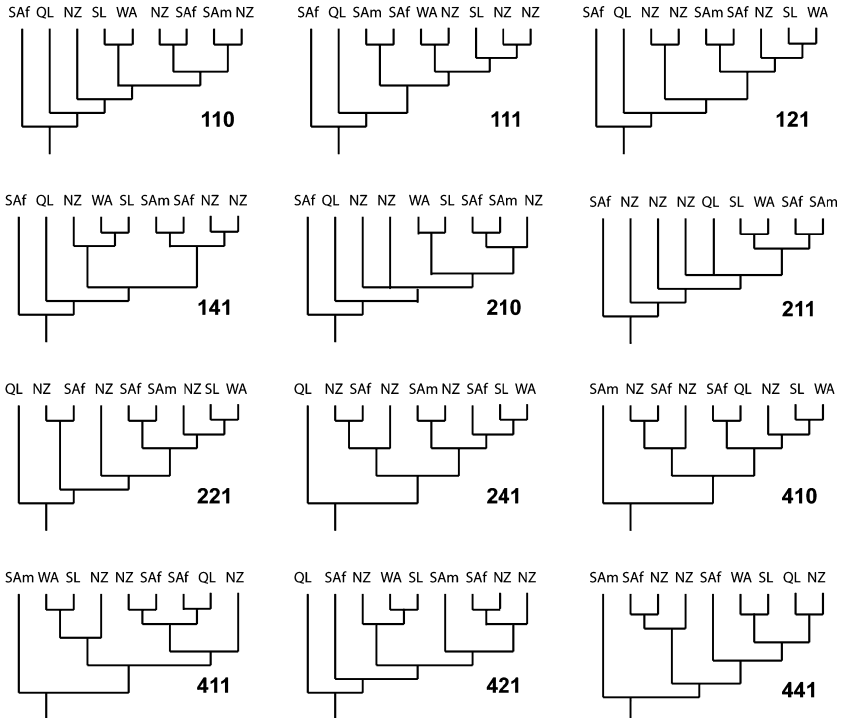

Fig. 3. Summary of biogeographical scenarios found in direct optimization sensitivity analysis of molecular data. The strict consensus tree for each parameter set is shown. Parameter set codes correspond to step matrices in Table 3. Geographical area codes: SAf, South Africa; NZ, New Zealand; QL, Queensland, Australia; SAm, South America; SL, Sri Lanka; WA, Western Australia.

JF), the Queensland group (91% JF), *denticulata* group (98% JF) and *antipodiana* group (58% JF). These clades were also found with high support in the Bayesian analysis of 18S and 28S rRNA data, with the exception of the *antipodiana* group, which received only 58% posterior probability.

Nuclear coding gene

In the parsimony analysis of the prealigned histone H3 data set using POY, the strict consensus of the shortest trees from all parameter sets resulted in a poorly resolved tree, with only *Karripurcellia*, the Queensland group, and *Pettalus* resolved, in addition to some outgroup relationships. In the jackknife analysis under the 211 parameter set, *Parapurcellia* (73% JF) and the *denticulata* group (59% JF) were also retrieved. The Bayesian analysis of histone H3 found few nodes with posterior probability > 95%. This was the only analysis in which the New Caledonian family Troglosironidae grouped within Pettalidae, but the monophyly of the grouping was only supported with 79% posterior probability.

Mitochondrial genes

In the direct optimization analysis of 16S rRNA the strict consensus of the shortest trees from all parameter sets found a monophyletic Pettalidae, monophyletic New Zealand *antipodiana* clade, monophyletic Queensland clade, and a clade uniting *Karripurcellia* (Western Australia) with *Pettalus* (Sri Lanka). Under the 211 parameter set, *Chileogovea* was retrieved (85% JF) as well as some species groups from within the major New Zealand and Sri Lanka clades.

In the direct optimization analysis of COI the strict consensus of all shortest trees from all parameter sets yielded little resolution. Pettalidae was not retrieved as a monophyletic group, and only *Karripurcellia* and some subgroups of New Zealand taxa and *Pettalus* were retrieved. Under the 211 parameter set, Pettalidae was monophyletic (< 50% JF). Within the family, *Parapurcellia* (100% JF) was found to be sister to all other taxa. *Chileogovea* (89% JF), *Karripurcellia* (100% JF), *Pettalus* (JF < 50), the Queensland group (60% JF), *denticulata* group and *antipodiana* group were all retrieved as monophyletic groups. Although this analysis retrieved the same groups as most other analyses, JFs were generally low.

Bayesian analysis of the COI data retrieved monophyly of Pettalidae with 100% posterior probability (PP hereafter). Within the family, *Parapurcellia* (100% PP) was found to be sister to all other taxa. *Chileogovea* (100% PP), *Karripurcellia* (100% PP), the Queensland group (100% PP), *denticulata* group (100% PP) and *antipodiana* group (96% PP) were all monophyletic.

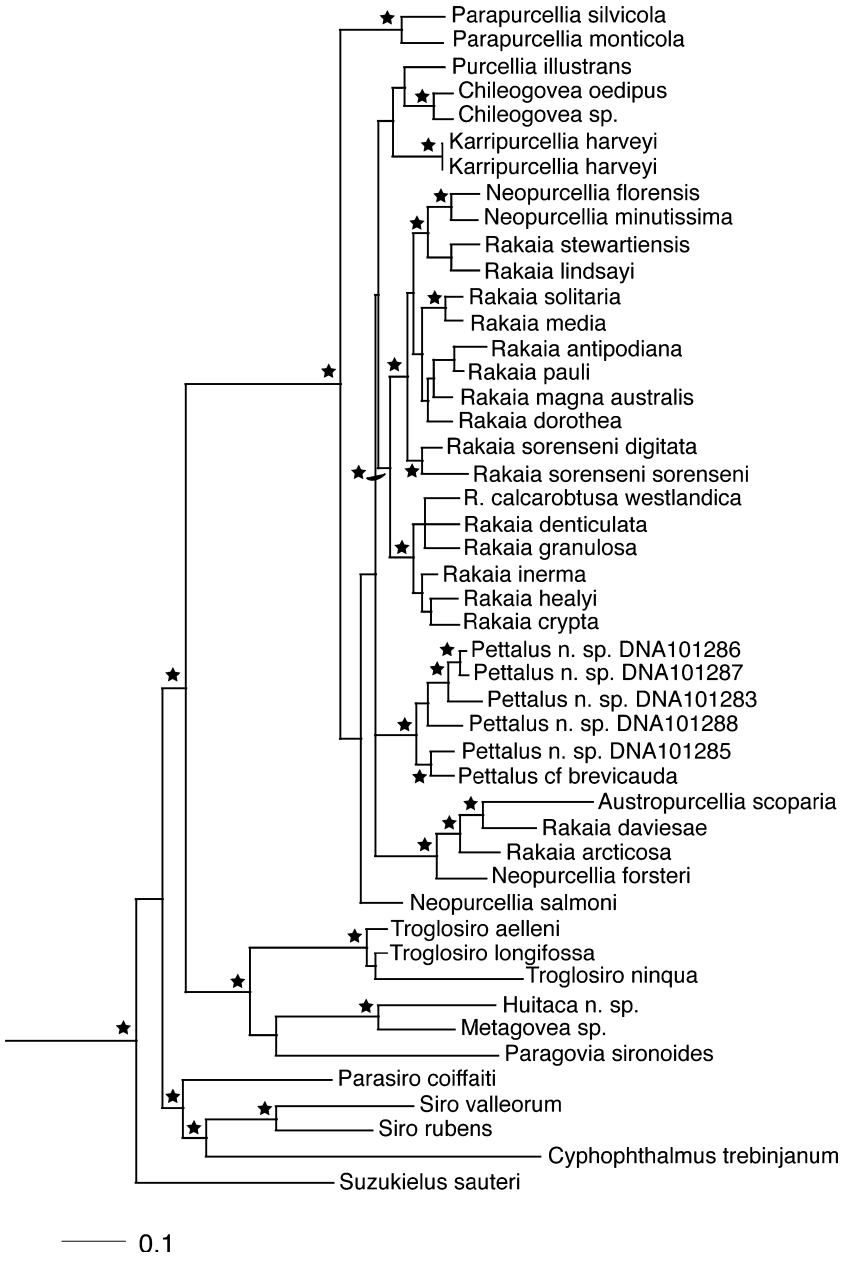

Fig. 4. Phylogeny of Pettalidae based on Bayesian analysis of 18S rRNA, 28S rRNA, histone H3 and COI data sets using unlinked models, indicating relative branch lengths. Stars indicate nodes supported with greater than 95% posterior probability. Members of the family Stylocellidae have been removed from this figure to better illustrate branch lengths within Pettalidae.

Taxonomy

Revision of pettalid genera from Australia and New Zealand

Current taxonomy of Pettalidae includes four genera in Australia and New Zealand: *Austropurcellia* Juberthie, 1988 (Queensland), *Karripurcellia* Giribet, 2003 (Western Australia), *Neopurcellia* Forster, 1948 (New Zealand and Queensland) and *Rakaia* Hirst, 1925 (New Zealand and Queensland). The results of this study clearly indicate that a revision of these genera is necessary. Here, we rediagnose *Austropurcellia* (''the Queensland group''), *Neopurcellia* and *Rakaia* (''the *antipodiana* group''), and erect the new genus *Aoraki* for the members of ''the *denticulata* group''.

Diagnosis of Austropurcellia *Juberthie, 1988*

Ozophores in dorsal 45° position. Eyes present, incorporated into ozophores, without lenses (Fig. 6A). No projections surrounding gonostome. Male exocrine glands present in anal region. Scopulae present in anal

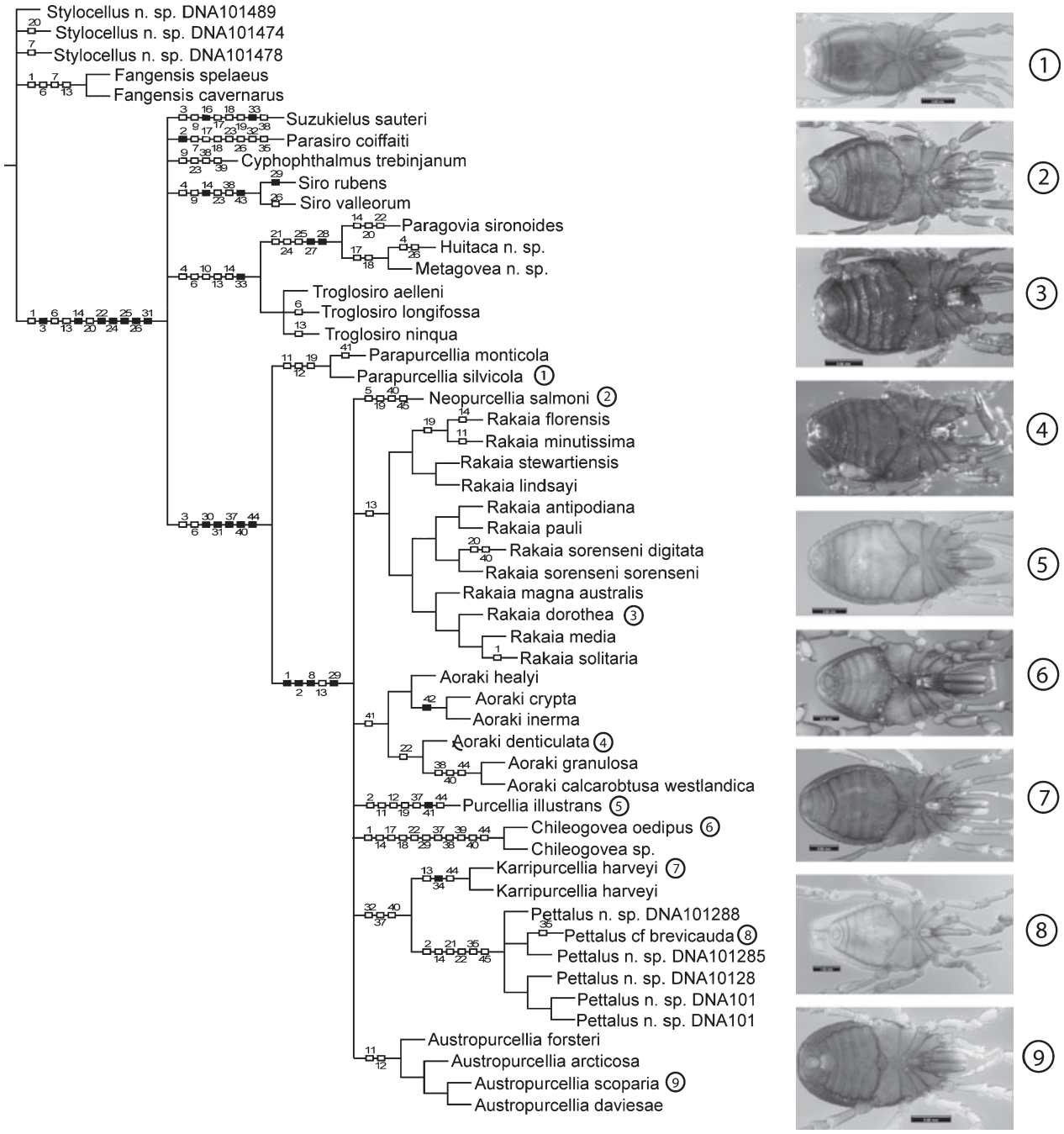

Fig. 5. Phylogeny of Family Pettalidae based on direct optimization analysis of combined molecular and morphological data for parameter set 211. Strict consensus of four trees at 8927 weighted steps. Morphological characters are optimized on the tree. Boxes on branches represent unambiguous character changes; numbers above boxes indicate the character number. Black boxes indicate that the character state is not homoplastic. Photographs of holotypes representing each genus are provided; numbers beside species names indicate corresponding images. Species names reflect the taxonomic revisions proposed in this paper.

plate; scopulae on tergite VIII absent (Fig. 8J). Tergite IX divided. Robust ventral process on the chelicera absent; prominent apodeme on chelicera (as in Fig. 6C). Prominent ventral process on trochanter of palp (as in Fig. 6E). Solea in tarsus I (as in Fig. 7A,B). Male tarsus IV bisegmented dorsally to fully bisegmented (as in Fig. 7F). Adenostyle extremely robust, with height no more than twice base length.

Type species: *Austropurcellia scoparia* Juberthie, 1988.

Species included: *Austropurcellia scoparia* Juberthie, 1988; *Austropurcellia forsteri* (Juberthie, 2000), **new combination**; *Austropurcellia capricornia* (Davies, 1977),

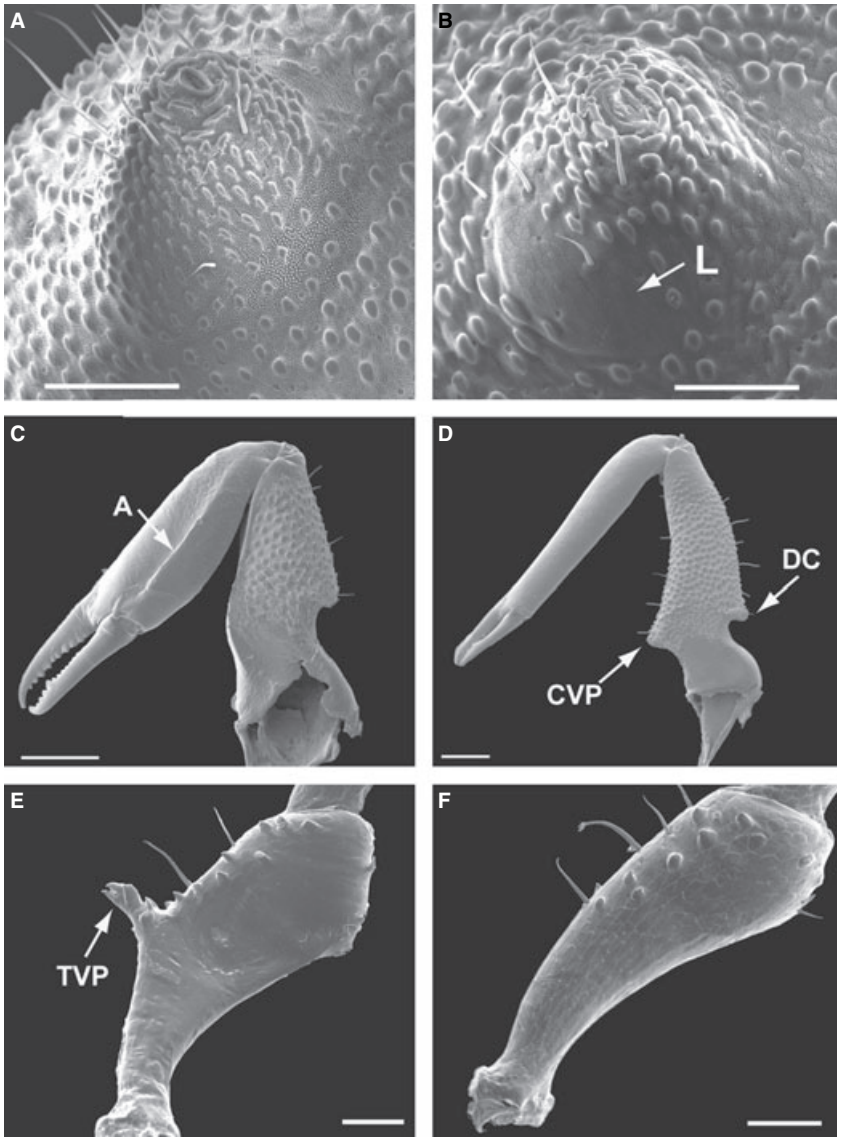

Fig. 6. Ozophore. Scale 100 μm. (A) *Neopurcellia forsteri*; (B) *Rakaia solitaria*. Eyes are found in most pettalids, incorporated at the base of the ozophore. In some species, a lens is present, indicated with an arrow and letter L in (B). In most species the eye is visible as a round white mass in LM but uniform ornamentation of the ozophore obscures the presence of the eye in SEM, as in (A). Chelicera. Scale 200 μm. (C) *Rakaia pauli*; (D) *R. calcarobtusa westlandica*. The chelicera comprises a complex suite of characters. Some characters include the cheliceral ventral process, marked with letters CVP in (D), dorsal crest, marked with letters DC in (D), and the apodeme, marked with A in (D). Trochanter of the palp. Scale 50 μm. (E) *Purcellia illustrans*; (F) *Rakaia healyi*. The trochanter of the palp may bear a ventral process, indicated with an arrow and letters TVP in (E).

new combination; *Austropurcellia daviesae* (Juberthie, 1989), **new combination**; *Austropurcellia arcticosa* (Cantrell, 1980), **new combination**; *Austropurcellia woodwardi* (Forster, 1955), **new combination**.

Distribution: Queensland, Australia.

Remarks: This clade includes all the species known from Queensland, formerly included in the three genera *Austropurcellia*, *Neopurcellia* and *Rakaia*.

Diagnosis of Neopurcellia *Forster, 1948*

Ozophores in dorsal 45° position. Eyes present, incorporated into ozophores without lenses. No scopulae in anal plate. Two prominent curling scopulae present, each originating from the inner margin of tergite VIII (Fig. 9L). Tergite VIII forming two lobes lacking ornamentation on the dorsal surface. Ornamentation of the dorsal scutum non-uniform with granules becoming larger towards the posterior region of the animal. Tarsus IV of the male divided (as in Fig. 7E).

Type species: *Neopurcellia salmoni* Forster, 1948.

Species included: *Neopurcellia salmoni* Forster, 1948.

Distribution: New Zealand's South Island: West Coast and western Southland.

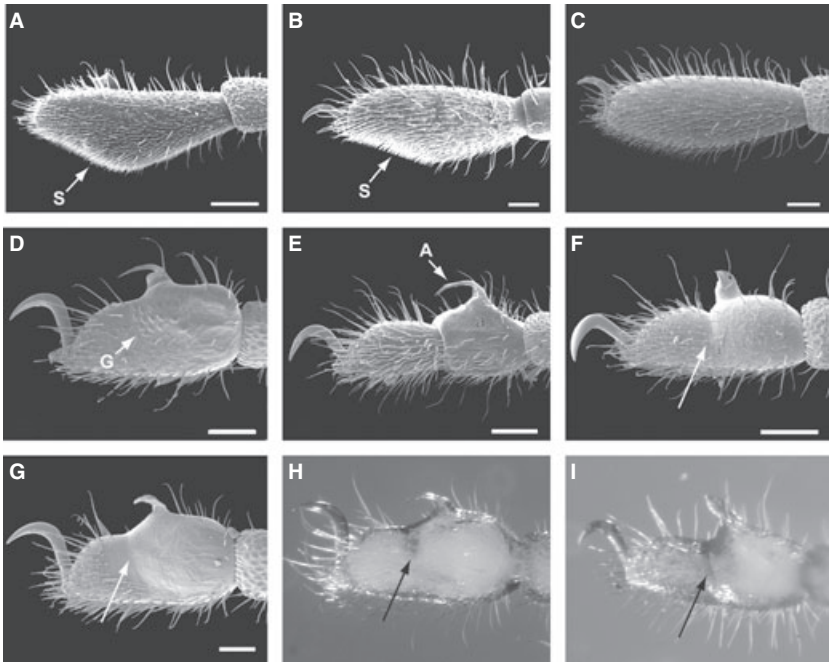

Fig. 7. Tarsi. Scale 100 μm. First tarsus: (A) *Pettalus brevicauda*, (B) *Rakaia inerma*, (C) *Neopurcellia florensis*. The first tarsus may bear a distinct solea (indicated by S), characterized by a sharp angle in the tarsus forming a flattened anterior ventral surface covered in a concentration of short setae, indicated with an arrow in (A) and (B). Some species have a first tarsus with some shorter setae in this area, but without the distinctive angled shape and flattened, presumably sensory, surface. Fourth tarsus of male: (D) *Rakaia denticulata*; (E) *Purcellia illustrans*; (F) *R. daviesae*; (G) *R. stewartiensis*; (H) *R. stewartiensis* viewed with LM; (I) *R. daviesae* viewed with LM. The fourth tarsus of the male bears an adenostyle (indicated by A) and may consist of one segment (D) or two segments (E). It also displays the intermediate character state of being bisegmented dorsally only, indicated with an arrow in (F) and (I). In some taxa, other smaller degrees of segmentation exist and present differently depending on the mode of microscopy used, indicated with an arrow in (G) and (H). Some species display granulation of the cuticle on the fourth tarsus of the male, indicated with an arrow and letter G in (D).

Remarks: This genus remains monotypic, although the single species has a broad distribution range that could include more than one cryptic species. Former members included in the genus have been transferred to the genera *Austropurcellia* and *Rakaia*.

Diagnosis of Rakaia *Hirst, 1925*

Ozophores in dorsal 45° position. Eyes present, incorporated into ozophores either with or without lenses (as in Fig. 6A,B). No projections surrounding gonostome. Scopulae present on anal plate, or scopulae originating from tergite VIII (Fig. 9F–K). Presence of a ventral process on the palp trochanter (as in Fig. 6E). Robust ventral process of the chelicera absent (Fig. 6C). Conspicuous longitudinal apodeme on second cheliceral segment. Lack of solea in tarsus I (Fig. 7C).

Type species: *Rakaia antipodiana* Hirst, 1925.

Species included: *Rakaia antipodiana* Hirst, 1925; *Rakaia dorothea* Phillips and Grimmett, 1932; *Rakaia florensis* (Forster, 1948), **new combination**; *Rakaia isolata* Forster, 1952; *Rakaia lindsayi* Forster, 1952; *Rakaia macra* Boyer and Giribet, 2003; *Rakaia magna australis* Forster, 1952; *Rakaia magna magna* Forster, 1948; *Rakaia media media* Forster, 1948; *Rakaia media insula* Forster, 1952; *Rakaia minutissima* (Forster, 1948), **new combination**; *Rakaia pauli* Forster, 1952; *Rakaia solitaria* Forster, 1948; *Rakaia sorenseni digitata* Forster, 1952; *Rakaia sorenseni sorenseni* Forster, 1952; *Rakaia stewartiensis* Forster, 1948; *Rakaia uniloca* Forster, 1952.

Distribution: New Zealand: North Island, South Island, Stewart Island, Little Barrier Island, and Motuara Island.

Remarks: This genus includes the New Zealand members of the old genera *Rakaia* and *Neopurcellia* that have a strong ventral process on the palp trochanter.

Diagnosis of Aoraki *gen. nov.*

Ozophores in dorsal 45° position. Eyes present, incorporated into ozophores, without lenses (as in Fig. 6A). No projections surrounding gonostome. Anal plate with either carina or scopulae on central ventral surface, or scopulae on posterior margin (Fig. 9A–E). Ventral process on the palp trochanter absent (Fig. 6F). Chelicera with prominent ornamented ventral process (Fig. 6D). Chelicea without a distinct apodeme on the second segment (Fig. 6D). Solea present in tarsus I (Fig. 7B). Male tarsus IV entire (Fig. 7D).

Type species: *Aoraki denticulata* (Forster, 1948), **new combination**.

Table 5
Morphological data matrix for the characters described in Appendix 1

	0 1 1234567890	1 2 1234567890	2 3 1234567890	3 4 1234567890	4 12345
Chileogovea oedipus	1320000111	00140-1100	0100110011	1120010110	-0000
Chileogovea sp.	1320000111	00140-1100	0100110011	1120010110	-0000
Parapurcellia monticola	0120000010	11020-0010	0000110011	1??0011001	30010
Parapurcellia silvicola	0120000010	11020-0010	0000110011	1??0011001	00010
Purcellia illustrans	2220000110	11120-0010	0000110001	1??0010001	40000
Pettalus cf. *brevicauda*	1220000111	00140-0000	1100110001	10-0310000	-0011
Pettalus n.sp. DNA101283	2220000111	00140-0000	1100110001	10-0110000	-0011
Pettalus n.sp. DNA101285	1220000111	00140-0000	1100110001	10-0110000	-0011
Pettalus n.sp. DNA101286	2220000111	?0140-0000	1100110001	10-0110000	-0011
Pettalus n.sp. DNA101287	2220000111	00140-0???	?1?0??????	1??0??????	??0??
Pettalus n.sp. DNA101288	1220000111	00140-0???	?1?0??????	1??0??????	??0??
Karripurcellia harveyi	2320000111	00020-0000	0000110001	10-1010000	-0000
Austropurcellia scoparia	2320000110	11130-0010	0000110001	1140011001	10010
Neopurcellia forsteri	2320000110	11130-0010	0000110001	1110011001	00010
Rakaia arcticosa	2320000110	11120-0020	0000110001	1??0011001	00010
Rakaia daviesae	2320000110	11130-0020	0000110001	1140011001	20010
Neopurcellia florensis	2320000110	01030-0010	0000110001	1??0011001	00011
Neopurcellia minutissima	2320000110	11020-0010	0000110001	1??0011001	00011
Neopurcellia salmoni	2320100111	00120-0010	0000110001	1??0011000	-0011
Rakaia antipodiana	2320100110	11020-0000	0000110001	1??0011001	00011
R. calcarobtusa westlandica	2320000111	00120-0000	0100110001	1120011100	-0000
Rakaia crypta	2320000111	00120-0000	0000110001	1120011001	31010
Rakaia denticulata	2320000111	00120-0000	0100110001	1120011001	30010
Rakaia dorothea	2320000110	11020-0000	0000110001	1??0011001	00011
Rakaia granulosa	2320000111	00120-0000	0100110001	1??0011100	-0000
Rakaia healyi	2320000111	00120-0000	0000110001	1120011001	30010
Rakaia inerma	2320000111	00120-0000	0000110001	1120011001	31010
Rakaia lindsayi	2320000110	00020-0000	0000110001	1??0011001	00010
Rakaia magna australis	2320100110	01020-0000	0000110001	1??0011001	00010
Rakaia media	2320000110	11020-0000	0000110001	1120011001	00010
Rakaia pauli	2320100110	11020-0000	0000110001	1??0011001	00011
Rakaia solitaria	1320000110	11020-0000	0000110001	1??0011001	00011
Rakaia sorenseni sorenseni	2320100110	11020-0000	0000110001	1??0011001	00011
Rakaia sorenseni digitata	2320000110	11020-0005	0000110001	1??0011000	-0011
Rakaia stewartiensis	2320000110	00020-0000	0000110001	1??0011001	00010
Cyphophthalmus trebinjanum	010001??00	000????000	0?1?1100?0	01103-0110	-0?00
Parasiro coiffaiti	0000011010	0002111100	0010100010	00-0100000	-0000
Siro rubens	0101010000	00010-0000	0010110020	01103-0100	-0100
Siro valleorum	0101010000	00010-0000	0010100010	01103-0100	-0100
Suzukielus sauteri	0120010000	0002101110	0000110010	0130010100	-0000
Troglosiro aelleni	0101000211	0013110000	0000110010	01003-0000	-0000
Troglosiro longifossa	0101010211	0013110000	0000110010	01003-0000	-0000
Troglosiro ninqua	0101000211	0003110000	0000110010	01003-0000	-0000
Huitaca n.sp.	0100000211	0013111100	100100111-	01003-0000	-0000
Metagovea n.sp.	0101000211	0013111100	100101111-	01003-0000	-0000
Paragovia sironoides	0101000011	0015110005	110101111-	01003-0000	-0000
Fangensis cavernarus	0110011010	00050-0001	0101000010	2110000000	-0000
Fangensis spelaeus	0110011010	00050-0001	0101000010	2110000000	-0000
Stylocellus n.sp. DNA101474	111000001?	00150-0000	0101000010	2??0000000	-0000
Stylocellus n.sp. DNA101478	111000101?	00150-0001	0101000010	2??0000000	-0000
Stylocellus n.sp. DNA101489	111000001?	00150-0001	0101000010	2??0000000	-0000

"?" indicates missing data; "-" indicates inapplicable data.

Species included: *Aoraki calcarobtusa calcarobtusa* (Forster, 1952), **new combination**; *Aoraki calcarobtusa westlandica* (Forster, 1952), **new combination**; *Aoraki crypta* (Forster, 1948), **new combination**; *Aoraki denticulata denticulata* (Forster, 1948), **new combination**; *Aoraki denticulata major* (Forster, 1948), **new combination**; *Aoraki granulosa* (Forster, 1952), **new combination**; *Aoraki healyi* (Forster, 1948), **new combination**; *Aoraki inerma inerma* (Forster, 1948), **new combination**; *Aoraki inerma stephenesis* (Forster, 1952), **new combination**; *Aoraki longitarsa* (Forster, 1952), **new combination**; *Aoraki tumidata* (Forster, 1948), **new combination**.

Etymology: Aoraki, meaning "cloud piercer", is the Maori name for Mount Cook in the South Island of New

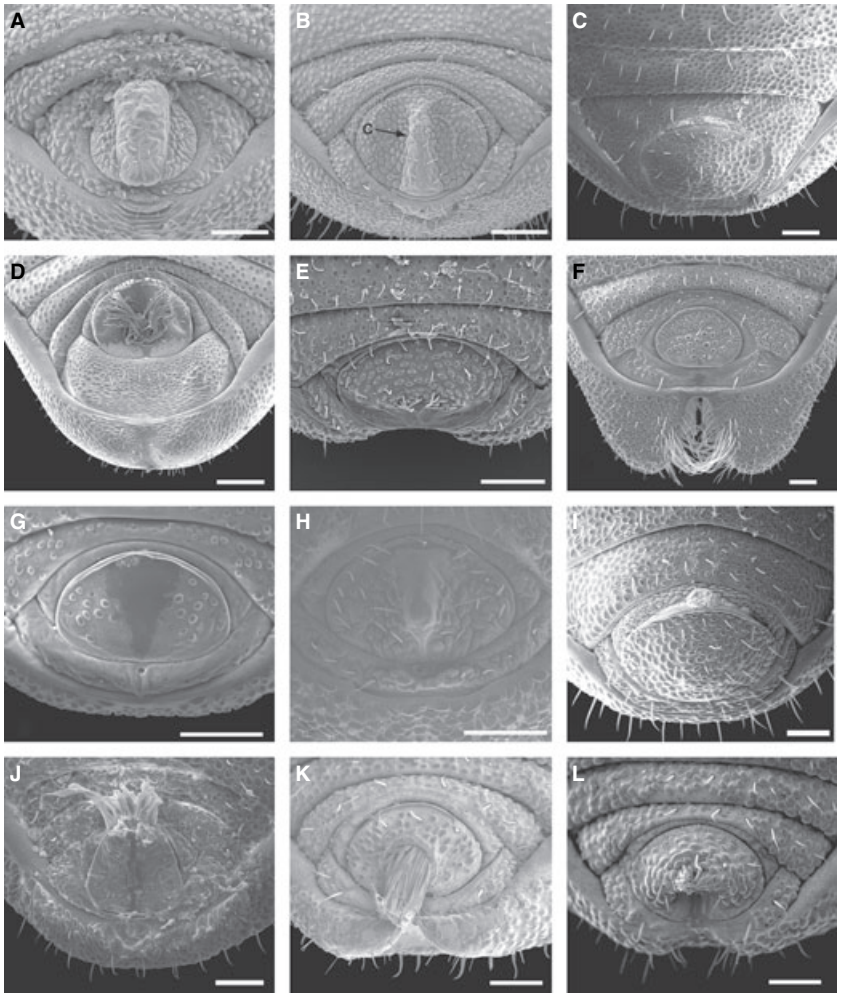

Fig. 8. Posterior ventral region. Scale 100 μm. (A) *Siro rubens*; (B) *Suzukielus sauteri*; (C) *Huitaca* n.sp. Boyacá; (D) *Purcellia illustrans*; (E) *Parapurcellia monticola*; (F) *Pettalus brevicauda*; (G) *Chileogovea jocasta*; (H) *Chileogovea oedipus*; (I) *Karripurcellia harveyi*; (J) *Austropurcellia scoparia*; (K) *Neopurcellia foresteri*; (L) *Rakaia daviesae*. This region comprises many different characters, including the relative positions of sternites and tergites surrounding the anal plate, ornamentation of the anal plate, presence of absence of a longitudinal carina (indicated by arrow and C in (B)), and scopulae (coarse hairs) on the anal plate, tergite IX, and tergite VIII.

Zealand. Gender feminine. The southernmost range of this genus occurs at a tiny patch of forest named Governor's Bush in the Aoraki/Mt. Cook National Park, the type locality for *Aoraki longitarsa,* a species which is known for only two collections: the original holotype collection by J. T. Salmon prior to 1952, and by the authors and Greg Edgecombe on January 14, 2006.

Distribution: *Aoraki* is distributed across the whole of the North Island of New Zealand, and in the South Island of New Zealand from Aoraki/Mt. Cook and points north (including Stephens Island).

Remarks: The genus *Aoraki* includes several New Zealand species formerly included in the genus *Rakaia*. It can be distinguished from the genera *Austropurcellia* and *Rakaia* by the overall appearance of the chelicera, which has a gracile rather than robust aspect and a clear ventral process in the proximal segment (as in Fig. 6D rather than 6C). The genus can also be distinguished from *Austropurcellia* and the majority of *Rakaia* species by the absence of a process on the palp of the trochanter (Fig. 6F rather than 6E), and it can be distinguished from all *Rakaia* by the absence of a solea in tarsus I (Fig. 7B vs 7C). *Aoraki* is distinguished from *Neopurcellia* by the absence of long curling scopulae originating from the inner margins of tergite 8.

Discussion

Concurrence of results from different analyses

The overwhelming majority of results from different analyses of different data sets find the same patterns: the temperate Gondwanan harvestman family Pettalidae is

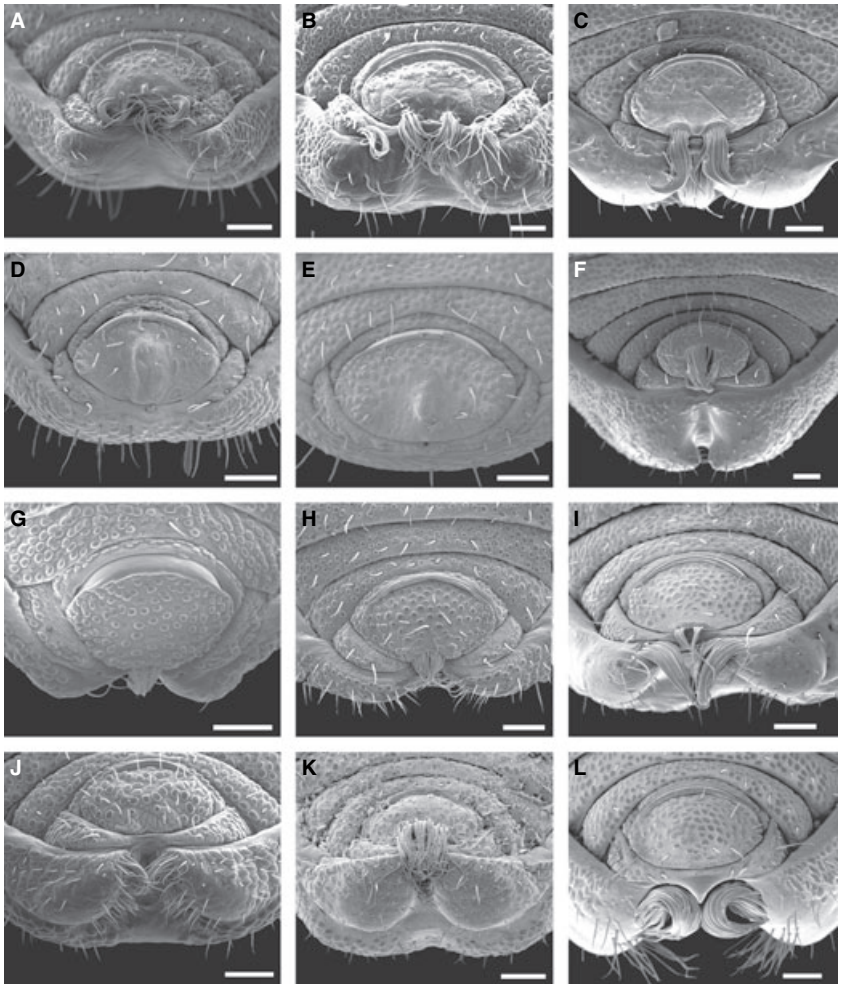

Fig. 9. Posterior ventral region. Scale 100 μm. (A) *Rakaia denticulata*; (B) *R. crypta*; (C) *R. healyi*; (D) *R. granulosa*; (E) *R. calcarobtusa westlandica*; (F) *R. stewartiensis*; (G) *R. media*; (H) *R. solitaria*; (I) *R. dorothea*; (J) *R. sorenseni digitata*; (K) *Neopurcellia minutissima*; (L) *N. salmoni*. This region comprises many different characters, including the relative positions of sternites and tergites surrounding the anal plate, ornamentation of the anal plate, and scopulae (coarse hairs) on the anal plate, tergite IX and tergite VIII.

a stable, strongly supported monophyletic group, within which several continent-specific clades are found (Fig. 2). The different analyses included direct optimization with parsimony as the optimality criterion, and maximum likelihood and Bayesian analyses of manually aligned data (Fig. 4). The fact that these extremely disparate approaches to data analysis all yielded consistent results indicates that the phylogenetic signal present in the data is not methodology-dependent. Despite concordance in most phylogenetic results, the relationships among the taxa occurring on each of the former Gondwanan landmasses remain mostly unresolved, though certain biogeographical trends are evident (see Discussion below).

Systematics of Pettalidae

The family Pettalidae currently comprises 52 described species and subspecies in 11 genera (Giribet, 2003a; Sharma and Giribet, 2006), including the new genus *Aoraki* proposed in this study. Thorell (1876) described the first pettalid as *Cyphophthalmus cimiciformis*, a species from Sri Lanka. Pocock (1897) subsequently described *Pettalus brevicauda* from Sri Lanka and transferred *C. cimiciformis* to *Pettalus*. The genus *Purcellia* from South Africa was described by Hansen and Sørensen (1904), followed in South Africa by *Speleosiro* Lawrence (1931) and *Parapurcellia* Rosas Costa (1950); although the current generic assignation of the members of *Purcellia* and *Parapurcellia* awaits re-study. Hirst (1925) described the first known pettalid from New Zealand, *Rakaia antipodiana*; subsequently Forster described 27 New Zealand species and subspecies in the genera *Rakaia* and *Neopurcellia* between 1948 and 1952, and an additional species was described by Boyer and Giribet (2003). Members of *Rakaia* and *Neopurcellia* were also described from Queensland (Australia) by Forster (1955), Davies (1977), Cantrell (1980)

and Juberthie (1989). A new monotypic genus from Queensland, *Austropurcellia*, was described by Juberthie (1988b), and Giribet (2003a) described *Karripurcellia*, with three species from Western Australia. The Chilean genus *Chileogovea* was described by Roewer (1961), and the genus *Manangotria* from Madagascar by Shear and Gruber (1996).

Shear (1980) erected the family Pettalidae based on a non-numerical cladistic analysis of the suborder Cyphophthalmi. In two recent cladistic analyses of morphological data by Giribet and Boyer (2002) and Giribet (2003a), Pettalidae was found to be monophyletic, and analyses of molecular data for Cyphophthalmi including preliminary subsets of the current data for pettalids also retrieved the family as a clade (Giribet and Boyer, 2002; Boyer et al., 2005; Schwendinger and Giribet, 2005). Strongly supported and stable monophyly of Pettalidae is further corroborated in this study.

The pettalid genera outside of Queensland and New Zealand are supported by this analysis: *Chileogovea* (represented by two species from Chile), *Parapurcellia* (represented by two species from South Africa) and *Pettalus* (represented by six species from Sri Lanka) are each shown to be monophyletic groups. (The genus *Purcellia* is only represented by one individual, and *Karripurcellia* is represented by two individuals from the same species.) In contrast, the genera *Neopurcellia* and *Rakaia* are both shown to be polyphyletic. The Queensland species form a well-supported monophyletic group, including species formerly assigned to the genera *Austropurcellia*, *Neopurcellia* and *Rakaia*, indicating that in this case biogeography prevails over traditional taxonomy. However, the Queensland clade (*Austropurcellia* following our new generic emendation) is not sister to *Karripurcellia* from Western Australia, once more corroborating the idea that large continents cannot be treated as single biogeographical units (e.g., Sanmartín and Ronquist, 2004); instead, the use of microareas should be used as proposed by Giribet and Edgecombe (2006; see also Weston and Crisp, 1994).

In the case of New Zealand, more than one clade of pettalids needs to be postulated. The New Zealand species form two well-supported clades plus the monotypic *Neopurcellia salmoni*, with relationships between these three lineages mostly unresolved. After the taxonomic proposal presented in this study *Austropurcellia* refers to all known species from Queensland (Australia), while among the three New Zealand clades *Rakaia* refers to the clade including *R. antipodiana* (the nominal species of the genus), and *Neopurcellia* is restricted to *N. salmoni* (the nominal species of the genus). A new genus, *Aoraki*, is erected to accommodate the remaining clade of New Zealand species with a smooth palp trochanter and gracile chelicerae with a conspicuous ventral process. Although few morphological characters are specific to *Rakaia* and *Aoraki* (Figs 8 and 9), unique combinations of characters distinguish each genus, as indicated in our taxonomic revision. The results of the present analyses confirm our previous suggestions that neither *Rakaia* nor *Neopurcellia*, as originally described with species in both Queensland and New Zealand, is monophyletic (Boyer and Giribet, 2003).

The tarsus of walking leg IV of Cyphophthalmi is typically unsegmented, unlike in most other Opiliones. The adult males of all Cyphophthalmi bear a specialized secretory organ on their tarsus IV called the adenostyle whose function is probably related to spermatoposition. This organ confers some often dramatic modifications to the tarsus IV, and in the males of certain species of pettalids and sironids, the tarsus IV becomes bisegmented (e.g., Shear, 1980; Giribet and Boyer, 2002) (Fig. 7D–I). This is found in the monotypic Japanese *Suzukielus* and in some American species of the genus *Siro* (both in the family Sironidae), as well as in all the South African species of Pettalidae, and in some species from Queensland and New Zealand—the members of the old genera *Austropurcellia* and *Neopurcellia* (Figs 2 and 5). When he erected the genus *Neopurcellia*, Forster separated it from *Rakaia* based on the fourth tarsus of the male consisting of one segment (*Rakaia*) versus two segments (*Neopurcellia*). He hypothesized that *Neopurcellia* was "undoubtedly" related to the South African genus *Purcellia* due to the shared character of a bisegmented male tarsus IV (Forster, 1947). The existence of a variety of conditions in the male tarsus IV, including animals with partially bisegmented tarsi or tarsi that appear bilobed but not bisegmented (Fig. 7G,H) suggests that the emphasis placed on this character is misleading. In addition, the results of our phylogenetic analysis do not indicate a close relationship between South African and New Zealand taxa with bisegmented tarsi, therefore confirming the lability of this character, as it was already shown for the family Sironidae (Shear, 1980). Instead, several parameter sets suggest that *Parapurcellia* from South Africa is sister to all other pettalids (Fig. 3). The presence of bisegmented tarsus IV in several other clades may indicate that this character optimizes at the base of the pettalid tree. Taxa with bisegmented and partially bisegmented male tarsi IV are indicated in Fig. 2.

Another key morphological feature of Pettalidae is the eyes, which were thought to be absent in the family until recently (Sharma and Giribet, 2006; see also Juberthie, 1989). Examination of material for this study revealed that eyes are in fact present in the majority of Pettalidae, though they are often incorporated at the base of the ozophores and typically lack lenses, rendering them invisible in SEM (Fig. 6A). Pettalidae is likely the sister to all other Cyphophthalmi, though the family Stylocellidae is also a candidate for this position (Boyer et al., in press). Stylocellids have lateral eyes with distinct lenses positioned ventrally relative to the ozophores; therefore, either Pettalidae or Stylocellidae

as the sister to all other Cyphophthalmi would resolve eyes as plesiomorphic in the suborder. Within Pettalidae, eyes are lacking in *Parapurcellia* but present in the remaining members of the family (character 1, Fig. 5). Given the presence of eyes in the outgroups as well as in Stylocellidae, it is most likely that eyes were lost in the common ancestor of *Parapurcellia*. Other important characters evolving only once within Pettalidae at this particular split include ozophore position, which shifts from a position slightly above the carapace in *Parapurcellia* to a more dorsal position in all other pettalids (character 2), and the dentition of the mobile digit of the chelicerae, which changes from uniform in *Parapurcellia* to a special condition with two types of teeth in all other pettalids (character 8).

Morphological characters uniting the family Pettalidae include the relative height of the gonostome (character 30), spiracle shape (character 31), and the presence of a bilobed tergite VIII (character 37) and bilobed tergite IX (character 44) in males (Fig. 5). Another important character for this group is the special configuration of the opisthosomal sternites 8 and 9 and tergite IX (character 36). Within Pettalidae, most species have sternites 8, 9, and tergite IX all free (Figs 8 and 9). The exceptions are found in the genus *Pettalus*, where most species have sternites 8 and 9 medially fused, and an unusual arrangement is seen in *Pettalus* cf. *brevicauda*, which has a corona analis but with some vestige of sutures among the plates still apparent (Fig. 8F). The anal region of males usually bears scopulae in Pettalidae (character 40), originating from the anal plate or from tergite VIII or IX. The function of these structures is unknown, but a role in courtship, mating, or species recognition seems likely given the sexually dimorphic nature of this complex of characters. The scopulae are taxonomically informative, as discussed in the diagnosis of *Aoraki*, *Austropurcellia*, *Neopurcellia* and *Rakaia*.

Biogeography of Pettalidae and the breakup of Gondwana

Gondwana formed the southern portion of the supercontinent Pangaea during the Triassic, and broke into fragments starting approximately 165–160 Ma when the continental block formed by Madagascar and India began to rift from both Australia and Africa; 135–130 Ma the South Atlantic Ocean opened at the far south tip of Africa and South America. It was not until 110–165 Ma that Africa and Antarctica finally separated. Approximately 88–84 Ma India and Madagascar separated from one another, with India finally colliding with Asia around 50 Ma. New Zealand, South America and Australia were originally connected across Antarctica; 80 Ma New Zealand began to drift away from West Antarctica, opening the Tasman Sea. Final terrestrial connections between New Zealand and Australia were broken by 60 Ma, though Australia and South America remained in contact across Antarctica until at least the early Eocene. At this time Antarctica had a temperate climate and was home to *Nothofagus* forests, but by 46 Ma cold conditions were severe enough that overland dispersal by temperate-adapted organisms would have been impaired. Southern South America and Antarctica still remained in contact through the Antarctic Peninsula until the opening of the Drake Passage at the Eocene–Oligocene boundary (30–28 Ma). This led to the establishment of the Antarctic Circumpolar Current and the onset of the first Antarctic glaciation (Sanmartín, 2002; Sanmartín and Ronquist, 2004).

The Temperate Gondwanan family Pettalidae, found across all the landmasses that once surrounded Antarctica, is retrieved as a monophyletic, highly supported clade, consistent with previous analyses. This family is not closely related to the other Tropical Gondwanan and New Caledonian Cyphophthalmi. Members of Neogoveidae are found in equatorial West Africa, northern South America and Florida (Tropical Gondwana) and are found to comprise a monophyletic group separate from Pettalidae. This is consistent with the findings of Sanmartín and Ronquist (2004), who showed that there is little biotic exchange between the northern tropical and southern temperate regions of South America. Rather, Neogoveidae are retrieved as sister to Troglosironidae from New Caledonia with high support and stability. It should be noted that New Caledonia is believed to have separated from Australia about 65 Ma, and subsequently drifted in a north-easterly direction, reaching its present position about 50 Ma (Coleman, 1980; Raven, 1979; Murienne et al., 2005). However, in our analyses the New Caledonian family Troglosironidae is consistently found to be sister to the Tropical Gondwanan family Neogoveidae, from northern South America and Africa, rather than part of the Temperate Gondwanan family Pettalidae including all Australian species (see also Giribet and Boyer, 2002; Boyer et al., in press). This intriguing result will be investigated in greater detail in future studies of the New Caledonian fauna (P. Sharma and G. Giribet, work in progress).

The fact that members of the family Pettalidae from the majority of the various fragments of Gondwana form continent-specific clades supports our model of diversification in this group driven by vicariance. One exception to this general rule is found in the South African species, where *Parapurcellia*, from eastern South Africa is the sister to all other pettalid species, and *Purcellia*, from western South Africa, is sister to *Chileogovea*, from Chile. These relationships could correspond to ancient distributions, as western South Africa was adjacent to southern South America during the Late Jurassic (Fig. 1). The Table Mountain formation, home to both *Purcellia illustrans* and *Speleosiro argasiformis*—the latter a troglobiont not included in our study—consists of an eroded layer of sandstone

deposited 450 Ma on top of more ancient granite and sandstone; the geological history of this area may have played a significant role in diversification of Pettalidae in South Africa. Only four of the eight described South African species were included in this study and we hope that future work will include molecular data for the monotypic genus *Speleosiro* as well as representatives from other South African regions such as the Transvaal, or the several undescribed species from the coastal forests of eastern South Africa.

Another notable exception to the "one area, one clade" rule occurs in New Zealand, where three different lineages exist, diagnosed here as *Neopurcellia*, *Rakaia* and *Aoraki*. In fact this is the only region where more than one pettalid lineage overlaps in distribution (unlike the South African and Australian species). Under the new taxonomy *Neopurcellia* becomes monotypic and does not group with other New Zealand genera; instead, it appears as the sister group to all other pettalids except for the eastern South African species. With respect to the other two larger New Zealand clades, in the Bayesian analysis of the data, *Rakaia* and *Aoraki* appear as sister clades, whereas in the direct optimization parsimony analyses they generally do not. Biogeographically, *Neopurcellia salmoni* is found west of the Southern Alps in the South Island; *Rakaia* is found to the east of the Southern Alps, Stewart Island, Nelson, Marlborough, and the North Island; and *Aoraki* is found in Nelson, Marlborough, and the North Island exclusively. This striking biogeographical pattern will be explored in greater detail in future studies (authors' work in progress).

Based on studies of biogeography in other Australian taxa, as well as the morphology of the Australian pettalid genera, we are not surprised that *Karripurcellia* from Western Australia and *Austropurcellia* from Queensland are not each other's closest relatives. The central region of Australia, now home to extensive deserts, was once humid and temperate with *Nothofagus* rainforest spreading across the entire continent as late as 37 Ma (BMR Paleogeographic Group, 1990). Cyphophthalmi may have dispersed across Australia during this time, but in this ancient group it is also possible that the Western Australia and Queensland lineages arose independently and dispersed to their present Australian locations from adjacent land masses now separate from Australia. In either case, it is clear that it would be inappropriate to treat extant Australian Pettalidae as a single biogeographical unit, consistent with findings in other taxa such as centipedes in the genus *Paralamyctes* (Giribet and Edgecombe, 2006), and waratahs (Weston and Crisp, 1994).

Several biogeographical trends are present in the data. Most analyses agree that *Parapurcellia*, from South Africa, is sister to all other Pettalidae (e.g., Figs 2–5). The direct optimization analysis under the optimal parameter set reveals a pattern in which *Parapurcellia* is sister to a grade of taxa from New Zealand and Queensland, followed by the remaining groups. The result from the Bayesian analysis of the data shares the common theme of *Parapurcellia* from South Africa as sister to all other Pettalidae, within which *Neopurcellia salmoni* from New Zealand is sister to all other taxa (Fig. 4). These patterns suggest the southern part of Gondwana as the point of origination for the family; alternative topologies found in the sensitivity analyses resolve the Queensland clade or *Chileogovea* (Chile) as the sister to all other pettalids; neither *Karripurcellia* (Western Australia) nor *Pettalus* (Sri Lanka) appears at the base of the tree when all molecular data are considered together. This result contradicts previous historical biogeographical scenarios proposed for Pettalidae, in which genera from Madagascar and Western Australia appeared as the sister group to all others (Giribet, 2003a), although the same analyses suggested Chile as a possible candidate, a result also obtained under some parameter sets (410, 411, 441; Fig. 3).

In addition to the basal split between *Parapucellia* and all other Pettalidae, three patterns that are found in many analyses, including the results under the optimal parameter set, are: (1) The genera from Queensland and New Zealand form a paraphyletic grade; (2) the genera from Western Australia and Sri Lanka are sister taxa; and (3) the genus *Chileogovea* from South America is the sister of *Purcellia* from South Africa. All three of these biogeographical patterns can be easily interpreted in light of the geography of pre-breakup Gondwana. Reconstructions indicate that Queensland and New Zealand were more or less adjacent to one another, as were Western Australia and Sri Lanka, as well as South America and South Africa (Fig. 1).

Although biogeographical trends are apparent within the phylogeny of the family Pettalidae, it should be acknowledged that the deep nodes within the tree remain poorly supported. Several factors may be contributing to this lack of resolution. First, branches within the family Pettalidae are short (Fig. 4), indicating that the main lineages may have arisen rapidly, possibly during the rapid expansion of *Glossopteris* forests throughout Temperate Gondwana. Secondly, pettalids may very well have been distributed throughout the forests of Antarctica and Central Australia during the periods when these areas were humid and temperate. Sanmartín and Ronquist (2004) provide an exhaustive summary of phylogenetic studies of Gondwana-distributed taxa, and conclude that in animal groups there is a close relationship between South American and Australian taxa due to geological contact between Australia and South America via Antarctica up until the early Eocene. *Nothofagus* fossils are known from Antarctica from as late as the early Miocene (Swenson et al., 2001b). It is reasonable to suppose that Pettalidae inhabited Antarctica during this time, and that massive extinction has occurred both in

Antarctica and in Central Australia, possibly contributing to the difficulty in resolving the tree using data from extant species only. It is worth noting, though, that the markers used were able to retrieve monophyly of the family and monophyly of major geographic areas and most genera (with the exception of the previously misdiagnosed Queensland–New Zealand genera). Therefore, the information content of the markers employed spans through the geological time prior to the origin to the family until at least the speciation events that gave origin to the modern genera.

The phylogeny presented here features taxon sampling across Temperate Gondwana comparable with the best sampled phylogenies for any Gondwanan group. They show that the family Pettalidae, inhabiting all these Gondwanan landmasses, forms a monophyletic entity but that it is unrelated to the Cyphophthalmi found in New Caledonia. Our results are consistent with a model of diversification of major lineages driven by vicariance, despite the fact that we were not able to elucidate the exact sequence of such vicariance events. With extant members on every fragment of the former supercontinent (except Antarctica), the family Pettalidae represents a new model Gondwanan taxon.

Acknowledgments

For help in the field, the authors would like to thank Greg Edgecombe, Cyrille D'Haese, Prashant Sharma, Indika Karunarathna, Lorenzo Prendini, Nobuo Tsurusaki, Michele Nishiguchi, Stephanie Huff, Phil Sirvid and Ricardo Palma. Ron Clouse generously shared sequences from undescribed *Stylocellus* species. Peter Schwendinger provided stylocellid specimens. Gustavo Hormiga provided material from *Chileogovea*. Prashant Sharma assisted with SEM images for New Zealand *Aoraki, Neopurcellia,* and *Rakaia*; Ligia Benavides provided SEM images for Neogoveidae; and Richard Schalek from Harvard CIMS provided technical assistance with the scanning electron microscope. The New Zealand DOC, and in particular Ian Millar at the Nelson office, were extremely helpful and organized in arranging collecting permits for us. Michael Ethier at the Harvard Center for Genomic Research helped with analyses performed on the CGR supercomputing cluster. Finally, we are indebted to all the curators of the museums that lent us pettalid specimens for their long-term loans, longer than originally requested (we promise we will return them some day): Janet Beccalioni and Paul Hillyard from The Natural History Museum (London), Debbie Jennings from the Natal Museum (Pietermaritzburg), Margie Cochrane from the South African Museum (Cape Town), Charles Griswold and Darrell Ubick from the California Academy of Sciences (San Francisco), Bruce Haliday from the Australian National Insect Collection (Canberra), Mark Harvey from the Western Australian Museum (Perth), Norman Platnick and Lorenzo Prendini from the American Museum of Natural History (New York), Petra Sierwald from The Field Museum of Natural History (Chicago), Phil Sirvid from Te Papa Tongarewa (Wellington), Simon Pollard from the Canterbury Museum (Christchurch), Abigail Blair from the Otago Museum (Dunedin), and Grace Hall at the New Zealand Arthropod Collection of Manaaki Whenua Landcare Research (Auckland). Lorenzo Prendini and two anonymous reviewers provided comments. This material is based upon work supported by the National Science Foundation under Grant no. 0236871. Field work for this project was also supported by Harvard Museum of Comparative Zoology Putnam Expedition Grants to the authors.

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Appendix 1

Morphological characters used in the phylogenetic analysis and character discussion.

GB indicates character number from the matrix presented by Giribet and Boyer (2002); G, character number from the matrix by Giribet (2003a); DG, character matrix by de Bivort and Giribet (2004).

1. Eyes: (0) absent; (1) present with lens; (2) present, incorporated into ozophore (GB 2; DG 1). Most Cyphophthalmi have been described as lacking eyes, with distinct eyes (positioned laterally, although they may correspond to the median eyes of other Opiliones) present only in the South-east Asian genus *Stylocellus* (Shear, 1980; Giribet and Boyer, 2002; Giribet et al., 2002). Although Pettalidae were originally described as blind animals, eyes located at the base of the ozophore have recently been discovered in members of the pettalid genera *Pettalus* and *Chileogovea* (Sharma and Giribet, 2006). Following this discovery, comparisons of images of ozophores in SEM and light microscope have revealed that eyes are present across almost all pettalids. In some species the eye has a lens that can be detected in SEM (Fig. 6B), while in others the eye is completely incorporated into the ozophore without a lens, appearing as a round white mass below the surface of the cuticle when viewed with a light microscope but invisible in SEM images (Fig. 6A). Within Pettalidae, eyes with a lens are found in *Chileogovea,* some members of *Pettalus*, *Rakaia solitaria*, and an undescribed *Rakaia* from Kapiti Island, New Zealand. All other *Pettalus* and *Rakaia,* as well as all members of *Aoraki*, *Austropurcellia*, *Karripurcellia*, *Neopurcellia* and *Purcellia* have eyes incorporated into the base of their ozophores.

2. Ozophore position: (0) type 1; (1) type 2; (2) type 3; (3) dorsal, facing 45° (GB 2; G 1; DG 2). Juberthie (1970) recognized three ozophore positions relative to the carapace. Type 1 is completely lateral, type 2 is slightly raised on the carapace, and type 3 is completely dorsal. In addition, we recognize a fourth position, intermediate between type 2 and type 3: dorsal, facing 45° as described by de Bivort and Giribet (2004).

3. Ozophore opening type: (0) subterminal ozopore; (1) infolded; (2) terminal ozopore, with circular opening; (3) labial; (4) disc-shaped (DG 3). This character was originally described as having a state referred to as "plugged ozopore". Further examination of ozophores with "plugs" has revealed that the smooth "plugs" visible on the tips of ozophores in all Sironidae (except *Suzukielus*), Neogoveidae and Troglosironidae are in fact secretions from the ozophore opening (Novak and Giribet, 2006). Therefore, we have renamed this state "subterminal ozopore", referring simply to the position of the opening. All pettalids have a terminal ozopore with circular opening (Fig. 6A,B).

4. Spiral ornamentation of the ozophore: (0) absent; (1) present (DG 4).

5. Protruding chelicerae: (0) absent; (1) present (G 2).

6. Widest part of the cheliceral distal article: (0) near base; (1) near articulation with mobile digit (DG 5).

7. Distal segment of chelicerae ornamentation: (0) absent; (1) present (GB 4; DG 6).

8. Dentition of the mobile digit of the chelicerae: (0) uniform; (1) dentition non-uniform with largest tooth occurring in the center of the row of teeth; (2) bilobed with smaller lobe distal (GB 6; DG 7). Many pettalids have two separate and very distinct types of dentition, as exemplified by *Karripurcellia harveyi*. In other species, such as *Rakaia pauli*, the dentition is not uniform but is not so neatly divisible into two categories. In many specimens the appearance of the dentition is influenced by the amount of wear on the teeth and the angle at which the chelicera is mounted on the SEM stub. Therefore, we have broadened the coding of this character state to "non-uniform with largest tooth central", effectively homologizing the type of dentition seen in *Karripurcellia harveyi* with the type of dentition seen in *Rakaia pauli*.

9. Basal article of chelicerae with a dorsal crest: (0) absent; (1) present (GB 7; G 5; DG 8).

10. Basal article of chelicerae with a basal ventral process: (0) absent; (1) present (GB 8; G 6; DG 9). We are using the restrictive coding developed by de Bivort and Giribet (2004) for this character, resulting in a recoding of this character for several pettalids (e.g., *Purcellia illustrans*). We want to draw attention to the fact that this process is basal in its position on the chelicera, to distinguish it from the second ventral process present in *Stylocellus globosus* and *Stylocellus ramblae* (DG 10) even though the second ventral process is not included as a character in this analysis. See Fig. 6(C,D).

11. Apodeme on chelicera: (0) absent; (1) present. This character was originally described as a unique feature of *Rakaia macra* (Boyer and Giribet, 2003) but we have since discovered that this previously undocumented feature is present in many species of Pettalidae from New Zealand (e.g., Fig. 6C) as well as species from the genera *Parapurcellia* and *Purcellia*.

12. Palp trochanter with ventral process: (0) absent; (1) present (GB 10; G 7; DG 11) (Fig. 6E,F).

13. Solea in tarsus 1: (0) absent; (1) present (GB 12; G 9; DG 13) (Fig. 7A–C).

14. Leg II ornamentation: (0) all segments smooth; (1) metatarsus and tarsus smooth; (2) metatarsus partially ornamented and tarsus smooth; (3) metatarsus ornamented and tarsus smooth; (4) metatarsus and dorso-basal part of the tarsus ornamented; (5) metatarsus ornamented and tarsus almost entirely ornamented.

15. Claw of leg II with modifications: (0) absent; (1) present (DG 16).

16. Claw of leg II with special row of teeth forming a comb: (0) absent; (1) present (DG 17).

17. Claw of leg III with modifications: (0) absent; (1) present (DG 18).

18. Claw of leg IV with modifications: (0) absent; (1) present (DG 19).

19. Male tarsus IV: (0) entire; (1) bisegmented; (2) bisegmented dorsally only (GB 15; G 11; DG 21). Most pettalids have a unisegmented (entire) male tarsus IV (Fig. 7D), while in some species it is bisegmented (Fig. 7E). In *Rakaia arcticosa* and *Rakaia daviesae* from Queensland, the fourth tarsus of the male is bisegmented dorsally only (Fig. 7F,I). In *Rakaia lindsayi* and *Rakaia stewartiensis* from Stewart Island (New Zealand), the fourth tarsus of the male appears bisegmented when examined in a light microscope but SEM images reveal no external evidence of segmentation (Fig. 7G,H). Like *R. arcticosa* and *R. daviesae*, *R. lindsayi* and *R. stewartiensis* are closely related to species with bisegmented fourth tarsi. In this analysis, we have coded *R. lindsayi* and *R. stewartiensis* as having an entire fourth tarsus.

20. Adenostyle: (0) lamelliform; (1) ending in a tuft of setae; (2) fimbriate; (3) triangular and heavily sclerotized; (4) plumose; (5) digitiform; (6) bilobed tip (GB 16; G 12; DG 21). The adenostyle of most cyphophthalmids is lamelliform (Fig. 7D–I). Within Pettalidae, one species from New Zealand included in this analysis, *Rakaia sorenseni digitata*, has a digitiform adenostyle. This state is also seen in a closely related undescribed *Rakaia* species from New Zealand not included in the current analysis. Additional states for this character have been included in previous studies to describe autapomorphic states in genera in the families Neogoveidae, Ogoveidae, and Sironidae (DG 21). While shape information is difficult to incorporate into discrete morphological characters, it is clear that the extremely robust adenostyle of all species from Queensland is a diagnostic character for the rediagnosed genus *Austropurcellia*.

21. Adenostyle in the most-basal region of the tarsus: (0) absent; (1) present (DG 22). Within pettalids, all species of *Pettalus* for which males were available for this analysis have an adenostyle with the proximal edge emerging at a distance from the metatarsus less than the width of the adenostyle.

22. Ornamentation of tarsi III and IV: (0) absent; (1) present (DG 23).

23. Proximal end of male coxae I meeting along the midline: (0) absent; (1) present (DG 24).

24. Second coxae: (0) free; (1) fused to coxae of leg III (GB 11; G 8; DG 25).

25. Proximal end of male coxae III meeting along the midline: (0) absent; (1) present (DG 26).

26. Coxae II and III endites with processes running along their suture: (0) absent; (1) present (DG 27).

27. Gonostome of male in anterior position: (0) absent; (1) present (DG 29).

28. Shape of the gonostome: (0) semicircular-trapezoidal; (1) subhexagonal (DG 30).

29. Anterior projections of male coxae IV endite: (0) no projections; (1) projections in gonostome wall; (2)

projections adjacent to coxal pore; (3) projections along suture of coxae IV (DG 31). Within Pettalidae, projections of male coxae IV are only known in *Parapurcellia* and *Chileogovea*. NOTE: This character was misdescribed by de Bivort and Giribet (2004) as "projections of male coxae III".

30. Endites of coxae IV running adjacent to midline suture for a length longer than gonostome: (0) absent; (1) present (DG 32).

31. Spiracle shape: (0) circular; (1) open circle; (2) "C" shaped (GB 21; G 14; DG 33).

Male exocrine glands on opisthosoma: Characters 32–33

Homology of the sternal glands of Troglosironidae and Neogoveidae to the anal glands found in some Pettalidae (e.g., Fig. 9E), Sironidae, and Stylocellidae has been proposed by Sharma and Giribet (2005). No specimen of Cyphophthalmi has ever been described with exocrine glands on the opisthosoma in both the sternal region and the anal region. In this study we have explicitly homologized these glands. Previously, male exocrine glands were coded by Giribet and Boyer (2002), Giribet (2003a) and de Bivort and Giribet (2004) in two separate characters: one for the presence/absence of sternal glands, and one for the presence/absence of anal glands.

32. Exocrine glands on opisthosoma: (0) absent; (1) present.

33. Position of opisthosomal exocrine glands: (0) on anterior sternal region; (1) on tergite VIII; (2) on tergite IX; (3) on tergites VIII + IX; (4) on tergite IX + anal plate.

34. V-shaped modification of sternites 6–8: (0) absent; (1) present (G 15; DG 36).

35. Sternites 8, 9, and tergite IX: (0) all free; (1) sternites 8 and 9 medially fused; (2) sternite 9 and tergite IX fused, but sternite 8 free; (3) all fused into corona analis; (4) sternites 8 and 9 completely fused, tergite IX free (GB 24; G 16; DG 37). Within Pettalidae, most species have sternites 8, 9, and tergite IX all free (Figs 8 and 9). The exceptions are found in the genus *Pettalus*, where most species have sternites 8 and 9 medially fused. The only species displaying a different configuration of plates is *Pettalus* cf. *brevicauda,* which has a corona analis but with some vestige of sutures among the plates still apparent. This condition is not readily apparent in examination with a light microscope but clearly visible in SEM (Fig. 8F).

36. Relative position of sternite 9 and tergite IX: (0) stylocellid type; (1) pettalid type (GB 25; DG 38) (Fig. 7).

37. Male tergite IX: (0) entire; (1) bilobed (GB 26; G 17). Previously, this character had been described as male tergite IX divided, rather than bilobed (Giribet and Boyer, 2002; Giribet, 2003a). The problem in this coding of the character is that many Pettalidae, particularly species from New Zealand, have a tergite IX, which is dramatically bilobed but with both lobes still narrowly connected in the center (e.g., Fig. 9L). We have reformulated this character because we consider the bilobed condition to be homologous to the divided condition. We consider tergite IX to be divided if it is significantly narrower and significantly diminished in ornamentation at its center. This changes the coding of this character for the species *Neopurcellia minutissima* and *N. salmoni*, which we previously considered to have an entire male tergite IX.

38. Longitudinal carina in male anal plate: (0) absent; (1) present (G 18; DG 39). Previous to this study, among pettalids, only *Chileogovea oedipus* (Fig. 8G) and *Ankaratra franzi* were known to have a longitudinal carina in the anal plate. Though it was not noted in the original descriptions, *Rakaia calcarobtusa westlandica* (Fig. 9E), *R. granulosa* (Fig. 9D), and *R. tumidata* also have this feature. It is also found in an undescribed species from Northland, New Zealand.

39. Lack of ornamentation in the midline of male anal plate: (0) absent; (1) present (DG 40).

Scopulae on the male anal plate: Characters 40–41

Many male Pettalidae have a scopula of unknown function in the anal plate. This scopula can be found in many orientations, and we have chosen to represent the scopula with two characters: presence/absence of the scopula, and position of the origin of the scopula on the anal plate. Scopulae can emerge from the posterior margin (Fig. 9H), anterior margin (Fig. 8J), posterior ventral surface (Fig. 9B), central ventral surface (Fig. 8D), or anterior ventral surface (Fig. 8E) of the anal plate.

40. Scopula on male anal plate: (0) absent; (1) present (GB 27; G 20).

41. Position of the origin of scopula: (0) posterior margin; (1) anterior margin; (2) posterior ventral surface; (3) central ventral surface; (4) anterior ventral surface.

42. Scopulae on male tergite IX: (0) absent; (1) present. *Rakaia crypta* and *R. inerma* from the North Island of New Zealand both have scopulae originating from each lobe of tergite IX (Fig. 9B).

43. Posterior elongation in female: (0) absent; (1) present (DG 43).

44. Male tergite VIII bilobed: (0) absent; (1) present (G 28; G 21).

45. Two scopulae originating from each inner margin of tergite VIII: (0) absent; (1) present (G 22).