Evolutionary and biogeographical history of an ancient and global group of arachnids (Arachnida: Opiliones: Cyphophthalmi) with a new taxonomic arrangement

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We investigate the phylogeny, biogeography, time of origin and diversification, ancestral area reconstruction and large-scale distributional patterns of an ancient group of arachnids, the harvestman suborder Cyphophthalmi. Analysis of molecular and morphological data allow us to propose a new classification system for the group; Pettalidae constitutes the infraorder Scopulophthalmi **new clade**, sister group to all other families, which are divided into the infraorders Sternophthalmi **new clade** and Boreophthalmi **new clade**. Sternophthalmi includes the families Troglosironidae, Ogoveidae, and Neogoveidae; Boreophthalmi includes Stylocellidae and Sironidae, the latter family of questionable monophyly. The internal resolution of each family is discussed and traced back to its geological time origin, as well as to its original landmass, using methods for estimating divergence times and ancestral area reconstruction. The origin of Cyphophthalmi can be traced back to the Carboniferous, whereas the diversification time of most families ranges between the Carboniferous and the Jurassic, with the exception of Troglosironidae, whose current diversity originates in the Cretaceous/Tertiary. Ancestral area reconstruction is ambiguous in most cases. Sternophthalmi is traced back to an ancestral land mass that contained New Caledonia and West Africa in the Permian, whereas the ancestral landmass for Neogoveidae included the south-eastern USA and West Africa, dating back to the Triassic. For Pettalidae, most results include South Africa, or a combination of South Africa with the Australian plate of New Zealand or Sri Lanka, as the most likely ancestral landmass, back in the Jurassic. Stylocellidae is reconstructed to the Thai-Malay Peninsula during the Jurassic. Combination of the molecular and morphological data results in a hypothesis for all the cyphophthalmid genera, although the limited data available for some taxa represented only in the morphological partition negatively affects the phylogenetic reconstruction by decreasing nodal support in most clades. However, it resolves

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the position of many monotypic genera not available for molecular analysis, such as *Iberosiro*, *Odontosiro*, *Speleosiro*, *Managotria* or *Marwe*, although it does not place *Shearogovea* or *Ankaratra* within any existing family. The biogeographical data show a strong correlation between relatedness and formerly adjacent landmasses, and oceanic dispersal does not need to be postulated to explain disjunct distributions, especially when considering the time of divergence. The data also allow testing of the hypotheses of the supposed total submersion of New Zealand and New Caledonia, clearly falsifying submersion of the former, although the data cannot reject the latter. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, ••, ••–••.

ADDITIONAL KEYWORDS: biogeography – distribution modelling – Gondwana – Laurasia – MAXENT – New Caledonia – New Zealand – Pangea.

INTRODUCTION

The harvestman suborder Cyphophthalmi (Fig. 1) constitutes an ancient lineage of arachnids and was probably one of the earliest inhabitants of terrestrial ecosystems. Currently distributed on all continental landmasses (with the exception of Antarctica) and on most large islands of continental origin, the group is considered to have been in close association to these landmasses since its origins (Juberthie & Massoud, 1976; Boyer *et al.*, 2007b). The fact that deep genetic divergences in cytochrome *c* oxidase subunit I (COI) have been reported within one species (Boyer, Baker & Giribet, 2007a), and are suspected for many others (R. Clouse & P. Sharma, unpubl. data), corroborates the observations that individuals may live a long time (Juberthie, 1960b) and do not disperse far during the course of life history. These, together with the old history of the group [a Burmese amber specimen probably belonging to Stylocellidae is known from the Early Cretaceous (Poinar, 2008) and the origins of the group has been estimated to have taken place during the Devonian or Carboniferous using molecular dating techniques (Giribet *et al.*, 2010)] have resulted in a broad use of Cyphophthalmi for biogeographical inferences and zoogeographical discussions (Rambla, 1974; Juberthie & Massoud, 1976; Boyer, Karaman &

Giribet, 2005; Boyer & Giribet, 2007; Clouse & Giribet, 2007; Giribet & Kury, 2007; Boyer *et al.*, 2007b; Boyer & Giribet, 2009; Clouse, de Bivort & Giribet, 2009; Karaman, 2009; Murienne & Giribet, 2009; Sharma & Giribet, 2009a; Clouse & Giribet, 2010; de Bivort & Giribet, 2010; Murienne, Karaman & Giribet, 2010b; Clouse *et al.*, 2011). These include some recent and more general debates on the total submersion of large fragment islands such as New Caledonia and New Zealand (Sharma & Giribet, 2009a; Giribet & Boyer, 2010; Giribet *et al.*, 2010).

However, to use a system for biogeographical inferences, a sound systematic hypothesis of the group is required. The taxonomy of Cyphophthalmi has benefitted from the contributions of many studies, especially the synthetic work of Hansen & Sørensen (1904), who produced the first and still best monograph on the group, and established the first classification system of the suborder Cyphophthalmi with one family, Sironidae, and two subfamilies, Stylocellini (including the genera *Stylocellus* Westwood, 1874, *Ogovia* Hansen & Sørensen, 1904, which was preoccupied and became *Ogovea* Roewer, 1923, and *Miopsalis* Thorell, 1890) and Sironini (including *Pettalus* Thorell, 1876, *Purcellia* Hansen & Sørensen, 1904, *Siro* Latreille, 1796, and *Parasiro* Hansen & Sørensen, 1904). Another major contributor was

Figure 1. Habitus. A, *Karripurcellia harveyi* (Pettalidae) from Warren National Park, Western Australia, July 2004. B, *Pettalus thwaitesi* (Pettalidae) from Peradeniya Botanical Gardens, Central Province, Sri Lanka, October 2007. C, *Rakaia pauli* (Pettalidae) from Kelcey's bush, near Waimate, North Island, New Zealand, February 2008. D, *Aoraki longitarsa* (Pettalidae) from Governor's bush, Mt Cook, South Island, New Zealand, January 2006. E, male *Pettalus thwaitesi* (Pettalidae) from Peradeniya Botanical Gardens, Central Province, Sri Lanka, June 2004. F, *Ogovea cameroonensis* (Ogoveidae) from Ototomo Forest, Central province, Cameroon, June 2009. G, *Parogovia* sp. (Neogoveidae) from Mt. Koupé, South-West Province, Cameroon, June 2009. H, two species of *Parogovia* from Campo Reserve, Littoral Province, Cameroon, June 2009; upper left, adult specimen of *Parogovia* n. sp.; lower right, juvenile specimen of *Parogovia* cf. *sironoides*. I, juvenile specimen of *Paramiopsalis ramulosus* (Sironidae) from P.N. Peneda Gerés, Portugal, May 2008. J, *Paramiopsalis ramulosus* (Sironidae) from P.N. Peneda Gerés, Portugal, May 2008. K, *Parasiro minor* (Sironidae) from Monte Rasu, Sardinia, Italy, March 2008. L, *Suzukielus sauteri* (Sironidae) from Mt. Takao, Tokyo Prefecture, Honshu, Japan, April 2005. M, juvenile specimen of *Leptopsalis* sp. (Stylocellidae) from Bantimurung-Bulusaraung N.P., Sulawesi Selatan, Indonesia, June 2006. N, female *Leptopsalis* sp. (Stylocellidae) from Bantimurung-Bulusaraung N.P., Sulawesi Selatan, Indonesia, June 2006.

Juberthie, who described and monographed many genera (e.g. Juberthie, 1956, 1958, 1960a, 1961, 1962, 1969, 1970a, b; Juberthie & Muñoz-Cuevas, 1970; Juberthie, 1979) in addition to his contributions to the biology of the group; the regional work of Forster (1948, 1952) in New Zealand, that of Lawrence (1931, 1933, 1939, 1963) in South Africa, that of Rambla (Rambla & Fontarnau, 1984, 1986; Rambla, 1991, 1994) in the Iberian Peninsula and southeast Asia, to mention just a few of them. More recently, Shear has contributed with descriptions of numerous species in almost all cyphophthalmid families (Shear, 1977, 1979a, b, 1985, 1993a, b, c; Shear & Gruber, 1996). He also proposed the bases of modern cyphophthalmid systematics in a seminal first cladistic analysis of the group (Shear, 1980), with five families, three of which were new, and two infraorders, equivalent to Hansen and Sørensen's subfamilies (Table 1). A sixth family, Troglosironidae, was also proposed a few years later (Shear, 1993b).

Two decades after Shear's classification system appeared, Giribet (2000) compiled all the cyphophthalmid literature to date, recognizing 113 species in 26 genera. A subsequent analysis including representatives of most genera and based on a numerical cladistic analysis of 32 morphological characters (Giribet & Boyer, 2002) recognized most of the families erected by Shear (1980) but also challenged some of his systematic propositions because the root of the tree, based on a limited molecular data set also published in the same study, was placed between stylocellids and the rest (rendering Tropicophthalmi paraphyletic) or between pettalids and the rest (rendering Temperophthalmi paraphyletic). Shear (1993b) had also proposed the new family Troglosironidae as sister to (Pettalidae + Sironidae) and this result was refuted by Giribet & Boyer (2002), who found it nested within an unresolved Neogoveidae. After some minor familial reassignments – *Huitaca* Shear, 1979 was removed from Ogoveidae (Giribet & Prieto, 2003)

Table 1. Classification system of Shear (1980, 1993)

Suborder Cyphophthalmi
  Infraorder Tropicophthalmi Shear, 1980
    Superfamily Stylocelloidea Hansen & Sørensen, 1904
      Family Stylocellidae Hansen & Sørensen, 1904
    Superfamily Ogoveoidea Shear, 1980
      Family Ogoveidae Shear, 1980
      Family Neogoveidae Shear, 1980

  Infraorder Temperophthalmi Shear, 1980
    Superfamily Sironoidea Simon, 1879
      Family Sironidae Simon, 1879
      Family Pettalidae Shear, 1980
      Family Troglosironidae Shear, 1993

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and subsequently included in Neogoveidae (Giribet, 2007b); *Fangensis* Rambla, 1994 was transferred from Sironidae to Stylocellidae (Schwendinger & Giribet, 2005); *Metasiro* was transferred from Sironidae to Neogoveidae (Giribet, 2007b); *Meghalaya* Giribet, Sharma & Bastawade, 2007 was included in Stylocellidae (Clouse *et al.*, 2009); and *Shearogovea mexasca* (Shear, 1977) was excluded from Neogoveidae (Benavides & Giribet, 2007; Giribet, 2011) – the families are currently considered to be stable.

Recent phylogenetic analyses based on nucleotide sequence data have resolved the relationship among some of these families, providing strong support for a relationship of Troglosironidae and Neogoveidae (Boyer *et al.*, 2007b; Boyer & Giribet, 2009; Sharma & Giribet, 2009a; Giribet *et al.*, 2010), a result also obtained in a recent analysis of morphometric characters (de Bivort, Clouse & Giribet, 2010). Monophyly of Pettalidae is well supported both by discrete and continuous morphological characters (Giribet & Boyer, 2002; Giribet, 2003a; Boyer & Giribet, 2007; de Bivort *et al.*, 2010; de Bivort & Giribet, 2010), as well as a diversity of molecular analyses (Boyer & Giribet, 2007, 2009; Boyer *et al.*, 2007b; Giribet *et al.*, 2010). Stylocellidae is also well supported based on morphology (Giribet & Boyer, 2002; Clouse *et al.*, 2009) and molecules (Schwendinger & Giribet, 2005; Clouse & Giribet, 2007; Boyer *et al.*, 2007b; Clouse *et al.*, 2009; Clouse & Giribet, 2010; Giribet *et al.*, 2010). However, monophyly of Sironidae, especially the membership of the Mediterranean genus *Parasiro* and the Japanese *Suzukielus* Juberthie, 1970, remains controversial, both based on morphology (Giribet & Boyer, 2002; de Bivort & Giribet, 2004; de Bivort *et al.*, 2010), as well as on molecular analyses (Boyer *et al.*, 2005; Boyer & Giribet, 2007; Giribet *et al.*, 2010).

In addition to the uncertainty about the monophyly of Sironidae, which we approach here by including an expanded taxon sampling in problematic genera previously represented by a single species (*Parasiro*), we include a much larger diversity of Neogoveidae, both from the Neotropics (29 species versus six used in Boyer *et al.*, 2007b; including data on the new Brazilian genus *Canga* DaSilva, Pinto-da-Rocha & Giribet, 2010) and from the Afrotropics (12 terminals versus seven used in Boyer *et al.*, 2007b). Most importantly, we include the first molecular data on the family Ogoveidae, from specimens collected in Cameroon in 2009. In total, we provide novel sequence data for 34 species (of a total of 162 molecular terminals), include 27 genera and a family previously unsampled, and include new landmasses (Mindanao, the eastern Neotropics, the westernmost distribution of the Afrotropics) not considered in previous phylogenetic analyses. The present study also provides the first total evidence analysis of molecules and

morphology for the whole suborder Cyphophthalmi and new data on the timing of diversification and cladogenesis of the group, aiming to revisit interesting biogeographical topics. Finally, we provide an estimate of the ancestral area for each lineage and present the first habitat suitability and distributional patterns analysis for this dispersal-limited, yet globally-distributed group of arthropods. Studying macroecological patterns in Cyphophthalmi is complicated as a result of the scarce occurrence data for most species. Thus, species-level assessment of large-scale distributional patterns and their primary ecological and evolutionary drivers is difficult. Recently, theoretical and practical arguments for the utility of modelling distributional patterns or even ecological niche characteristics above the species level have been proposed (Heino & Soininen, 2007; Hadly, Spaeth & Li, 2009; Diniz, De Marco & Hawkins, 2010). Despite some obvious limitations (Diniz *et al*., 2010), this approach may be very useful to evaluate patterns in groups with limited distributional data such as insects and other arthropods including Cyphophthalmi.

MATERIAL AND METHODS
SPECIMENS
Most specimens used in the molecular part of this study (Fig. 2) were collected by one or more of the authors through direct sifting of leaf litter and transferred to approximately 95% ethanol for molecular and morphological study. Museum specimens have also been used for the morphological studies. A detailed discussion of the specimen collecting effort is provided in the Supporting information (Appendix S1).

The study includes the first molecular data for the family Ogoveidae (*Ogovea cameroonensis* Giribet & Prieto, 2003) and includes additional sampling within all other families, building upon previous studies on the phylogenies of Pettalidae (Boyer & Giribet, 2007; Boyer *et al*., 2007b). Stylocellidae (Clouse *et al*., 2009; Clouse & Giribet, 2010; Clouse *et al*., 2011), Troglosironidae (Sharma & Giribet, 2009a), and Sironidae (Boyer *et al*., 2005; Giribet & Shear, 2010; Murienne *et al*., 2010b). However, data for Neogoveidae were restricted to a single previous study (Boyer *et al*., 2007b), and the family was poorly sampled. For the African diversity, we are now able to add data on another described species, *Parogovia gabonica* (Juberthie, 1969), from near its type locality (Ipassa Reserve, Makokou, Gabon). We also add new data on two new species from Mount Koupé and the Campo reserve, in Cameroon, and an additional specimen of *Parogovia* cf. *sironoides* also from the Campo reserve in Cameroon. The third African species, *Parogovia pabsgarnoni* Legg, 1990, is known only from its type locality in Sierra Leone, resulting in a large biogeographical gap from the known distribution of species in the Gulf of Guinea, and differs morphologically from the other species in the genus in many key characters, showing very different spermatopositor
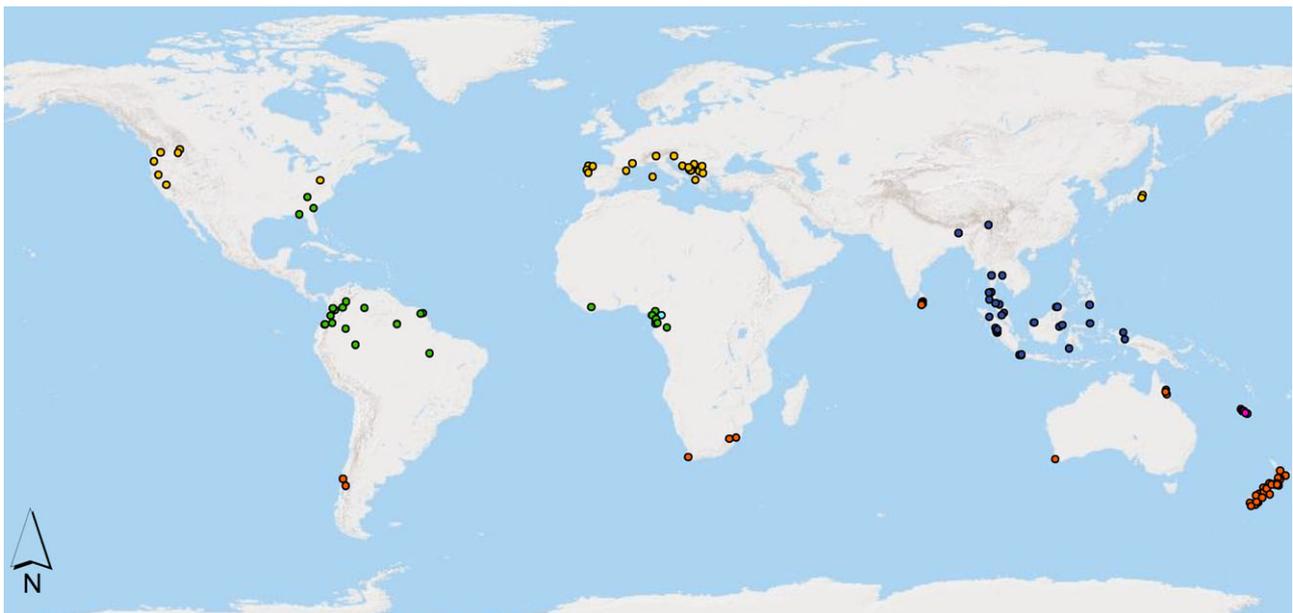
Figure 2. Distribution map of the sampled specimens for the molecular study (Table 2). Pettalidae are represented in red, Troglosironidae in purple, Ogoveidae in cyan, Neogoveidae in green, Sironidae in orange, and Stylocellidae in navy blue.

from the species in the Gulf of Guinea (Legg & Pabs-Garnon, 1989; Legg, 1990). A possible close relative to this species is included here, based on data from a female collected in Ivory Coast. The South American sampling has also been enriched considerably. The monotypic genus *Huitaca* is now represented by data from seven species all from Colombia, including the nominal *Huitaca ventralis* Shear, 1979. *Metagovea* is now represented by 13 specimens in 12 putative new species, including one from Guyana. These include the Colombian species identified as *Neogovea* in our previous studies, although they appear to be related to *Metagovea*. A large biogeographical gap in our previous studies was the easternmost distribution of the genus *Neogovea* (type species *Neogovea immsi* Hinton, 1938, from Amapá, Brazil). We now include putative representatives of this clade based on specimens collected in French Guiana and Guyana, including specimens from the recently described *N. virginie* Jocqué & Jocqué, 2011. With the exception of one specimen from Guyana clustering with *Metagovea*, these specimens group with the unidentified juvenile from Venezuela used in Boyer *et al*. (2007b) and with a species from the 'Tepuis' in Colombia, which we reassign here to the genus *Brasilogovea* Martens, 1969, previously considered a synonym of *Neogovea* (Shear, 1980; Giribet, 2000). Finally, we were able to include data on the monotypic genus *Canga* based on a specimen from its type locality (DaSilva *et al*., 2010). However, large areas of the Neotropics with known specimens of Neogoveidae remain unsampled in our molecular phylogeny, and they should be included in future studies (Benavides & Giribet, 2007: fig. 1).

MOLECULAR DATA

DNA extraction, amplification, and sequencing were performed as described in several of our previous studies on molecular systematics of Cyphophthalmi using the same markers (Schwendinger & Giribet, 2005; Boyer *et al*., 2007b; Boyer & Giribet, 2009; Sharma & Giribet, 2009a; Clouse & Giribet, 2010). We used the five markers as in these previous studies, including the nuclear ribosomal 18S and 28S rRNA, the nuclear protein-encoding histone H3, the mitochondrial ribosomal 16S rRNA, and the mitochondrial protein-encoding COI genes. For outgroups, we used seven noncyphophthalmid Opiliones from the suborders Eupnoi, Dyspnoi, and Laniatores (Table 2). Published sequence data from these studies and the novel data presented here are deposited in GenBank and are shown in Table 2.

All sequence files for each gene were prepared with MacGDE (Linton, 2005). 18S rRNA sequence data were divided into six fragments and it was available for 170 terminals. The 28S rRNA fragment was divided into ten regions and was available for 169 terminals. 16S rRNA was divided into eight fragments and was available for 127 terminals. All the ribosomal genes were submitted to direct optimization or to multiple sequence alignment for homology assignment. The 143 COI sequences, unlike in many other organisms, show clade-specific considerable sequence length variation, and hence the gene was divided into seven fragments and analyzed under dynamic homology (Wheeler, 2005) or submitted to multiple sequence alignment. The histone H3 data were available for 108 terminals and were treated as prealigned in all analyses because they show no length variation.

MORPHOLOGICAL DATA MATRIX

A morphological matrix of 62 characters was compiled for 161 taxa based in part on our previous studies (Giribet & Boyer, 2002; Giribet, 2003a; de Bivort & Giribet, 2004; Boyer & Giribet, 2007; de Bivort & Giribet, 2010), direct observation of specimens, mostly through scanning electron microscopy, and complemented by some new literature sources (Karaman, 2009). All 19 multistate characters were unordered. Spermatogenesis in Cyphophthalmi is a promising source of phylogenetic characters, as recently outlined by Alberti, Giribet & Gutjahr (2009; see also Juberthie & Manier, 1976; Juberthie, Manier & Boissin, 1976; Juberthie & Manier, 1978; Alberti, 1995, 2005), although taxon sampling is still sparse and these characters were not considered in this data set (G. Alberti & G. Giribet, unpubl. data). We did not have access to specimens of a few species that were included in the data matrix based entirely on literature sources. These have missing data for several characters, especially those observed through scanning electron microscopy, such as the prosomal sternal characters. These species include *Ankaratra franzi* Shear & Gruber, 1996, *Manangotria taolanaro* Shear & Gruber, 1996, and *Odontosiro lusitanicus* Juberthie, 1961. Similarly, several *Cyphophthalmus* Joseph, 1868 species, included in our molecular matrix, were not scored for several morphological characters because males were never available for examination, and their published descriptions do not include scanning electron micrographs of the relevant characters and their descriptions and illustrations are inadequate for scoring those features. Finally, a few species scored in the matrix are not known for one gender, and therefore the corresponding scorings are missing. The total number of missing cells was thus 1798 (17% of cells). In the present study, we were not able to use morphometrics, as we have done in previous studies (Clouse, 2010; de Bivort *et al*., 2010; de

Table 2. Specimen and collection data with GenBank accession numbers

	Voucher	Locality	Coordinates	18S rRNA	28S rRNA	16S rRNA	COI	H3
FAMILY PETTALIDAE								
Aoraki calcarobtusa westlandica	DNA101129	New Zealand	-41.78387, 172.36903	EU673626	DQ518038	DQ518070	EU673667	EU673703
Aoraki crypta	DNA101289	New Zealand	-37.53404, 175.74140	DQ518000	DQ518043	DQ518068	DQ518120	DQ518156
Aoraki denticulata denticulata	DNA100955	New Zealand	-42.09283, 171.34096	EU673618	EU673654	EU673584	DQ992309	EU673698
Aoraki denticulata major	DNA100959	New Zealand	-43.03408, 171.76464	EU673620	EU673656	EU673585	DQ992203	EU673700
Aoraki granulosa	DNA101841	New Zealand	-39.93478, 175.64046	DQ517999	DQ518039	DQ518071	–	–
Aoraki healyi	DNA100940	New Zealand	-41.08673, 174.13826	DQ518002	DQ518042	DQ518067	DQ518122	DQ518160
Aoraki inerma	DNA100966	New Zealand	-38.79686, 177.12472	EU673622	EU673658	–	–	EU673702
Aoraki longitarsa	DNA101806	New Zealand	-43.73666, 170.09222	EU673613	EU673652	–	DQ992313	EU673695
Aoraki cf. tumidata	DOC094	New Zealand	-39.667, 175.637*	EU673614	–	–	DQ992318	–
Aoraki sp.	DNA101126	New Zealand	-41.08708, 174.13709	EU673624	EU673659	–	DQ992319	–
Austropurcellia arcticosa	DNA100951	Queensland, Australia	-16.16610, 145.41560	DQ517984	DQ518023	–	DQ518111	DQ518147
Austropurcellia daviesae	DNA100947	Queensland, Australia	-17.24560, 145.64207	DQ517985	DQ518022	–	DQ518112	DQ518148
Austropurcellia forsteri	DNA100945	Queensland, Australia	-16.06151, 145.46217	DQ517983	DQ518021	DQ518064	DQ518110	DQ518146
Austropurcellia scoparia	DNA100946	Queensland, Australia	-16.59458, 145.27927	DQ517982	DQ518020	DQ518065	DQ518108	EU673678
Chileogovea oedipus	DNA100413	Chile	-41.50833, -72.61666	DQ133721	DQ133733	DQ518055	DQ133745	EU673672
Chileogovea sp.	DNA100490	Chile	-39.66666, -73.28333*	DQ133722	DQ133734	DQ518054	DQ133746	DQ518143
Karripurcellia harveyi	DNA101303	Western Australia	-34.49500, 115.97527	DQ517980	DQ518010	DQ518062	DQ518106	EU673694
Neopurcellia salmoni	DNA100939	New Zealand	-44.10780, 169.35527	DQ517998	EU673650	DQ518066	DQ825638	DQ518135
Parapurcellia monticola	DNA100386	South Africa	-29.05347, 29.38516	DQ518973	DQ518009	–	DQ518098	DQ518136
Parapurcellia silvicola	DNA100385	South Africa	-28.74421, 31.13763	AY639494	DQ518008	DQ518053	AY639582	EU673677
Pettalus thwaitesi	DNA101223	Sri Lanka	7.27251, 80.59333	EU673592	EU673633	EU673569	EU673666	EU673676
Pettalus sp.	DNA101282	Sri Lanka	7.38483, 80.81696	DQ825537	EU673632	–	DQ825636	DQ518137
Pettalus sp.	DNA101283	Sri Lanka	7.38483, 80.81696	DQ517974	DQ518016	DQ518056	DQ518100	DQ518138
Pettalus sp.	DNA101285	Sri Lanka	6.92517, 80.81949	DQ517976	DQ518017	DQ518058	DQ518102	DQ518139
Pettalus sp.	DNA101286	Sri Lanka	6.92517, 80.81949	DQ517977	DQ518013	DQ518059	DQ518103	DQ518140
Pettalus sp.	DNA101287	Sri Lanka	6.82359, 80.84996	DQ517978	DQ518014	DQ518060	DQ518104	DQ518141
Pettalus sp.	DNA101288	Sri Lanka	6.55551, 80.37030	DQ517979	DQ518015	DQ518061	DQ518105	DQ518142
Purcellia illustrans	DNA100387	South Africa	-33.98294, 18.42464	EU673589	EU673629	DQ518052	EU673665	EU673673
Rakaia antipodiana	DNA100957	New Zealand	-43.25145, 171.36761	DQ517988	DQ518031	DQ518072	DQ518115	DQ518151
Rakaia dorothea	DNA100943	New Zealand	-41.28163, 174.90961	DQ517990	DQ518033	DQ518077	DQ992331	–
Rakaia florensis	DNA101295	New Zealand	-40.83258, 172.96896	DQ517986	DQ518025	DQ518083	DQ518113	DQ518149
Rakaia lindsayi	DNA101128	New Zealand	-46.89327, 168.10398	DQ517995	DQ518027	DQ518081	DQ518118	DQ518154
Rakaia macra	DNA101808	New Zealand	-45.92000, 170.02805	EU673596	EU673636	EU673571	EU673668	–
Rakaia magna australis	DNA100962	New Zealand	-42.33225, 172.17126	EU673601	EU673640	EU673575	DQ992333	EU673684
Rakaia media	DNA101292	New Zealand	-39.93478, 175.64046	DQ517996	DQ518030	DQ518074	DQ518125	DQ518157
Rakaia minutissima	DNA101291	New Zealand	-39.41641, 175.21858	DQ517987	DQ518026	DQ518082	DQ518114	DQ518150
Rakaia pauli	DNA100968	New Zealand	-44.70073, 170.96557	DQ517992	DQ518032	DQ518073	EU673670	DQ518161
Rakaia solitaria	DNA101294	New Zealand	-41.46852, 175.44885	DQ517997	DQ518034	DQ518075	DQ518119	DQ518155
Rakaia sorenseni sorenseni	DNA100969	New Zealand	-46.10967, 167.69034	DQ517993	DQ518036	DQ518079	DQ518116	DQ518153
Rakaia sorenseni digitata	DNA100970	New Zealand	-46.58177, 169.20901	DQ517989	DQ518035	DQ518078	DQ518123	DQ518162
Rakaia stewartiensis	DNA100944	New Zealand	-46.89327, 168.10398	DQ517994	DQ518028	DQ518080	DQ518117	–
Rakaia uniloca	DNA101812	New Zealand	-41.22083, 173.43944	EU673599	EU673638	–	EU673671	EU673691
Rakaia sp.	DNA101297	New Zealand	-40.97595, 175.11747	EU673608	EU673647	EU673579	DQ992344	EU673689
Rakaia sp.	DNA101807	New Zealand	-45.90166, 169.46277	EU673606	EU673645	–	–	EU673681
Rakaia sp.	DNA100958	New Zealand	-43.80869, 173.02144	EU673597	EU673637	EU673573	DQ992349	–
Rakaia sp.	DNA101293	New Zealand	-40.85181, 174.93233	EU673610	EU673649	EU673581	DQ992322	EU673693
Rakaia sp.	DNA100954	New Zealand	-41.15757, 175.02168	EU673603	EU673642	EU673576	DQ992348	EU673686

Table 2. *Continued*

	Voucher	Locality	Coordinates	18S rRNA	28S rRNA	16S rRNA	COI	H3
FAMILY SIRONIDAE								
Cyphophthalmus corfuanus	DNA102111	Greece	39.61056, 20.33944	FJ946390	FJ946415	FJ946364	FJ946438	–
Cyphophthalmus duricorius	DNA100487	Slovenia	46.01667, 14.66667	AY639461	DQ513120	AY639526	AY639556	–
Cyphophthalmus ere	DNA100499	Serbia	43.83333, 20.05	AY639462	DQ825593	AY639527	AY639557	AY639444
Cyphophthalmus cf. *giorgjevici*	DNA100498	Macedonia	41.96667, 21.35	AY639464	DQ825587	AY639529	AY639559	–
Cyphophthalmus gordani	DNA100495	Montenegro	42.45, 19.26667	AY639467	DQ825592	AY639532	–	AY639446
Cyphophthalmus hlavaci	DNA102099	Croatia	43.41344, 16.91244	FJ946384	FJ946409	FJ946358	FJ946433	–
Cyphophthalmus markoi	DNA100497	Macedonia	41.41667, 22.26667	AY639469	AY639504	AY639534	AY639561	AY639447
Cyphophthalmus martensi	DNA100494	Montenegro	42.4, 18.76667	AY639471	DQ825589	AY639536	AY639563	AY639449
Cyphophthalmus minutus	DNA100493	Montenegro	42.65, 18.66667	AY639473	DQ825591	AY639537	AY639565	AY639450
Cyphophthalmus ognjenovici	DNA101039	Bosnia & Herzegovina	43.01667, 18.51667	AY639475	DQ825594	–	AY639567	AY639451
Cyphophthalmus rumijae	DNA100492	Montenegro	42.16667, 19.33333	AY639477	DQ825588	AY639539	AY639569	AY639453
Cyphophthalmus serbicus	DNA102098	Serbia	43.27917, 22.06389	FJ946383	FJ946408	FJ946357	FJ946432	–
Cyphophthalmus teyrovskyi	DNA100910	Montenegro	42.23333, 19.06667	AY639482	DQ513118	AY639544	AY639571	AY639454
Cyphophthalmus trebinjanus	DNA101038	Bosnia & Herzegovina	42.23333, 19.16667	AY639483	DQ513119	–	AY639572	–
Cyphophthalmus zetae	DNA100907	Montenegro	42.93333, 18.5	AY639485	AY639515	AY639546	AY639574	AY639456
Paramiopsalis eduardoi	DNA101878	Spain	43.41718, –8.06356	EU638284	EU638287	EU638281	EU638288	JF786415
Paramiopsalis ramulosus	DNA100459	Spain	42.31580, –8.48697	AY639489	DQ513121	AY639550	DQ825641	–
Paramiopsalis ramulosus	DNA103538	Portugal	41.56944, –8.14027	JF934956	JF934990	JF935023	JF786389	–
Paramiopsalis sp.	DNA104624	Spain	43.31968, –6.87282	JF934957	JF934991	JF935024	JF786390	JF786416
Parasiro coiffaiti	DNA101383	Sardinia, Italy	42.15251, 1.93039	AY918872	DQ513122	AY918877	DQ825642	AY918882
Parasiro minor	DNA103535	Sardinia, Italy	40.43047, 9.00948	JF934958	JF934992	JF935025	JF786391	–
Siro acaroides	DNA100488	Oregon, USA	44.5833, –123.5166*	AY639490	DQ513128	AY639551	DQ825643	–
Siro boyerae	DNA101614	Washington, USA	46.99221, –121.84641	DQ513139	DQ513125		DQ513112	–
Siro calaveras	DNA101623	California, USA	38.27744, –120.30543	DQ513146	DQ513133*			–
Siro exilis	DNA100489	Maryland, USA	39.4833, –79.4333	AY639491	DQ825585	–	AY639579	–
Siro cf. *kamiakensis*	DNA101611	Idaho, USA	47.74646, –116.70207	DQ513147	DQ513134*	–	DQ513115	–
Siro kamiakensis	DNA101613	Idaho, USA	46.86777, –117.15777	JF934959	JF934993			–
Siro rubens	DNA100457	France	44.08338, 3.58140	AY428818	DQ825584	–	DQ513111	–
Siro shasta	DNA101622	California, USA	41.06367, –122.36045	DQ513149	DQ513136*	–	–	–
Siro valleorum	DNA100461	Italy	45.9833, 9.8666*	AY639492	DQ513123	AY639552	AY639580	AY639457.1
Suzukielus sauteri	DNA101543	Japan	35.63440, 139.24122	DQ513138	DQ513116	DQ518086	DQ513108	DQ518166
Suzukielus sauteri	DNA101550	Japan	34.83333, 138.93166	DQ825541	DQ825583	DQ825615	DQ825640	DQ825520
FAMILY OGOVEIDAE								
Ogovea cameroonensis	DNA104617	Cameroon	3.64621, 11.29079	JF934960	JF934994	JF935026	JF786392	JF786417
FAMILY TROGLOSIRONIDAE								
Troglosiro aelleni	DNA100345	New Caledonia	–21.1833, 165.3059	AY639497	DQ825580	AY639555	AY639584	DQ518164
Troglosiro juberthiei	DNA100344	New Caledonia	–22.0500, 166.4667	DQ825540	EU887121	EU887077	EU887047	–
Troglosiro longifossa	DNA100867	New Caledonia	–22.3527, 166.9736	DQ518089	DQ825582	DQ518084	DQ825639	DQ518165
Troglosiro monteithi	DNA101580	New Caledonia	–21.6000, 165.7167	EU887101	EU887116	EU887074	EU887043	–
Troglosiro ninqua	DNA100577	New Caledonia	–21.7500, 166.1500	DQ518088	DQ825581	DQ518055	DQ518128	–
Troglosiro urbanus	DNA101710	New Caledonia	–22.1945, 166.5017	EU887102	EU887119	EU887073	EU887040	JF786340
Troglosiro wilsoni	DNA102324	New Caledonia	–22.1770, 166.5106	EU887107	EU887125	EU887075	EU887061	–

Table 2. *Continued*

Taxon	Voucher	Locality	Coordinates					
FAMILY STYLOCELLIDAE								
Fangensis insulanus	DNA100388, DNA101063	Thailand	7.885, 98.43694	GQ488337	DQ825551	–	–	GQ488181
Fangensis spelaeus	DNA100669	Thailand	14.29972, 98.98306	DQ133712	DQ825554	GQ488195	AY639583	AY639460
Leptopsalis lydekkeri	DNA101064	New Guinea, Indonesia	-2.71667, 134.5*	DQ133717	GQ488439	–	GQ488153	–
Leptopsalis novaguinea	DNA101510	New Guinea, Indonesia	-0.8333, 134.0333*	GQ488322	GQ488451	GQ488230	–	–
Leptopsalis sp.	DNA101514	Borneo, Malaysia	1.76667, 110.31667	GQ488317	GQ488435	DQ825611	GQ488178	GQ488114
Leptopsalis sp.	DNA101932	Java, Indonesia	-6.79833, 107.01583	GQ488264	GQ488382	GQ488206	GQ488144	GQ488121
Leptopsalis sp.	DNA101944, DNA101945	Java, Indonesia	-6.75694, 106.52333	GQ488267	GQ488385	GQ488226	GQ488146	GQ488123
Leptopsalis sp.	DNA101093, DNA100496	Thailand	6.67, 101.15*	GQ488283	GQ488402	GQ488221	GQ488137	–
Leptopsalis sp.	DNA101483	Malaysia	4.39694, 102.43056	DQ825532	GQ488454	DQ825610	GQ488182	GQ488128
Leptopsalis sp.	DNA101489	Malaysia	3.71639, 101.73861	DQ518095	GQ488456	DQ518087	GQ488184	–
Leptopsalis sp.	DNA101930	Java, Indonesia	-6.74, 107.01278	GQ488262	GQ488380	GQ488204	–	GQ488119
Leptopsalis sp.	DNA101937	Sulawesi, Indonesia	1.49028, 125.15278	GQ488298	GQ488422	GQ488211	GQ488167	GQ488132
Leptopsalis sp.	DNA101938	Sulawesi, Indonesia	-5.0425, 119.73556	GQ488299	GQ488359	GQ488212	GQ488168	GQ488133
Leptopsalis sp.	DNA102032	Sumatra, Indonesia	-0.10583, 100.66389	GQ488308	GQ488361	GQ488188	GQ488171	GQ488134
Leptopsalis sp.	DNA102033, DNA102048	Sumatra, Indonesia	0.34611, 100.06917	GQ488307	GQ488428	–	GQ488170	–
Leptopsalis sp.	DNA102039	Sumatra, Indonesia	-0.94583, 100.54361	GQ488250	GQ488433	GQ488190	GQ488175	GQ488136
Leptopsalis sp.	DNA102042	Sumatra, Indonesia	3.22111, 98.49722	GQ488314	GQ488434	GQ488213	GQ488176	GQ488135
Leptopsalis sp.	DNA102061	Sumatra, Indonesia	-0.47722, 100.35389	GQ488312	GQ488432	–	GQ488174	GQ488127
Leptopsalis sp.	DNA103250	Thailand	9.76667, 98.41389	GQ488278	GQ488394	GQ488192	GQ488155	–
Meghalaya sp.	DNA101094, DNA101500	Thailand	7.88528, 98.43722	DQ825534	GQ488352	–	GQ488158	–
Meghalaya sp.	DNA101494, DNA101506, DNA101765	Thailand	9.91806, 98.94278	DQ825530	GQ488398	–	DQ825632	–
Meghalaya sp.	DNA101767	Thailand	6.97, 100.10*	GQ488276	GQ488390	–	GQ488154	–
Meghalaya sp.	DNA102051	India	25.50778, 90.23167	GQ488261	GQ488379	–	–	GQ488118
Meghalaya sp.	DNA103242, DNA103243, DNA103244	China	27.68833, 98.27778	GQ488233	GQ488377	GQ488219	–	GQ488117
Meghalaya sp.	DNA103251	Thailand	9.76667, 98.41389	GQ488280	GQ488396	GQ488196	–	–
Meghalaya sp.	DNA103265	Thailand	14.25, 101.98*	GQ488239	GQ488392	–	–	–
Miopsalis sp.	DNA101519	Borneo, Indonesia	0.64, 117.09*	DQ825526	GQ488436	GQ488228	GQ488180	GQ488115
Miopsalis sp.	DNA103259	Borneo, Malaysia	5.81, 116.24*	GQ488260	GQ488375	GQ488193	GQ488142	GQ488116
Miopsalis sp.	DNA101468, DNA101950	Borneo, Indonesia	0.64, 117.09*	GQ488328	GQ488444	–	–	–
Miopsalis sp.	DNA101517	Borneo, Indonesia	1.06667, 117.83333*	DQ825527.1	DQ825564	–	GQ488179	DQ825508.1
Miopsalis sp.	DNA102032, DNA102053, DNA102058	Sumatra, Indonesia	-0.10583, 100.66389	GQ488305	GQ488425	–	–	–
Miopsalis sp.	DNA103249	Borneo, Malaysia	6.01, 116.53*	GQ488252	GQ488367	GQ488194	GQ488139	–
Miopsalis sp.	DNA103254	Borneo, Malaysia	1.75833, 110.32972	GQ488257	GQ488371	–	–	–
Miopsalis sp.	DNA104981	Mindanao, Philippines	6.48, 125.09*	HQ593868	HQ593869	–	HQ593870	HQ593871
FAMILY NEOGOVEIDAE								
Brasilogovea sp.	DNA101665	Colombia	0.17972, -72.62333	JF934963	JF935011	JF935028	JF786414	JF786430
'*Brasilogovea*' sp. Tobogan	DNA100869	Venezuela	5.65000, -67.63333	DQ825545	DQ825600	DQ825617	–	–

Table 2. *Continued*

	Voucher	Locality	Coordinates	18S rRNA	28S rRNA	16S rRNA	COI	H3
Canga renatae	DNA105680	Brazil	−6.41055, −50.32319	JF934964	JF934997	JF935029	JF786395	JF786420
Huitaca ventralis	DNA101674	Colombia	7.41667, −72.43333	JF934980	JF935014	–	JF786399	JF786421
Huitaca sp.	DNA101683	Colombia	3.55833, −76.58278	JF934979	JF935016	–	JF786396	–
Huitaca sp.	DNA101407	Colombia	5.77956, −73.45377	DQ518090	DQ825596	DQ518050	DQ518129	DQ518167
Huitaca sp.	DNA101681	Colombia	5.09956, −75.40594	JF934977	JF935015	JF935032	JF786397	JF786422
Huitaca sp.	DNA102150	Colombia	3.55833, −76.58278	JF934981	JF935012	JF935033	–	JF786423
Huitaca sp.	DNA104646	Colombia	3.55833, −76.58278	JF934982	JF935017	JF935030	JF786398	–
Huitaca sp.	DNA101671	Colombia	7.41667, −72.43333	JF934978	JF935013	JF935031	JF786400	JF786424
Metagovea sp.	DNA101680	Colombia	5.09542, −75.39075	JF934972	JF934999	JF935036	–	–
Metagovea sp.	DNA104647	Colombia	3.55833, −76.58278	JF934988	JF935003	JF935037	–	–
Metagovea sp.	DNA104648	Colombia	3.55833, −76.58278	JF934989	JF935004	JF935038	–	–
Metagovea sp.	DNA101408	Colombia	−4.04495, −69.98979	DQ825543	DQ825598	DQ825618	GQ912860	DQ825514
Metagovea sp.	DNA101410	Colombia	1.28500, −78.07367	DQ518091	DQ825597	JF935034	JF786401	DQ518168
Metagovea sp.	DNA101654	Colombia	1.25, −78.25*	JF934970	JF935000	JF935035	JF786402	JF786425
Metagovea sp.	DNA102151	Colombia	5.48583, −76.01667	JF934971	JF935001	–	JF786403	–
Metagovea sp.	DNA101685	Colombia	3.56889, −76.58861	JF934973	JF934998	–	–	–
Metagovea sp.	DNA101670	Colombia	1.61639, −76.10417	JF934984–5	JF935002	–	–	JF786426
Metagovea sp.	DNA101409	Colombia	1.28500, −78.07367	DQ825544	DQ825599	DQ825619	DQ825646	–
Metagovea sp.	DNA101642	Colombia	3.55833, −76.58278	JF934986	JF935006	JF935042	JF786404	–
Metagovea sp.	DNA101686	Colombia	3.56889, −76.58861	JF934987	JF935005	–	JF786408	–
Metagovea sp.	DNA105826	Guyana	1.33655, −58.96510	JF934983	JF935010	JF935041	DQ825645	DQ825513
Metasiro americanus	DNA101532	Florida, USA	30.56489, −84.95163	DQ825542	DQ825595	DQ825616	JF786393	JF786418
Metasiro americanus	DNA105644	South Carolina, USA	35.06231, −82.795	JF934961	JF934995	–	JF786394	JF786419
Metasiro americanus	DNA105645	South Carolina, USA	32.18923, −81.08	JF934962	JF934996	JF935027	JF786405	–
Neogovea virginie	DNA104823	French Guiana	4.19511, −52.14936	JF934974	JF935007	–	JF786406	–
Neogovea virginie	DNA105824	French Guiana	4.08813, −52.67520	JF934975	JF935008	JF935039	JF786407	–
Neogovea sp.	DNA105825	Guyana	1.38803, −58.94632	JF934976	JF935009	JF935040	JF786411	–
Parogovia gabonica	DNA104620	Gabon	0.50448, 12.79525	JF934969	JF935019	JF935047	–	–
Parogovia sironoides	DNA101059	Bioko, Equatorial Guinea	3.72570, 8.83828	DQ518092	DQ825606	DQ518051	DQ518131	DQ518169
Parogovia sironoides	DNA101061	Bioko, Equatorial Guinea	3.70284, 8.87520	DQ825550	DQ825607	JF935043	DQ825650	DQ825519
Parogovia cf. *sironoides*	DNA100462	Equatorial Guinea	2.18305, 9.80305	AY639493	DQ825603	–	–	AY639459
Parogovia cf. *sironoides*	DNA101053	Equatorial Guinea	1.65815, 10.31143	DQ825548	DQ825604	DQ825623	DQ825650	DQ825517
Parogovia cf. *sironoides*	DNA101056	Equatorial Guinea	1.44858, 9.78086	DQ825549	DQ825605	DQ825624	DQ825650	DQ825518
Parogovia cf. *sironoides*	DNA104619	Cameroon	2.74108, 9.88181	JF934967	JF935022	JF935045	JF786409	JF786428
Parogovia sp.	DNA101052	Equatorial Guinea	1.65815, 10.31143	DQ825546	DQ825601	DQ825620	DQ825648	DQ825516
Parogovia sp.	DNA101057	Equatorial Guinea	2.13119, 9.87187	DQ825547	DQ825602	DQ825621	–	DQ825515
Parogovia sp.	DNA104615	Cameroon	4.80084, 9.66326	JF934966	JF935021	JF935044	JF786410	JF786427
Parogovia sp.	DNA104618	Cameroon	2.74108, 9.88181	JF934968	JF935020	JF935046	JF786412	JF786429
Parogovia sp.	DNA105671	Ivory Coast	5.83333, −7.35000*	JF934965	JF935018	JF935048	JF786413	–
OUTGROUPS								
Protolophus singularis	DNA101033	California, USA		EF028095	EF028096	EF108581	EF108586	EF108592
Megalopsalis sp.	DNA100783	SI, New Zealand		EF108573	EF108576	EF108582	EF108587	EF108593
Hesperonemastoma modestum	DNA100312	Oregon, USA		AF124942	EF108577	EF108583	EF108588	EF108594
Dendrolasma parvulum	DNA100318	Japan		EF108574	EF108578	EF108584	EF108589	–
Equitius doriae	DNA100607	Australia		U37003	EF108579	–	EF108590	EF108595
Sandokan malayanus	DNA100321	Malaysia		EF108575	EF108580	EF108585	EF108591	EF108596

Asterisks indicate approximate coordinates.

Bivort & Giribet, 2010), as a result of the larger number of specimens based on literature sources and the lack of scanning electron micrographs of several species.

When selecting the morphological terminals, we attempted to maximize overlapping with the molecular matrix and also attempted to include the type species of each genus, with a few exceptions. All monotypic genera were also included, irrespective of whether molecular data were available or not. Monotypic genera not represented by molecular data are *Ankaratra* Shear & Gruber, 1996, *Iberosiro* de Bivort & Giribet, 2004, *Manangotria* Shear & Gruber, 1996, *Marwe* Shear, 1985, *Odontosiro* Juberthie, 1961, *Speleosiro* Lawrence, 1931, and *Stylocellus*. Similarly, *Shearogovea mexasca*, now not considered as a member of Neogoveidae or *Neogovea* (Benavides & Giribet, 2007; Giribet, 2011), is not represented by molecular data but was included in the combined analysis.

When a species was represented by multiple molecular terminals, the morphological data matrix was replicated so all molecular terminals were represented by the same morphological codings. This applies to the three populations of *Metasiro americanus* (Davis, 1933), the two specimens of *Parogovia sironoides* Hansen, 1921 and four specimens of *P.* cf. *sironoides*, the two specimens of *Metagovea* sp. (DNA104648 and DNA104647), two specimens of *Neogovea virginie*, and two specimens of *Suzukielus sauteri* (Roewer, 1916).

The annotated morphological data matrix has been deposited in Morphobank (morphobank.org) with accession number P199 (http://morphobank.org/permalink/?P199).

PHYLOGENETIC ANALYSIS: DYNAMIC HOMOLOGY UNDER PARSIMONY

Parsimony analysis under direct optimization (Wheeler, 1996) used the software POY, version 4.1.2 (Varón, Sy Vinh & Wheeler, 2010) on six processors on a Quad-Core Intel Xeon 3 GHz Mac Pro or on 40 processors in the Odyssey cluster at Harvard University FAS Research computing facility. Timed searches (multiple Wagner trees followed by SPR + TBR + ratchet and tree fusing) of 6–12 h each were run for the combined analyses of all molecules under six analytical parameter sets (see below). Two additional rounds of sensitivity analysis tree fusing (SATF) (Giribet, 2007a), taking all input trees from the previous round of analyses, were conducted for the combined analysis of molecules under the multiple parameter sets evaluated. These were also 6-h timed searches, and the results of these were plotted to check for stability in the results. Once a parameter set stabilized and the optimal result was found multiple times, we stopped that inquiry but continued with additional rounds of searches for those parameter sets that continued improving or that found the optimal solution only once. The results of these analyses are shown in Table 3.

Because a broad parameter space has already been explored in detail in earlier studies (Boyer *et al.*, 2007b), we restricted the dynamic homology analyses to six parameter sets, named 111, 121, 211, 221, 3221, and 3211. Parameter set 3221 (indel opening cost = 3; indel extension cost = 1; transversions = transitions = 2) has been favoured in many analyses and has been justified philosophically as the best way of analyzing data under direct optimization (De Laet, 2010). In addition, we explored a parameter set, named 3211, where transversions and transitions receive different costs (indel opening cost = 3; indel extension cost = 1; transversion cost = 2; transition cost = 1), extending the idea of mixed-parameter sets of Sharma *et al.* (2011). Four other parameter sets 111, 121, 211, and 221, optimal in the analyses of Boyer *et al.* (2007b) and aiming to limit the difference between indel costs and transformation costs (Spagna & Álvarez-Padilla, 2008), were explored. To calculate the $_W$ILD (Wheeler, 1995; Sharma *et al.*, 2011) each individual partition, or the combination of the two nuclear ribosomal RNA partitions, were run with a

Table 3. Search strategy and tree length stabilization after subsequent rounds of sensitivity analysis tree fusing (TF*N*) for each parameter set

	TF4	TF5	TF6	TF7	TF8	TF9
111	27101	27074	27074	–	–	–
121	41849	41773	41773	–	–	–
211	28975	28944	28940	28940	–	–
221	45211	45179	45131	45118	45115	45115
3221	55982	55744	55729	55729	–	–
3211	43121	42874	42854	42854	–	–

111 and 121 stabilized after five rounds of tree fusing; 221 stabilized after eight rounds of tree fusing

Table 4. Tree lengths for different data partitions (rib, nuclear ribosomal genes; coi, cytochrome *c* oxidase subunit I; 16s, 16S rRNA; h3, histone H3; mol, all molecular partitions) analyzed and incongruence length differences (ILD) between the data sets

	rib	coi	16s	h3	Mol	wILD
111	5852	12315	6857	1449	27074	0.02220
121	8846	18664	11350	1974	41773	0.02248
211	6659	12502	7692	1449	28940	0.02205
221	10312	18890	12897	1974	45115	0.02310
3211	9268	18810	11861	1967	42851	0.02205
3221	*12212*	*24996*	*14397*	*2898*	*55713*	*0.02172*

Parameter set *3221* (in italics) minimizes the ILD value.

similar search strategy as described above with a 2-h timed search. The resulting $_W$ILD values are shown in Table 4.

A jackknife resampling analysis (Farris *et al*., 1996) with 1000 replicates and a probability of deletion of each character of 0.36 was applied to assess nodal support. Because resampling techniques may be meaningless under dynamic homology, different strategies can be applied. Dynamic characters can be converted to a static set, although this tends to inflate support values because it is based on the implied alignment that favours the topology. Instead, we resample characters that were static a priori (morphology and pre-aligned protein-encoding genes), as well as fragments of the dynamic characters by both using the number of fragments (eight fragments for 16S rRNA, six fragments for 18S rRNA, and ten fragments for 28S rRNA), as well as the command auto_sequence_partition, which evaluates each predetermined fragment. If a long region appears to have no indels, then the fragment is broken inside that region.

PHYLOGENETIC ANALYSIS: PROBABILISTIC APPROACHES

Maximum likelihood (ML) analyses were conducted on static alignments, which were inferred as follows. Sequences of ribosomal genes were aligned using MUSCLE, version 3.6 (Edgar, 2004) with default parameters, and subsequently treated with GBLOCKS, version 0.91b (Castresana, 2000) to cull positions of ambiguous homology. For these genes, indels were permitted within blocks. Sequences of the protein-encoding genes COI and histone H3 were aligned using MUSCLE, version 3.6 with default parameters as well, although alignments were confirmed using protein sequence translations before treatment with GBLOCKS, and no gaps were permitted within blocks (COI has length variation, so these regions were excluded in GBLOCKS). The size of

data matrices for each gene before and subsequent to treatment with GBLOCKS is provided in the Appendix (Table A1).

ML analysis was conducted using RaxML, version 7.2.7 (Stamatakis, 2006) on 40 CPUs of a cluster at Harvard University, FAS Research Computing (http://rc.fas.harvard.edu/faq/odyssey). For the maximum likelihood searches, a unique GTR model of sequence evolution with corrections for a discrete gamma distribution (GTR + Γ) was specified for each data partition, and 500 independent searches were conducted. Nodal support was estimated via the rapid bootstrap algorithm (1000 replicates) using the GTR-CAT model (Stamatakis, Hoover & Rougemont, 2008), through the CIPRES, version 3, gateway, using the Abe Dell Intel 64 Linux teragrid cluster housed at the National Center for Supercomuting Applications (University of Illinois). Bootstrap resampling frequencies were thereafter mapped onto the optimal tree from the independent searches.

ESTIMATION OF DIVERGENCE TIMES

Ages of clades were inferred using BEAST, version 1.6.1 (Drummond *et al*., 2006; Drummond & Rambaut, 2007). We assigned the best fitting models (a GTR model of sequence evolution with corrections for a discrete gamma distribution and a proportion of invariant sites, GTR + Γ+ I) selected by MODELTEST, version 3.7 (Posada & Crandall, 1998; Posada, 2005) to each partition. Protein-encoding genes were partitioned into two sets by codon positions, separating third codon positions from the set of first and second positions. An uncorrelated lognormal clock model was inferred for each partition, and a Yule speciation process was assumed for the tree prior. We selected the uncorrelated lognormal model because its accuracy is comparable to an uncorrelated exponential model, although it has narrower 95% highest posterior density (HPD) intervals. Additionally, the

variance of the uncorrelated lognormal model can better accommodate data that are already clock-like (Drummond *et al*., 2006). Priors were sequentially optimized in a series of iterative test runs (data not shown). Markov chains were run for 50 000 000 generations, sampling every 1000 generations. Convergence diagnostics were assessed using TRACER, version 1.5 (Rambaut & Drummond, 2007).

Fossil taxa were used to calibrate divergence times. We constrained the age of Eupnoi to 410 Mya using the Devonian harvestman *Eophalangium sheari* [Dunlop *et al*. 2004 [Dunlop *et al*., 2003; 2004 (for 2003)]; a normal distribution with a standard deviation of 5 Myr was applied to this node to account for uncertainty in estimation of fossil age. Dyspnoi were constrained using a normal distribution with a mean of 300 Mya and a standard deviation of 10 Myr, on the basis of the Carboniferous fossils *Eotrogulus fayoli* Thevenin, 1901 and *Nemastomoides elaveris* Thevenin, 1901 (Dunlop, 2007).

We explored constraining the family Stylocellidae using the Early Cretaceous Burmese amber fossil *Palaeosiro burmanicum* Poinar, 2008 (Poinar, 2008)[1]. We used a gamma distribution with shape parameters $(\alpha, \beta) = (8, 14)$, and an offset of 105 Myr for the diversification of Stylocellidae; such a prior distribution establishes a floor in the age of stylocellids (105 Mya), at the same time enabling estimates of diversification as early as the Late Permian, in accordance with previous estimates (Boyer *et al*., 2007b; Clouse & Giribet, 2010). However, because the inclusion of this last constraint did not affect the age estimate of Stylocellidae, we ultimately did not include it in the analysis.

ANCESTRAL AREA RECONSTRUCTION

Likelihood analysis of ancestral area reconstruction was conducted using the software LAGRANGE (Ree *et al*., 2005; Ree & Smith, 2008). We divided the dated tree from BEAST analysis into three parts for analytical tractability: (1) the Pettalidae subtree; (2) the (Troglosironidae + Ogoveidae + Neogoveidae) subtree; and (3) the (Sironidae + Stylocellidae) subtree. For each subtree, we implemented stratified dispersal constraint matrices for multiple spans of time for the relevant areas inhabited by the constituent taxa of each subtree. Geological events used to delimit the

[1]*Palaeosiro burmanicum* Poinar, 2008 was placed within Sironidae in the original description based on the lack of a sternal apophysis with gland pores and dentition on the tarsal claw of leg II, although these only rule out placement within Troglosironidae and Neogoveidae. Moreover, the shape and position of the ozophores, the presence of eyes, the carina of the anal plate (similar to some *Fangensis* Schwendinger & Giribet, 2005), and the collecting locality of the fossil, are all consistent with an early diverging lineage of Stylocellidae.

time spans are *sensu* Sanmartín & Ronquist (2004) and Hall (2002). The maximum number of areas in ancestral ranges was held at two (this convention reflects empirical observations of Cyphophthalmi species, the majority of which are narrowly distributed endemics), and dispersal constraints were set to 1.0 (if landmasses were connected), 0.1 (if landmasses were disjunct) or 0 (if landmasses did not exist). Areas and geological intervals for each subtree are indicated in the Appendix Table A2 (the Python scripts specifying dispersal constraint matrices are available upon request from the authors).

HABITAT SUITABILITY AND DISTRIBUTION MODELLING

To generate predictions of habitat suitability and potential lineage distributions, habitat suitability models (HSMs) of the major lineages of Cyphophthalmi were reconstructed using the 19 bioclimatic variables of Hijmans *et al*. (2005: http://www.worldclim.org/). These variables provide a summary of the monthly temperature and precipitation worldwide. These variables are well documented and are widely used in studies relaying on niche and distribution modelling (Evans *et al*., 2009; Smith & Donoghue, 2010). By contrast to the raw temperature and precipitation data, they do provide biologically relevant information. We have used all 19 variables at 10 arc minutes resolution. In addition, analyses with a subset of the environmental variables representing only the most important variables were performed (thus reducing the dimensionality of the analyses and the risk of over fitting) and the results obtained were compared. To evaluate the variables significance, we used jackknife (as implemented in MAXENT).

HSMs were built using the maximum entropy algorithm implemented in MAXENT, version 3.3.3a (Phillips, Anderson & Schapire, 2006; Phillips & Dudik, 2008). Maximum entropy has shown a high performance score in comparison with other methods (Araujo & Rahbek, 2006) and also allows working with fewer data points (Pearson *et al*., 2007). The total number of unique localities with occurrence observations used for the modelling of habitat suitability was: Pettalidae, $N = 107$; Sironidae, $N = 60$; Stylocellidae, $N = 127$; and Sternophthalmi, $N = 90$. To evaluate the performance of the model, cross-validation as implemented in MAXENT (ten replicates) was used in all runs.

To test the sensitivity of the results to the modelling algorithm, we have run the same set of analysis using the simpler BIOCLIM (Nix, 1986) profile method as implemented in openModeller, version 1.1.0 (de Souza Muñoz *et al*., 2011). Climatic envelopes' extent and distribution were modelled world-

Figure 3. Phylogenetic tree based on the parsimony direct optimization analysis of molecular data under parameter set 3221 (55 713 weighted steps). Clade colours correspond to those in Fig. 2. Navajo rugs indicate monophyly (black) or non-monophyly (white) of a given node under the parameter set specified in the legend. Numbers above nodes indicate jackknife support values. ▶

wide to compare the actual linage distributions with the distribution of potentially suitable climates.

The software package ENMTools, version 1.3 (Warren, Glor & Turelli, 2010) was used to access climatic envelopes' differentiation. ENMTools implements the I, Schoener's D and relative rank metrics to compare models predictions (Schoener, 1968; Warren, Glor & Turelli, 2008). The three indices measure similarity of predicted habitat suitability distributions and range from 0, indicating no overlap, to 1, indicating complete overlap. In addition, habitat suitability score differences were evaluated by comparing the similarity indices (models overlap) for the models built from the actual occurrences of the two species to a null distribution generated by nonparametric resampling. Comparisons were performed using the niche identity test (Warren *et al*., 2008) implemented in ENMTools.

RESULTS

Analysis of the combined molecular data matrix under selected parameter sets for direct optimization resulted in topologies that agree on several basic aspects of cyphophthalmid phylogeny, including monophyly of the suborder, a sister group relationship of Pettalidae to all other families, and a clade containing all members of the families Troglosironidae, Ogoveidae, and Neogoveidae. All parameter sets also resulted in very similar $_{W}$ILD numbers, with 3221 being slightly favoured above all others ($_{W}$ILD = 0.02172; the worst parameter set being 121, with $_{W}$ILD = 0.02248). Stabilization of parameter set 3221 occurred after nine rounds of tree fusing. The optimal tree, along with the Navajo rugs (Giribet, 2003b) for the familial monophyly and relationships, is presented in Figure 3. A clade containing the families Sironidae and Stylocellidae is also found under most analytical conditions (Fig. 3).

Monophyly of Pettalidae, Troglosironidae, Stylocellidae, and Ogoveoidea (= Ogoveidae + Neogoveidae) is supported under every analyzed parameter set, as are many internal clades within the families Stylocellidae, Sironidae, and Neogoveidae. However, Sironidae is not monophyletic under any parameter set when combining all data (Sironidae is monophyletic when nuclear ribosomal genes are analyzed alone). In this case, a clade containing the genera *Siro*, *Paramiopsalis*, and *Cyphophthalmus* is stable to parameter variation, although *Parasiro* and

Suzukielus often appear at the base of Stylocellidae, or as sister to a clade including the families Stylocellidae, Troglosironidae, Ogoveidae, and Neogoveidae (parameter set 3211). The North American *Siro* and the European *Siro* form reciprocally monophyletic groups and this clade is sister to *Paramiopsalis* + *Cyphophthalmus*. In the case of Neogoveidae, most parameter sets find *Metasiro* to be the sister genus to all other neogoveids but, under parameter sets 111 and 211, *Ogovea* appears as sister to the African genus *Parogovia*, both forming the sister clade to *Metasiro*. These are the only parameter sets that find monophyly of the South American neogoveids, with *Canga* as sister genus to all other South American genera. All other parameter sets instead support monophyly of Neogoveidae, *Metasiro* as the sister genus to all other species, the Brazilian genus *Canga* as sister to the African genus *Parogovia*, and the stable relationship of ((*Brasilogovea*, *Neogovea*) (*Huitaca*, *Metagovea*)). Relationships of Stylocellidae are well resolved, as: (*Fangensis* (*Meghalaya* (*Miopsalis*, *Leptopsalis*))). Although all pettalid genera are supported, their relationships remain unstable to parameter set variation, and stable are only the sister group relationships of *Purcellia* to *Chileogovea* Roewer, 1961 and of *Karripurcellia* Giribet, 2003 to *Pettalus*. Two genera appear as candidate sister groups to all other pettalids, the South African genus *Parapurcellia* Rosas Costa, 1950 or the north-eastern Australian endemic *Austropurcellia* Juberthie, 1988. Jackknife support values for the pettalid generic relationships are, for the most part, below 50%.

The maximum likelihood analysis resulted in a tree topology with $\ln L = -103\,563.078879$. The likelihood tree topology (Fig. 4) is largely comparable to results from parsimony analyses but notably recovers a monophyletic Sironidae (i.e. including the genera *Parasiro* and *Suzukielus*), albeit with low nodal support (BS = 44%). As in the direct optimization optimal tree, *Parapurcellia* is sister to all other pettalid genera, and *Purcellia* + *Chileogovea* form a supported clade (66% bootstrap support; BS), whereas *Karripurcellia* and *Pettalus* form a clade without significant nodal support. No other generic relationships find high support. Troglosironidae is sister to Ogoveoidea (84% BS), and the structure of Neogoveidae is almost identical to that of the optimal direct optimization tree, with the exception that *Brasilogovea* is here monophyletic (the sequences for one terminal
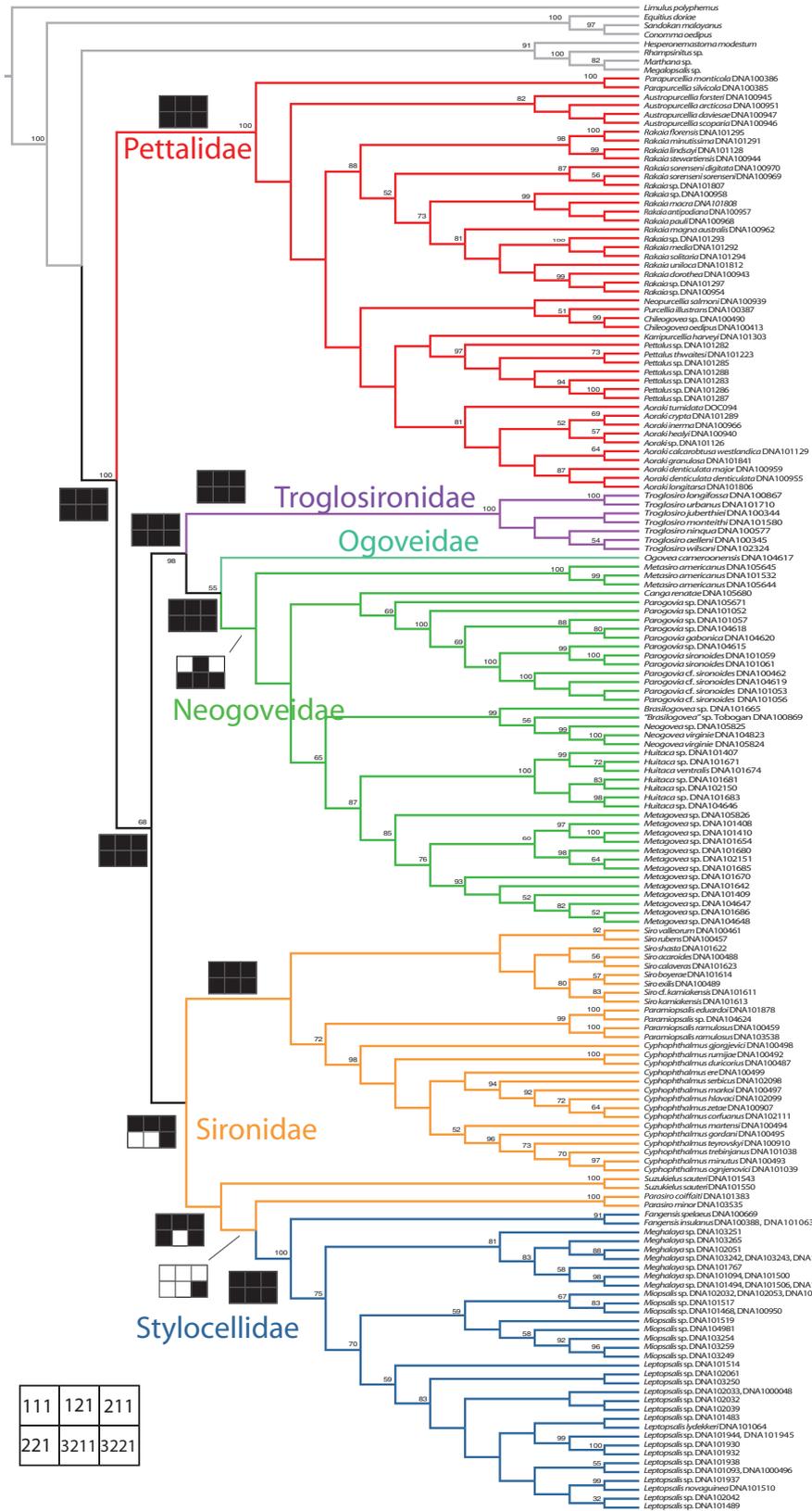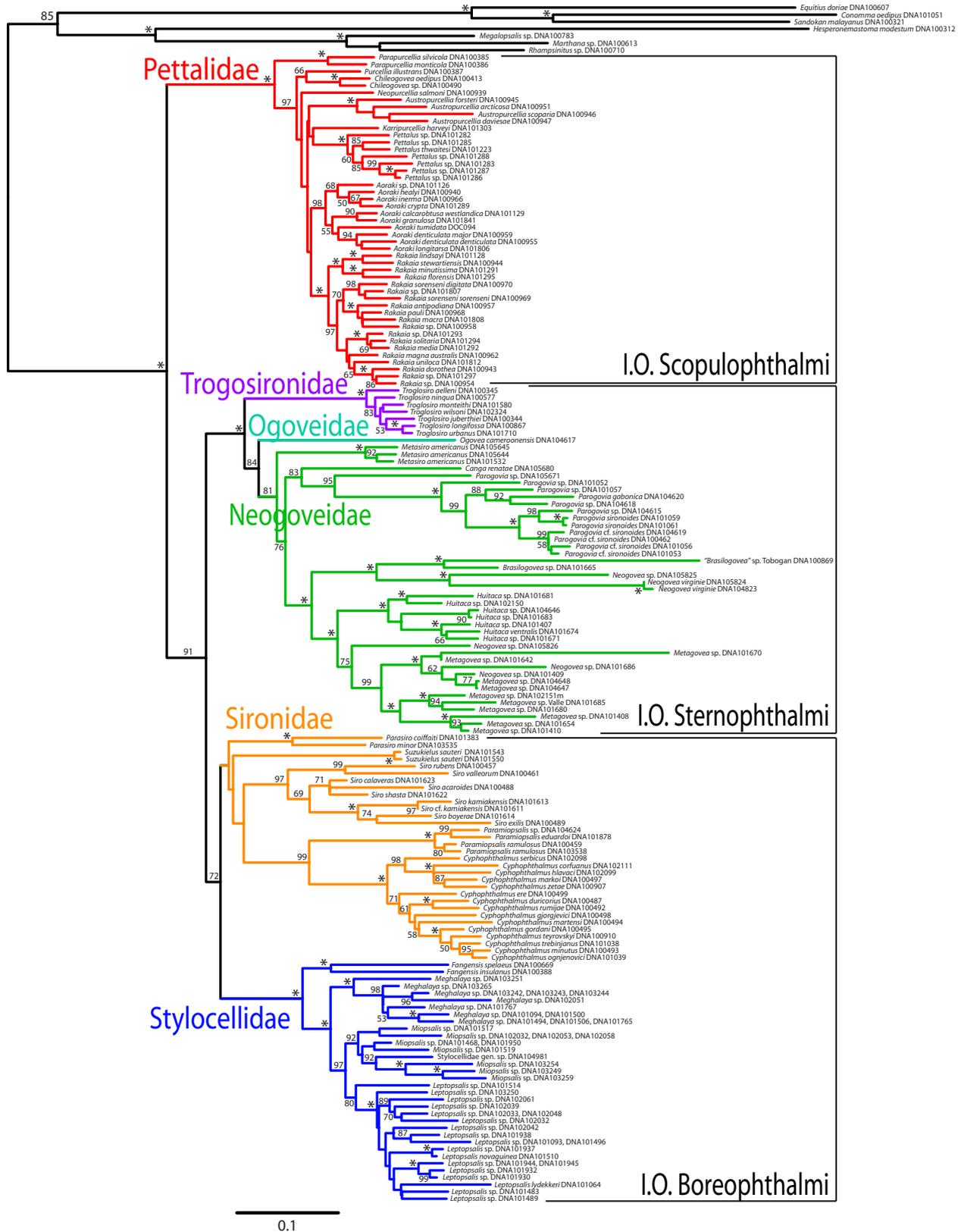
Figure 4. Single most likely tree (ln*L* = −103 563.078879) for the combined molecular data set aligned using MUSCLE and subsequently trimmed with GBLOCKS and analyzed in RAxML under GTR + Γ. Clade colours correspond to those in Fig. 2. Bootstrap support values are represented above each node; asterisks indicate 100% bootstrap value.

are based on a juvenile specimen, so the assignment to this genus is tentative). Within Sironidae, *Parasiro* is sister to all other genera, followed by *Suzukielus*, although bootstrap support for these basal nodes is low, as is the clade including the remaining sironid genera. In this case, there is also reciprocal monophyly of the European and North American *Siro*, and these form the sister group of *Paramiopsalis* + *Cyphophthalmus*. Structure of the genera within Stylocellidae matches that of the direct optimization analyses.

The run of BEAST reached stationarity after 10 000 000 generations; 20 000 000 generations were discarded as burn-in. The tree topology recovered by BEAST (Fig. 5) is almost identical to that of the parsimony analysis under the parameter set 3221, with *Parasiro* and *Suzukielus* forming a paraphyletic grade at the base of Stylocellidae, although posterior probabilities for the corresponding nodes are low (0.788 and 0.880, respectively). In all other aspects, it also resembles the topology of the maximum likelihood analysis, especially in the internal relationships among the pettalid genera.

The diversification of Cyphophthalmi is estimated at approximately 332 Mya (95% HPD: 297–362 Mya). Diversification times for the described families of Cyphophthalmi are estimated as: Neogoveidae, 236 Mya (95% HPD: 208–266 Mya); Pettalidae, 183 Mya (95% HPD: 148–218 Mya); Sironidae (excluding *Parasiro* and *Suzukielus*), 278 Mya (95% HPD: 243–311 Mya); Stylocellidae, 167 Mya (95% HPD: 140–195 Mya); and Troglosironidae, 57 Mya (95% HPD: 40–73 Mya). Ogoveidae, represented by a single exemplar, diverged from Neogoveidae 261 Mya (95% HPD: 231–292 Mya), and Troglosironidae diverged from Ogoveoidea 279 Mya (95% HPD: 248–311 Mya). These results largely corroborate previous estimates of divergence times (Boyer *et al.*, 2007b; Giribet *et al.*, 2010), with the exception of Stylocellidae, the diversification of which is recovered as younger than previously reported (Clouse & Giribet, 2010). Although some species represented by multiple terminals are young (e.g. *Suzukielus sauteri*, *Neogovea virginie*, *Parogovia sironoides*), *Metasiro americanus* is an old species, perhaps reflecting the existence of cryptic species along its range.

All probabilistic approaches recognize a clade of *trans*-Tasman Cyphophthalmi (the Australian and New Zealand genera), although none of these landmasses or their constituent terranes appears monophyletic (Fig. 6). The ancestral area reconstruction of this clade is ambiguous, with the highest probability for an origin in the Australian plate of New Zealand. The ancestral area of the family shows more ambiguity, the three most likely scenarios being a mixed South Africa/New Zealand Australian plate

(P = 0.291), South African (P = 0.207) or mixed South Africa/Sri Lankan (P = 0.194). The ancestral area reconstruction of the clade including the three families with sternal opisthosomal gland openings (Fig. 7) is mostly West African/New Caledonian (P = 0.787), with the ogoveoid families being most likely West African (P = 0.662) or mixed between West Africa and the south-eastern USA (P = 0.206), the latter being once connected to West Africa. A South American (Amazonian) origin of the family Neogoveidae receives little support.

COMBINED ANALYSIS OF MOLECULES AND MORPHOLOGY

The position of morphology-only taxa was unstable in the first rounds of analyses, which (for example) did not group the two *Ogovea* species, one represented by morphology only, whereas the other one was represented by molecules and morphology, despite being almost identical for the morphological data matrix. This appears to be a problem of the Wagner addition, as designed in most phylogenetic software, and was resolved by fusing a jackknife tree and a first tree obtained during a normal search, as described above. The resulting trees of each subsequent analysis were then fused to the previous pool of trees until results (topology and tree length) stabilized. The combined analysis of molecules and morphology in POY required eight rounds of tree fusing until stabilizing in a tree length of 56 984 weighted steps and finding three trees differing only in the position of some of the morphology-only taxa (Fig. 9).

The overall topology is very similar to those of the analyses with molecular data only, with a few exceptions, and lowered jackknife support values. Pettalidae is monophyletic (63%), and includes both *Speleosiro* and *Manangotria* from the morphology-only taxa. *Speleosiro* appears as sister to *Purcellia* and *Managotria* is sister to *Karripurcellia*, although these relationships, as with most other intergeneric pettalid relationships, receive low support. *Ankaratra* does not appear within Pettalidae and, instead, is basal to the clade containing Sironidae and Stylocellidae.

Troglosironidae appears as sister to Ogoveoidea, although this tree differs from all previous trees in that Neogoveidae is paraphyletic with respect to *Ogovea*, which is sister to *Parogovia*, constituting an African clade, sister to all the American species, with *Canga* as the sister group to *Metasiro*, and this clade being sister to the remaining neogoveids [56% jackknife frequency (JF)]. The type species and morphology-only species of *Neogovea* and *Brasilogovea* appear in a clade, although there is little correspondence between the complete taxa and those
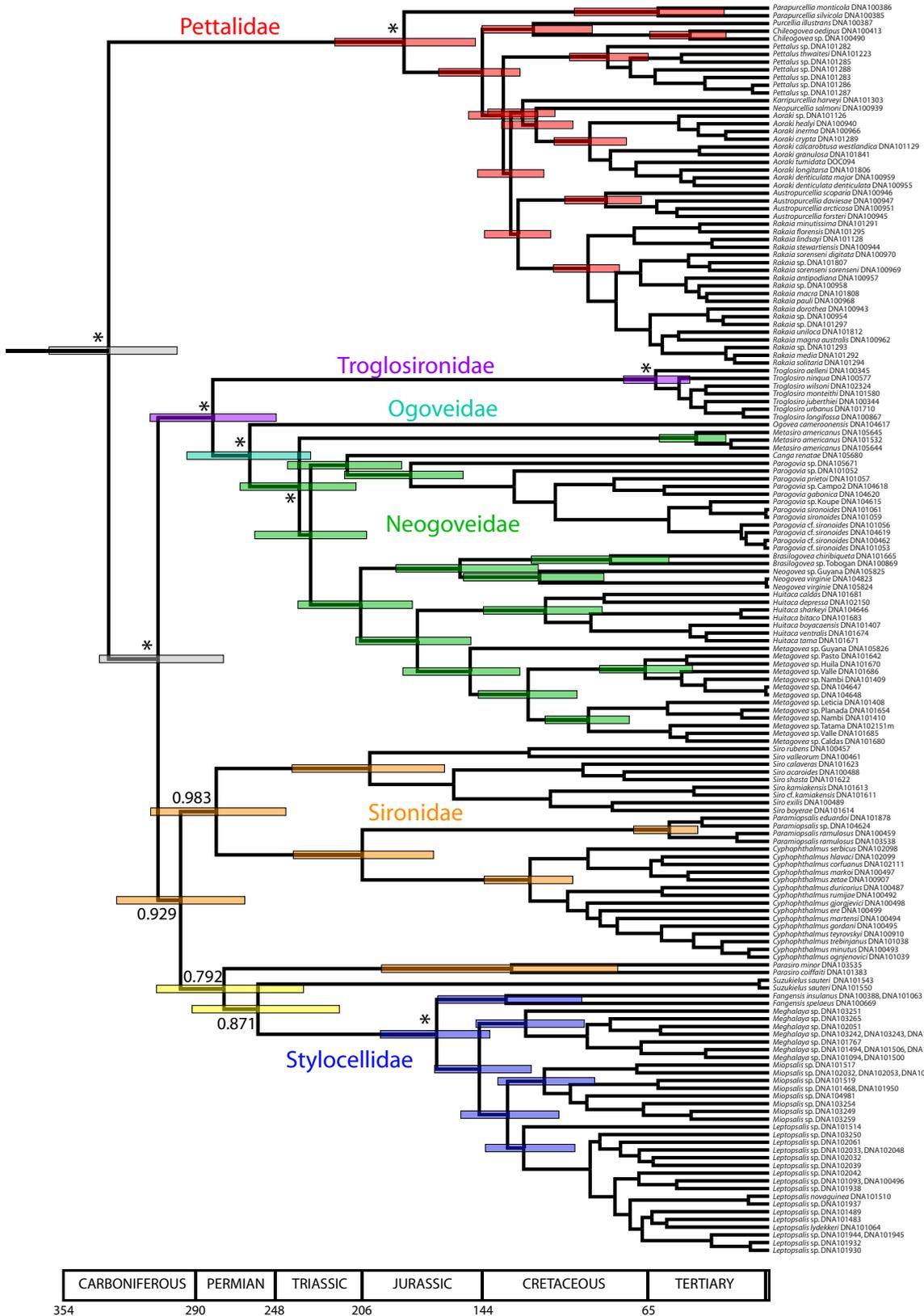
Figure 5. Evolutionary time-tree of Cyphophthalmi inferred from BEAST analysis of all molecular data. Clade colours correspond to those in Fig. 2. Coloured bars indicate 95% highest posterior density (HPD) intervals for nodes of interest. Number on nodes indicate posterior probabilities; asterisks indicate posterior probability of 1.00.
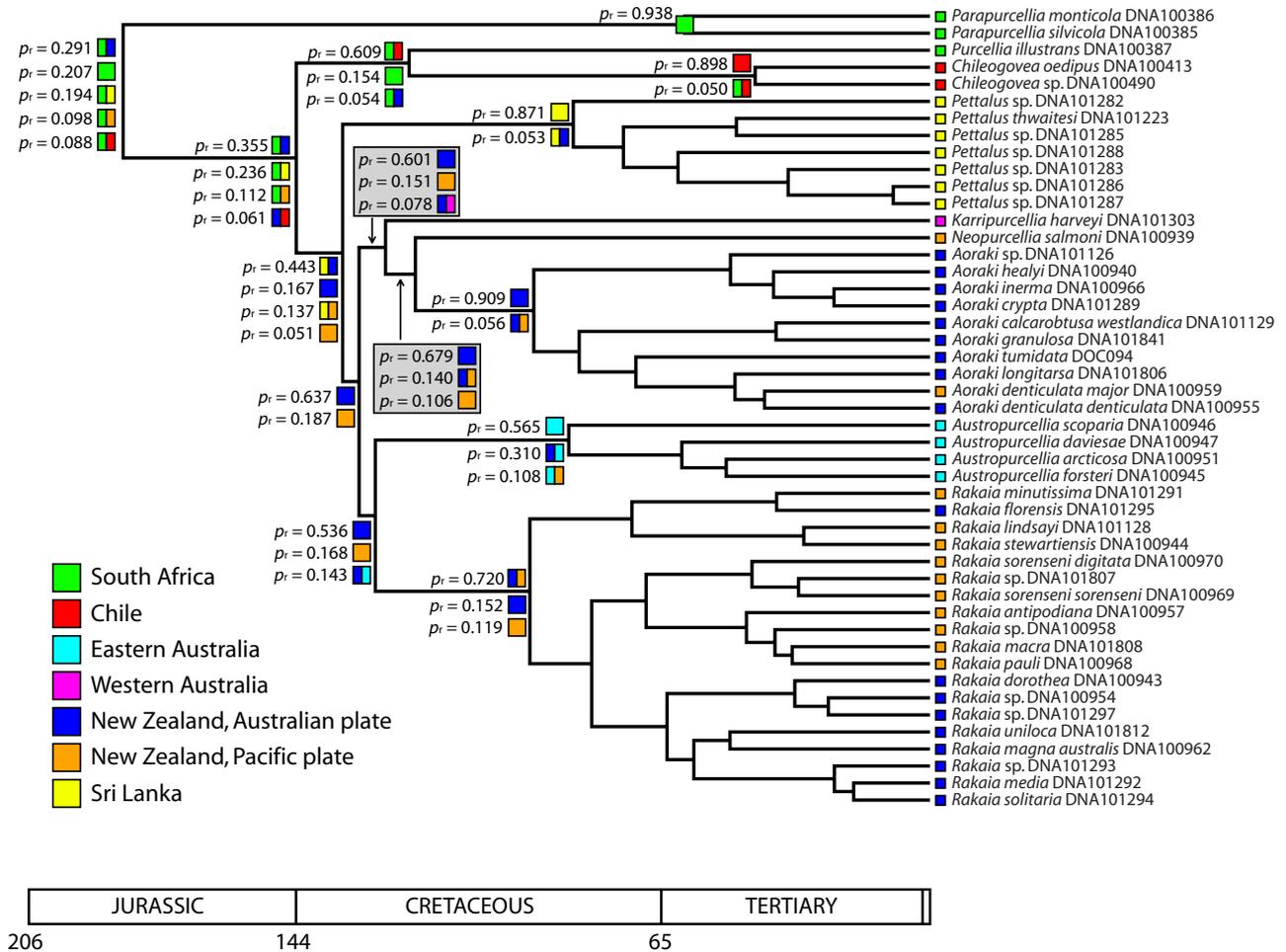
Figure 6. Ancestral range reconstructions for Pettalidae inferred by Lagrange analysis, using stratified models. Coloured squares at terminals indicate ranges occupied by sampled species. Coloured squares on nodes indicate ranges reconstructed for hypothetical ancestors. Numbers on nodes indicate relative probability of ranges reconstructed.

represented by morphology only (i.e. *Neogovea* and *Brasilogovea* are not reciprocally monophyletic).

Ankaratra and *Shearogovea* form a grade at the base of the Sironidae – Stylocellidae clade, with Sironidae paraphyletic, as in the prior POY and BEAST analyses. *Marwe* and *Iberosiro* form a clade with *Paramiopsalis*, and *Odontosiro* forms a clade with *Parasiro*. Stylocellidae is monophyletic (63% JF), including the morphology-only species *Stylocellus sumatranus* Westwood, 1874, *Meghalaya annandalei* Giribet, Sharma & Bastawade, 2007, *Miopsalis pulicaria* Thorell, 1890, and *Leptopsalis beccarii* Thorell, 1882–1883. *Stylocellus sumatranus*, the type species of *Stylocellus*, appears nested within the molecular *Meghalaya* clade; *Meghalaya annandalei*, the type species of *Meghalaya*, appears unresolved at the base of the molecular *Leptopsalis* clade; *Miopsalis pulicaria* and *Leptopsalis beccarii*, the type species of their respective genera, appear nested deep within

the clade *Leptopsalis*. Although the stylocellid results make little sense, this may be a result of the lack of discrete characters useful for resolving their phylogenetic relationships (see below).

A NEW CLASSIFICATION SYSTEM FOR CYPHOPHTHALMI

Based on the results reported above, we provide a new classification system for Cyphophthalmi, introducing three new infraorders: Scopulophthalmi **new clade**, Sternophthalmi **new clade**, and Boreophthalmi **new clade** (Table 6). Scopulophthalmi is diagnosed as Pettalidae, and the name refers to the presence of a scopula in the anal region of the male in many pettalid species. Sternophthalmi includes the families Troglosironidae, Ogoveidae, and Neogoveidae, with its etymology referring to the presence of an exocrine gland opening in the opisthosomal
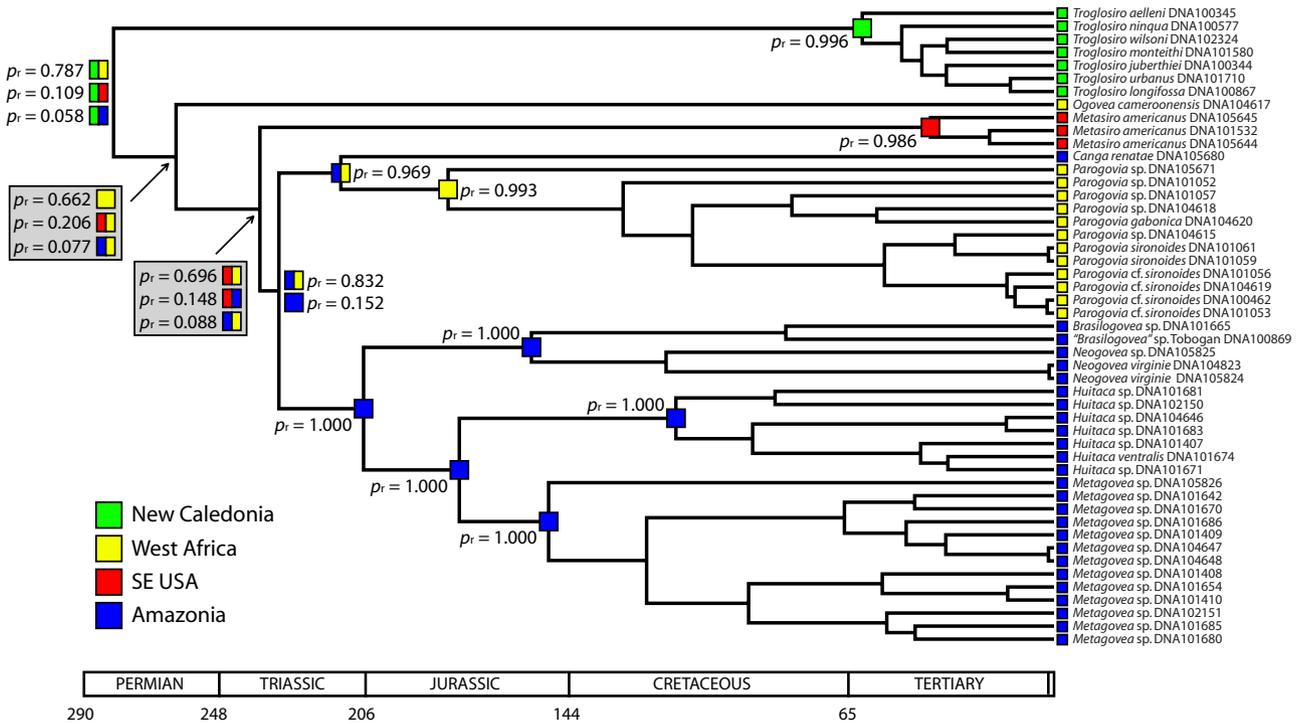
Figure 7. Ancestral range reconstructions for Sternophthalmi (Troglosironidae, Ogoveidae, Neogoveidae) inferred by Lagrange analysis, using stratified models. Coloured squares at terminals indicate ranges occupied by sampled species. Coloured squares on nodes indicate ranges reconstructed for hypothetical ancestors. Numbers on nodes indicate relative probability of ranges reconstructed.

sternal region of males in all troglosironids, all ogoveids, and most neogoveids, as opposed to the other three families where the opisthosomal exocrine glands, when present, open in the posterior tergites. We maintain Shear's superfamily Ogoveoidea, and restrict Sironoidea to the family Sironidae and Stylocelloidea to the family Stylocellidae, although we do not introduce other superfamilies because they would each contain a single family. Boreophthalmi includes the families Stylocellidae and Sironidae, which subsequent to Hansen & Sørensen's (1904), had been considered the representatives of the two main cyphophthalmid clades (Shear, 1980). The term refers to the mostly northern hemisphere distribution of these two families, although the origin of Stylocellidae can be probably traced to northern Gondwana (Clouse & Giribet, 2010). Sternophthalmi is sister group to Boreophthalmi.

The following taxa are thus abandoned as a result of being non-monophyletic according to our phylogenetic results: Infraorder Tropicophthalmi Shear, 1980 and Infraorder Temperophthalmi Shear, 1980. Shear's infraorders do not reflect the phylogenetic relationships obtained here, as suggested in previous studies (Giribet & Boyer, 2002; Boyer *et al.*, 2007b; Giribet *et al.*, 2010).

DISTRIBUTION MODELLING AND HABITAT SUITABILITY OVERLAP

Habitat suitability models predicted by both the MAXENT and BIOCLIM methods were highly congruent and therefore we present only results from MAXENT (Fig. 10) because it was found to outperform other modelling algorithms (Elith *et al.*, 2006). Model predictions were significantly distinct from random and area under the curve (AUC) values were high or moderately high (in the range 0.84–0.99) in all runs independently of the modelling algorithm and the set of variables used to build the model. For the analyses with a reduced number of variables, we kept all variables that had jackknife regularized training gain greater than one. As expected, when correlation among variables is present, using a lower number of variables does not change significantly the AUC values but reduces over-fitting; hence, the resulting models find broader areas with suitable conditions. These are, however, congruent with results from models built with all BIOCLIM variables and differences are generally associated with areas where habitat suitability is low (Fig. 10).

The variables with highest average relative contribution to the MAXENT habitat suitability model for
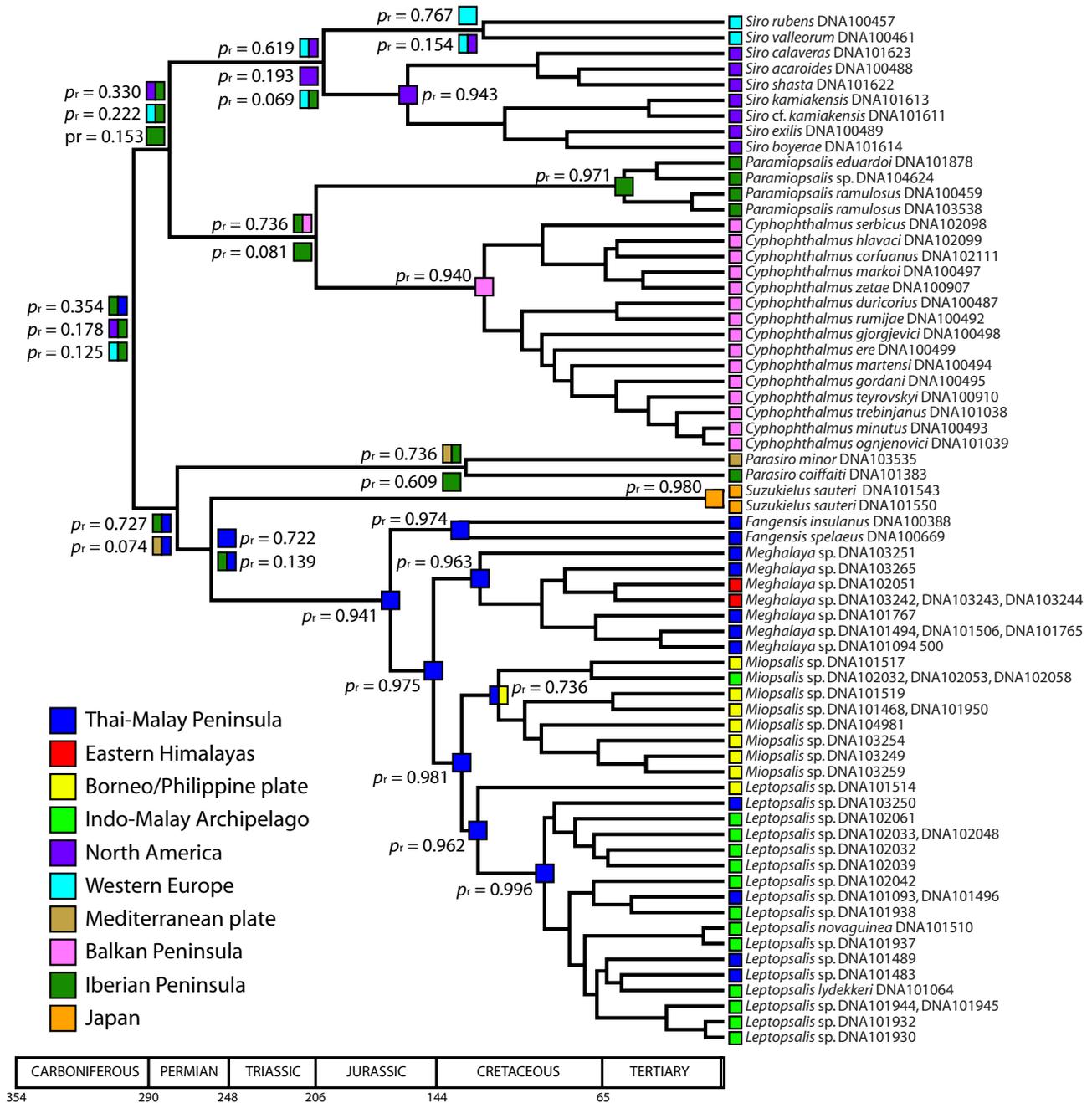
Figure 8. Ancestral range reconstructions for *Boreophthalmi* (*Sironidae, Stylocellidae*) inferred by Lagrange analysis, using stratified models. Coloured squares at terminals indicate ranges occupied by sampled species. Coloured squares on nodes indicate ranges reconstructed for hypothetical ancestors. Numbers on nodes indicate relative probability of ranges reconstructed.

Pettalidae were isothermality (33.8%), precipitation of the driest month (22.8%) and annual mean temperature (9.2%). Jackknife tests of variable importance indicate that temperature seasonality had the highest gain in isolation. Mean diurnal temperature range decreased the gain the most when omitted, suggesting that it contained the most information not present in the other variables. For Sironidae, the precipitation of the coldest quarter (40.0%), mean temperature of the coldest quarter (16.3%), and annual mean temperature were the variables with highest contribution. Mean temperature of the coldest quarter had the highest gain in isolation, and annual precipitation decreased the gain the most

Figure 9. Combined analysis of morphology and molecules. Strict consensus of three optimal trees based on the parsimony direct optimization analysis under parameter set 3221 (56 984 weighted steps). Clade colours correspond to those in Fig. 2; taxa in red are represented by morphology only. Numbers above nodes indicate jackknife support values.

Table 5. Habitat suitability overlap statistics based on the MAXENT analysis with all bioclim variables

Clade	Relative rank	I	D
Pettalidae versus Sironidae	0.727**	0.392	0.187
Pettalidae versus Stylocellidae	0.826* ($P = 0.015$)	0.525	0.234
Pettalidae versus Sternophthalmi	0.832**	0.638	0.329
Sironidae versus Stylocellidae	0.666**	0.126	0.038
Sironidae versus Sternophthalmi	0.768**	0.292	0.114
Stylocellidae versus Sternophthalmi	0.836 ($P = 0.133$)	0.819	0.554

Relative rank significance calculated using ENMtools identity test results. *$0.01 < P < 0.05$, **$P < 0.01$. I, the I statistic (Warren *et al*., 2008); D, Schoener's D (Schoener, 1968).

Table 6. Classification system for Cyphophthalmi, using established family and superfamily names

Suborder Cyphophthalmi
  Infraorder Scopulophthalmi new clade
    Family Pettalidae Shear, 1980
  Infraorder Sternophthalmi new clade
    Family Troglosironidae Shear, 1993
  Superfamily Ogoveoidea Shear, 1980
    Family Ogoveidae Shear, 1980
    Family Neogoveidae Shear, 1980
  Infraorder Boreophthalmi new clade
  Superfamily Stylocelloidea Hansen & Sørensen, 1904 **new composition**
    Family Stylocellidae Hansen & Sørensen, 1904
  Superfamily Sironoidea Simon, 1879 **new composition**
    Family Sironidae Simon, 1879

when omitted. The variables with highest contribution for Stylocellidae were temperature seasonality (42.9%), annual precipitation (26.3%), and precipitation of the warmest quarter (11.8%). Annual precipitation had the highest gain in isolation, and precipitation of the warmest quarter decreased the gain the most when omitted. For the clade Sternophthalmi, the variables with the highest contribution were annual precipitation (33.8%), precipitation of the driest quarter (24.1%), and isothermality (13.9%). Temperature annual range had the highest gain in isolation and also reduced gain the most when omitted.

Results of the identity test for the MAXENT models based on all variables are shown in Table 5. Results from the analysis using the Bioclim algorithm are congruent (not shown). The identity test shows that, when considering relative ranks, the calculated habitat suitability scores for most of the groups are significantly distinct except for Stylocellidae versus Sternophthalmi, the two tropical clades. Habitat suitability identity cannot be rejected either for Pettalidae versus Stylocellidae at the 0.01% significance level. The higher values for I and D in those two cases also show that there is significant overlap of the suitable habitat of these clades. Pettalidae versus Sternophthalmi shows also high values of I and D but identity tests reject the null hypothesis of habitat suitability identity.

DISCUSSION

The present data, of worldwide scope, and spanning the geological scale from the Palaeozoic to the present, allow us to study a group of soil arthropods to a level of detail rarely seen in biogeographical and phylogenetic studies. Taxonomic representation in the molecular data includes species from all non-monotypic genera and several monotypic genera; all genera are represented in the morphological data set. Geographical coverage includes all known world regions where Cyphophthalmi have been reported, with the exception of Mexico (a few specimens from two caves; Shear, 1977, 1980), Madagascar (four specimens known in total for two species; Shear & Gruber, 1996), Kenya (five specimens known from a single cave; Shear, 1985), and the Philippine island of Palawan (a single adult specimen known; Shear, 1993c).

Our phylogenetic results provide the basis for a new classification of the suborder Cyphophthalmi. The results also set the geological time framework for the origin and diversification of each family and the evolution of the niche preference in selected families or suprafamilial clades. This allows testing specific biogeographical hypotheses, such as the supposed total submersion of New Caledonia (Murienne *et al*., 2005) or New Zealand (Goldberg, Trewick & Paterson, 2008), or the reconstruction of the ancestral areas of each cyphophthalmid lineage.

DIRECT OPTIMIZATION ANALYSIS

To a lesser degree than for static homology, dynamic homology searches are difficult to evaluate in terms of optimality. In the present study, we used a strategy of SATF with multiple rounds of analyses to decide when to stop the searches, and saw that searches of 6–12 h run on a desktop computer stabilized after five to ten rounds, depending on the parameter set. The stability of the results is used here as a criterion for

reporting results, in the same fashion that driven searches and similar techniques have been applied to the computational problem of tree searching (Giribet, 2007a; Goloboff, Farris & Nixon, 2008).

In previous studies of cyphophthalmid and harvestmen data, analyses based on direct optimization have yielded results sometimes differing from those of analyses based on static homology (Boyer *et al*., 2007b; Giribet *et al*., 2010). However, this is not the case in the present study, where taxon sampling and geographical representation have been thoroughly optimized. One major difference remains, the monophyly of Sironidae (see below), although some of the static homology analyses (Fig. 5) are congruent with the direct optimization tree (Fig. 3), whereas the maximum likelihood tree (Fig. 4) differs from the Bayesian estimate (Fig. 5). Another major difference (but, again, among analyses, and not necessarily the result of differences between dynamic and static notions of homology) is the internal resolution of the pettalid genera (see below).

Systematics

The monophyly of Cyphophthalmi has been well supported in all morphological analyses (Giribet & Boyer, 2002), as well as from the earliest molecular analyses using just a few sequences in the families Sironidae and Stylocellidae (Giribet *et al*., 1999; Shultz & Regier, 2001; Giribet *et al*., 2002), a few representatives of the suborder (Giribet & Boyer, 2002) or, more recently, in several much denser analyses (Boyer *et al*., 2007b; Giribet *et al*., 2010). Our new data add corroboration to this well-delimited taxon, with the familial inter-relationships and their internal structure being the real focus of the study, although, in the combined analysis including taxa with morphological data only, support for the monophyly of Cyphophthalmi decreases to 61%, probably as a result of some effects of the missing data (see below). Among these, Pettalidae, Stylocellidae, Troglosironidae, and Neogoveidae are monophyletic in most of our analyses (but see discussion on Neogoveidae), Ogoveidae is represented by a single specimen in the molecular analyses, and Sironidae remains contentious, especially with respect to the placement of the two genera *Suzukielus* and *Parasiro*.

One of the outstanding issues in cyphophthalmid phylogenetics has been the placement of the root, which was suggested to occur: (1) between Stylocellidae and the remaining families; (2) between Pettalidae and the remaining families; or (3) between a clade containing *Suzukielus* and Pettalidae and the remaining families (Giribet & Boyer, 2002), based on the molecular rooting of a morphological tree, because most cyphophthalmid morphological characters are inapplicable or meaningless outside the suborder. Subsequent analyses found alternative resolutions placing the root between Pettalidae and the rest or between Stylocellidae and the rest (Boyer *et al*., 2007b), depending on the analysis and optimality criterion employed. Different studies have assumed either one of these alternative rootings until a recent broader Opiliones study found the root between Pettalidae and the rest (Sternophthalmi + Boreophthalmi), this time without distinction among optimality criteria or method of analysis (Giribet *et al*., 2010). This latter result is further corroborated in the present study. This position of Pettalidae as sister group to all other cyphophthalmid families falsifies the two infraorders introduced by Shear (1980), which should be abandoned, and allows for a much clearer reconstruction of the cyphophthalmid ancestor, which must have had laterally positioned simple ocelli (Alberti, Lipke & Giribet, 2008), a lamelliform adenostyle in the male fourth tarsus, and opisthosomal exocrine glands opening in the anal region in the male.

Internal resolution of Pettalidae does not differ considerably from the source studies of this pettalid data set (Boyer & Giribet, 2007, 2009) and, as in these studies, South Africa, New Zealand and Australia are not monophyletic. Diversification of the family started 183 Mya, and therefore paralogy of some of its landmasses is easily explained by cladogenesis prior to the split of Gondwana into its current continents. Nonetheless, relationships within Pettalidae remain unstable or poorly supported and important African diversity is missing from the molecular sampling, both from South Africa (de Bivort & Giribet, 2010) and Madagascar (Shear & Gruber, 1996), although the combined analyses with morphology place *Speleosiro* as sister group to *Purcellia* (64% JF) (Giribet, 2003a; de Bivort *et al*., 2010; de Bivort & Giribet, 2010), and *Manangotria* as sister group to *Karripurcellia*, although with low nodal support.

Results within Pettalidae are congruent among methods of analysis in the monophyly of each genus, although their relationships remain contentious. A *trans*-Tasman clade is found, albeit with low support, in the probabilistic analyses but not in the direct optimization analysis. Similarly, the most-basal position of *Parapurcellia* is not universally accepted. Other relationships discussed above are poorly supported, with the exception of a *Chileogovea* + *Purcellia* clade. Whether the deficient sampling in South Africa (whose genera appear to have influence at the base of the tree) or perhaps lineage extinction during the cooling of Antarctica are responsible for the lack of resolution in the pettalid relationships, remains untested.

The present study introduces the first genetic data for the monogeneric family Ogoveidae, which clearly forms part of the previously established Troglosironidae–Neogoveidae clade (Boyer *et al.*, 2007b; Sharma & Giribet, 2009a), now named Sternophthalmi. Ogoveidae forms a clade with Neogoveidae in all analyses, corroborating Shear's superfamily Ogoveoidea, although not his infraorder Tropicophthalmi, because Stylocellidae are unrelated to Ogoveoidea. Ogoveoidea is thus a Pantropical clade of probable African origin, although its original diversification dates back to 261 Mya. Some analyses (two suboptimal parameter sets under direct optimization) place Ogoveidae as ingroup Neogoveidae, although most analyses support monophyly of Neogoveidae. This is also found in the combined analysis with morphology, where *Ogovea* and *Parogovia* form a clade of African Ogoveoidea, although support for this clade is low. The latter clade is sister to a clade of American neogoveids. However, because of the unique morphology of ogoveids (Juberthie, 1969; Giribet & Prieto, 2003), and monophyly of Neogoveidae in most analyses, the family Ogoveidae is maintained as valid (after rediagnosis from Giribet & Prieto, 2003). Shear (1980) included the genus *Huitaca* in this family, although, earlier, he had postulated a sister group relationship of *Huitaca* and *Metagovea* (Shear, 1979a), as shown in our analyses.

Neogoveidae began its own diversification soon after (236 Mya), long before the opening of the Atlantic Ocean, as illustrated by the amphi-Atlantic clade relating the Eastern Brazilian genus *Canga* with the African *Parogovia* (specimens from Cameroon, Gabon, and Equatorial Guinea), or the sister group relationships of the North American genus *Metasiro* to the Amazonian/West African clade. The specimen from Ivory Coast, probably related to *P. pabsgarnoni*, constitutes a new genus that will be described elsewhere. Other than *Canga*, the South American species form a well supported clade that we currently assign to four genera: *Brasilogovea*, which we resurrect here, includes species from Amazonia and the 'Tepuis' region of Colombia; *Neogovea*, represented by two species from Guyana and French Guiana; *Huitaca*, still endemic to Colombia, including a large number of undescribed species; and *Metagovea*, including not only most specimens from the Andean region, but also some Amazon specimens from Leticia and a specimen from Guyana, with the latter being sister to all other *Metagovea* and possibly constituting another new genus (L. Benavides & G. Giribet, unpubl. data). This species is clearly unrelated to the genus *Neogovea*, occurring in this part of the Neotropics, and it is characterized by a conspicuous opisthosomal middorsal longitudinal sulcus; an adenostyle ending in a brush of setae and located at the base or towards the centre of the dorsal side of tarsus IV; absence of opisthosomal exocrine glands; and a spermatopositor complex with a crown-shaped structure at the tip, with additional perpendicular projections (L. Benavides & G. Giribet, unpubl. data). Our *Metagovea* clade includes specimens that we previously placed in the genera *Metagovea* and *Neogovea* (Boyer *et al.*, 2007b; Giribet *et al.*, 2010) because they differ considerably in their anatomy. Further subdivision of *Metagovea* may be warranted, although not until specimens from the Manaus area (Brazil) are available for molecular study. Nonetheless, relationships among the four genera are well established, with *Brasilogovea* + *Neogovea* being the sister group to a clade including *Huitaca* and *Metagovea*, and the latter genus generally divided among small species, or 'typical' *Metagovea* and larger species more similar to *Neogovea*. The large sampling within the superfamily, including all the currently recognized genera, and new data for many mostly undescribed species and genera not represented in previous studies, allows us to provide a more comprehensive understanding of this Pantropical group. The addition of morphological data of the types of the genera *Neogovea* and *Brasilogovea* did not fully resolve this clade, although this is considered to be a result of the poor preservation of these specimens (missing the ventral opisthosomal region) that does not allow examination of key characters such as the sternum or the opisthosomal exocrine glands.

The sister group of Ogoveoidea is without doubt the New Caledonia endemic genus *Troglosiro*, and both separated approximately 279 Mya at a time when New Caledonia was geographically located at the eastern margin of Gondwana. Diversification of Troglosironidae is, however, much more recent (57 Mya) and the error associated with this date does not allow for an unambiguous interpretation of the postulated total submersion of the island (Grandcolas *et al.*, 2008; Murienne *et al.*, 2008; Murienne, 2009). The analyses recognize a group with sternal opisthosomal depressions associated with the sternal exocrine glands of the males, *sensu* Sharma & Giribet (2009a).

Stylocellidae have gone from being the most poorly-known group to arguably the most stable and best understood phylogenetically. The results of the present study corroborate those from the recent studies mostly by R. Clouse (Clouse & Giribet, 2007; Clouse *et al.*, 2009; Clouse, 2010; Clouse & Giribet, 2010; Clouse *et al.*, 2011), from which all the data included here were derived; see also Schwendinger & Giribet (2005). *Fangensis*, a clade with its origins in the terrane that today constitutes the Thai-Malay peninsula, is sister to all other stylocellids, which diversified towards the north in the genus *Meghalaya* and towards the south in the genera *Miopsalis* and

Leptopsalis, the former mostly found on Borneo, although giving rise to species in the Philippines and Sumatra, and the latter radiating rapidly as Sumatra, Java, and Sulawesi became accessible, and also extending to New Guinea. The family diversified 167 Mya and includes the only reported cases of possible transoceanic dispersal in Cyphophthalmi (Clouse & Giribet, 2007; see also Clouse *et al*., 2011). Morphological analysis of discrete character data also support earlier studies excluding the nominal genus *Stylocellus* from any of the four genera adopted here, with *Stylocellus* remaining monotypic (Clouse *et al*., 2009). However, the addition of the type species of the genera *Leptopsalis*, *Meghalaya*, *Miopsalis*, and *Stylocellus*, not available for molecular analysis, does not result in a well-resolved taxonomy. The problem, however, lies in the nature of the data because the type of *Stylocellus*, an old, pinned, deformed specimen, is difficult to position based on discrete-characters only (Clouse *et al*., 2009), whereas the type of *Miopsalis* is a female and thus misses most discrete characters coded for other specimens, and was not available to be included in the morphometric analyses of Clouse *et al*. (2009). *Leptopsalis* is, however, well placed within its supposed molecular clade, although the type of *Meghalaya* does not find good support.

Sironidae monophyly has been disputed in previous analyses based on morphology and molecules, where two genera, *Parasiro* and *Suzukielus*, often do not cluster with the remaining sironids (in the genera *Siro*, *Cyphophthalmus*, *Paramiopsalis*, and *Iberosiro*) (Giribet & Boyer, 2002; de Bivort & Giribet, 2004; Boyer *et al*., 2007b; Giribet *et al*., 2010). *Odontosiro*, never included in a molecular analysis, is sister to *Parasiro* outside of the typical sironids. The Kenyan *Marwe* has been placed within sironids in some analyses based on morphological data (de Bivort & Giribet, 2004), as also shown here, and appears related to *Paramiopsalis* and *Iberosiro*. Sironids found their monophyly, however, in a recent morphological analysis of continuous characters (de Bivort *et al*., 2010) and in the maximum likelihood analysis of Giribet *et al*. (2010), as does the maximum likelihood analysis of the present data set, albeit with bootstrap support below 50%. Monophyly of Sironidae is also found in the analysis of the nuclear ribosomal data under direct optimization, suggesting that the non-monophyly of the family may be an artefact introduced most probably by their unusual COI evolution (Boyer *et al*., 2005). However, the membership in Sironidae of the genera *Iberosiro*, *Odontosiro*, or even *Marwe* remains untested with molecular data and future sampling effort in the north-western Iberian Peninsula and in Kenya should focus on these highly controversial genera.

MORPHOLOGICAL DATA

It is well known that combined analyses of molecules and morphology are fundamental for understanding the systematics of groups that include many taxa for which molecular data cannot be obtained (Eernisse & Kluge, 1993; Nixon & Carpenter, 1996). A typical example of the latter case is provided by fossil taxa (Giribet, 2010; Murienne, Edgecombe & Giribet, 2010a; Pyron, 2011). When dealing with such taxa, missing data can become a concern, although it has been shown, both with simulation and with empirical results, that missing data in and of themselves are not always problematic; instead, it is information content in the data at hand what really matters (Wiens, 2003; Goloboff *et al*., 2009; Hejnol *et al*., 2009; Wiens, 2009).

The fossil record of Cyphophthalmi is scarce (Dunlop & Giribet, 2003; Poinar, 2008; Dunlop & Mitov, 2011), and it does not add important diversity that can be coded into an explicit data matrix. However, the problem of missing data is of great importance in Cyphophthalmi as a result of the group's almost global but highly localized distribution, making collecting an arduous task. For these reasons, many species are known only from old museum material, from a single male, or even from only females or juveniles, making it impossible to include them in the molecular matrix or presenting considerable amounts of missing data in our morphological matrix. To mention just a few examples, the type species of the genera *Miopsalis* and *Ogovea* are known only from female individuals (Thorell, 1890–1891; Hansen & Sørensen, 1904); the second species in the genus *Pettalus*, *Pettalus brevicauda* Pocock 1897, was based on a juvenile specimen (Giribet, 2008); *Stylocellus sumatranus*, currently the only species in the genus, is based on a deformed specimen in very poor condition (Clouse *et al*., 2009); and several monotypic genera have never been examined under a scanning electron microscope: *Ankaratra*, *Manangotria*, *Marwe*, and *Odontosiro*.

When trying to maximize the diversity represented in the present study, we included all currently recognized genera in our morphological matrix, although some of the species representing these genera are missing important characters. Despite this problem, we followed earlier recommendations into a combined analysis in POY under the optimal parameter set and submitted it to a jackknife analysis. The resulting tree was not too different from that of an early analysis of all cyphophthalmid genera (Giribet & Boyer, 2002) with respect to the lack of resolution for many clades, which is otherwise well supported by the molecular data sets. Notable results are the placement of *Managotria taolanaro* within Pettalidae (63%

jackknife support), the monophyly of Stylocellidae (including the types of the genera *Leptopsalis*, *Megalaya*, *Miopsalis*, and *Stylocellus*, despite the lack of molecular data; 63% jackknife support) or the monophyly of the Neotropical Neogoveidae (excepting *Canga*), including the types and morphology-only species of *Neogovea* [*N. immsi*, *Neogovea kartabo* (Davis, 1937)], *Neogovea kamakusa* Shear, 1977), and *Brasilogovea microphaga* Martens, 1969 (56% jackknife support). The inclusion of *Parogovia pabsgarnoni* affects the monophyly of the African neogoveids, as *Parogovia* sp. DNA105671 does not form a clade with the other *Parogovia* (54% jackknife support). However, the instability of species such as *Shearogovea mexasca* and *Ankaratra franzi* affects the monophyly of groups that are otherwise robust to molecular analysis such as Sternophthalmi + Boreophthalmi, Sternophthalmi, Ogoveoidea, Neogoveidae or Boreophthalmi.

The current results combining morphology with molecules lowered overall support for the tree. This is an unfortunate result because simulations have shown that the accuracy in the phylogenetic placement of fossils often improves or stays the same when using molecular data and that only in a few cases accuracy was significantly decreased (Wiens, 2009). The problem here may be related to the low numbers of discrete morphological characters available for these Opiliones, often limited to variation among groups of species; hence, the recent use of continuous characters in some analyses of the group (Clouse *et al.*, 2009; de Bivort *et al.*, 2010; de Bivort & Giribet, 2010). Some characters show low levels of homoplasy, greatly structuring the data (some of these characters were the basis for older classification systems) but many of our wild taxa show 'unexpected' states in these characters. Character 7 is notable in this respect. The coxae of the walking legs of Cyphophthalmi show different degrees of fusion, with coxae III and IV of each side always fused and coxae I remaining moveable. Coxa II can be free (state 0) or fused to coxae III and IV; among the former are most members of the families Pettalidae, Troglosironidae, and Sironidae (except for the genera *Paramiopsalis* and *Iberosiro*); among the latter are the members of the families Ogoveidae, Stylocellidae, and Neogoveidae (except for *Canga* and *Metasiro*). It is therefore not unexpected that this character defined the major groups Sironoidea and Stylocelloidea *sensu* Hansen & Sørensen (1904), and that a genus such as *Metasiro* was considered a member of Sironidae in previous studies, nor that these genera are among the most unstable ones when morphology is used. The presence/absence of eyes (character 1), ozophore type (character 2), and spiracle shape (character 49) are also characters with relatively low levels of

homoplasy, which have played an important role in cyphophthalmid systematics, and, again, it is not unexpeced that the taxa that present odd character states become unstable.

BIOGEOGRAPHICAL PATTERNS IN CONTINENTS

Cyphophthalmi have been shown to present a high correlation of their systematic position and landmass affinity (Juberthie & Massoud, 1976; Shear, 1980; Giribet, 2000), to show strong genetic structure across short distances (Boyer *et al.*, 2007a), and have been used as models to study vicariance biogeography (Giribet, 2003a; Boyer *et al.*, 2005; Boyer & Giribet, 2007; Giribet & Kury, 2007; Boyer *et al.*, 2007b; Boyer & Giribet, 2009; Clouse *et al.*, 2009; Sharma & Giribet, 2009a; Clouse, 2010; Clouse & Giribet, 2010; de Bivort & Giribet, 2010; Murienne *et al.*, 2010b; Clouse *et al.*, 2011). This study corroborates earlier findings that suggest a temperate Gondwanan clade (Pettalidae; Fig. 6), a Pantropical clade (Sternophthalmi; Fig. 7), one clade originating in the Thai-Malay Peninsula (Stylocellidae; Fig. 8), and two or more Laurasian clades whose ancestral area is difficult to reconstruct with high probability but that includes the Iberian Peninsula, North America, and Western Europe (Sironidae; Fig. 8). The origin of all these clades is ancient, preceding the fragmentation of Pangea and therefore suggesting that many cladogenetic events were older than the vicariant events that followed. This has important biogeographical implications with respect to using vicariant events as calibration points because the mismatch between the two events could be very large (Kodandaramaiah, 2011).

Most biogeographical patterns observed, in conjunction with a well-dated phylogenetic hypothesis and a reconstruction of the ancestral landmasses for each clade, allow a thorough explanation of each clade. The ancestral area reconstruction of the family Pettalidae (Fig. 6) involves several cladogenetic events at the genus-level because each genus is currently recognized to be restricted to a single landmass or to adjacent terranes (Boyer & Giribet, 2007). Although resolution among the genera finds low support, most analyses suggest the South African genus *Parapurcellia* to be the sister group to all other genera, and place the other South African genus, *Purcellia*, in that clade, lending support to South Africa as one of the possible centres of origin of the family. A relationship between South Africa (*Purcellia*) and South America (*Chileogovea*) is found in most analyses, as is also found in the members of the peripatopsid Onychophora, with similar distribution and habitat requirements as pettalids (Allwood *et al.*, 2010). It is also notable that the two Australian genera *Austro-*
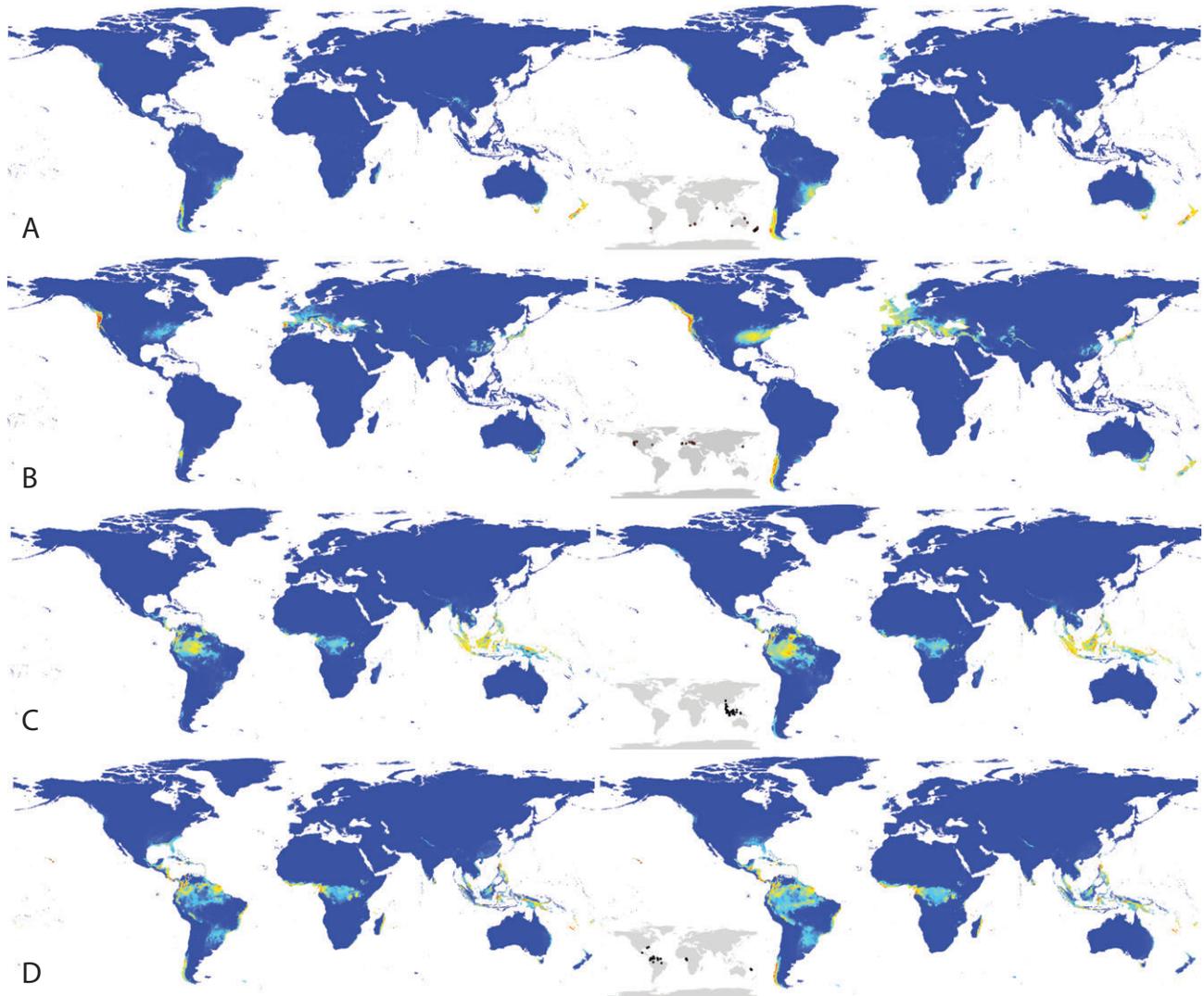
Figure 10. MAXENT models of habitat suitability. Left column with all bioclim variables, right column with variables with jackknife regularized training gain greater than one. Warmer (red-yellow) colours represent more suitable habitats. Maps in miniature represent actual presence observations. A, *Pettalidae*; B, *Sironidae*; C, *Stylocellidae*; D, *Sternophthalmi* (*Troglosironidae* + *Ogoveidae* + *Neogoveidae*).

purcellia (Queensland) and *Karripurcellia* (Western Australia) never form a clade, supporting earlier views about using microareas in biogeographical studies of small soil organisms (Giribet & Edgecombe, 2006). A relationship of Sri Lanka–Australia–New Zealand is found in several analyses.

The biogeographical patterns of Sternophthalmi (Fig. 7) are easily reconstructed, with two ancestral lineages occurring in the Neotropics (*Canga* is sister to the African *Parogovia* clade), two ancestral lineages in Africa (*Ogovea* and *Parogovia*), and one lineage in North America (*Metasiro*), which separated from the remaining neogoveids during the Triassic. Although older analyses suggested a relationship of *Metasiro* to *Parogovia*, this was based on analyses

without several neogoveid lineages and without ogoveids, and the current results are very stable. The sister group relationship of Ogoveoidea to the New Caledonian endemic genus *Troglosiro* has been found in previous studies and it is discussed in more detail below. No paralogy is needed in this tree when considering the timing of the diversification events, as the separation of the Neotropics from the Afrotropics is dated at 95 Mya (Raven & Axelrod, 1972; Sanmartín, 2002).

Stylocellid biogeography and their ancestral areas have been discussed recently (Clouse & Giribet, 2010) and our results corroborate this earlier analysis. The Thai-Malay Peninsula is reconstructed as the ancestral terrane for the family with subsequent

expansions to the Eastern Himalayas during the Cretaceous/Tertiary boundary, and radiations into the Borneo/Philippine plate and into the Indo-Malay Archipelago during the Cretaceous. Several lineages may have returned to the Thai-Malay Peninsula or moved between islands around the Cretaceous/Tertiary boundary during a period in which southeast Asia was subjected to drastic changes and the Indo-Malay Archipelago variously connected (Hall, 2002; Ali & Aitchison, 2008).

Reconstruction of the biogeographical history of Sironidae remains hindered by the instability of the relationships of *Suzukielus* and *Parasiro*; the former endemic to Japan and the latter found in the Iberian and Mediterranean plates. *Parasiro* has its origins in the Jurassic/Cretaceous of the Iberian Peninsula, where cyphophthalmids are so far restricted to areas with Paleozoic rocks (Murienne & Giribet, 2009). The main sironid clade includes three genera found in North America (*Siro*), Western Europe (*Siro*), the Iberian Peninsula (*Paramiopsalis*), and the Balkan region and Eastern Europe (*Cyphophthalmus*). *Siro* shows reciprocal monophyly of the two landmasses, the lineages separating during the Triassic, a result not supported in a recent analysis of the North American diversity (Giribet & Shear, 2010). The sister-group relationship of the Iberian/Balkan clade has been discussed thoroughly in recent studies (Boyer *et al*., 2005; Murienne *et al*., 2010b), which have also illustrated a correlation between an evolutionary explosion and the coming into contact of ancestral landmasses in the Mediterranean region (Murienne *et al*., 2010b). From a geological point of view, the Balkan Peninsula, supporting the explosive evolution of *Cyphophthalmus*, includes the margin of both Eurasia (the Moesian microplate) and Gondwana (the Adria microplate), as well as remnants of the Tethys and related marginal seas (made up of oceanic crust) (Karamata, 2006). The Adria microplate is the largest lithospheric fragment in the Central Mediterranean region. It was connected to Iberia in the west and to north-west Africa in the south (Wortmann *et al*., 2001) until the Middle–Late Triassic episodes of rifting and breakup (Channell, D'Argenio & Horváth, 1979; Pamic, Gusic & Jelaska, 1998), around the cladogenesis time for the split between *Paramiopsalis* and *Cyphophthalmus*. For most of the time, the Adria microplate was in a shallow-water environment (Scheibner & Speijer, 2008) in which the Southern Tethyan Megaplatform formed before disintegrating into several carbonate platforms in the Early Jurassic (Vlahovic *et al*., 2005), before the diversification of *Cyphophthalmus* during the Jurassic/Cretaceous, when cycles of land submergence and emergence have been recorded in some carbonate platforms (Vlahovic *et al*., 2005; Márton *et al*., 2008). The ancestral area of the family is however difficult to infer, perhaps, amongst other factors, as a result of the large number of terranes that existed around the Tethys.

BIOGEOGRAPHY IN CONTINENTAL ISLANDS: THE CASES OF NEW CALEDONIA AND NEW ZEALAND

Cyphophthalmi are present in most islands of continental origin (fragment islands *sensu* Gillespie & Roderick, 2002), including Sri Lanka (Pocock, 1897; Sharma & Giribet, 2006; Giribet, 2008; Sharma, Karunarathna & Giribet, 2009), Chiloé (Roewer, 1961; Juberthie & Muñoz-Cuevas, 1970; Shear, 1993a), Corsica and Sardinia (Simon, 1872; Juberthie, 1958), Honshu (Roewer, 1916; Juberthie, 1970b; Suzuki & Ohrui, 1972; Giribet, Tsurusaki & Boyer, 2006), and the Indo-Malay archipelago (Westwood, 1874; Thorell, 1882–1883; Pocock, 1897; Hansen & Sørensen, 1904; Shear, 1979b; Rambla, 1991; Shear, 1993c; Giribet, 2002; Schwendinger & Giribet, 2005; Clouse & Giribet, 2007; Clouse *et al*., 2009; Clouse & Giribet, 2010), and, in all these cases, their presence in these islands is best explained as a result of vicariance. Similarly, New Caledonia and New Zealand host a considerable diversity of Cyphophthalmi, although their presence in these islands as a result of one or more vicariant evens has been recently disputed.

New Caledonia currently has 13 described species in the genus *Troglosiro*, the only genus in the family Troglosironidae (Juberthie, 1979; Shear, 1993b; Sharma & Giribet, 2005, 2009a; Sharma & Giribet, 2009b) considered to be endemic to the Grande Terre and unambiguously recovered as the sister group to the Equatorial Ogoveoidea from Equatorial West Africa and the Equatorial Neotropical belt. Geological data on the origins of the New Caledonian biodiversity argue in favour of a series of submersions during the Palaeocene and Eocene (Paris, Andreieff & Coudray, 1979; Aitchison *et al*., 1998; Pelletier, 2006), which has been used to support a total submersion of the island, re-emerging 37 Mya (Murienne *et al*., 2005; Grandcolas *et al*., 2008; Murienne *et al*., 2008). Indeed, molecular dating analyses of several New Caledonian clades has supported diversification processes post-dating the critical date of 37 Mya (Murienne *et al*., 2005; Page *et al*., 2005; Murienne *et al*., 2008; Espeland & Johanson, 2010; Murienne, Edgecombe & Giribet, 2011), which has led some studies to suggest that the entirety of the New Caledonian terrestrial biota must have arrived to the islands via dispersal and that no trace of ancient vicariance is left. One notable exception may be the family Troglosironidae, whose diversification has been dated at 28–49 Mya by Boyer *et al*. (2007b) and 52–102 Mya by Giribet *et al*. (2010), although these studies used few

troglosironid samples. Refined analyses here suggest a Late Cretaceous–Early Tertiary diversification of the family (57 Mya), predating the supposed re-emergence of New Caledonia, although the error associated with this date does not allow unambiguous distinction of the hypothesis owing to the temporal proximity of the re-emergence of the island (37 Mya) and the floor of the diversification age estimate (95% HPD: 40–73 Mya). The ancestral area reconstruction for the split between Troglosironidae and Ogoveoidea is supported as a contiguous landmass containing West Africa and New Caledonia, deep in the Permian, indicating that the range of the clade was much broader than it currently is (Figs 5, 7), and that massive extinctions may have occurred during the period comprised between 279–57 Mya. However, relict taxa (and Troglosironidae certainly is such an example) and the problem of extinction, especially in the absence of a fossil record, are mysteries that are difficult to address in biogeography (Crisp, Trewick & Cook, 2011). This is indeed a unique case, where Troglosironidae constitute a special lineage in this respect.

Another possibility is a *trans*-Pacific dispersal, again during the 279–57 Mya period, a phenomenon also observed in at least two other opilionid lineages (e.g. the families Zalmoxidae and Samoidae; Sharma & Giribet, 2011). However, dispersals in the Cenozoic are possible to reconstruct unambiguously in Zalmoxidae and Samoidae insofar as lineages in one part of the Pacific form a grade with respect to a clade in another part of the Pacific. In both these cases, Neotropical lineages form the paraphyletic grade with respect to Pacific island lineages, rendering the ancestral area reconstruction for the origin of these radiations as Neotropical. By contrast, Troglosironidae and the clade (Ogoveidae + Neogoveidae) form reciprocally monophyletic groups that diverged 279 Mya, which is inconsistent with recent dispersal. Moreover, the Permian origin of Troglosironidae also suggests that any putative dispersal event had to have occurred sometime between 279–57 Mya, a hypothesis that is difficult to test. As stated previously, we submit that the biogeographical history of Troglosironidae is inherently difficult to reconstruct as a result of the relictual nature of this lineage (Sharma & Giribet, 2009a).

A similar case has been proposed for New Zealand, which includes 29 species in three pettalid genera (*Aoraki*, *Neopurcellia*, and *Rakaia*) (Forster, 1948, 1952; Boyer & Giribet, 2003, 2007) found in two geological terranes (the Australian plate and the Pacific plate) (Boyer & Giribet, 2009). New Zealand's geology and biota reflect a dynamic history of ancient Gondwanan origin, long-term isolation from other continental landmasses, marine inundating during the Oligocene, glaciation during the Pleistocene, and evolutionary radiations that have produced a spectacular proportion of endemic species (Gibbs, 2006). Studies have focused on New Zealand's biogeography with particular vigour over the past two decades because molecular systematics has provided new tools with which to approach evolutionary questions. Molecular systematists have addressed topics such as the number and location of Pleistocene refugia (Marske *et al*., 2009; Buckley, Marske & Attanayake, 2010), the Alpine Fault Hypothesis (Heads & Craw, 2004), and, most contentiously, a vicariance versus dispersal-based origin of New Zealand's terrestrial biota (Trewick, Paterson & Campbell, 2007; Phillips *et al*., 2010). Although studies have long recognized that land area was drastically reduced (i.e. to less than 15% of its current size) during the marine incursions of the Oligocene (Cooper & Cooper, 1995), more recently Waters & Craw (2006) have suggested that there is no strong evidence for continuously emergent land throughout the period (Landis *et al*., 2008). Trewick *et al*. (2007) and Wallis & Trewick (2009) asserted that the preponderance of biogeographical evidence favours a scenario of complete submergence during the Oligocene, and some studies have gone further, suggesting that the entire terrestrial biota arrived via dispersal during the last 22 Myr (Landis *et al*., 2008), and that it is therefore more like that of an oceanic archipelago than a continent (Goldberg *et al*., 2008). Few have questioned this new trend in New Zealand biogeography (Knapp *et al*., 2007; Edgecombe & Giribet, 2008; Boyer & Giribet, 2009; Allwood *et al*., 2010; Giribet & Boyer, 2010).

The evolutionary history of the New Zealand cyphophthalmid genera (*Aoraki*, *Rakaia*, and *Neopurcellia*) has long been of interest as part of the evaluation of a hypothesis proposing total submersion of New Zealand in the Oligocene (Waters & Craw, 2006; Trewick *et al*., 2007; Goldberg *et al*., 2008; Landis *et al*., 2008; Wallis & Trewick, 2009; Giribet & Boyer, 2010; Phillips *et al*., 2010). The persistence of these lineages through the Oligocene bottleneck was considered to represent evidence of incomplete submersion of this landmass (Boyer & Giribet, 2007, 2009), although this hypothesis was not previously accompanied by molecular dating. Consequently, the ages of diversification of these lineages have been open to interpretation as very young (e.g. approximately 5 Mya; Goldberg *et al*., 2008). Moreover, Crisp *et al*. (2011) suggested that an important criterion for evidence of vicariance events is diversification time coincident with the timing of the geological event that precipitated the vicariance; in this case, the rifting of Zealandia from the Australian plate approximately 85 Mya, although cladogenesis could be expected to be

much older than the vicariant event in taxa with low vagility and small distribution ranges.

The present study, utilizing a robust methodology for simultaneous estimation of tree topology and clade divergence times (*sensu* Crisp *et al.*, 2011), and calibrated using fossil taxa exclusively (Kodandaramaiah, 2011), obtains the following diversification times for the New Zealand endemic genera *Rakaia* and *Aoraki*: 91 Mya (95% HPD: 72–108 Mya) and 90 Mya (95% HPD: 75–108 Mya), respectively. These diversification age estimates coincide with the rifting of Zealandia in the Late Cretaceous. We present evidence, therefore, based upon tree topology and clade divergence times, of the persistence of multiple lineages through the Oligocene. In addition, the present study reconstructs the origin of the genus *Aoraki* to the Australian plate during the Cretaceous and that of the genus *Rakaia* to a composite terrane in the Pacific and Australian plate also in the middle of the Cretaceous, although, later on, our study clearly assigns a clade to each terrane (Figs 5, 6). Unfortunately, the generic relationships are highly unstable across methods and parameter sets and further speculation about the relationships of the Australian and New Zealand genera awaits further data. We submit that these data falsify the hypothesis of complete submersion of New Zealand during the Oligocene Drowning. Recent and forthcoming studies of other invertebrate lineages (Allwood *et al.*, 2010; Giribet & Boyer, 2010; Murienne *et al.*, 2010a; Marshall, 2011) are anticipated to corroborate this conclusion.

HABITAT SUITABILITY MODELS

One common characteristic of all models that we present here is the larger suitable habitat than the area actually occupied by the four clades of interest. This constitutes further evidence for the old cladogenesis and low dispersal abilities of Cyphophthalmi because many areas of suitable habitat have never been in contact with a landmass occupied by the clade of interest. This pattern also corroborates the hypothesis that tectonic movements and vicariance events have defined distributions and driven diversification in this group of soil arthropods. Mysteries remain because certain temperate clades have migrated to warmer climates (e.g. *Pettalus* in Sri Lanka or *Austropurcellia* in Queensland, Australia), whereas others may not have been able to adapt to changing climates. This suggests that, in several lineages, processes of niche evolution might have taken place. However, the lack of detailed occurrence observations for many species does not currently allow studying the niche evolution in Cyphophthalmi in greater detail.

CONCLUDING REMARKS

Cyphophthalmi constitute an ancient lineage of Opiliones distributed in temperate to tropical rainforests worldwide but restricted for the most part to continents and islands of continental origin, representing an ideal group of organisms for studying vicariance biogeography. Both phylogenetic patterns derived from molecular and morphological data and molecular dating using Opiliones fossils as calibration points corroborate the old age of the group and of its constituent clades. Ancestral area reconstruction further corroborates our biogeographical predictions by requiring only minimal switches between landmasses, most of them through contiguous land, therefore showing that the actual distribution is much more restricted than the potential distribution defined by the modelled habitat suitability for the different familial/suprafamilial clades. The data also permit tests of more general biogeographical hypotheses, such as the total submersion of New Caledonia and New Zealand and, at least in the former case, contradict a scenario of complete inundation. The present study provides refinement not only of the phylogenetic relationships and taxonomy of the group, but also its evolutionary and biogeographical history.

ACKNOWLEDGEMENTS

Guyana, Eduardo Mateos for Spanish samples, and Ricardo Pinto-da-Rocha for Brazilian samples. Greg Edgecombe, Salvador Carranza, and Michele Nishiguchi accompanied us on many collecting trips. We are also indebted to many museums and curators for their long-term loans that made this research possible, especially Lorenzo Prendini and Norman Platnick from the American Museum of Natural History, New York, NY; Charles Griswold from the California Academy of Sciences, San Francisco, CA; Petra Sierwald from the Field Museum, Chicago, IL; Jan Beccaloni from The Natural History Museum, London; Arturo Muñoz Cuevas from the Muséum national d'Histoire naturelle, Paris; Phil Sirvid from Te Papa Tongarewa, Wellington; Jonathan Coddington from the US National Museum (Smithsonian Institution), Washington, DC; Nikolaj Scharff from the Zoological Museum, Natural History Museum of Denmark, Copenhagen; and Jason Dunlop from the Zoologischen Museums, Berlin. Finally, Laura Leibensperger has assisted with specimen loans during all these years. The editor John A. Allen, an anonymous reviewer, and Gustavo Hormiga provided comments that helped to improve upon an earlier version of this manuscript.

REFERENCES

Aitchison JC, Ireland TR, Clarke GL, Cluzel D, Davis AM, Meffre S. 1998. Regional implications of U/Pb SHRIMP age constraints on the tectonic evolution of New Caledonia. *Tectonophysics* **299:** 333–343.

Alberti G. 1995. Comparative spermatology of Chelicerata: review and perspective. In: Jamieson BGM, Ausió J, Justine J-L, eds. *Advances in spermatozoal phylogeny and taxonomy*. Mémoires du Muséum National d'Histoire Naturelle **166:** 203–230.

Alberti G. 2005. Double spermatogenesis in Chelicerata. *Journal of Morphology* **266:** 281–297.

Alberti G, Giribet G, Gutjahr M. 2009. Ultrastructure of spermatozoa of different species of Neogoveidae, Sironidae, and Stylocellidae (Cyphophthalmi: Opiliones). *Contributions to Natural History – Scientific papers from the Natural History Museum Bern* **12:** 53–69.

Alberti G, Lipke E, Giribet G. 2008. On the ultrastructure and identity of the eyes of Cyphophthalmi based on a study of *Stylocellus* sp. (Opiliones, Stylocellidae). *Journal of Arachnology* **36:** 379–387.

Ali JR, Aitchison JC. 2008. Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian sub-continent from the Middle Jurassic through latest Eocene (166–35 Ma). *Earth-Science Reviews* **88:** 145–166.

Allwood J, Gleeson D, Mayer G, Daniels S, Beggs JR, Buckley TR. 2010. Support for vicariant origins of the New Zealand Onychophora. *Journal of Biogeography* **37:** 669–681.

Araujo MB, Rahbek C. 2006. How does climate change affect biodiversity? *Science* **313:** 1396–1397.

Benavides LR, Giribet G. 2007. An illustrated catalogue of the South American species of the cyphophthalmid family Neogoveidae (Arthropoda, Opiliones, Cyphophthalmi) with a report on 37 undescribed species. *Zootaxa* **1509:** 1–15.

de Bivort B, Clouse RM, Giribet G. 2010. A morphometrics-based phylogeny of the temperate Gondwanan mite harvestmen (Opiliones, Cyphophthalmi, Pettalidae). *Journal of Zoological Systematics and Evolutionary Research* **48:** 294–309.

de Bivort B, Giribet G. 2010. A systematic revision of the South African Pettalidae (Arachnida : Opiliones : Cyphophthalmi) based on a combined analysis of discrete and continuous morphological characters with the description of seven new species. *Invertebrate Systematics* **24:** 371–406.

de Bivort BL, Giribet G. 2004. A new genus of cyphophthalmid from the Iberian Peninsula with a phylogenetic analysis of the Sironidae (Arachnida : Opiliones : Cyphophthalmi) and a SEM database of external morphology. *Invertebrate Systematics* **18:** 7–52.

Boyer SL, Baker JM, Giribet G. 2007a. Deep genetic divergences in *Aoraki denticulata* (Arachnida, Opiliones, Cyphophthalmi): a widespread 'mite harvestman' defies DNA taxonomy. *Molecular Ecology* **16:** 4999–5016.

Boyer SL, Clouse RM, Benavides LR, Sharma P, Schwendinger PJ, Karunarathna I, Giribet G. 2007b. Biogeography of the world: a case study from cyphophthalmid Opiliones, a globally distributed group of arachnids. *Journal of Biogeography* **34:** 2070–2085.

Boyer SL, Giribet G. 2003. A new *Rakaia* species (Opiliones, Cyphophthalmi, Pettalidae) from Otago, New Zealand. *Zootaxa* **133:** 1–14.

Boyer SL, Giribet G. 2007. 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. *Cladistics: The International Journal of the Willi Hennig Society* **23:** 337–361.

Boyer SL, Giribet G. 2009. Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones, Cyphophthalmi). *Journal of Biogeography* **36:** 1084–1099.

Boyer SL, Karaman I, Giribet G. 2005. The genus *Cyphophthalmus* (Arachnida, Opiliones, Cyphophthalmi) in Europe: a phylogenetic approach to Balkan Peninsula biogeography. *Molecular Phylogenetics and Evolution* **36:** 554–567.

Buckley TR, Marske K, Attanayake D. 2010. Phylogeography and ecological niche modelling of the New Zealand stick insect *Clitarchus hookeri* (White) support survival in multiple coastal refugia. *Journal of Biogeography* **37:** 682–695.

Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17:** 540–552.

Channell JET, D'Argenio B, Horváth F. 1979. Adria, the African Promontory, in Mesozoic Mediterranean Paleogeography. *Earth Science Reviews* **15:** 213–292.

Clouse RM. 2010. Molecular and morphometric phylogenetics and biogeography of a Southeast Asian arachnid family (Opiliones, Cyphophthalmi, Stylocellidae). PhD Thesis, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge.

Clouse RM, de Bivort BL, Giribet G. 2009. A phylogenetic analysis for the South-east Asian mite harvestman family Stylocellidae (Opiliones : Cyphophthalmi) – a combined analysis using morphometric and molecular data. *Invertebrate Systematics* **23:** 515–529.

Clouse RM, General DM, Diesmos AC, Giribet G. 2011. An old lineage of Cyphophthalmi (Opiliones) discovered on Mindanao highlights the need for biogeographical research in the Philippines. *Journal of Arachnology* **39:** 147–153.

Clouse RM, Giribet G. 2007. Across Lydekker's Line – first report of mite harvestmen (Opiliones : Cyphophthalmi : Stylocellidae) from New Guinea. *Invertebrate Systematics* **21:** 207–227.

Clouse RM, Giribet G. 2010. When Thailand was an island – the phylogeny and biogeography of mite harvestmen (Opiliones, Cyphophthalmi, Stylocellidae) in Southeast Asia. *Journal of Biogeography* **37:** 1114–1130.

Cooper A, Cooper RA. 1995. The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proceedings of the Royal Society of London Series B, Biological Sciences* **261:** 293–302.

Crisp MD, Trewick SA, Cook LG. 2011. Hypothesis testing in biogeography. *Trends in Ecology & Evolution* **26:** 66–72.

DaSilva MB, Pinto-da-Rocha R, Giribet G. 2010. *Canga renatae*, a new genus and species of Cyphophthalmi from Brazilian Amazon caves (Opiliones: Neogoveidae). *Zootaxa* **2508:** 45–55.

De Laet J. 2010. A problem in POY tree searches (and its work-around) when some sequences are observed to be absent in some terminals. *Cladistics: The International Journal of the Willi Hennig Society* **26:** 453–455.

Diniz JAF, De Marco P, Hawkins BA. 2010. Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. *Insect Conservation and Diversity* **3:** 172–179.

Drummond AJ, Ho SY, Phillips MJ, Rambaut A. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biology* **4:** e88.

Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7:** 214.

Dunlop JA. 2007. Paleontology. In: Pinto-da-Rocha R, Machado G, Giribet G, eds. *Harvestmen: the biology of Opiliones*. Cambridge, MA: Harvard University Press, 247–265.

Dunlop JA, Anderson LI, Kerp H, Hass H. 2003. Preserved organs of Devonian harvestmen. *Nature* **425:** 916.

Dunlop JA, Anderson LI, Kerp H, Hass H. 2004. for 2003). A harvestman (Arachnida: Opiliones) from the Early Devonian Rhynie cherts, Aberdeenshire, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94:** 341–354.

Dunlop JA, Giribet G. 2003. The first fossil cyphophthalmid (Arachnida: Opiliones), from Bitterfeld amber, Germany. *Journal of Arachnology* **31:** 371–378.

Dunlop JA, Mitov PG. 2011. The first fossil cyphophthalmid harvestman from Baltic amber. *Arachnologische Mitteilungen* **40:** 47–54.

Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32:** 1792–1797.

Edgecombe GD, Giribet G. 2008. A New Zealand species of the trans-Tasman centipede order Craterostigmomorpha (Arthropoda : Chilopoda) corroborated by molecular evidence. *Invertebrate Systematics* **22:** 1–15.

Eernisse DJ, Kluge AG. 1993. Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules, and morphology. *Molecular Biology and Evolution* **10:** 1170–1195.

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermannm NE. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29:** 129–151.

Espeland M, Johanson KA. 2010. The effect of environmental diversification on species diversification in New Caledonian caddisflies (Insecta: Trichoptera: Hydropsychidae). *Journal of Biogeography* **37:** 879–890.

Evans ME, Smith SA, Flynn RS, Donoghue MJ. 2009. Climate, niche evolution, and diversification of the 'birdcage' evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*). *American Naturalist* **173:** 225–240.

Farris JS, Albert VA, Källersjö M, Lipscomb D, Kluge AG. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics: The International Journal of the Willi Hennig Society* **12:** 99–124.

Forster RR. 1948. The sub-order Cyphophthalmi Simon in New Zealand. *Dominion Museum Records in Entomology* **1:** 79–119.

Forster RR. 1952. Supplement to the sub-order Cyphophthalmi. *Dominion Museum Records in Entomology* **1:** 179–211.

Gibbs G. 2006. *Ghosts of Gondwana. The history of life in New Zealand*. Nelson: Craig Potton Publishing.

Gillespie RG, Roderick GK. 2002. Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology* **47:** 595–632.

Giribet G. 2000. Catalogue of the Cyphophthalmi of the World (Arachnida, Opiliones). *Revista Ibérica de Aracnología* **2:** 49–76.

Giribet G. 2002. *Stylocellus ramblae*, a new stylocellid

(Opiliones, Cyphophthalmi) from Singapore, with a discussion of the family Stylocellidae. *Journal of Arachnology* **30:** 1–9.

Giribet G. 2003a. *Karripurcellia*, a new pettalid genus (Arachnida : Opiliones : Cyphophthalmi) from Western Australia, with a cladistic analysis of the family Pettalidae. *Invertebrate Systematics* **17:** 387–406.

Giribet G. 2003b. Stability in phylogenetic formulations and its relationship to nodal support. *Systematic Biology* **52:** 554–564.

Giribet G. 2007a. Efficient tree searches with available algorithms. *Evolutionary Bioinformatics* **3:** 1–16.

Giribet G. 2007b. Neogoveidae Shear, 1980. In: Pinto-da-Rocha R, Machado G, Giribet G, eds. *Harvestmen: the biology of Opiliones*. Cambridge, MA: Harvard University Press, 95–97.

Giribet G. 2008. On the identity of *Pettalus cimiciformis* and *P. brevicauda* (Opiliones, Pettalidae) from Sri Lanka. *Journal of Arachnology* **36:** 199–201.

Giribet G. 2010. A new dimension in combining data? The use of morphology and phylogenomic data in metazoan systematics. *Acta Zoologica (Stockholm)* **91:** 11–19.

Giribet G. 2011. *Shearogovea*, a new genus of Cyphophthalmi (Arachnida, Opiliones) of uncertain position from Oaxacan caves, Mexico. *Breviora* **528:** 1–7.

Giribet G, Boyer SL. 2002. A cladistic analysis of the cyphophthalmid genera (Opiliones, Cyphophthalmi). *Journal of Arachnology* **30:** 110–128.

Giribet G, Boyer SL. 2010. 'Moa's Ark' or 'Goodbye Gondwana': is the origin of New Zealand's terrestrial invertebrate fauna ancient, recent, or both? *Invertebrate Systematics* **24:** 1–8.

Giribet G, Edgecombe GD. 2006. The importance of looking at small-scale patterns when inferring Gondwanan biogeography: a case study of the centipede *Paralamyctes* (Chilopoda, Lithobiomorpha, Henicopidae). *Biological Journal of the Linnean Society* **89:** 65–78.

Giribet G, Edgecombe GD, Wheeler WC, Babbitt C. 2002. Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data. *Cladistics: The International Journal of the Willi Hennig Society* **18:** 5–70.

Giribet G, Kury AB. 2007. Phylogeny and biogeography. In: Pinto-da-Rocha R, Machado G, Giribet G, eds. *Harvestmen: the biology of Opiliones*. Cambridge, MA: Harvard University Press, 62–87.

Giribet G, Prieto CE. 2003. A new Afrotropical *Ogovea* (Opiliones, Cyphophthalmi) from Cameroon, with a discussion on the taxonomic characters in the family Ogoveidae. *Zootaxa* **329:** 1–18.

Giribet G, Rambla M, Carranza S, Baguñà J, Riutort M, Ribera C. 1999. Phylogeny of the arachnid order Opiliones (Arthropoda) inferred from a combined approach of complete 18S and partial 28S ribosomal DNA sequences and morphology. *Molecular Phylogenetics and Evolution* **11:** 296–307.

Giribet G, Shear WA. 2010. The genus *Siro* Latreille, 1796 (Opiliones, Cyphophthalmi, Sironidae), in North America

with a phylogenetic analysis based on molecular data and the description of four new species. *Bulletin of the Museum of Comparative Zoology* **160:** 1–33.

Giribet G, Tsurusaki N, Boyer SL. 2006. Confirmation of the type locality and the distributional range of *Suzukielus sauteri* (Opiliones, Cyphophthalmi) in Japan. *Acta Arachnologica* **55:** 87–90.

Giribet G, Vogt L, Pérez González A, Sharma P, Kury AB. 2010. A multilocus approach to harvestman (Arachnida: Opiliones) phylogeny with emphasis on biogeography and the systematics of Laniatores. *Cladistics: The International Journal of the Willi Hennig Society* **26:** 408–437.

Goldberg J, Trewick SA, Paterson AM. 2008. Evolution of New Zealand's terrestrial fauna: a review of molecular evidence. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **363:** 3319–3334.

Goloboff PA, Catalano SA, Mirande JM, Szumik CA, Arias JS, Källersjö M, Farris JS. 2009. Phylogenetic analysis of 73 060 taxa corroborates major eukaryotic groups. *Cladistics: The International Journal of the Willi Hennig Society* **25:** 211–230.

Goloboff PA, Farris JS, Nixon KC. 2008. TNT, a free program for phylogenetic analysis. *Cladistics: The International Journal of the Willi Hennig Society* **24:** 774–786.

Grandcolas P, Murienne J, Robillard T, DeSutter-Grandcolas L, Jourdan H, Guilbert E. 2008. New Caledonia: a very old Darwinian island? *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **363:** 3309–3317.

Hadly EA, Spaeth PA, Li C. 2009. Niche conservatism above the species level. *Proceedings of the National Academy of Sciences of the United States of America* **106:** 19707–19714.

Hall R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences* **20:** 353–431.

Hansen HJ, Sørensen W. 1904. *On two orders of Arachnida: Opiliones, especially the suborder Cyphophthalmi, and Ricinulei, namely the family Cryptostemmatoidea*. Cambridge: Cambridge University Press.

Heads M, Craw R. 2004. The Alpine Fault biogeographic hypothesis revisited. *Cladistics: The International Journal of the Willi Hennig Society* **20:** 184–190.

Heino J, Soininen J. 2007. Are higher taxa adequate surrogates for species-level assemblage patterns and species richness in stream organisms? *Biological Conservation* **137:** 78–89.

Hejnol A, Obst M, Stamatakis A, Ott M, Rouse GW, Edgecombe GD, Martinez P, Baguñà J, Bailly X, Jondelius U, Wiens M, Müller WEG, Seaver E, Wheeler WC, Martindale MQ, Giribet G, Dunn CW. 2009. Assessing the root of bilaterian animals with scalable phylogenomic methods. *Proceedings of the Royal Society of London Series B, Biological Sciences* **276:** 4261–4270.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for

global land areas. *International Journal of Climatology* **25:** 1965–1978.

Juberthie C. 1956. Une nouvelle espèce d'Opilions *Sironidae* de France et d'Espagne: *Parasiro coiffaiti* n. sp. *Bulletin du Muséum National d'Histoire Naturelle, 2e série* **28:** 394–400.

Juberthie C. 1958. Révision du genre *Parasiro* (Opilions, Sironidae) et descriptions de *Parasiro minor* n. sp. *Bulletin du Muséum National d'Histoire Naturelle, 2e série* **30:** 159–166.

Juberthie C. 1960a. Contribution a l'étude des opilions cyphophthalmes: description de *Metasiro* gen. n. *Bulletin du Muséum National d'Histoire Naturelle, 2e série* **32:** 235–241.

Juberthie C. 1960b. Sur la biologie d'un opilion endogé, *Siro rubens* Latr. (Cyphophthalmes). *Comptes rendus des séances de L'Académie des Sciences* **251:** 1674–1676.

Juberthie C. 1961. Étude des opilions cyphophthalmes (arachnides) du Portugal: description d'*Odontosiro lusitanicus* g. n., sp. n. *Bulletin du Muséum National d'Histoire Naturelle, 2e série* **33:** 512–519.

Juberthie C. 1962. Étude des opilions cyphophthalmes Stylocellinae du Portugal. Description de *Paramiopsalis ramulosus* gen. n., sp. n. *Bulletin du Muséum National d'Histoire Naturelle, 2e série* **34:** 267–275.

Juberthie C. 1969. Sur les opilions cyphophthalmes Stylocellinae du Gabon. *Biologia Gabonica* **5:** 79–92.

Juberthie C. 1970a. Les genres d'opilions Sironinae (Cyphophthalmes). *Bulletin du Muséum National d'Histoire Naturelle, 2e série* **41:** 1371–1390.

Juberthie C. 1970b. Sur *Suzukielus sauteri* (Roewer, 1916) opilion cyphophthalme du Japon. *Revue d'Écologie et de Biologie du Sol* **7:** 563–569.

Juberthie C. 1979. Un cyphophthalme nouveau d'une grotte de Nouvelle-Caledonie: *Troglosiro aelleni* n. gen., n. sp. (Opilion, Sironinae). *Revue suisse de Zoologie* **86:** 221–231.

Juberthie C, Manier JF. 1976. *Les grands traits de la spermiogenese chez les opilions Comptes Rendus de la Troisième Réunion des Arachnologistes d'Expression Française. Station biologique des Eyzies*. Les Eyzies: Académie de Paris, 74–82.

Juberthie C, Manier JF. 1978. Étude ultratructurale comparée de la spermiogenèse des opilions et son intérêt phylétique. *Symposium of the Zoological Society of London* **42:** 407–416.

Juberthie C, Manier JF, Boissin L. 1976. Étude ultrastructurale de la double espermiogenèse chez l'opilion cyphophthalme *Siro rubens* Latreille. *Journal de Microscopie et de Biologie Cellulaire* **25:** 137–148.

Juberthie C, Massoud Z. 1976. Biogéographie, taxonomie et morphologie ultrastructurale des opilions cyphophthalmes. *Revue d'Écologie et de Biologie du Sol* **13:** 219–231.

Juberthie C, Muñoz-Cuevas A. 1970. Revision [sic] de *Chileogovea oedipus* Roewer (Opiliones: Cyphophthalmi: Sironinae). *Senckenbergiana biologica* **51:** 109–118.

Karaman IM. 2009. The taxonomical status and diversity of Balkan sironids (Opiliones, Cyphophthalmi) with descriptions of twelve new species. *Zoological Journal of the Linnean Society* **156:** 260–318.

Karamata S. 2006. The geological development of the Balkan Peninsula related to the approach, collision and compression of Gondwanan and Eurasian units. In: Robertson AHF, Mountrakis D, eds. *Tectonic development of the Eastern Mediterranean region*. London: Geological Society, 155–178.

Knapp M, Mudaliar R, Havell D, Wagstaff SJ, Lockhart PJ. 2007. The drowning of New Zealand and the problem of *Agathis*. *Systematic Biology* **56:** 862–870.

Kodandaramaiah U. 2011. Tectonic calibrations in molecular dating. *Current Zoology* **57:** 116–124.

Landis CA, Campbell HJ, Begg JG, Mildenhall DC, Paterson AM, Trewick SA. 2008. The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geological Magazine* **145:** 173–197.

Lawrence RF. 1931. The harvest-spiders (Opiliones) of South Africa. *Annals of the South African Museum* **29:** 341–508.

Lawrence RF. 1933. The harvest-spiders (Opiliones) of Natal. *Annals of the Natal Museum* **7:** 211–241.

Lawrence RF. 1939. A contribution to the opilionid fauna of Natal and Zululand. *Annals of the Natal Museum* **9:** 225–243.

Lawrence RF. 1963. The Opiliones of the Transvaal. *Annals of the Transvaal Museum* **24:** 275–304.

Legg G. 1990. *Parogovia pabsgarnoni*, sp. n. (Arachnida, Opiliones, Cyphophthalmi) from Sierra Leone, with notes on other African species of *Parogovia*. *Bulletin of the British Arachnological Society* **8:** 113–121.

Legg G, Pabs-Garnon EB. 1989. The life history of a tropical forest cyphophthalmid from Sierra Leone (Arachnida, Opiliones). In: Haupt J, ed. *Xi europäisches arachnologisches colloquium*. Berlin: Technische Universität Berlin, 222–230.

Linton EW. 2005. *MacGDE: Genetic Data Environment for MacOS X*, Version 2.0. Available at: http://www.msu.edu/~lintone/macgde/

Marshall BA. 2011. A new species of *Latia* Gray, 1850 (Gastropoda: Pulmonata: Hygrophila: Chilinoidea: Latiidae) from Miocene Palaeo-lake Manuherikia, southern New Zealand, and biogeographic implications. *Molluscan Research* **31:** 47–52.

Marske KA, Leschen RAB, Barker GM, Buckley TR. 2009. Phylogeography and ecological niche modelling implicate coastal refugia and trans-alpine dispersal of a New Zealand fungus beetle. *Molecular Ecology* **18:** 5126–5142.

Márton E, Cosovic V, Moro A, Zvocak S. 2008. The motion of Adria during the Late Jurassic and Cretaceous: new paleomagnetic results from stable Istria. *Tectonophysics* **454:** 44–53.

Murienne J. 2009. Testing biodiversity hypotheses in New Caledonia using phylogenetics. *Journal of Biogeography* **36:** 1433–1434.

Murienne J, Edgecombe GD, Giribet G. 2010a. Including secondary structure, fossils and molecular dating in the centipede tree of life. *Molecular Phylogenetics and Evolution* **57:** 301–313.

Murienne J, Edgecombe GD, Giribet G. 2011. Comparative phylogeography of the centipedes *Cryptops pictus* and *C. niuensis* in New Caledonia, Fiji and Vanuatu. *Organisms Diversity & Evolution* **11:** 61–74.

Murienne J, Giribet G. 2009. The Iberian Peninsula: ancient history of a hot spot of mite harvestmen (Arachnida: Opiliones: Cyphophthalmi: Sironidae) diversity. *Zoological Journal of the Linnean Society* **156:** 785–800.

Murienne J, Grandcolas P, Piulachs MD, Bellés X, D'Haese C, Legendre F, Pellens R, Guilbert E. 2005. Evolution of a shaky piece of Gondwana: is local endemism recent in New Caledonia? *Cladistics: The International Journal of the Willi Hennig Society* **21:** 2–7.

Murienne J, Karaman I, Giribet G. 2010b. Explosive evolution of an ancient group of Cyphophthalmi (Arachnida: Opiliones) in the Balkan Peninsula. *Journal of Biogeography* **37:** 90–102.

Murienne J, Pellens R, Budinoff R, Wheeler WC, Grandcolas P. 2008. Phylogenetic analysis of the endemic New Caledonian cockroach *Lauraesilpha*. Testing competing hypotheses of diversification. *Cladistics: The International Journal of the Willi Hennig Society* **24:** 802–812.

Nix HA. 1986. A biogeographic analysis of Australian elapid snakes. In: Longmore R, ed. *Australian flora and fauna series number 7. Atlas of elapid snakes of Australia*. Canberra: Australian Government Publishing Service, 4–15.

Nixon KC, Carpenter JM. 1996. On simultaneous analysis. *Cladistics: The International Journal of the Willi Hennig Society* **12:** 221–241.

Page TJ, Baker AM, Cook BD, Hughes JM. 2005. Historical transoceanic dispersal of a freshwater shrimp: the colonization of the South Pacific by the genus *Paratya* (Atyidae). *Journal of Biogeography* **32:** 581–593.

Pamic J, Gusic I, Jelaska V. 1998. Geodynamic evolution of the Central Dinarides. *Tectonophysics* **297:** 251–268.

Paris JP, Andreieff P, Coudray J. 1979. Sur l'âge Eocène supérieur de la mise en place de la nappe ophiolitique de Nouvelle-Calédonie. *Comptes rendus de l'Académie des sciences, série B* **288:** 1659–1661.

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography* **34:** 102–117.

Pelletier B. 2006. Geology of the New Caledonia region and its implications for the study of the New Caledonian biodiversity. In: Payri C, Richer de Forges B, eds. *Compendium of marine species from New Caledonia*. Doc. Sci. Tech. IRD. IRD, II 7, 17–30.

Phillips MJ, Gibb GC, Crimp EA, Penny D. 2010. Tinamous and moa flock together: mitochondrial genome sequence analysis reveals independent losses of flight among ratites. *Systematic Biology* **59:** 90–107.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190:** 231–259.

Phillips SJ, Dudik M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* **31:** 161–175.

Pocock RI. 1897. Descriptions of some new Oriental Opiliones recently received by the British Museum. *Annals and Magazine of Natural History, series 6* **19:** 283–292.

Poinar G. 2008. *Palaeosiro burmanicum* n. gen., n. sp., a fossil Cyphophthalmi (Arachnida: Opiliones: Sironidae) in Early Cretaceous Burmese amber. In: Makarov SE, Dimitrijevic RN, eds. *Advances in arachnology and developmental biology. Papers dedicated to Prof. Dr. Bozidar Curcic*. Vienna, Belgrade, Sofia: Faculty of Life Sciences, University of Vienna, and Serbian Academy of Sciences and Arts, 267–274.

Posada D. 2005. *Modeltest*, Version 3.7. Available at: http://darwin.uvigo.es

Posada D, Crandall KA. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics (Oxford, England)* **14:** 817–818.

Pyron RA. 2011. Divergence time estimation using fossils as terminal taxa and the origins of Lissamphibia. *Systematic Biology* **60:** 466–481.

Rambaut A, Drummond AJ. 2007. *Tracer*, Version 1.5. Available at: http://beast.bio.ed.ac.uk/Tracer

Rambla M. 1974. Consideraciones sobre la biogeografía de los Opiliones de la Península Ibérica. *Miscellanea Alcobé* **Special volume:** 45–56.

Rambla M. 1991. A new *Stylocellus* from some caves of Borneo, Malaysia (Opiliones, Cyphophthalmi, Stylocellidae). *Mémoires de Biospéologie* **18:** 227–232.

Rambla M. 1994. Un nouveau Cyphophthalme du sud-est asiatique, *Fangensis leclerci* n. gen. n. sp. (Opiliones, Sironidae). *Mémoires de Biospéologie* **21:** 109–114.

Rambla M, Fontarnau R. 1984. Les Opilions Cyphophthalmes (Arachnida) de la faune ibérique: I. Sur *Paramiopsalis ramulosus* Juberthie, 1962. *Revue Arachnologique* **5:** 145–152.

Rambla M, Fontarnau R. 1986. Les Opilions Cyphophthalmes (Arachnida) de la faune ibérique: III. Sur *Odontosiro lusitanicus* Juberthie, 1961. *Mémoirs de la Société royale belge d'Entomologie* **33:** 171–178.

Raven PH, Axelrod DI. 1972. Plate tectonics and Australasian paleobiogeography. *Science* **176:** 1379–1386.

Ree RH, Moore BR, Webb CO, Donoghue MJ. 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution* **59:** 2299–2311.

Ree RH, Smith SA. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* **57:** 4–14.

Roewer CF. 1916. 7 neue Opilioniden des Zoolog. Museums in Berlin. *Archiv für Naturgeschichte* **81:** 6–13.

Roewer CF. 1961. Opiliones aus Süd-Chile. *Senckenbergiana biologica* **42:** 99–105.

Sanmartín I. 2002. *A paleogeographic history of the Southern Hemisphere*. Uppsala: Uppsala University.

Sanmartín I, Ronquist F. 2004. Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology* **53:** 216–243.

Scheibner C, Speijer RP. 2008. Late Paleocene-early Eocene Tethyan carbonate platform evolution – a response

to long- and short-term paleoclimatic change. *Earth Science Reviews* **90**: 71–102.

Schoener TW. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**: 704–726.

Schwendinger PJ, Giribet G. 2005. The systematics of the south-east Asian genus *Fangensis* Rambla (Opiliones : Cyphophthalmi : Stylocellidae). *Invertebrate Systematics* **19**: 297–323.

Sharma P, Giribet G. 2005. A new *Troglosiro* species (Opiliones, Cyphophthalmi, Troglosironidae) from New Caledonia. *Zootaxa* **1053**: 47–60.

Sharma P, Giribet G. 2006. A new *Pettalus* species (Opiliones, Cyphophthalmi, Pettalidae) from Sri Lanka with a discussion on the evolution of eyes in *Cyphophthalmi*. *Journal of Arachnology* **34**: 331–341.

Sharma P, Giribet G. 2009a. A relict in New Caledonia: phylogenetic relationships of the family Troglosironidae (Opiliones: Cyphophthalmi). *Cladistics: The International Journal of the Willi Hennig Society* **25**: 279–294.

Sharma P, Karunarathna I, Giribet G. 2009. On the endemic Sri Lankan genus *Pettalus* (Opiliones, Cyphophthalmi, Pettalidae) with the description of a new species and a discussion on the magnitude of its diversity. *Journal of Arachnology* **37**: 60–67.

Sharma PP, Giribet G. 2009b. *The family Troglosironidae (Opiliones: Cyphophthalmi) of New Caledonia Zoologia Neocaledonica 7. Biodiversity Studies in New Caledonia*. Paris: **196**, 83–123.

Sharma PP, Giribet G. 2011. The evolutionary and biogeographic history of the armoured harvestmen – Laniatores phylogeny based on ten molecular markers, with the description of two new families of Opiliones (Arachnida). *Invertebrate Systematics* **25**: 106–142.

Sharma PP, Vahtera V, Kawauchi GY, Giribet G. 2011. Running $_{\mathrm{W}}$ILD: the case for exploring mixed parameter sets in sensitivity analysis. *Cladistics: The International Journal of the Willi Hennig Society* **27**: 538–549.

Shear WA. 1977. The opilionid genus *Neogovea* Hinton, with a description of the first troglobitic cyphophthalmid from the western hemisphere (Opiliones, Cyphophthalmi). *Journal of Arachnology* **3**: 165–175.

Shear WA. 1979a. *Huitaca ventralis*, n. gen., n. sp., with a description of a gland complex new to cyphophthalmids (Opiliones, Cyphophthalmi). *Journal of Arachnology* **7**: 237–243.

Shear WA. 1979b. *Stylocellus sedgwicki* n.sp., from Penang Island, Malaysia (Opiliones, Cyphophthalmida, Stylocellidae). *Bulletin of the British Arachnological Society* **4**: 356–360.

Shear WA. 1980. A review of the Cyphophthalmi of the United States and Mexico, with a proposed reclassification of the suborder (Arachnida, Opiliones). *American Museum Novitates* **2705**: 1–34.

Shear WA. 1985. *Marwe coarctata*, a remarkable new cyphophthalmid from a limestone cave in Kenya (Arachnida, Opiliones). *American Museum Novitates* **2830**: 1–6.

Shear WA. 1993a. The genus *Chileogovea* (Opiliones, Cyphophthalmi, Petallidae [sic]). *Journal of Arachnology* **21**: 73–78.

Shear WA. 1993b. The genus *Troglosiro* and the new family Troglosironidae (Opiliones, Cyphophthalmi). *Journal of Arachnology* **21**: 81–90.

Shear WA. 1993c. New species in the opilionid genus *Stylocellus* from Malaysia, Indonesia and the Philippines (Opiliones, Cyphophthalmi, Stylocellidae). *Bulletin of the British Arachnological Society* **9**: 174–188.

Shear WA, Gruber J. 1996. Cyphophthalmid opilionids new to Madagascar: two new genera (Opiliones, Cyphophthalmi, ?Pettalidae). *Bulletin of the British Arachnological Society* **10**: 181–186.

Shultz JW, Regier JC. 2001. Phylogenetic analysis of Phalangida (Arachnida, Opiliones) using two nuclear protein-encoding genes supports monophyly of Palpatores. *Journal of Arachnology* **29**: 189–200.

Simon E. 1872. Notice sur les Arachnides cavernicoles et hypogés. *Annales de la Société entomologique de France, 5e série* **2**: 215–244.

Smith SA, Donoghue MJ. 2010. Combining historical biogeography with niche modeling in the *Caprifolium* clade of *Lonicera* (Caprifoliaceae, Dipsacales). *Systematic Biology* **59**: 322–341.

de Souza Muñoz ME, De Giovanni R, Ferreira de Siqueira M, Sutton T, Brewer P, Scachetti Pereira R, Llange Canhos DA, Perez Canhos V. 2011. openModeller: a generic approach to species' potential distribution modelling. *Geoinformatica* **15**: 111–135.

Spagna JC, Álvarez-Padilla F. 2008. Finding an upper limit for gap costs in direct optimization parsimony. *Cladistics: The International Journal of the Willi Hennig Society* **24**: 787–801.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics (Oxford, England)* **22**: 2688–2690.

Stamatakis A, Hoover P, Rougemont J. 2008. A rapid bootstrap algorithm for the RAxML Web servers. *Systematic Biology* **57**: 758–771.

Suzuki S, Ohrui M. 1972. Opiliones of the Izu Peninsula, Central Japan. *Acta Arachnologica* **24**: 41–50. [In Japanese.

Thorell T. 1882–1883. Descrizione di alcuni Aracnidi inferiori dell' Arcipelago Malese. *Annali del Museo civico di Storia naturale di Genova* **18**: 21–69.

Thorell T. 1890–1891. Aracnidi di Pinang raccolti nel 1889 dai Sig.ri L. Loria e L. Fea. *Annali del Museo civico di Storia naturale di Genova* (Ser. 2a) **10**: 269–383.

Trewick SA, Paterson AM, Campbell HJ. 2007. Hello New Zealand. *Journal of Biogeography* **34**: 1–6.

Varón A, Sy Vinh L, Wheeler WC. 2010. POY version 4: phylogenetic analysis using dynamic homologies. *Cladistics: The International Journal of the Willi Hennig Society* **26**: 72–85.

Vlahovic I, Tisljar J, Velic I, Maticec D. 2005. Evolution of the Adriatic carbonate platform: palaeogeography, main events and depositional dynamics. *Palaeogeography Palaeoclimatology Palaeoecology* **220**: 333–360.

Wallis GP, Trewick SA. 2009. New Zealand phylogeography: evolution on a small continent. *Molecular Ecology* **18:** 3548–3580.

Warren DL, Glor RE, Turelli M. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* **62:** 2868–2883.

Warren DL, Glor RE, Turelli M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* **33:** 607–611.

Waters JM, Craw D. 2006. Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. *Systematic Biology* **55:** 351–356.

Westwood JO. 1874. *Thesaurus entomologicus oxoniensis; or, illustrations of new, rare, and interesting insects, for the most part contained in the collections presented to the University of Oxford by the Rev. F.W. Hope . . . with forty plates from drawings by the author*. Oxford: Clarendon Press.

Wheeler WC. 1995. Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data. *Systematic Biology* **44:** 321–331.

Wheeler WC. 1996. Optimization alignment: the end of multiple sequence alignment in phylogenetics? *Cladistics: The International Journal of the Willi Hennig Society* **12:** 1–9.

Wheeler WC. 2005. Alignment, dynamic homology, and optimization. In: Albert VA, ed. *Parsimony, phylogeny, and genomics*. Oxford: Oxford University Press, 71–80.

Wiens JJ. 2003. Missing data, incomplete taxa, and phylogenetic accuracy. *Systematic Biology* **52:** 528–538.

Wiens JJ. 2009. Paleontology, genomics, and combined-data phylogenetics: can molecular data improve phylogeny estimation for fossil taxa? *Systematic Biology* **58:** 87–99.

Wortmann UG, Weissert H, Funk H, Hauck J. 2001. Alpine plate kinematics revisited: the Adria problem. *Tectonics* **20:** 134–147.

SUPPORTING INFORMATION

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

Appendix S1. Specimen sampling. Detailed accounts of specimens and collecting data.

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APPENDIX

Table A1. Size of data matrices for each gene before and subsequent to treatment with GBLOCKS

Data partition	Number of positions after treatment with MUSCLE	Number of positions after treatment with GBLOCKS
16S rRNA	598	403
18S rRNA	1769	1769
28S rRNA	2267	2016
COI	820	657
Histone H3	327	327

Table A2. Lagrange analyses.

Subtree: Pettalidae
Areas:
(a) South Africa
(b) Chile
(c) Eastern Australia
(d) Western Australia
(e) New Zealand, Australian plate
(f) New Zealand, Pacific plate
(g) Sri Lanka

Geological intervals:
(1) 0–35 Ma (disconnection of all landmasses)
(2) 35–60 Ma (fragmentation of transantarctic connections between Australian plate and temperate South America)
(3) 60–75 Ma (disconnection of Australia and Zealandia)
(4) 75–110 Ma (disconnection of South America and West Africa)
(5) 110–120 Ma (Sri Lanka + Madagascar + India separated from Africa)
(6) 120–167 Ma (East Gondwana separated from West Gondwana)
(7) 167–184 Ma (connection of all landmasses)

Subtree: Sternophthalmi
Areas:
(a) Southeast USA
(b) Amazonia
(c) Tropical West Africa
(d) New Caledonia

Geological intervals:
(1) 0–35 Ma (disconnection of all three landmasses)
(2) 35–45 Ma (submersion of New Caledonia)
(3) 45–60 Ma (New Caledonia emergent and disconnected)
(4) 60–75 Ma (submersion of New Caledonia)
(5) 75–110 Ma (transantarctic connections between the Australian plate and temperate South America; disconnection of South America and West Africa)
(6) 110–206 Ma (connection of all landmasses)

Subtree: Boreophthalmi
Areas:
(a) Thai-Malay Peninsula
(b) Eastern Himalayas
(c) Borneo
(d) Indo-Malay Archipelago
(e) North America
(f) Western Europe
(g) Mediterranean
(h) Balkans
(i) Iberia
(j) Japan

Geological intervals
0–35 Ma (separation of Mediterranean plate from Western Europe; separation of Japan from Eurasia; connection of Iberia to Eurasia)
35–45 Ma (separation of Borneo and Indo-Malay Archipelago from Eurasia)
45–60 Ma (Balkans connected to Western Europe; Iberia connected to Mediterranean plate, Balkans and Japan)
60–75 Ma (Iberia separated from Mediterranean plate, Balkans and Japan; North America separated from Western Europe; emergence of Indo-Malay Archipelago)
75–110 Ma (Mediterranean plate separated from North America; Iberia connected to western Laurasia; Balkans separated from North America and Western Europe)
110–120 Ma (Iberia disconnected from other landmasses; Western Europe, Mediterranean plate and North America separated from Eastern Laurasia; emergence of Borneo; Indo-Malay Archipelago nonexistent)
120–180 Ma (Iberia disconnected from other landmasses; Western Europe, Mediterranean plate and North America separated from Eastern Laurasia; Borneo and Indo-Malay Archipelago nonexistent)
180–250 Ma (Thai-Malay Peninsula disconnected from other landmasses; Eastern Himalayas disconnected from North America, Western Europe and Iberia; Borneo and Indo-Malay Archipelago nonexistent)
250–296 Ma (Borneo and Indo-Malay Archipelago nonexistent; other landmasses connected)