A Phylogeny and Timescale for the Evolution of Pseudocheiridae (Marsupialia: Diprotodontia) in Australia and New Guinea

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Abstract Pseudocheiridae (Marsupialia: Diprotodontia) is a family of endemic Australasian arboreal folivores, more commonly known as ringtail possums. Seventeen extant species are grouped into six genera (Pseudocheirus, Pseudochirulus, Hemibelideus, Petauroides, Pseudochirops, Petropsuedes). Pseudochirops and Pseudochirus are the only genera with representatives on New Guinea and surrounding western islands. Here, we examine phylogenetic relationships among 13 of the 17 extant pseudocheirid species based on protein-coding portions of the ApoB, BRCA1, ENAM, IRBP, Rag1, and vWF genes. Maximum parsimony, maximum likelihood, and Bayesian methods were used to estimate phylogenetic relationships. Two different relaxed molecular clock methods were used to estimate divergence times. Bayesian and maximum parsimony methods were used to reconstruct ancestral character states for geographic provenance and maximum elevation occupied. We find robust support for the monophyly of Pseudocheirinae (Pseudochirus + Pseudocheirus), Hemibelidinae (Hemibelideus + Petauroides), and Pseudochiropsinae (Pseudochirops + Petropsuedes), respectively, and for an association of Pseudocheirinae and Hemibelidinae to the exclusion of Pseudochiropsinae. Within Pseudochiropsinae, Petropsuedes grouped more closely with the New Guinean Pseudochirops spp. than with the Australian Pseudochirops archeri, rendering Pseudochirops paraphyletic. New Guinean species belonging to Pseudochirops are monophyletic, as are New Guinean species belonging to Pseudocheirus. Molecular dates and ancestral reconstructions of geographic provenance combine to suggest that the ancestors of extant New Guinean Pseudochirops spp. and Pseudocheirus spp. dispersed from Australia to New Guinea ~12.1–6.5 Ma (Pseudochirops) and ~6.0–2.4 Ma (Pseudocheirus). Ancestral state reconstructions support the hypothesis that occupation of high elevations (>3000 m) is a derived feature that evolved on the terminal branch leading to Pseudochirops cupreus, and either evolved in the ancestor of Pseudocheirus forbesi, Pseudocheirus mayeri, and Pseudochirups caroli, with subsequent loss in P. caroli, or evolved independently in P. mayeri and P. forbesi. Divergence times within the New Guinean Pseudochirops clade are generally coincident with the uplift of the central cordillera and other highlands. Diversification within New Guinean Pseudocheirus occurred in the Plio-Pleistocene after the establishment of the Central Range and other highlands.

Keywords Marsupialia · New Guinea · Phylogenetic bracketing · Pseudocheiridae · Relaxed molecular clocks · Stratigraphic bounding

Introduction

The marsupial family Pseudocheiridae (Marsupialia: Diprotodontia) includes six extant genera (Pseudocheirus, Pseudocheirus, Pseudochirops, Petropsuedes, Hemibelideus, Pseudocheirus, Pseudochirops, Petropsuedes, Hemibelideus, Pseudochirops, Petropsuedes).
deus, Petauroidea) and 16 to 17 (Nowak and Dickman 2005; Groves 2005) species commonly known as ringtail possums. With the exception of Petauroidea, which has consistently been recognized as a genus, the other genera have variably been recognized as subgenera in Pseudocheirus (e.g., Tate 1945). Pseudocheirids inhabit mainland Australia, Tasmania, New Guinea, and islands (Japen, Salawatti) to the west of New Guinea, and commonly occur in montane rainforests. Four of the five Pseudochirrops species and five of the seven Pseudochirulus species are found only in New Guinea (Flannery 1995b; Fig. 1). Ringtail possums are arboreal folivores. Adaptations to arboreality include forcipate hands, in which the first two digits are at least partly opposable to the latter three, and a prehensile tail. Adaptations to folivory include selenodont molars and an enlarged cecum that acts as a fermentation chamber. In addition to extant pseudocheirid genera, extinct pseudocheirids have been referred to five genera: Paljara, Pildra, Marlu, Pseudokoala, and Gawinga (Woodburne et al. 1987; Bassarova and Archer 1999; Roberts et al. 2007, 2008, 2009). Paljara, Pildra, and Marlu are known from late Oligocene to early Miocene sediments in South Australia and Oligo-Miocene deposits of the Riversleigh World Heritage Area in Queensland (Woodburne et al. 1987; Bassarova and Archer 1999; Roberts et al. 2007). Pseudokoala is known from Plio-Pleistocene sediments in South Australia, Victoria, and Queensland (Turnbull and Lundelius 1970; Crosby et al. 2004). The fossil record of Gawinga is restricted to Riversleigh’s Faunal Zone B, which has been interpreted as early Miocene in age based on bio-correlation (Roberts et al. 2007).

The most comprehensive phylogenetic studies of Pseudocheiridae are based on microcomplement fixation studies with albumin (Baverstock et al. 1990b), single-copy DNA-DNA hybridization data (Springer et al. 1992), craniodental characters (Springer 1993), and concatenated nuclear gene sequences (Meredith et al. 2009a). Baverstock et al. (1990b) treated all pseudocheirid species except for Petauroidea volans as members of the genus Pseudocheirus, but their taxonomic sampling included representatives of all pseudocheirid genera as currently recognized by Groves (2005). Baverstock et al.’s (1990b) microcomplement fixation analyses provided support for three primary lineages: Pseudochirulus + Pseudocheirus, Hemibelideus + Petauroidea, and Pseudochirrops + Petropseudes (Baverstock et al. 1990b). Neither the New Guinean Pseudochirrops spp. nor Pseudochirulus spp., respectively, were recovered as monophyletic (Baverstock et al. 1990b). DNA-DNA hybridization analyses included representatives of all pseudocheirid genera (sensu Groves 2005) excepting Petropseudes, and provided additional support for Pseudochirulus + Pseudocheirus, Hemibelideus + Petauroidea, and Pseudochirrops domed
Cladistic analyses of craniodental characters are generally in agreement with microcomplement fixation and DNA-DNA hybridization results and supported a sister group relationship between *Petroseudes* and representative species of *Pseudocheiridae*, a sister group relationship between *Hemibelideus* and *Petauridae* (Springer 1993), and an association of *Pseudocheirus* with *Pseudochirulus* (Springer 1993). None of the cladistic analyses of craniodental characters recovered the New Guinean *Pseudochirops* spp. as monophyletic (Springer 1993). Groves (2005), following Kirsch et al. (1997), divided Pseudocheiridae into the subfamilies Pseudochirinae (*Pseudocheiridae*), Hemibelidinae (*Hemibelideus + Petauridae*), and Pseudocheirinae (*Pseudocheirus + Pseudochirulus + Petroseudes*), although it should be noted that whereas Groves included *Petroseudes* in Pseudocheirinae, the taxonomic affinities of *Petroseudes* were not explicitly addressed in Kirsch et al.’s (1997) classification. Analyses based on concatenated nuclear DNA sequences (Meredith et al. 2009a) are in general agreement with microcomplement fixation (Baverstock et al. 1990a, b), DNA-DNA hybridization (Springer et al. 1992; Kirsch and Springer 1993), and craniodental analyses (Springer 1993), and provide additional support for *Hemibelideus + Petauridae, Pseudocheirus + Pseudochirulus, and Petroseudes + Petroseudes*. However, *Pseudochirips* was found to be paraphyletic with *Petroseudes* grouping more closely to *Petroseudes cupreus* than to *Pseudochirips archeri* (Meredith et al. 2009a). As a result, Meredith et al. (2009a) suggested subsuming *Petroseudes dahli* into *Petroseudes as Pseudochirips (Petroseudes) dahli*. Furthermore, Meredith et al. (2009a) found strong support for a basal split between the *Pseudochirips + Petroseudes* clade and all other extant pseudocheirids.

Hypotheses in historical biogeography are informed and underpinned by robust phylogenetic hypotheses, accurate estimates of divergence times, and reliable paleogeographic reconstructions. The present distribution of pseudocheirids, as well as other marsupial groups that currently inhabit Australia and New Guinea, have been explained through elements of both vicariance and dispersal. Flannery (1988) suggested a vicariant origin for the New Guinean mammal fauna, but a robust phylogenetic hypothesis for interrelationships among Australasian mammals was not available. Flannery (1988) synthesized the paleogeographic works of Dow (1977), Pieters et al. (1983), and Dow and Sukamoto (1984), and suggested a continuous connection between southern New Guinea and northern Australia from the late Paleocene into the Oligocene, which allowed for extensive faunal interchange. Flannery (1988) further suggested that the connection between Australia and New Guinea was severed in the early Miocene, although he allowed for the possibility of infrequent interchange between the Australian and New Guinean mammal faunas via waif dispersal subsequent to the vicariant sundering of Australia and New Guinea. Tropical rainforest pseudocheirids are “extremely poor dispersers” (Flannery 1995a) as a consequence of their largely or strictly arboreal lifestyle (Pahl et al. 1988; Laurance 1990; Laurance and Laurance 1999), and are therefore among the least probable candidates for waif dispersal. Australia and New Guinea remained isolated from each other until the Pleistocene (Dow 1977), when eustatic lowering of sea level allowed for interchange between the Australian and New Guinean mammal faunas (Flannery 1988).

If Flannery’s (1988) hypothesis is correct, we should expect to find two sets of divergences dates between Australian and New Guinean taxa: (1) divergence dates that predate the Miocene and reflect the vicariant separation of Australia and New Guinea, and (2) divergence dates from the latest Pliocene/Pleistocene that reflect resurgent land connections that developed at this time in conjunction with eustatic lowering of sea level. Flannery’s (1988) hypothesis was subsequently tested by Aplin et al. (1993) with microcomplement fixation data, and Kirsch and Springer (1993) with single-copy DNA hybridization data. Aplin et al. (1993) suggested a complex history of faunal interchanges between Australia and New Guinea in the Miocene (12–10 Ma) and Plio–Pleistocene (4.7–2.7 Ma) based on an albumin molecular clock and microcomplement fixation trees that contradicted the monophyly of New Guinean species of *Pseudochirlops* and *Pseudochirulus*, respectively. Kirsch and Springer (1993) included a smaller number of taxa and suggested that representative Australian species belonging to *Pseudochirlops* (*P. archeri*) and *Pseudochirulus* (*P. herbertensis*) separated from their New Guinean congeners (*Pseudochirlops cupreus* and *Pseudochirulus forbesi*) 10.3 Ma and 10.9 Ma, respectively. Thus, the molecular studies of both Aplin et al. (1993) and Kirsch and Springer (1993) suggest the possibility of land bridges between Australia and New Guinea during the Miocene (Aplin et al. 1993; Kirsch and Springer 1993), or that marsupials are better dispersers than has previously been thought (Kirsch and Springer 1993). In support of possible land connections in the late Tertiary, Aplin et al. (1993) cited Pigram et al. (1989) and Davies (1990). Pigram et al. (1989) found that carbonate sedimentation on the Papuan platform was progressively replaced by more clastic deposition during the late Tertiary, and that clastic deposition terminated with widespread paralic sedimentation in the Pliocene. Davies (1990) found Miocene paraconformities in the stratigraphy of the Papuan platform that “could well represent depositional hiatuses” (Aplin et al. 1993: 142). These paraconformities date to 9 Ma and 4.5 Ma, and are in the range of Aplin et al.’s (1993) estimated dates for marsupial dispersal events. The main difficulty with
previous molecular studies that have reconstructed the historical biogeography of pseudocheirids is that they have not been underpinned by a robust phylogeny that includes extensive taxonomic sampling.

The evolutionary history of the New Guinean mammal fauna has been impacted not only by vicariance/dispersal events, but also by tectonic forces that have shaped New Guinea’s physiography. New Guinea is a type locality of island arc-continent collision that occurred during the Cenozoic (van Ufford and Cloos 2005). The geological history of New Guinea is complex, and the number and timing of Cenozoic tectonic events has been debated (van Ufford and Cloos 2005). Tectonic models of New Guinea range from one discrete collisional event to prolonged and piecemeal accretion involving at least 32 distinct tectono-stratigraphic terranes (reviewed in van Ufford and Cloos 2005). The most recent synthesis of available geological data (Cloos et al. 2005; van Ufford and Cloos 2005) suggests that the Cenozoic tectonic history of New Guinea involved two distinct orogenic events. The first event, the Peninsular orogeny of Oligocene age (~35–30 Ma), was restricted to the Papuan Peninsula in easternmost New Guinea and created the Peninsular Range. The second event, the Central Range orogeny, commenced in the latest middle Miocene and resulted in the mountainous spine of New Guinea that extends from the Bird’s Neck region to the Papuan Peninsula (van Ufford and Cloos 2005). By about 5 million years ago, the central cordillera in western New Guinea included topography that was between 3000 and 5000 m high. New Guinea has distinct zoogeographic provinces, which roughly correspond to its geological provinces (Flannery 1995b). Within these zoogeographic provinces, species belonging to Pseudochiropus and Pseudochirulus both show altitudinal zonation (Table 1; Fig. 1) that has been shaped by climate and possibly species competition (Flannery 1995b). Up to four pseudocheirid species, each in a distinct weight class and with unique nesting habits, are known to exist sympatrically in New Guinea (Flannery 1995b; Fig. 1).

In this paper, we use a nuclear protein-coding DNA data set to infer a phylogeny and timescale for 13 extant pseudocheirids. We also perform relaxed clock analyses and ancestral state reconstructions for geographic provenance to determine the number and timing of dispersal events to New Guinea within the Pseudochirulus and Pseudochiropus clades. Finally, we combine phylogeny, divergence times, reconstructions of geographic provenance and maximum elevation occupied, and recent information on the geological history of New Guinea to evaluate whether or not pseudocheirid species diversified in synchrony with the uplift of the New Guinean cordillera and highlands or filled in habitats with pre-existing altitudinal differentiation.

### Materials and methods

#### Taxon sampling

We included 13 of 17 recognized pseudocheirid species (Groves 2005) and nine marsupial outgroups with representatives from all other petauroid families (Acrobatidae, Petauridae, Tarsipedidae). Previous molecular studies provide robust support for petauroid monophyly (Springer and Kirsch 1991; Kirsch et al. 1997; Kavanagh et al. 2004; Phillips and Pratt 2008; Meredith et al. 2009a; Springer et al. 2009). Taxon sampling and GenBank accession numbers are given in Table 2.

#### Gene sampling

Genomic DNA was extracted following Meredith et al. (2009a). Portions of protein coding regions of six nuclear genes that were used in this study were chosen based on their utility in previous mammalian phylogenetic studies (Amrine-Madsen et al. 2003; Meredith et al. 2008a, b, c; Meredith et al. 2009a, b, c). ApoB, BRCA1, IRBP, Rag1, and vWF were amplified, cleaned, and sequenced following the protocols outlined in Meredith et al. (2009a). Approximately 900 bp of the 5’ end of exon 10 of the enamelin gene (ENAM) were amplified, cleaned, and sequenced following the protocols outlined in Meredith et al. (2009b).

#### Alignments

We identified alignment ambiguous regions using SOAP v1.2a4 (Löytynoja and Milinkovitch 2001) with gap opening (11–19) and gap extension (3–11) penalties in steps of two (25 total alignments). Prior to the removal of the alignment ambiguous regions, the resultant alignment was manually re-aligned with Se-Al (Rambaut 1996) to keep gaps in synchrony with codons. We removed entire codon positions from the alignment in cases where partial codons were included in the ambiguous region. Twenty-one base pairs were identified and removed from the BRCA1 alignment. The remaining 6928 sites were retained for subsequent analyses (ApoB=760 sites; BRCA1=2477 sites; ENAM=900 sites; IRBP=1276 sites; Rag1=544 sites; vWF=971 sites). The aligned nexus file is given in Supplementary Information.

#### Data compatibility

Bootstrap compatibility tests (de Queiroz 1993; Teeling et al. 2002) were performed with RAXML 7.0.4 (Stamatakis 2006) to assess the appropriateness of combining individual gene segments into a concatenated data set. Bootstrap analyses for each gene segment included 500 bootstrap...
Table 1  Geographic range, habitat, diet, and altitudinal for Australian and New Guinean pseudocheirids included in this study (data from Tate 1945; Thomson and Owen 1964; Flannery 1995b; Meynecke 2004; Helgen 2007a, b)

| Geographic Range | Habitat | Diet | Altitude (meters) |
|------------------|---------|------|-------------------|
| *Pseudocheirus peregrinus* | Parts of Queensland, New South Wales, Victoria, South Australia, and Tasmania | Scrub, sclerophyll forest, rainforest | Mostly leaves, but also flowers and fruits (dietary preferences vary geographically) | Sea level—1500 |
| *Pseudocheirulus herbertensis* | Queensland (between Ingham and Cairns) | Tropical rainforest; occasionally tall open forests of Flooded Gum that fringe rainforests | Mostly leaves | >350 m |
| *Pseudocheirulus canescens* | Widespread throughout lowland New Guinea | Lowland forests | Mosses, ferns, lichens, leaves | Sea level—1700 |
| *Pseudocheirulus caroli* | Irian Jaya (Weyland Range, Noord River basin, Baliem Valley, Maokop Range) | Noord River basin, Weyland Range, Baliem Valley, Noord River basin, Weyland Range, Baliem Valley, | No information | 0-2200 |
| *Pseudocheirulus moyeri* | New Guinean central cordillera | Moss forests | Leaves, mosses, ferns, lichens, fungus, and pollen | 1200–4200 (most abundant > 2000) |
| *Pseudocheirulus forbesi* | Eastern half of the New Guinean central cordillera, Vogelkop Peninsula North Coast Ranges, Huon Peninsula | Montane forests | Primarily leaves, includes those of Medinella | 450–3800 |
| *Hemibelideus lemuroides* | Queensland (between Ingham and Cairns, Mount Carbine Tableland) | Tropical rainforest | Mostly leaves; also certain flowers and the outer covering of the yellow walnut | >450 |
| *Petauroides volans* | Eastern Australia (Queensland, New South Wales, Victoria) | Sclerophyll forest | Almost exclusively eucalypt leaves | >1000 |
| *Petropseudes dahli* | Western Australia (northeastern Kimberley region), Northern Territory (Katherine and Roper Rivers region, Groote Eylandt), Queensland (northwestern region) | Rocky outcrops | Flowers, fruits, leaves | <1000 |
| *Pseudochirops archeri* | Queensland (between Paluma and the Mount Windsor Tableland, west of Mossman) | Tropical rainforest | Almost exclusively leaves, mainly from several species of fig | 300–1200 |
| *Pseudochirops corinnae* | Huon Peninsula, New Guinean central cordillera | Lower montane rainforest | Primarily leaves | 900–2900 (most common at 1800–2200) |
| *Pseudochirops cupreus* | New Guinean central cordillera; Wissel Lakes Region | Rainforest; scrub and herbfield at 3700 m in Prinz Wilhelm V Range in Irian Jaya | Primarily leaves | 1350–4000 (most common above 2500) |
| *Pseudochirops albertisii* | New Guinea (Arfak Mountains, Weyland Range, North Coast Ranges), Japen Island | Lower montane rainforest | Known stomach contents include leaves, fruits, and buds of *Ficus* sp. | 300–2500 |
replicates, and either the GTR+Γ (ApoB, BRCA1, ENAM) or GTR+I+Γ (IRBP, Rag1, vWF) model of sequence evolution (see Phylogenetic analyses). All bootstrap analyses were started from randomized MP starting trees, employed the fast hill-climbing algorithm, and estimated free model parameters. No conflicting nodes were found at or above the 90% bootstrap support level. PAUP 4.0b10 (Swofford 2002) was used to implement the partition homogeneity test (Farris et al. 1994) with six partitions corresponding to each of the gene segments, 1000 replicates, and ten taxon input orders per replicate. The results of the partition homogeneity test were significant (p=0.003). However, Cunningham (1997), Barker and Lutzoni (2002), and Darlu and Lecointre (2002) suggested that a significance threshold of 0.05 might be too conservative for the partition homogeneity test; Cunningham (1997) suggested using a critical alpha value between 0.01 and 0.001. In contrast to Cunningham (1997) and others, Dowton and Austin (2002) showed that the partition homogeneity test sometimes results in estimates of congruence that are too high. Given the conflicting results reported above for the bootstrap compatibility and partition homogeneity tests, and the uncertainty associated with interpreting the results of partition homogeneity tests, we chose to combine the six individual gene segments into a single concatenation based on the results of bootstrap compatibility tests.

### Phylogenetic analyses

Maximum likelihood (ML), Bayesian, and maximum parsimony (MP) analyses were performed with RAxML (7.0.4) (Stamatakis 2006), MrBayes v3.1.1 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003), and PAUP 4.0b10 (Swofford 2002), respectively. Gaps were treated as missing data in all analyses. ML bootstrap analyses employed 500 replicates. MP bootstrap analyses implemented 1000 replicates, 10 randomized taxon input orders per replicate, and tree-bisection and reconnection branch swapping.

### Table 2 GenBank accession numbers and taxonomy followed in this study. New sequences are indicated with asterisks

| TAXON | ApoB       | BRCA1      | IRBP        | Rag1        | vWF         | ENAM         |
|-------|------------|------------|-------------|-------------|-------------|--------------|
| Petauroidea |            |            |             |             |             |              |
| Petauridae |            |            |             |             |             |              |
| Petaurus breviceps | AY243433 | EU160443   | AY243441    | AY243400    | AY243417    | GU199289*    |
| Petaurus norfolcensis | FJ623979 | FJ623999   | FJ624017    | FJ624041    | FJ624065    | GU199290*    |
| Petaurus abidi | GU199269* | GU199275*  | GU199303*   | GU199309*   | GU199315*   | GU199288*    |
| Gymnobelideus leadbeateri | FJ623975 | EFO25766   | FJ624013    | FJ624037    | FJ624061    | GU199285*    |
| Dactylopsila palpatior | FJ623972 | FJ623994   | FJ624010    | FJ624034    | FJ624058    | GU199282*    |
| Dactylopsila trivirgata | FJ623973 | FJ623995   | FJ624011    | FJ624035    | FJ624059    | GU199283*    |
| Pseudocheiridae |            |            |             |             |             |              |
| Hemibelideus lemuroides | FJ623976 | FJ623997   | FJ624014    | FJ624038    | FJ624062    | GU199286*    |
| Petauridae |            |            |             |             |             |              |
| Acrobates pygmaeus | FJ603115 | FJ603119   | FJ603126    | FJ603131    | FJ603136    | GU199281*    |
| Distoechurus pennatus | FJ623974 | FJ623996   | FJ624012    | FJ624036    | FJ624060    | GU199284*    |

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For the ML and Bayesian analyses we performed partitioned analyses, which allowed each gene to have its own parameters, and non-partitioned analyses, which treated the concatenation as a single gene. In addition, we performed a ML analysis on each gene segment. Best-fit models of molecular evolution were chosen using the Akaue Information Criterion as implemented in Modeltest 3.06 (Posada and Crandall 1998). Models chosen were GTR+Γ (ApoB); TVM+Γ (BRCA1); HKY+Γ (ENAM); TVM+I+Γ (IRBP); TIM+I+Γ (Rag1); TrNef+I+Γ (vWF); GTR+I+Γ (concatenation). If the model of sequence evolution suggested by Modeltest was not available in MrBayes, we used the next most general model. RAxML only implements the GTR substitution matrix, and the results of Modeltest were only used to inform the possible inclusion of a rate-heterogeneity parameter (Γ or Γ+I). ML analyses were started from randomized MP starting trees, employed the fast hill-climbing algorithm, and estimated free model parameters. Bayesian analyses used default settings for priors, random starting trees, eight Markov chains (seven hot and one cold) sampled every 1000 generations, and were terminated once the average standard deviation of the split frequencies for the simultaneous analyses fell below 0.01 (at least 5 million generations).

Molecular dating analyses

The likelihood ratio statistic rejected the molecular clock hypothesis for each of the six genes and the concatenation (P<0.001). We therefore employed two relaxed clock Bayesian methods, BEAST v1.4.8 (Drummond et al. 2006; Drummond and Rambaut 2007) and Multidivtime (version 9-25-03; Kishino et al. 2001; Thorne and Kishino 2002), to estimate posterior probabilities of divergence times. BEAST v1.4.8 allows for the incorporation of multiple constraints from the fossil record, simultaneously estimates both the phylogeny and divergence times, allows for complex models of molecular evolution, does not assume that rates among lineages are correlated, and permits both “soft” and “hard” bounded constraints (Hedges and Kumar 2004; Yang and Rannala 2006). In contrast, Multidivtime requires a rooted tree topology, only allows for fixed minimum and maximum constraints, and assumes autocorrelated rates of molecular evolution among lineages (Thorne et al. 1998; Kishino et al. 2001; Thorne and Kishino 2002).

The data set was treated both as non-partitioned (one model of sequence evolution for all genes) and partitioned (individual models of sequence evolution for each gene). Modeltest (Posada and Crandall 1998) was used to guide model selection for BEAST analyses, with the caveat that BEAST only implements two substitution models [HKY (two rates); GTR (six rates)], with or without a gamma distribution of rates and an allowance for a proportion of invariant sites. If Modeltest suggested more than two substitution rates, but fewer than six substitution rates, we used the more general GTR model.

Analyses with BEAST v1.4.8 implemented the uncorrelated lognormal distribution (UCLN) model, which draws the rate of each lineage independently from a lognormal distribution, with a Yule tree prior. For both the non-partitioned and partitioned data sets, BEAST analyses were run for 30 million generation with sampling every 1000 generations and a burnin of three million generations. Tracer v1.4.1 (Drummond and Rambaut 2007) was used to inspect stationarity/mixing and to verify that the estimated sample size was greater than 200 for all parameters. In soft-bounded analyses, prior probabilities for fossil-calibrated nodes followed a normal distribution, with 95% of the distribution between the specified minima and maxima and 2.5% in each tail. We also performed hard-bounded analyses that employed uniform priors with fixed minima and maxima on the calibrated nodes. The monophyly of the ingroup (Tarsipedidae+Petauridae+Pseudocheiridae) was constrained, but monophyly was not constrained for any other nodes.

For the Multidivtime analyses, we used the topology shown in Figs. 2 and 3 with Acrobatidae as the outgroup. We employed the F84+Γ model of sequence evolution (Swofford et al. 1996) which is the most complicated model implemented by Multidivtime. Among-site rate heterogeneity was approximated with four discrete categories for the Γ distribution, which along with the transition/transversion parameter were estimated with Paup 4.0b10 (Swofford 2002). Branch lengths were estimated with estbranches. We used 38.2 million years as the mean age of the prior distribution for the base of Tarsipedidae+Petauridae+Pseudocheiridae based on a previous molecular estimate for the age of this clade (Meredith et al. 2009a). We set the mean prior for the rate of molecular evolution at the ingroup root node equal to the median amount of evolution from the ingroup root node to the ingroup tips divided by the mean age of the prior distribution for the root of Tarsipedidae+Petauridae+Pseudocheiridae. All analyses were run for one million generations with chain sampling every 100 generations and a burnin of 100,000 generations.

Fossil constraints

We used minimum and maximum age constraints for nine different nodes (Fig. 4). Node numbers in Fig. 4 correspond to labeled nodes on the chronogram in Fig. 5. For the Multidivtime analyses, the minimum and maximum constraints for nodes 1 and 9 were not available because the outgroup (Acrobatidae) was trimmed from the tree by estbranches prior to running Multidivtime. Woodburne et al.
(1993), Myers and Archer (1997), Gradstein et al. (2004), Archer et al. (2006), and Travouillon et al. (2006) were used for biocorrelation and geologic dates of Australasian deposits. The age of Riversleigh Faunal Zone A is based on Myers and Archer’s (1997) correlation of this unit to the Ngama Local Fauna, which Woodburne et al. (1993) dated at 25.0–24.7 Ma. The ages of Riversleigh Faunal Zones B (23.03–15.97 Ma) and C (15.97–11.61 Ma) are based on correlations with Gradstein et al.’s (2004) timescale. Fossils from Mt. Etna were given ages in millions of years based on their presumed epoch (e.g. middle Pleistocene ∼0.5 Ma; Hocknull et al. 2007). Minimum ages were assigned based on the age of the oldest unequivocal fossil belonging to a given clade (Fig. 4). Maximum ages were assigned based on the maximum of stratigraphic bounding (Benton and Donoghue 2007), phylogenetic bracketing (Reisz and Müller 2004; Müller and Reisz 2005), and phylogenetic uncertainty. Stratigraphic bounding uses the age of underlying fossil-bearing deposits that lack fossils for a given clade to establish a maximum age; phylogenetic bracketing uses the age of the oldest fossils for the next node below a divergence event to establish a maximum age; and phylogenetic uncertainty allows that the age of a clade may be as old as described fossils of uncertain phylogenetic affinity that may or may not belong to a clade. Hedges et al. (2006: 770) correctly point out a limitation of the phylogenetic bracketing approach, i.e., that the oldest fossil of the most closely related group is “only a minimum for its own lineage and the true maximum—and splitting event—could be much older.” Viewed another way, the fossil of the

![Bayesian tree obtained from the gene partitioned Bayesian analysis. Values above and below branches correspond to the mean Bayesian posterior probabilities (expressed as percentages) based on the two simultaneous runs, and ML bootstrap support percentages for the RAxML gene-partitioned analysis, respectively.](image-url)
The maximum may turn out to be older based on other criteria such as stratigraphic bounding and/or phylogenetic uncertainty. Given the sketchy record of Australasian mammal fossils, we followed Meredith et al.’s (2008b) recommendations and did not restrict stratigraphic bounding to the immediately underlying fossil-bearing deposit or the sister group (= 1st outgroup), respectively. Rather, the maximum age based on stratigraphic bounding encompassed two successive underlying fossil-bearing deposits that did not contain any fossils from the lineage of interest. Similarly, phylogenetic bracketing encompassed the age of the oldest fossils that were up to two nodes below the divergence event (i.e., the oldest fossils belonging to either the 1st or 2nd outgroup) to establish a maximum age (see Fig. 4; Table 3). All fossils that were incorporated into our compendium of minimum and maximum constraints were personally examined by us (K.K.R.) or were obtained from fully described/figured specimens in refereed articles. In cases where the oldest fossil was from a late Oligocene site, we used the age of the Tingamarra Local Fauna near

**Fig. 3** Maximum likelihood phylogram obtained from the RAxML gene partitioned analysis (GTR+I+ model of sequence evolution) using protein-coding portions of ApoB, BRCA1, ENAM, IRBP, Rag1, and vWF.
Murgon (54.6±0.05 Ma; Godthelp et al. 1992; Beck et al. 2008), as this is the only marsupial-bearing deposit in Australasia that pre-dates the late Oligocene.

a. Node 1 (Acrobatidae): The oldest described/figured acrobatids (*Acrobates* sp.) come from Mount Etna deposits in Queensland (∼0.50–0.28 Ma; Hocknull 2005; Hocknull et al. 2007). Putative acrobatids have been reported from Riversleigh (23.03–15.97 Ma; Archer et al. 1999), but these fossils have not been formally described/figured and were not reported in Archer et al. (2006). As a result, the Riversleigh acrobatids were not used as fossil constraints in our analyses. The oldest described tarsipedid, pseudocheirid, or petaurid, which together comprise the 1st outgroup, are the pseudocheirids *Paljara* sp. A from Zone A of the Etadunna Formation (25.7–25.5 Ma; Woodburne et al. 1993), and *Pildra antiquus* from the Pinpa Local Fauna of the Namba Formation, which has been biocorrelated with Zone A of the Etadunna Formation (Woodburne et al. 1987, 1993). We used a minimum of 0.28 Ma and a maximum of 25.7 Ma (phylogenetic bracketing) for node 1.

b. Node 2 (Petauridae): Fossils belonging to *Petaurus* sp. have been described from a Pliocene Hamilton Local Fauna (4.46±0.1 Ma; Turnbull et al. 2003) in Victoria. Turnbull et al. (2003: 534) note that the Hamilton *Petaurus* fossils include individual specimens that are near living *P. norfolcensis*, *P. breviceps*, and *P. australis*, but also allow for the possibility that all of the Hamilton *Petaurus* specimens belong to “one highly variable species.” Fossils of *Dactylopsila* spp. have been described from Queensland (Mount Etna; ∼0.5–0.28 Ma; Hocknull 2005; Hocknull et al. 2007). Fossils belonging to *Dactylopsila* sp. have also been reported from Riversleigh (15.97–11.61 Ma, Archer et al. 1999), but these fossils have yet to be described/figured and were not reported in Archer et al. (2006). As a result, the Riversleigh *Dactylopsila* sp. was not

![Fig. 4 Visual representation of the methodology used to determine fossil constraints employed in this study. Fossil/Faunal zones used to determine the oldest representative of a given lineage are given in Table 3. Ages of epoch boundaries are based on Gradstein et al. (2004). Plio.=Pliocene; Pl.=Pleistocene.](image-url)

Table 3. Ages of epoch boundaries are based on Gradstein et al. (2004). Plio.=Pliocene; Pl.=Pleistocene.
used as a fossil constraint in our analyses and we used a minimum of 4.36 Ma for node 2. *Paljara* sp. A and *Pildra antiquus* are the oldest representatives of the first outgroup, Pseudocheiridae (see node 1), and establish a maximum of 25.7 Ma (phylogenetic bracketing) for node 2.

c. Node 3 (Pseudocheiridae): The oldest described crown pseudocheirids are from the Hamilton Local Fauna (4.46 Ma; Turnbull et al. 2003; see nodes 5–6) and Pliocene Bluff Downs Local Fauna (3.6 Ma; Mackness et al. 2000; Mackness and Archer 2001; see node 5). We used a minimum of 4.36 Ma for node 3. The oldest stem pseudocheirids (1st outgroup) are *Paljara* sp. A and *Pildra antiquus* (25.7–25.5 Ma; Woodburne et al. 1993). We used a maximum of 25.7 Ma (phylogenetic bracketing) for node 3.

**Fig. 5** Timeline in millions of years before present for pseudocheirid evolution based on the BEAST partitioned analysis. Grey bars indicate 95% highest posterior densities. Numbers within open circled nodes indicate calibrated nodes. Plio. = Pliocene; Pl. = Pleistocene.
d. Node 4 (Petropseudes+Pseudochirops): Two Pseudochirops spp. have been reported from Riversleigh Faunal Zone C deposits (15.97–11.61 Ma; Archer et al. 2006). These species have since been identified as belonging to an extinct, undescribed genus (Roberts et al. unpublished). Pseudochirops winteri from the Pliocene Bluff Downs Local Fauna (3.62 ± 0.5 Ma; Mackness et al. 2000; Mackness and Archer 2001) is the oldest described member of Pseudochirops. Petropseudes dahli has been reported from Riversleigh Pliocene Rackham’s Roost Site (5.3–2.6 Ma; Archer et al. 1997). The fossil has yet to be described or figured, but is included in Archer et al. (2006) and is the only fossil record for Petropseudes. One of us (K.K.R.) has examined the putative Petropseudes specimen and considers that whereas it could belong to Petropseudes, there is insufficient material to confirm this identification. The specimen should therefore be considered Pseudocheiridae gen. et sp. indet., and the presence of Petropseudes cannot be assumed for the Pliocene. The oldest described fossils of Pseudocheirinae or Hemibelidinae, which together comprise the 1st outgroup, are from the Hamilton Local Fauna (4.46±0.1 Ma; Turnbull et al. 2003). The oldest described stem pseudocheirids (2nd outgroup) are Paljara sp. A and Pildra antiquus (25.7–25.5 Ma; Woodburne et al. 1993). We used a minimum of 3.12 Ma and a maximum of 25.7 Ma (phylogenetic bracketing) for node 4.

e. Node 5 (Hemibelideus+Petauroides): Petauroides spp. (Mount Etna; ~0.5–0.28 Ma; Hocknull 2005; Hocknull et al. 2007) and Petauroides stirtoni (Hamilton Local Fauna; 4.46±0.1 Ma; Turnbull et al. 2003) are the

Table 3 Fossil localities that were utilized in determining minimum and maximum fossil constraints

| Fossil/Faunal Zone Local Fauna | Reference(s) |
|--------------------------------|--------------|
| Cave Sites (late Pleistocene)  | Long et al. 2002 |
| Mt. Etna deposits (~0.28–0.50 Ma) | Hocknull 2005; Hocknull et al. 2007 |
| Late Pliocene to early Pleistocene | Piper et al. 2006 |
| Childer’s Cove (~1.81–2.59 Ma)  | Rich 1991 |
| Dog Rocks Local Fauna (~1.81–2.59 Ma) | Rich 1991; Tedford et al. 1992 |
| Awe Local Fauna New Guinea (2.59–3.60 Ma) | Rich 1991 |
| Chinchilla Sands (3.4 Ma)       | Rich 1991 |
| Curramulka Local Fauna (3.6 Ma) | Rich 1991 |
| Bow Local Fauna (3.62 Ma)       | Rich 1991 |
| Kanunka Local Fauna (3.4 Ma)    | Rich 1991 |
| Bluff Downs Local Fauna (3.62 Ma) | Rich 1991; Mackness et al. 2000; Mackness and Archer 2001 |
| Rackham Roost Site (~2.6–5.3 Ma) | Archer et al. 2006 |
| Coimadai Local Fauna (3.60–5.33 Ma) | Piper et al. 2006 |
| Hamilton Local Fauna (4.46±0.1 Ma) | Turnbull et al. 2003; Tedford et al. 2006 |
| Riversleigh Two Trees Site (~2.6–5.3 Ma) | Archer et al. 2006 |
| Late Miocene                    | Megirian et al. 1996; Murray and Megirian 1992 |
| Alcoota/Ongeva Local Fauna (~7–8 Ma) | Archer et al. 2006 |
| Riversleigh Encore Local Fauna (~10 Ma) | Murray and Megirian 1992 |
| Middle Miocene                 | Archer et al. 2006 |
| Riversleigh Faunal Zone C (11.61–15.97 Ma) | Archer et al. 2006 |
| Early Miocene                  | Archer et al. 2006 |
| Late Oligocene                 | Tedford and Kemp 1998 |
| Geilston Bay Deposits (23±0.5 Ma) | Megirian et al. 2004 |
| Kangaroo Well Local Fauna (~23.03 Ma) | Woodburne et al. 1993 |
| Etadunna Formation (24.2–25.7 Ma) | Rich 1991; Woodburne et al. 1993 |
| Namba Fm (~equivalent to Etadunna Fm) | Archer et al. 2006 |
| Riversleigh Faunal Zone A (24.7–25.0 Ma) | Godthelp et al. 1992 |

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oldest described species of either Hemibelideus or Petauroidea. We used a minimum of 4.36 Ma for node 5. All of the described fossils belonging to the 1st outgroup (Pseudocheirinae) and 2nd outgroup (Pseudochirops + Petropseudes) are ≤4.46 Ma, so we used a maximum of 15.97 Ma for node 5 based on stratigraphic bounding (Fig. 4).

f. Node 6 (Pseudochirulus + Pseudocheirus): Pseudochirulus sp. 1 (Mount Emu; ~0.5–0.28 Ma; Hocknull et al. 2005; Hocknull et al. 2007), Pseudocheirus marshalli (Hamilton Local Fauna; 4.46±0.1 Ma; Turnbull et al. 2003), and Pseudocheirus spp. (Mount Emu; ~0.5–0.28 Ma; Hocknull et al. 2007) are the oldest described species belonging to Pseudochirulus or Pseudocheirus. We used a minimum of 4.36 Ma for node 6. All of the described fossils belonging to the 1st outgroup (Hemibelidinae) and 2nd outgroup (Pseudochirops + Petropseudes) are ≤4.46 Ma, so we used a maximum of 15.97 Ma for node 6 based on stratigraphic bounding (Fig. 4).

g. Node 7 (Petauridae + Pseudocheiridae): The oldest described fossils belonging to Petauridae or Pseudocheiridae are Paljara sp. A and Pildra antiquus (25.7–25.5 Ma; Woodburne et al. 1993; see node 3). Extinct pilkipildrids are sometimes included in an unresolved crown-clade with petaurids and pseudocheirids (Crosby et al. 2004), but the fossil record of pilkipildrids only extends as far back as the fossil record of pseudocheirids. The oldest fossils belonging to Tarsipedidae (1st outgroup) and Acrobatidae (2nd outgroup) are much younger than the oldest pseudocheirids. No petaurids are known from the Tingamarra Local Fauna near Murgon (54.6±0.05 Ma; Godthelp et al. 1992; Beck et al. 2008). We used a minimum of 25.5 Ma and a maximum of 54.65 Ma (stratigraphic bounding) for node 7.

h. Node 8 (Tarsipedidae + Petauridae + Pseudocheiridae): The earliest fossils belonging to Tarsipedidae are late Pleistocene in age (Long et al. 2002). The oldest fossils belonging to Petauridae or Pseudocheiridae and Paljara sp. A and Pildra antiquus (25.7–25.5 Ma; Woodburne et al. 1987, 1993). The oldest fossils belonging to Acrobatidae (1st outgroup) or Australoplagiaulacoida (2nd outgroup) are stem kangaroos from Zone A of the Etadunna Formation (25.7–25.5 Ma; Woodburne et al. 1987, 1993). We used a minimum of 25.5 Ma and a maximum of 54.65 Ma (stratigraphic bounding) for node 8.

i. Node 9 (Petauroidea): The oldest marsupial bearing deposits in Australia are known from the Tingamarra Local Fauna (54.6±0.05 Ma; Queensland; Godthelp et al. 1992; Beck et al. 2008) and as of yet no petaurids have been identified. Fossil pseudocheirids from Oligo-Miocene deposits are the oldest described members of the Petauroidea (25.7–25.5 Ma; Woodburne et al. 1987, 1993). The oldest fossils belonging to Australoplagiaulacoida (1st outgroup) or Vombatiformes (2nd outgroup) are stem kangaroos and stem koalas, respectively, from Zone A of the Etadunna Formation (25.7–25.5 Ma; Woodburne et al. 1993). We used a minimum of 25.5 Ma and a maximum of 54.65 Ma (stratigraphic bounding) for node 9.

Ancestral state reconstructions

SIMMAP (version 1.0 B2.3.2; Bollick 2006) and MacClade 4.08 (Maddison and Maddison 2005) were used to estimate ancestral states for geographic provenance of origin for Pseudocheiridae [0: Australia and Tasmania; 1: New Guinea and surrounding islands], and maximum elevation [0: ≤ 1500 m; 1: between 1500 and 3000 m; and 2: ≥ 3000 m (ordered character)]. MacClade uses parsimony to infer the minimal number of steps needed to explain the distribution of characters found in the terminal branches. SIMMAP implements the methods of Nielsen (2002) and Huelsenbeck et al. (2003) for stochastically mapping discrete mutations onto phylogenies. SIMMAP uses a Bayesian approach to calculate a posterior probability distribution that accommodates uncertainty in ancestral states, evolutionary rates, and the phylogeny. The rate prior is described by the parameters α and β, which specify the mean (α/β) and variance (α/β²). We used 50 discrete categories to approximate the gamma distribution and rescaled branch lengths before applying the prior to maintain branch length proportionality. We used three sets of morphological priors (α=1 and β=1; α=3 and β=2; α=5 and β=5) to investigate the robustness of our estimates. An additional parameter, the bias parameter, is required for analyses with binary characters. The bias parameter prior was specified with α=1, which specifies an uninformative prior with equal prior probabilities. We used all post burn-in trees from one run of the partitioned Bayesian analysis (12212 trees) with ten draws from the prior distribution; acrobats, Tarsipes, and petaurids were excluded from the SIMMAP analyses, but the pseudocheirid trees remained rooted. The three different combinations of priors gave posterior probabilities that differed by no more than 0.1199 (ancestral areas) or 0.1007 (elevation) at a given node, and we only report the results for analyses with α=3 and β=2.

Results

Phylogenetic analyses

Concatenation

The maximum posterior probability tree based on the partitioned analysis is shown in Fig. 2, which also shows

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Bayesian posterior probabilities (BPP) and bootstrap support percentages for the partitioned analyses. The ML tree is shown in Fig. 3. Bayesian posterior probabilities, along with ML and MP bootstrap support percentages, are summarized in Table 4 for nodes that were not supported at the 100% bootstrap and 1.00 posterior probability levels.

All analyses recovered Acrobatidae, Petauridae, and Pseudocheiridae as monophyletic families. Within Petauridae, Gymnobelideus and Petaurus grouped to the exclusion of Dactylorhiza. Within Petaurus, P. breviceps and P. norfolcensis grouped to the exclusion of P. abidi.

Three groups within Pseudocheiridae were recovered in all analyses: Hemibelidinae (Petauroidea+Hemibelideus); a modified Pseudocheirinae (Pseudocheirus+Pseudochirulus) that does not include Petropseudes; and a modified Pseudochiropsinae that includes Pseudochirops and Petropseudes. In all analyses, Hemibelidinae grouped with Pseudocheirinae. Within Pseudochiropsinae, the basal split was between Pseudochirops archeri (Australia) and a clade containing Petropseudes dahli (Australia) and New Guinean species of Pseudochirops. Within the latter clade, Pseudochirops alberti and P. cupreus were sister taxa, P. corinnae was sister to these two, and Petropseudes dahli was sister to these three. Within Pseudocheirinae, Pseudocheirus and Pseudochirulus were recovered as sister taxa. Within Pseudochirulus, the Australian P. herbertensis was recovered as the sister taxon to a New Guinean clade that included all other Pseudochirulus species. In the New Guinean clade, P. mayeri and P. caroli grouped together, these two grouped with P. forbesi, and these three grouped to the exclusion of P. canescens.

**Individual genes**

ML phylogenograms based on the individual genes were generally concordant with the concatenated analyses (Fig. 6). Individual petaurid families were always recovered as monophyletic except in analyses with Rag1 (Fig. 6E), which nested Tarsipedidae within Petauridae in a clade with Dactylorhiza and Gymnobelideus. Within Petauridae, ENAM (Fig. 6C), IRBP (Fig. 6D), and vWF (Fig. 6F) grouped Gymnobelideus and Petaurus, BRCA1 (Fig. 6B) grouped Petaurus and Dactylorhiza, and ApoB (Fig. 6A) grouped Gymnobelideus and Dactylorhiza. Within Petaurus, all of the individual gene trees excepting ApoB recovered Petaurus as monophyletic, with P. breviceps and P. norfolcensis grouping to the exclusion of P. abidi. ApoB recovered P. breviceps as the sister taxon to all other petaurids (Fig. 6A). The three pseudocheirid subfamilies (Hemibelidinae, Pseudocheirinae, Pseudochiropsinae) were recovered as monophyletic in analyses with ApoB, BRCA1, ENAM, IRBP, and vWF (Fig. 6A–D, F), whereas analyses with Rag1 (Fig. 6E) failed to recover Petauroidea+Hemibelideus.

Within Pseudocheirinae, all analyses with individual genes recovered Pseudochirulus as monophyletic. ENAM was the only gene segment that failed to recover the monophyly of New Guinean Pseudochirulus species, and instead placed P. canescens as the sister taxon to all other Pseudochirulus species.

Within Pseudochiropsinae, all genes except for IRBP supported a basal split between Pseudochirops archeri and all other taxa, whereas IRBP supported Pseudochirops monophyly. Monophyly of the New Guinean species of

**Table 4** Posterior probabilities and bootstrap support percentages. All clades that were supported at the 100% bootstrap and 1.00 posterior probability levels are not shown. Posterior probabilities are given as the average of the two independent runs. Partitioned=each gene was modeled to have its own model of molecular evolution; Non-partitioned=ApoB, BRCA1, IRBP, Rag1, vWF, ENAM were treated as a single gene; MP=maximum parsimony; ML=maximum likelihood

| Phylogenetic Hypothesis | MP | ML | Bayesian Analyses |
|-------------------------|----|----|------------------|
|                         |    |    |                  |
|                         |    |    | Partitioned      |
|                         |    |    | Non-Partitioned  |
| Gymnobelideus+Petaurus  | 88 | 98 | 1.00             |
| Petaurus breviceps+Petaurus norfolcensis | 65 | 75 | 0.98 |
| Pseudochirulus forbesi+P. mayeri + P. caroli | 79 | 75 | 0.75 |
| Pseudochirulus mayeri+P. caroli | 77 | 75 | 0.96 |
| Pseudochirulus monophyly (excluding Petropseudes) | 0.3 | 0 | 0.00 |
| Petropseudes+New Guinean Pseudochirops spp. | 92 | 94 | 1.00 |
| Pseudochirops corinnae+P. cupreus+P. albertisi | 42 | 73 | 0.97 |
| Hemibelidinae+Pseudocheirinae | 99 | 99 | 1.00 |

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Pseudochirops (P. cupreus, P. albertisii, P. corinnae) was supported by BRCA1 and IRBP. All six genes supported a sister group relationship between *P. cupreus* and *P. corinnae*.

Molecular dating

Figure 5 shows the timescale for Petauroidea based on the partitioned BEAST analyses. Point estimates and 95%
highest posterior densities (BEAST) or 95% credibility intervals (Multidivtime) for all nodes are given in Table 5. Dates for the soft-bounded, partitioned BEAST analyses were 0.03 million years older, on average, than soft-bounded, non-partitioned BEAST dates. Dates for the hard-bounded, partitioned BEAST analyses were 0.03 million years younger, on average, than hard-bounded, non-partitioned BEAST dates. Soft-bounded, partitioned BEAST dates were 0.15 million years younger, on average, than hard-bounded, non-partitioned BEAST dates. Dates for partitioned Multidivtime analyses were 0.02 million years older, on average, than non-partitioned Multidivtime dates. BEAST dates were 1.2 million years younger, on average, than Multidivtime dates.

All of the point estimates suggest that Petauridae split from Pseudocheiridae ∼30–29 Ma. Petaurids last shared a common ancestor ∼21–18 Ma. Within Petaurus, P. abidi last shared a common ancestor with P. norfolcensis+P. breviceps ∼3–2 Ma, and P. norfolcensis split from P. breviceps ∼2–1 Ma. Pseudocheirids last shared a common ancestor in the early Miocene (∼22–20 Ma). Hemibelidinae last shared a common ancestor with Pseudocheiriinae ∼20–18 Ma. Diversification within the crown-clades Hemibelidinae, Pseudocheiriinae, and Pseudochiroptinae commenced in the middle to late Miocene (∼22–20 Ma). Hemibelidinae (∼12–10 Ma); Pseudocheiriinae (∼12–11 Ma); and Pseudochiroptinae (∼12–9 Ma). Within Pseudochiroptinae, the Australian Petropseudes dahlia split from the New Guinean Pseudochirus species ∼10–7 Ma, and the three New Guinean species last shared a common ancestor ∼10–5 Ma. Within Pseudochirulus, the Australian P. herbertensis split from the New Guinean clade ∼6 Ma, and the New Guinean taxa last shared a common ancestor 3–2 Ma.

**Ancestral state reconstructions**

Figures 7 and 8 show the ancestral state reconstructions for geographic provenance and maximum elevation, respectively, based on SIMMAP (α=3 and β=2) and MacClade. SIMMAP posterior probabilities for ancestral state reconstructions are shown in Table 6.

MacClade reconstructions recovered Pseudocheiriidae, Hemibelidinae+Pseudocheiriinae, Hemibelidinae, Pseudochiroptinae, and Pseudocheiriinae as having Australian origins, whereas the New Guinean clades of Pseudochirulus and Pseudochirus, respectively, were reconstructed as having common ancestries in New Guinea (Fig. 7). In the SIMMAP analysis, the ancestral reconstructions for Pseudocheiriidae, Hemibelidinae+Pseudocheiriinae, Hemibelidinae, and Pseudocheiriinae were reconstructed as having high posterior probabilities (>0.96) for an Australian origin. The ancestor of Pseudochirulus was most likely Australian in origin (>0.75 posterior probability), and New Guinean species of Pseudochirulus were reconstructed as having a posterior probability of 1.00 for a New Guinea origin. The ancestor of Pseudochiroptinae was reconstructed as originating in Australia (>0.91 posterior probability). In contrast to MacClade, SIMMAP reconstructed the common ancestor of Petropseudes and the New Guinean Pseudocheiris clade as having a New Guinean origin (>0.87). New Guinean Pseudochirus species were also reconstructed as New Guinean in origin (1.00 posterior probability).

MacClade and SIMMAP reconstructions (Fig. 8) both suggest that occupation of high elevations (>3000 m) occurred independently in Pseudochirulus and Pseudochirus. In Pseudochirus, occupation of elevations above 3000 m evolved on the terminal branch leading to Pseudochirus cupreus. In Pseudochirulus, high altitude occupation evolved in the ancestor of Pseudochirulus forbesi, Pseudochirulus mayeri, and Pseudochirulus caroli, with loss of high altitude occupation on the terminal branch leading to P. caroli (SIMMAP and acctran parsimony reconstructions; Fig. 8), or evolved independently on the branches leading to Pseudochirulus forbesi and Pseudochirulus mayeri (deltran parsimony reconstruction). The common ancestors of New Guinean Pseudochirulus and Pseudochirus, respectively, were both reconstructed as having maximum elevations between 1500 and 3000 m.

**Discussion**

**Phylogenetic relationships**

**Petauroidea**

Within Petauroidea, our results strongly support an association of Petauridae and Pseudocheiriidae to the exclusion of Tarsipedidae. These results are consistent with other molecular studies (Kavanagh et al. 2004; Phillips and Pratt 2008; Meredith et al. 2009a, c).

**Petauridae**

Our analyses grouped Petaurus and Gymnobelideus to the exclusion of Dactylorhiza with strong support. This result is consistent with morphology (Smith 1984; Aplin and Archer 1987; Archer 1984), chromosomal characters (McKay 1984), brain encephalization (Nelson and Stephan 1982), serological data (Kirsch and Calaby 1977; Kirsch 1977), single-copy DNA–DNA hybridization studies (Springer et al. 1994), and classifications (Kirsch 1977; Archer 1984).
| Clade                                      | Multidivtime Partitioned | Multidivtime Non-partitioned | BEAST Partitioned Soft Bounds | BEAST Partitioned Hard Bounds | BEAST Non-partitioned Soft Bounds | BEAST Non-partitioned Hard Bounds |
|--------------------------------------------|--------------------------|------------------------------|-------------------------------|-------------------------------|-----------------------------------|----------------------------------|
| Petauroidea                               | N/A                      | N/A                          | 35.71 (28.37–43.00)           | 35.41 (28.82–42.77)           | 35.69 (28.52–43.09)               | 35.52 (28.85–42.85)              |
| Tarsopedidae + Petauridae + Pseudocheiridae | 33.44 (28.41–39.11)      | 33.36 (28.34–38.81)          | 33.62 (27.07–40.86)           | 33.23 (27.59–39.91)           | 33.53 (26.74–40.40)               | 33.28 (27.62–39.96)              |
| Petauridae + Pseudocheiridae              | 30.30 (26.00–35.12)      | 30.03 (28.34–35.18)          | 29.29 (23.17–35.39)           | 29.13 (25.50–34.58)           | 29.33 (23.44–35.70)               | 29.21 (25.50–34.63)              |
| Acrobatidae                               | N/A                      | N/A                          | 19.53 (13.52–25.63)           | 20.38 (15.12–25.70)           | 19.70 (13.71–26.20)               | 20.31 (15.16–25.70)              |
| Petauridae                                | 21.33 (17.54–25.17)      | 20.74 (16.93–24.81)          | 18.34 (13.83–23.17)           | 18.89 (14.45–24.21)           | 18.31 (13.60–22.98)               | 18.80 (14.25–23.81)              |
| Pseudocheiridae                           | 22.06 (18.29–25.41)      | 20.55 (16.86–23.86)          | 20.09 (15.85–24.52)           | 20.50 (16.45–25.14)           | 20.02 (15.69–24.33)               | 20.57 (16.57–25.20)              |
| Hemibelidinae + Pseudocheiriinae          | 20.46 (16.79–23.88)      | 20.40 (16.78–23.65)          | 18.39 (14.48–22.59)           | 18.78 (14.89–23.15)           | 18.31 (15.69–24.33)               | 18.83 (14.90–23.13)              |
| Hemibelidae                               | 12.06 (9.25–15.01)       | 12.20 (9.29–15.15)           | 10.28 (7.17–13.47)            | 10.51 (6.77–14.44)            | 10.19 (7.23–13.47)                | 10.49 (6.91–14.39)               |
| Pseudocheirinae                           | 12.00 (9.30–14.92)       | 12.02 (9.14–15.01)           | 11.37 (8.66–14.29)            | 11.72 (8.65–15.03)            | 11.37 (8.70–14.28)                | 11.82 (8.85–15.12)               |
| Pseudochirulus                            | 5.85 (4.09–7.90)         | 5.63 (3.87–7.66)             | 5.81 (3.99–7.72)              | 5.92 (4.09–7.99)              | 5.83 (4.11–7.74)                  | 5.99 (4.10–8.05)                 |
| New Guinean Pseudochirulus spp.           | 2.56 (1.56–3.85)         | 2.35 (1.49–3.49)             | 2.49 (1.62–3.44)              | 2.52 (1.61–3.49)              | 2.53 (1.68–3.50)                  | 2.58 (1.71–3.60)                 |
| Pseudochirulus forbesi + P. mayeri + P. caroli | 1.92 (1.10–2.94)    | 2.09 (1.30–3.13)             | 2.21 (1.39–3.08)              | 2.23 (1.40–3.12)              | 2.22 (1.43–3.10)                  | 2.26 (1.43–3.17)                 |
| Pseudochirulus mayeri + P. caroli         | 1.46 (0.77–2.33)         | 1.84 (1.21–2.81)             | 1.92 (1.15–2.75)              | 1.94 (1.16–2.81)              | 1.93 (1.14–2.73)                  | 1.97 (1.19–2.86)                 |
| Pseudochiropsinae                         | 11.50 (8.78–14.52)       | 12.12 (9.16–15.25)           | 8.83 (6.13–11.75)             | 8.61 (6.02–11.63)             | 8.71 (6.19–11.57)                 | 8.68 (6.11–11.54)                |
| Petropseudes + New Guinean Pseudechirops spp. | 9.71 (7.25–12.57)    | 10.26 (7.55–13.21)           | 7.18 (4.89–9.67)              | 7.02 (4.82–9.54)              | 7.11 (4.92–9.52)                  | 7.08 (4.92–9.58)                 |
| New Guinean Pseudechirops spp.            | 8.93 (6.59–11.70)        | 9.72 (7.12–12.64)            | 6.67 (4.42–9.04)              | 6.51 (4.36–8.89)              | 6.61 (4.53–8.94)                  | 6.58 (4.50–8.94)                 |
| Pseudechirops cupreus + P. albertisii     | 6.51 (4.56–8.86)         | 6.69 (4.61–9.18)             | 4.38 (2.65–6.25)              | 4.28 (2.62–6.20)              | 4.33 (2.76–6.18)                  | 4.33 (2.67–6.29)                 |
| Petaurus + Gymnobelideus                  | 19.98 (16.17–23.87)      | 18.56 (14.77–22.50)          | 16.05 (11.69–20.54)           | 16.53 (12.24–21.39)           | 15.97 (11.52–20.48)               | 16.38 (12.21–21.19)              |
| Dactylopsila                              | 7.51 (5.23–10.17)        | 7.85 (5.34–10.91)            | 5.30 (2.92–8.05)              | 5.31 (2.99–8.05)              | 5.25 (2.86–7.93)                  | 5.33 (3.08–8.10)                 |
| Petaurus                                  | 2.40 (1.29–3.84)         | 2.69 (1.68–4.10)             | 3.17 (1.91–4.33)              | 3.21 (1.94–4.61)              | 3.16 (1.95–4.53)                  | 3.23 (2.01–4.66)                 |
| Petaurus breviceps + P. norfolcensis      | 0.97 (0.27–1.88)         | 1.40 (0.75–2.31)             | 1.73 (0.92–2.63)              | 1.75 (0.95–2.66)              | 1.73 (0.94–2.61)                  | 1.77 (0.96–2.69)                 |
that place *Petaurus* and *Gymnobelideus* in the subfamily Petaurinae. In contrast, Meredith et al. (2009a) found moderate support for an association of *Dactylopsila* and *Gymnobelideus* with a data set that included one less gene (ENAM) and one fewer *Petaurus* species. Baverstock et al. (1990a) and Edwards and Westerman (1995) also found support for *Dactylopsila* + *Gymnobelideus* based on MC'F data and single copy DNA-DNA hybridization results, respectively. The ENAM gene provides additional support for *Petaurus* + *Gymnobelideus* and may explain the difference between the present results and Meredith et al.'s (2009a) earlier study.

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**Fig. 7** A SIMMAP ancestral state reconstructions for geographic provenance. Posterior probabilities of ancestral state reconstructions are depicted with pie graphs at each node. B MacClade ancestral state reconstruction for geographic provenance.
Our analysis included 13 of 16 (Nowak and Dickman 2005) or 17 (Groves 2005) extant species of Pseudocheiridae, and representatives of all six genera. Missing species (following Groves 2005) included three species of Pseudochirulus (P. cinereus, P. schlegeli, P. larvatus) and Pseudochirops coronatus. Of these, P. cinereus has previously been recognized as a subspecies of P. herbertensis (e.g., Tate 1945); P. schlegeli and P. larvatus have previously been recognized as subspecies of P. forbesi (e.g., Tate 1945); and P. coronatus has previously been recognized as a subspecies of Pseudochirops albertisii (e.g., Tate 1945). Previous work therefore suggests that holes in our taxonomic sampling are less important for evaluating intergeneric relationships than for assessing intrageneric relationships within Pseudochirulus and Pseudochirops.

Groves (2005) recognized three pseudocheirid subfamilies: Pseudocheirinae (Pseudocheirus, Pseudochirulus, Petropsuedes); Hemibelidinae (Hemibelideus, Petauroides), and Pseudochiropsinae (Pseudochirops). Previous phylogenetic analyses are generally in agreement with this.
classification (Baverstock et al. 1990b; Springer et al. 1992; Springer 1993; Kirsch et al. 1997; Meredith et al. 2009a), except that Petropseudes groups with Pseudocheirips rather than with Pseudocheirus and Pseudochirulus (Baverstock et al. 1990b; Springer 1993). Hemibelidinae is supported by karyology (Hayman and Martin 1974; McKay 1984; McQuade 1984), microcomplement fixation (Baverstock 1984; Baverstock et al. 1987, 1990a), craniodental cladistics (Archer 1984; Springer 1993), single-copy DNA–DNA hybridization (Springer et al. 1992), and nuclear DNA (Meredith et al. 2009a). Pseudocheirus+Pseudochirus is supported by single-copy DNA–DNA hybridization (Springer et al. 1992; Kirsch et al. 1997) and nuclear DNA (Meredith et al. 2009a). Finally, a clade comprising Pseudochirus and Petropseudes is supported by low chromosome numbers (Hayman and Martin 1974; Murray et al. 1990), dental characters (Archer 1984; Springer 1993), microcomplement fixation (Baverstock et al. 1987, 1990a), and nuclear DNA (Meredith et al. 2009a). We find robust support for all three of these lineages. We also find strong support for the basal split between Pseudocheiripsinae and all other pseudocheirids that was recovered by Meredith et al. (2009a). Based on the congruence of multiple phylogenetic studies, we recommend a revised classification for pseudocheirids that recognizes the same three subfamilies as Kirsch et al. (1997) and Groves (2005), but modifies the taxonomic composition of Groves’ Pseudocheirinae and Pseudochiripsinae by transferring Petropseudes dahlia from Pseudocheirinae to Pseudochiripsinae.

Craniodental characters (Springer 1993) and microcomplement results (Baverstock et al. 1990b) have supported Pseudochirus monophyly. Craniodental analyses suggested that Pseudochirus albertisii, P. cupreus, and P. archeri group together to the exclusion of P. corinnae, whereas microcomplement fixation data suggested P. albertisii, P. archeri, and P. corinnae group to the exclusion of P. cupreus. In contrast to cladistic analyses of craniodental characters and microcomplement fixation results, we find strong support for Pseudochirus paraphyly, i.e., Petropseudes dahlia and the New Guinean species of Pseudochirus (albertisii, cupreus, corinnae) group together to the exclusion of Pseudochirus archeri. Our finding that Pseudochirus is paraphyletic supports Meredith et al.’s (2009a) proposal that Petropseudes dahlia be recognized as Pseudochirus (Petropseudes) dahlia. Among New Guinean Pseudochirus species, an association of P. cupreus and P. albertisii was previously proposed by Tate (1945).

Within Pseudochirus we find strong support for the basal split between the Australian P. herbertensis and a New Guinean clade comprising the remainder of Pseudochirus species included in our study. Within the monophyletic New Guinean clade, our results suggest that P. forbesi groups with both P. mayeri and P. caroli to the exclusion of P. canescens. DNA–DNA hybridization studies suggested P. forbesi and P. canescens group together to the exclusion of P. herbertensis (Springer et al. 1992), but MC’F data (Baverstock et al. 1990b) suggested an association of P. herbertensis and P. forbesi to the exclusion of both P. mayeri and P. canescens. Cladistic analyses with craniodental analyses (Springer 1993) recovered a monophyletic New Guinean Pseudochirus clade with Dollo parsimony, and in a subset of analyses with Wagner parsimony, but not with Camin-Sokal parsimony.

### Table 6 SIMMAP results for ancestral state reconstructions of geographic provenance and maximum altitude occupied. Morphological priors were set to $\alpha=3$ and $\beta=2$

| Clade | Clade Frequency | Provenance | Posterior Probabilities | Altitude (meters) |
|-------|----------------|------------|-------------------------|-------------------|
|       |                | Australia | New Guinea | <1500 | 1500–3000 | >3000 |
| Pseudocheiridae | 1.0000 | 0.9694 | 0.0306 | 0.9853 | 0.0147 | 0.0000 |
| Hemibelidinae | 1.0000 | 0.9987 | 0.0013 | 0.9993 | 0.0007 | 0.0000 |
| Pseudocheirinae | 1.0000 | 0.9822 | 0.0178 | 0.9887 | 0.0113 | 0.0000 |
| Pseudochirus | 1.0000 | 0.7476 | 0.2524 | 0.7843 | 0.2148 | 0.0008 |
| New Guinean Pseudochirus spp. | 1.0000 | 0.0000 | 1.0000 | 0.0000 | 0.8397 | 0.1603 |
| Pseudochirus forbesi+P. mayeri+P. caroli | 0.7457 | 0.0000 | 1.0000 | 0.0000 | 0.0106 | 0.9894 |
| Pseudochirus mayeri+P. caroli | 0.9595 | 0.0000 | 1.0000 | 0.0000 | 0.1388 | 0.8612 |
| Pseudocheiriinae | 1.0000 | 0.9154 | 0.0846 | 0.9400 | 0.0600 | 0.0000 |
| Petropseudes+New Guinean Pseudochiridae spp. | 1.0000 | 0.1287 | 0.8713 | 0.1411 | 0.8589 | 0.0000 |
| New Guinean Petropseudes spp. | 0.9748 | 0.0002 | 0.9998 | 0.0001 | 0.9995 | 0.0004 |
| Pseudochirus cupreus+P. albertisii | 1.0000 | 0.0001 | 0.9999 | 0.0000 | 0.9272 | 0.0728 |
| Hemibelidinae+Pseudocheiriinae | 1.0000 | 0.9986 | 0.0014 | 0.9994 | 0.0006 | 0.0000 |
Petaurid divergence times

Our point estimates for the split between the *Petaurus abidi* and *Petaurus breviceps* + *Petaurus norfolcensis* are in the range of 3–2 Ma in the late Pliocene. These estimates are 6–10 million years younger than Malekian et al.’s (2009) estimate for this split (~12–9 Ma). Malekian et al. (2009) used BEAST to estimate divergence dates based on two mitochondrial protein-coding genes (ND2, ND4), but the only constrained node in Malekian et al.’s (2009) analyses was the split between *P. breviceps* and *P. norfolcensis*, which Malekian et al. (2009) constrained to have a minimum of 4.46 million years ago based on a fossil identified as similar to *P. norfolcensis*. However, this ignores Turnbull et al.’s (2003) more recent assessment that Hamilton Local Fauna fossils belonging to *Petaurus* may represent as many as three species (near *P. norfolcensis*, *P. breviceps*, and *P. australis*) or as few as one highly variable species. In contrast, our analyses were based on nuclear genes rather than mitochondrial genes, and employed multiple constraints, but did not impose a minimum constraint on the divergence between *P. norfolcensis* and *P. breviceps* given Turnbull et al.’s (2003) uncertain placement of *Petaurus* fossils from the Hamilton Local Fauna.

Malekian et al.’s (2009) molecular divergence dates suggest a much earlier origin for *Petaurus* (24–18 Ma) than does the fossil record (oldest *Petaurus* fossils are ~4.46 million years). Our taxon sampling did not include *Petaurus australis*, which prevented us from dating the most recent common ancestor of *Petaurus*, but did include representatives of the other major lineages that were sampled by Malekian et al. (2009). Malekian et al.’s (2009) divergence times for *P. abidi* to *P. breviceps* + *P. norfolcensis* (~12–9 Ma) and *P. breviceps* to *P. norfolcensis* (~9–7 Ma) are Miocene in age and are compatible with connectivity between northern Australia and southern New Guinea during the late Miocene when sea-level reductions (Byrne et al. 2008) and emergent land bridges (Hall 2001; Malekian et al. 2009) may have facilitated dispersal between New Guinea and Australia. Malekian et al. (2009: 11) further concluded that among *Petaurus* species included in their study there was no evidence of dispersal events during the Pleistocene when “Ice Age sea-level reductions led to cycles of land bridge connectivity between New Guinea and Australia.” In contrast, our point estimates for the separation of *P. breviceps* and *P. norfolcensis* are all in the Pleistocene. Coupled with Malekian et al.’s (2009) reconstruction of an ancestral area of New Guinea for this node, our divergence time estimates suggest that the ancestor of *P. norfolcensis* likely dispersed from New Guinea to Australia when there was land bridge connectivity between New Guinea and Australia during the Pleistocene.

Pseudocheirid divergence times, biogeography, and altitudinal zonation

In contrast to all previous analyses that have examined pseudocheirid relationships, we find strong support for the monophyly of New Guinean *Pseudocheirus* and New Guinean *Pseudocheirus*, respectively. In a parsimony framework, the monophyly of each New Guinean cohort can be explained by a single dispersal event. In contrast, SIMMAP reconstructions favor a New Guinean ancestor of the clade that includes the Australian *Petropseudes dahl* and the New Guinean *Pseudocheirus* species (Fig. 7; Table 6). This scenario requires back dispersal to Australia for the ancestor of the *Petropseudes* lineage. The only fossil described for the *Petropseudes* lineage is a molar tooth fragment from the Pliocene (~5.3–2.6 Ma) Riversleigh Rackham Roost site (Archer et al. 1997, 2006). This fossil postdates our divergence estimates for the common ancestor of *Petropseudes* and the New Guinean *Pseudocheirus* species (10–7 Ma), allowing enough time for the back dispersal. *Pseudocheirus* differs from all other pseudocheirids in that it inhabits rocky outcrops in northern Australia and is more terrestrial adapted than its cousins, climbing trees only at night to feed (Nowak and Dickman 2005). The SIMMAP reconstruction of a New Guinean common ancestry for *Petropseudes* and the New Guinean *Pseudocheirus* clade (Fig. 7A) may be a consequence of the short branch leading from this ancestor to the common ancestor of the New Guinean *Pseudocheirus* clade (Fig. 3). This branch was reconstructed as representing less than one million years in all *Multidivtime* and BEAST analyses (Table 5). Thus the probability of two separate dispersal events on longer branches that represent more time, one on the branch leading to *Petropseudes* and New Guinean *Pseudocheirus*, and a second on the branch leading to *Petropseudes*, was reconstructed by SIMMAP as more likely than a single dispersal on the shorter branch leading to the New Guinean *Pseudocheirus* species.

Our analyses suggest that the ancestor of the New Guinean *Pseudocheirus* clade arrived in New Guinea as early as ~12 million years ago (SIMMAP ancestral reconstructions; *Multidivtime* non-partitioned date for the split between *Pseudocheirus archeri* and other members of *Pseudocheirus* plus *Petropseudes*), and no later than ~6.5 million years ago (MacClade ancestral reconstructions; hard-bounded, partitioned BEAST date for the common ancestor of New Guinean *Pseudocheirus*) in the late Miocene, and that the ancestor of New Guinean *Pseudocheirus* arrived in New Guinea 6–2 Ma. Aplin et al. (1993) suggested multiple dispersal events between Australian and New Guinean in both *Pseudocheirus* and *Pseudocheirus* in the late Miocene (12–10 Ma) and Pliocene (4.7–2.7 Ma). Kirsch and Springer (1993) analyzed a smaller subset of
species for each genus and suggested that the common ancestors of New Guinean *Pseudochirulus* and *Pseudochirops* species, respectively, both arrived in New Guinea ~10 Ma. As mentioned above, Hall (2001) and Byrne et al. (2008) provide evidence for lower sea levels and land bridges between northern Australia and southern New Guinea in the late Miocene between ~10–7 Ma. Our molecular estimates for the dispersal of *Pseudochirops* species between Australia and New Guinea are compatible with dispersal during the late Miocene when land bridges may have existed. *Pseudochirulus* probably reached New Guinea at a later time, possibly in the early Pleistocene when sea levels were once again lower and land bridges connected Australia and New Guinea.

In contrast to our results, which suggest that pseudocheirids reached New Guinea no sooner than 12 Ma, relaxed molecular dates for phalangerids suggest that the ancestor of *Phalangerinus* + *Ailurops ursinus* + *Strigocuscus celebensis* dispersed from Australia to the New Guinean region between ~29 Ma and ~19 Ma (Raterman et al. 2006), or between ~17 Ma and ~14 Ma (Meredith et al. 2009a). The earlier dispersal of phalangerids than pseudocheirids to New Guinea and surrounding islands may reflect the superior dispersal and colonization abilities of the former (Flannery 1995a), which is evidenced by the presence of endemic phalangerid species, but not pseudocheirid species, on oceanic islands such as Woodlark Island (Flannery 1995a). In contrast to pseudocheirids, which have diets that are specialized for folivory, phalangerids typically have more diverse diets that include a wide variety of leaves, fruit, flowers, and in some cases even meat when available (Hume et al. 1993; Flannery 1995a). The more generalist diet of phalangerids may predispose them to successful colonization. Finally, the dispersal abilities of some pseudocheirids may be restricted by their largely or strictly arboreal lifestyles and reluctance to come to the ground (Pahl et al. 1988; Laurance 1990; Laurance and Laurance 1999).

Recent geological evidence suggests that New Guinea has been shaped by two orogenic events. The first event was the Peninsular orogeny, which resulted in the Papuan Peninsula during the Oligocene (35–30 Ma). The mountainous spine of New Guinea, in turn, was formed by the Central Range orogeny that commenced ~15 Ma when small isolated islands appeared (Cloos et al. 2005; van Ufford and Cloos 2005). The orogeny in the western Central Range began in earnest between 15 and 12 Ma, when the cordillera attained elevations that were hundreds of meters high. Between 12 and 8 Ma, proto-New Guinea continued to widen and reached elevations up to ~2 km. The most dramatic period of vertical uplift occurred between 8 and 4 Ma, when the core of the orogenic belt rose upwards and increased in width. Volcanism in the western Central Range began at ~7 Ma. At ~5 Ma, the cordillera of western New Guinea included topography between 3000 and 5000 m high (Cloos et al. 2005: fig. 19). Between 4 Ma and the present, current day altitudes and geography were established. Orogenic events in the eastern Central Range are sequentially younger by about three million years than those for the western Central Range—a result of the orientation of the plates and propagation of the tear in the subducting Australian plate (Cloos et al. 2005; van Ufford and Cloos 2005).

Relaxed clock dates for cladogenesis within the New Guinean *Pseudochiropus* clade are in the range of 9.7–6.5 Ma (*Multidivitine*) or 6.7–4.3 Ma (BEAST) and are generally coincident with the uplift of the central cordillera and other highlands of New Guinea. Diversification within the New Guinean *Pseudochirulus* clade has occurred in the last 2.5 Ma and postdates the origin and establishment of the central cordillera and other highlands in New Guinea. This suggests that *Pseudochirulus* species diversified into habitats with pre-existing, altitudinal differentiation.

Ancestral reconstructions suggest that cladogenic events in New Guinean *Pseudochiropus* occurred at elevations that were below 1500 m, or between 1500 and 3000 m. Occupation of altitudes above 3000 m is a derived feature that evolved in *Pseudochiropus cupreus*. Occupation of high elevations in *P. cupreus* is associated with scrub and herbfield at 3700 m in the Prinz Wilhelm V Range in Irian Jaya (Flannery 1995b). In *Pseudochirulus*, high altitude occupation (>3000 m) either evolved in the ancestor of *P. forbesi, P. mayeri, and P. caroli*, with subsequent loss in *P. caroli*, or evolved independently in *P. mayeri* and *P. forbesi*. *P. forbesi* is most common between 1200 and 2800 m, but has been recorded as high as 3800 m (Helgen 2007a, b). *P. mayeri* inhabits montane forests between 1200 and at least 4200 m along the central cordillera of New Guinea, and is most abundant in upper montane, moss forests that are above 2000 m, and in some cases 3000 m (Flannery 1995b; Helgen 2007a, b). In conjunction with its occupation of moss forests, *P. mayeri* has a unique diet among pseudocheirids that includes leaves, mosses, ferns, lichens, fungi, and pollen (Hume et al. 1993; Flannery 1995b).

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