

Populating a Continent:  
Phylogenomics Reveal the Timing of Australian Frog Diversification

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1     *Abstract*

2                 The Australian continent's size and isolation make it an ideal place for studying  
3     the accumulation and evolution of biodiversity. Long separated from the ancient  
4     supercontinent Gondwana, most of Australia's plants and animals are unique and  
5     endemic, including the continent's frogs. Australian frogs comprise a remarkable  
6     ecological and morphological diversity categorized into a small number of distantly-  
7     related radiations. We present a phylogenomic hypothesis based on an exon-capture  
8     dataset that spans the main clades of Australian myobatrachoid, pelodryadid hylids,  
9     and microhylid frogs. Our time-calibrated phylogenomic-scale phylogeny identifies great  
10    disparity in the relative ages of these groups which vary from Gondwanan relics to  
11    recent Asian immigrants and include arguably the continent's oldest living vertebrate  
12    radiation. This age stratification provides insight into the colonization of, and  
13    diversification on, the Australian continent through deep time, during periods of  
14    dramatic climatic and community changes. Contemporary Australian frog diversity  
15    highlights the adaptive capacity of anurans, particularly in response to heat and aridity,  
16    and explains why they are one of the continent's most visible faunas.

17

*Keywords:* Anuran; adaptive radiation; Gondwana; phylogenetics

18 *Introduction*

19 Frogs are an ancient vertebrate radiation originating in the Permian more than  
20 250 million years ago (Hime et al. 2021). They share a unique and unusual morphology  
21 yet are a spectacularly successful group, with more than 7,500 extant species spread  
22 across most of the world (AmphibiaWeb 2022). Despite their age, much of this diversity,  
23 potentially more than 95%, has developed since the Cretaceous-Paleogene mass  
24 extinction (65 mya) (Feng et al. 2017). Australia is one of the driest continents on Earth  
25 yet, surprisingly, it is home to nearly 250 frog species. Australia's frogs belong to just  
26 four anuran groups spread widely across the “modern frog” suborder Neobatrachia: (1)  
27 Myobatrachoidea comprising the Limnodynastidae (66 species) and Myobatrachidae (70  
28 spp.); (2) Hyloidea represented by the family Pelodryadidae (91 spp.); (3) the  
29 Microhylidae subfamily Asterophryinae (24 spp.); and (4) a single Ranidae species in the  
30 genus *Papurana*. These groups show very different levels of species richness and  
31 geographic spread across the continent (Fig.1). However, together they have radiated to  
32 inhabit almost every part of Australia including tropical rainforests, alpine streams,  
33 featureless boulder piles, and hyper-arid deserts.

34 While we know a great deal about many aspects of Australian frog biology (Tyler  
35 1998; Anstis 2017), the age of each of the major groups and the timing of their  
36 subsequent diversification, is poorly understood. Since the origin of frogs over 250  
37 million years ago, the landmass that is now Australia has traveled extensively. Long ago  
38 it was part of the supercontinent Pangea before separating as a component of  
39 Gondwana alongside South America, Africa, Antarctica, and India. Sometime around 50  
40 million years ago Australia separated from Antarctica and began drifting alone towards  
41 Asia (Hall 2002; Bijl et al. 2013). Given the long evolutionary history of frogs, and  
42 Australia's varied geographic affinities with other landmasses, we ask three related  
43 questions: (1) Where did Australia's frogs originate? (2) When did they get to

44 Australia? and (3) Who and where are their closest relatives? Answering these questions  
45 provides context for the varied species richness and ecological diversity of these groups  
46 and offers important insight into the evolution of a continental fauna.

47

48 *Materials and Methods*

49 We assembled an exon-capture dataset comprising 99 frog species spanning all  
50 major anuran clades and with particular focus on the families Pelodryadidae,  
51 Microhylidae, Limnodynastidae and Myobatrachidae (Table S1). This dataset includes  
52 near-complete (92%) genus-level sampling of Australia's frogs. We generated new  
53 Anchored Hybrid Enrichment (AHE—Lemmon et al. 2012) data for 83 samples and  
54 combined these with outgroup samples from Hime et al.'s (2021) amphibian  
55 phylogenomic dataset. Outgroup sampling was designed around maximizing commonly  
56 used anuran fossil calibrations to provide a consistent time-calibrated phylogenomic  
57 estimate of Australian frogs. Data from different AHE projects were combined using  
58 custom scripts which relied on *metablastr* to identify orthologous loci  
59 (*blast\_best\_reciprocal\_hit*) (Benoit & Drost 2021), *mafft* to align them (*--add, --*  
60 *keeplength*) (Katoh et al. 2013), and *AMAS* to manipulate alignments (Borowiec 2016).  
61 We reconstructed individual genealogies for our exon-capture data (n = 450) under  
62 maximum-likelihood in IQTREE (Nguyen et al. 2015), allowing the program to assign  
63 the best fitting model of nucleotide substitution using ModelFinder (Kalyaanamoorthy  
64 et al. 2017) and then perform 1,000 ultrafast bootstraps (Minh et al. 2013). We then  
65 estimated a species tree using the quartet-based summary method ASTRAL III (Zhang  
66 et al. 2018) with IQTREE gene trees as input. To estimate divergence times among taxa  
67 we applied a series of fossil calibrations first compiled by Feng et al. (2019) (Table S2)  
68 and used the Bayesian divergence time software MCMCTree (Rannala & Young 2007).  
69 We started by concatenating all loci and partitioning them into two partitions, first and

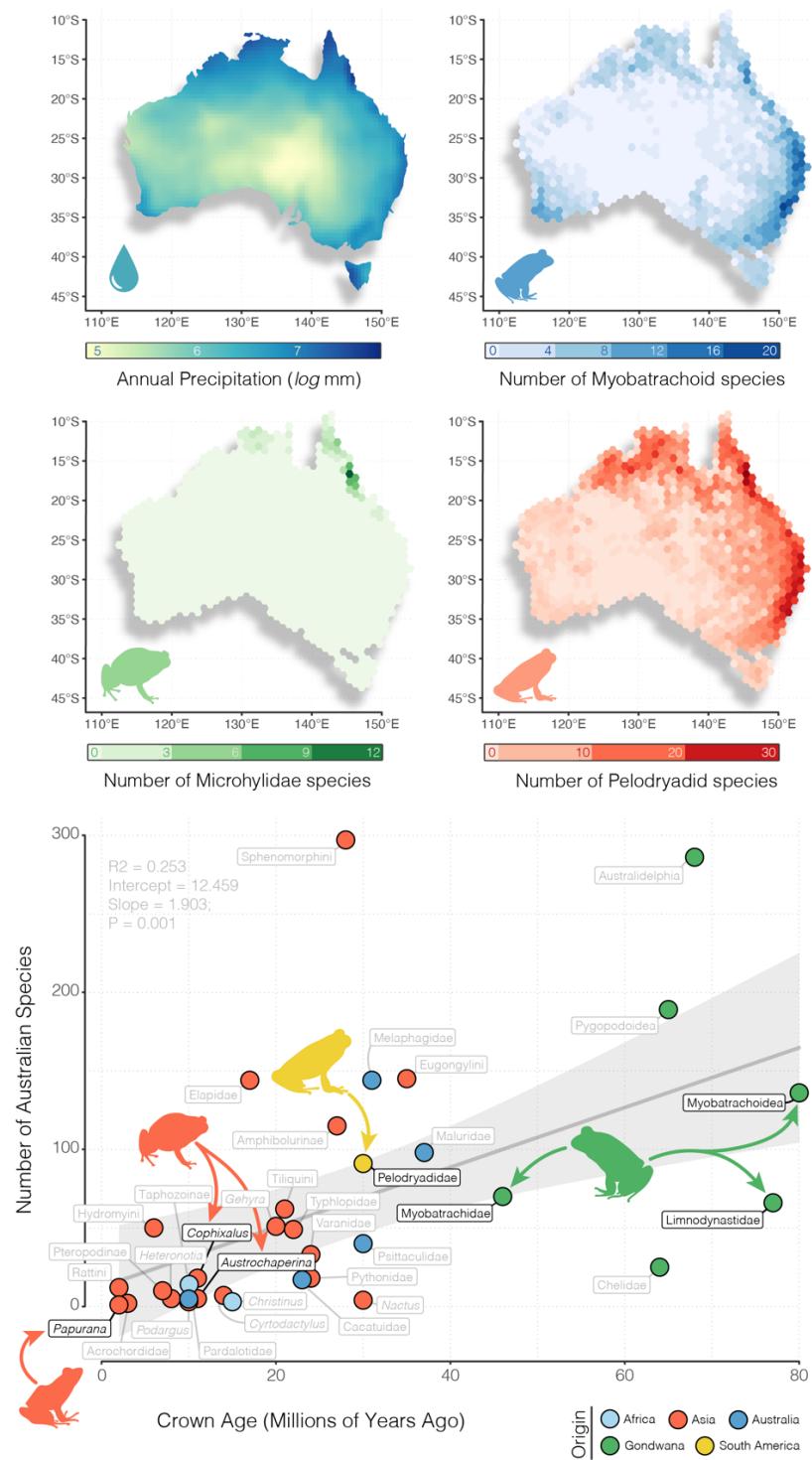
70 second codons together, and third codons separately. We then used *baseML* to estimate  
71 approximate likelihoods (dos Reis & Yang 2011) and branch lengths before running  
72 *mcmcTree* on the gradient and Hessian (in.BV file) for ten replicate analyses. We  
73 inspected mcmc files for stationarity and compared for convergence, then combined  
74 them using logCombiner, and used this combined mcmc file to summarize divergence  
75 times on our tree (*print* = -1 in .ctl file). Sample, alignment, and gene tree summary  
76 statistics are presented in Supplementary Material (Fig.S1-3) and are available alongside  
77 all other materials on Dryad (doi:10.5061/dryad.zpc866tcj) and GitHub  
78 ([https://github.com/IanGBrennan/Crown\\_Frogs](https://github.com/IanGBrennan/Crown_Frogs)).

79

80 *Results*

81 Crown divergences of the three Australian frog radiations can be clearly  
82 separated into old (Myobatrachidae and Limnodynastidae—80 mya), intermediate  
83 (Pelodryadidae—30 mya), and young (Asterophryinae—11 mya) (Fig.2). The youngest  
84 Australian group, microhylids in the genera *Austrochaperina* and *Cophixalus*, are  
85 embedded deeply within the subfamily Asterophryinae and appear to represent two  
86 separate, relatively recent ( $\approx$ 11 mya) invasions of Australia from New Guinea.  
87 Pelodryadidae tree frogs also share a complex biogeographic history across Australasia,  
88 with several species groups split across the Torres Strait (separating Australia and New  
89 Guinea), suggesting frequent biotic exchange. However, the origins of the Pelodryadidae  
90 are far older. Their closest relatives are the iconic Phyllomedusidae found throughout  
91 Central and South America, with the crown split between extant Pelodryadidae in  
92 Australia/New Guinea and South America estimated at approximately 40 million years  
93 ago. Australian myobatrachids and limnodynastids also have their closest relatives in  
94 South America—the Calyptocephalidae, represented here by *Calyptocephalla*, the  
95 Helmeted Water Toad of Chile. The crown split between extant myobatrachoids in

96 Australia and Chile is ancient, occurring more than 100 million years ago. The  
97 remaining phylogenomic topology and divergence estimates of frogs are broadly  
98 consistent with previous results (Feng et al. 2017; Hime et al. 2021) (Fig.2, S4, S5).  
99



100

101

102 Figure 1. Australian frogs show a pattern of increasing species richness with  
 103 precipitation, and with time. Above, maps of richness for the three focal radiations  
 104 (with Limnodynastidae and Myobatrachidae presented together as Myobatrachoidea)

105 are plotted alongside a map showing total annual precipitation. Greatest richness is  
106 concentrated along Australia's east coast, however this pattern falls away in cold areas  
107 of the far southeast, particularly in southwest Tasmania. Species occurrence records  
108 were collated from the Atlas of Living Australia (<https://ala.org.au>). Below, Australian  
109 radiations can be divided broadly into (1) relictual Gondwanan clades >40 myo (green),  
110 (2) ancient colonizing groups (>20 myo, <40 myo; varied colors), or (3) immigrant  
111 clades of Asian origin (orange). Each point is colored according to the region of  
112 hypothesized origin and labeled by the narrowest phylogenetic taxonomy. Black labels  
113 indicate focal groups and grey labels indicate other Australian vertebrate clades.  
114 Regression in background is fit to all points and shows a general pattern of increasing  
115 species richness with age.

116

### 117 *Discussion*

118 Here we present the first reliable estimates of relationships among all of  
119 Australia's frog genera and major clades of the mega-genus *Litoria*. Our investigation  
120 into the timing and origins of the Australian frog fauna reveals that each radiation  
121 originated or arrived during different periods in Australia's history, demonstrating a  
122 staggered colonization and population of the continent. This stratified arrival means  
123 each radiation established itself in a very different incarnation of the continent. Across  
124 these eras Australia has flourished through a warm and wet Eocene, cooling and drying  
125 following the onset of Antarctic glaciation in the Oligocene, warm and forested Miocene,  
126 and a gradual aridification leading to its present status (Byrne et al. 2011, Pross et al.  
127 2012, Macphail & Hill 2018, Mao & Retallack 2019).

128

### 129 *Origins and Biogeography*

130        The Myobatrachidae and Limnodynastidae (together—myobatrachoids) represent  
131    the oldest, most diverse (136 spp.), and only near-endemic of Australia’s frog radiations  
132    (one species—*Lechriodus aganoposis* is found in New Guinea). They share a long history  
133    with South America and its Gondwanan past. Anchored by a deep split with the South  
134    American *Calyptocephallela* (roughly 100 mya; Fig.2), early divergences among the  
135    Australian myobatrachoids, principally between myobatrachids and limnodynastids,  
136    occurred in the late Cretaceous (80–70 mya), preceding the isolation of Australia from  
137    Antarctica. This dates to a time when South America, Antarctica, and Australia were a  
138    continuous landmass that was likely temperate in climate (Palazzi & Barreda 2007;  
139    Mörs et al. 2020). The phylogenetic depth and distribution of myobatrachoids (including  
140    *Calyptocephallela*) across these now widely disjunct continents suggests a historically  
141    continuous distribution across southern Gondwana, including Antarctica. This idea is  
142    supported by the recent discovery of an extinct calyptocephallelid from mid-Miocene  
143    Antarctica that lived more than 40 mya (Mörs et al. 2020). The persistence of  
144    calyptocephallelids in Antarctica into the Late Eocene highlights the dichotomy between  
145    young extant myobatrachid and limnodynastid diversity (most species < 30 mya) and  
146    ancient splits between limnodynastids and myobatrachids and within limnodynastids (>  
147    70 mya). These long branches are likely the survivors of a much greater southern  
148    Gondwanan myobatrachoid diversity, potentially mirroring the diversity of extinct  
149    calyptocephallelids through southern South America and Patagonia (Nicoli et al. 2022).

150        Australian myobatrachoids however are not the only group with close  
151    connections to South America. The Pelodryadidae are a species rich (91 spp.) and  
152    morphologically diverse clade of Australasian frogs. Embedded within the primarily  
153    Neotropical treefrogs, they show a more recent late-Eocene divergence from their South  
154    American relatives the Phyllomedusidae, some 40 mya. Crown divergence of the  
155    pelodryadids occurred in the mid-to-late Oligocene (30 mya) before erupting into a

radiation across Australia and New Guinea in the early Miocene. This timing has spurred speculation about the origins of pelodryadids either as part of a young Gondwanan group or more recent over-water dispersers from South America (Pyron 2014). Divergence between phyllomedusids and pelodryadids 40 mya aligns with the opening of the Drake Passage and separation of South America from Antarctica (Toumoulin 2020). Unfortunately this does not provide any certainty about how pelodryadids arrived in Australia. While the Brazil Current would have provided a favorable trajectory for rafting frogs, the over-water distance between South America and Australia remained immense. A more likely scenario is that pelodryadids dispersed from South America through Antarctica and into Australia. Climate reconstructions suggest warm temperate/tropical habitats across Antarctica which would have been suitable through a long period of the Eocene (Pross et al. 2012). Dispersal via Antarctic land bridges would have had to occur prior to the Eocene-Oligocene cooling (34 mya) that blanketed Antarctica beneath an ice sheet (van den Ende et al. 2017).

Contrasting with the comparatively ancient limnodynastids, myobatrachids, and pelodryadids, Australia's youngest anuran radiation are the microhylids. Embedded deeply in the Asterophryinae subfamily, the two temporally adjacent clades (12–13 mya) of *Austrochaperina* and *Cophixalus* crossed the gap from New Guinea to Australia in the mid Miocene. This time frame coincides with a period of increased variation in sea surface levels driven by cooling global temperatures following the mid Miocene climatic optimum. Dropping sea levels likely repeatedly exposed a landbridge between southern New Guinea and northern Australia (both Cape York and the Top End) and facilitated biotic exchange between these landmasses (Mitchell et al. 2014). The young age of these clades, and existence of two other species-rich incumbent frog clades in the pelodryadids and myobatrachoids potentially explains why Australian microhylids are relatively species poor (*Austrochaperina*—5 spp., *Cophixalus*—18 spp.) and morphologically

182 conservative compared to their New Guinean neighbors (200+ spp.), reflecting a pattern  
183 seen in monitor lizards (Pavón-Vázquez et al. 2021).

184 The sole Australian ranid *Papurana daemeli* is native but not endemic to the  
185 continent, and can be found broadly across Australo-Papua, extending to just beyond  
186 the edge of the Sahul shelf (Reilly et al. 2022). It belongs to a clade of frogs distributed  
187 throughout southeast Asia, Wallacea, and Sahul, with other *Papurana* species found in  
188 New Guinea and the Solomon Islands (Oliver et al. 2015; Chan et al. 2020). Though not  
189 included in our phylogenomic sampling, *Papurana daemeli* is likely a relatively young  
190 species (<7 mya) with limited divergence between populations found in Wallacea and  
191 Sahul (Reilly et al. 2022). The broad distribution of *P. daemeli* across Australo-Papua  
192 suggests either a very recent colonization of Australia or vicariant speciation followed by  
193 subsequent dispersal out of Australia and back into New Guinea and Wallacea.

194 The staggered temporal origins of Australian frogs exemplifies the general  
195 colonization history of Australian vertebrates. Radiations of mammals, birds, frogs, and  
196 reptiles fall into discretized temporal groups broadly identified as (1) Gondwanan relicts  
197 >40 myo, (2) old colonizers (>20 myo, <40 myo) with varied origins, or (3) recent  
198 Asian immigrants (<20 myo). The Limnodynastidae and Myobatrachidae fall  
199 undoubtedly into the Gondwanan group alongside ancient Australian radiations like  
200 Australidelphian marsupial mammals which include koalas, kangaroos, and Tasmanian  
201 devils; side-necked chelid turtles; and pygopodoid geckos which include the bizarre  
202 limbless pygopodids. These groups—with the exception of pygopodoids—have close links  
203 to South American relatives based on molecular and fossil evidence (Georges et al. 1999;  
204 Mitchell et al. 2014). While a Pelodryadidae link with South America is clear, they are  
205 perhaps the sole radiation to have emigrated from South America to Australia since the  
206 continental breakup. Most other similarly aged Australian groups instead show signal of  
207 Asian or Australian origins. In comparison, the Australian microhylids

208 (*Austrochaperina*, *Cophixalus*) and the ranid *Papurana daemeli* are relatively young  
209 colonizers from New Guinea with deeper origins in Asian groups. Both the  
210 Asterophryinae and Ranidae, to which these species belong, have a long history in the  
211 Sunda and Wallacean regions, reflecting patterns of old diversity in this tectonically  
212 active area. Alongside a number of other groups such as pythons (Esquerré et al. 2020),  
213 monitor lizards (Brennan et al. 2021), honeyeater birds (Marki et al. 2017), dragon  
214 lizards (Tallowin et al. 2020), elapid snakes (Keogh 1998), various gekkonid gecko  
215 genera (Heinicke et al. 2011), megabats, frogmouth birds (Oliver et al. 2020), cockatoos  
216 and parrots (Schweizer et al. 2011), several skink subfamilies (Skinner et al. 2011), and  
217 two rodent groups (Roycroft et al. 2020), they share diversity across Australia and New  
218 Guinea with repeated exchange between the two islands. Many of these groups show a  
219 telltale stepping stone biogeographic pattern that links them back to mainland Asian  
220 ancestors, with Australo-Papuan members deeply phylogenetically nested. In general,  
221 these Australian clades show a pattern of increasing species richness with clade age,  
222 however the drivers of such a pattern are likely idiosyncratic (Fig.1).

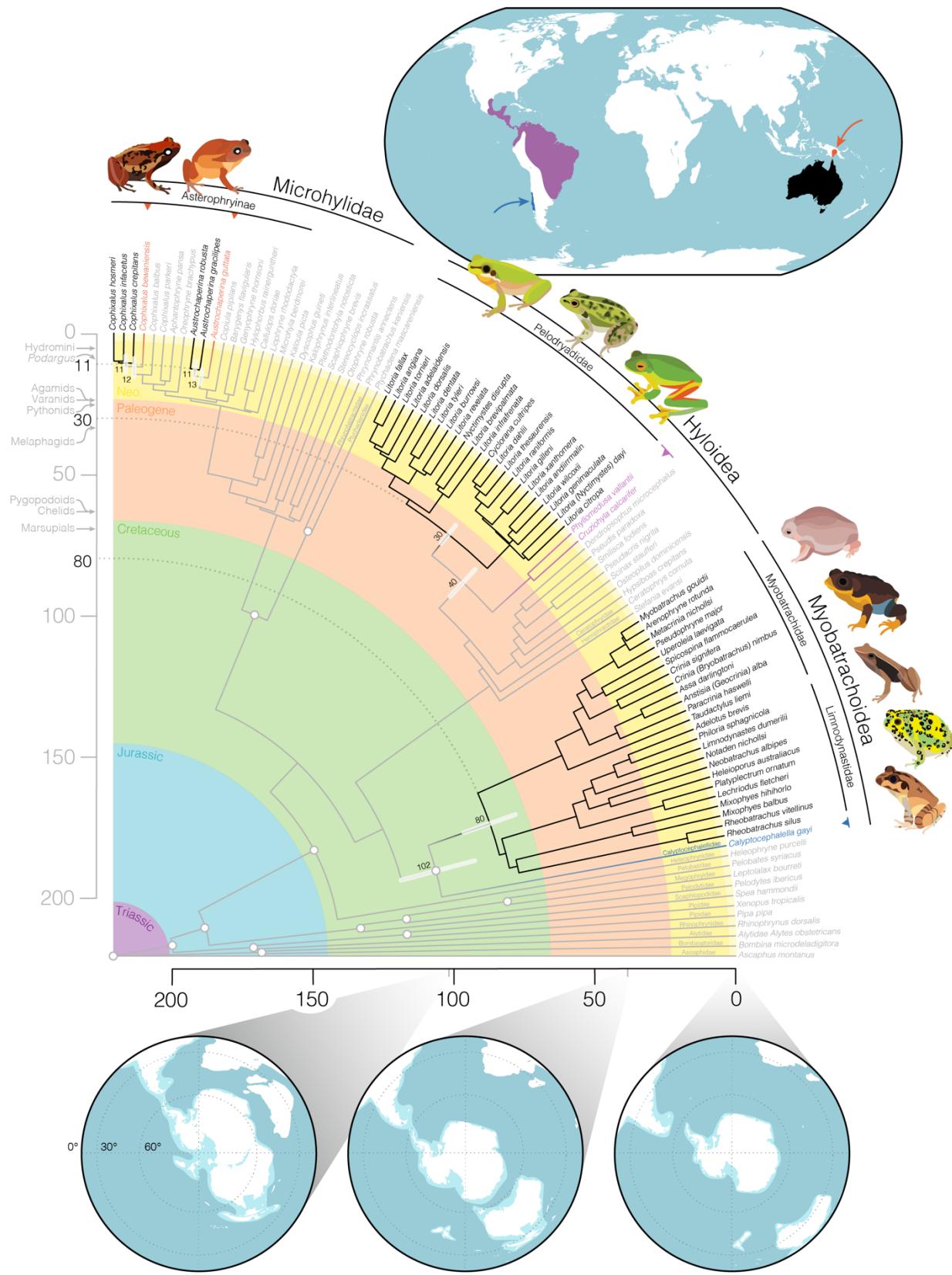
223

224 *Macroevolutionary Patterns*

225 The radiation of frogs in Australia has occurred over a deep timescale and across  
226 a changing climatic landscape. Old species-poor lineages have become confined to the  
227 mesic-temperate fringes of the continent, while new niches and species have popped up  
228 in the expanding arid zone. And while frogs are found across most of the Australian  
229 continent, their basic moisture requirements and desiccation sensitivity mean that  
230 Australian amphibian diversity shows a stark mesic-arid gradient (Fig.1), similar to that  
231 seen for birds and mammals, and the inverse of lizards (Powney et al. 2010). Not all has  
232 been lost in the red center though—several independent clades of dry-country  
233 inhabitants have evolved among Australia’s harsh sandy and stony deserts.

234 *Neobatrachus*, *Notaden*, and *Cyclorana* have all evolved to aestivate through the hottest  
235 and driest seasons. These genera (commonly known as the water-holding frogs) are  
236 capable of growing epidermal cocoons to retain moisture that may see them through  
237 periods of extreme drought lasting from months to years (van Beurden 1980).

238 Along with changes in habitat and ecology, Australia's frogs have also  
239 accumulated vast diversity in reproductive strategy, ontogenetic trajectory, and  
240 morphology (Crump 2015, Duellman 1992, Sherratt et al. 2018). While we do not  
241 present data on these topics, our well-resolved phylogenetic hypothesis provides new  
242 context for the macroevolution of some of these extreme traits. Bizarre rearing habits  
243 such as raising young in stomachs (*Rheobatrachus*), hip-pockets (*Assa*), or subterranean  
244 nests (*Myobatrachus*) exist on both long branches and deeply nested taxa suggesting a  
245 remarkable frequency of transition among states. Similarly, morphological variation has  
246 rapidly evolved to dramatic extremes. The long limbed highly aquatic *Litoria dahlii*  
247 with webbed feet and dorsally situated eyes is sister to the short-limbed burrowing  
248 water-holding frogs *Cyclorana* (Vidal-Garcia & Keogh 2015). Together these frogs are  
249 embedded deeply within the otherwise toe-padded and arboreal tree frogs, highlighting  
250 the adaptive capacity of pelodryadids. Myobatrachoids too have taken ecomorphology to  
251 the extreme, offering us what is perhaps the world's strangest living anuran, the turtle  
252 frog *Myobatrachus gouldii*. In pursuit of their backwards burrowing lifestyle and termite-  
253 heavy diet, *Myobatrachus* lack many of the characteristics we typically associate with  
254 frogs. Their beady black eyes are set in small heads and, alongside their sister taxon  
255 *Arenophryne*, they crawl—not jump—across the ground on short limbs that are  
256 incapable of hopping (Vidal-Garcia et al. 2014).



258 Figure 2. Time-calibrated frog phylogeny highlights the varied origins and staggered  
259 arrival of the four major frog families that comprise the Australian anuran fauna.  
260 Primarily Australian clades are identified by black branches and text, their closest living  
261 relatives outside of Australia are noted by colored branches and text, and outgroup taxa  
262 are grey. White circles at nodes identify the location of fossil calibrations (see Table S2).  
263 Upper inset map shows the general geographic location of: (red) closely related  
264 microhylids in New Guinea, (purple) phyllomedusid hylids in South America, and (dark  
265 blue) *Calyptocephalella* in Chile. Lower inset maps show the connection and proximity  
266 of Australia to other Gondwanan continents as Australia drifted away over the past 100  
267 million years. White indicates contemporary coastlines, light blue the continental plates,  
268 and dark blue the oceans. Maps were generated using GPlates and input files modified  
269 from Landis (2017). Partial fan phylogeny was plotted using *phytools* in the R  
270 programming environment. Annotations on vertical time axis show the age of crown  
271 divergences of other notable Australian groups for temporal context (see Fig.1). Species  
272 illustrated clockwise from top left: *Cophixalus infacetus*, *Austrochaperina robusta*,  
273 *Litoria fallax*, *Litoria dahlii*, *Litoria xanthomera*, *Myobatrachus gouldii*, *Spicospina*  
274 *flammocaerulea*, *Taudactylus acutirostris*, *Notaden bennettii*, *Mixophyes balbus*.

275

276 *Conclusion*

277 Australian frogs offer important insights into colonization, persistence, and  
278 diversification of a major continental group through deep time. The varied species  
279 richness, timing of diversification, and ecomorphological diversity among replicate  
280 radiations provides evidence of the processes dictating the accumulation of biodiversity.  
281 Beyond the temperate and tropical forests of the east and north coast, the Australian  
282 continent is an open country of habitat scarcely welcoming to frogs. Despite this,  
283 anurans have a long history in Australia and have diversified into an amazing array of

284 forms, colors, and lifestyles. This success is potentially the result of the stratified  
285 temporal arrival of the three main frog clades and possibly exaggerated by their  
286 ecological differences. Our phylogenetic framework provides a foundation for examining  
287 how temporal changes to climate, habitat, and niche space have influenced the  
288 diversification of one of Australia's richest and most unique vertebrate faunas.

289

290 *Data Accessibility*

291 Sequence alignments, analysis control files, and phylogenetic trees can be  
292 downloaded from Dryad (doi:10.5061/dryad.zpc866tcj) and GitHub  
293 ([https://github.com/IanGBrennan/Crown\\_Frogs](https://github.com/IanGBrennan/Crown_Frogs)). We also provide a temporary link to  
294 these files suitable for peer review:

295 <https://datadryad.org/stash/share/gZnvJUP7Ow7xlQjrJr3Z9IYlMWqshquiWGGahkNRji4>

296

297 *Conflicts of Interest*

298 The authors recognize no conflicts of interest, either direct or indirect, that might  
299 bias the conclusions, implications, or opinions stated in this work.

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472 *Figure Captions*

473 Figure 1. Australian frogs show a pattern of increasing species richness with  
474 precipitation, and with time. Above, maps of richness for the three focal radiations  
475 (with Limnodynastidae and Myobatrachidae presented together as Myobatrachoidea)  
476 are plotted alongside a map showing total annual precipitation. Greatest richness is  
477 concentrated along Australia's east coast, however this pattern falls away in cold areas  
478 of the far southeast, particularly in southwest Tasmania. Species occurrence records  
479 were collated from the Atlas of Living Australia (<https://ala.org.au>). Below, Australian  
480 radiations can be divided broadly into (1) relictual Gondwanan clades >40 myo (green),  
481 (2) ancient colonizing groups (>20 myo, <40 myo; varied colors), or (3) immigrant  
482 clades of Asian origin (orange). Each point is colored according to the region of  
483 hypothesized origin and labeled by the narrowest phylogenetic taxonomy. Black labels  
484 indicate focal groups and grey labels indicate other Australian vertebrate clades.  
485 Regression in background is fit to all points and shows a general pattern of increasing  
486 species richness with age.

487

488 Figure 2. Time-calibrated frog phylogeny highlights the varied origins and staggered  
489 arrival of the four major frog families that comprise the Australian anuran fauna.  
490 Primarily Australian clades are identified by black branches and text, their closest living  
491 relatives outside of Australia are noted by colored branches and text, and outgroup taxa  
492 are grey. White circles at nodes identify the location of fossil calibrations (see Table S2).  
493 Upper inset map shows the general geographic location of: (red) closely related  
494 microhylids in New Guinea, (purple) phyllomedusid hylids in South America, and (dark  
495 blue) *Calyptocephallela* in Chile. Lower inset maps show the connection and proximity  
496 of Australia to other Gondwanan continents as Australia drifted away over the past 100  
497 million years. White indicates contemporary coastlines, light blue the continental plates,

498 and dark blue the oceans. Maps were generated using GPlates and input files modified  
499 from Landis (2017). Partial fan phylogeny was plotted using *phytools* in the R  
500 programming environment. Annotations on vertical time axis show the age of crown  
501 divergences of other notable Australian groups for temporal context (see Fig.1). Species  
502 illustrated clockwise from top left: *Cophixalus infacetus*, *Austrochaperina robusta*,  
503 *Litoria fallax*, *Litoria dahlii*, *Litoria xanthomera*, *Myobatrachus gouldii*, *Spicospina*  
504 *flammoecaerulea*, *Taudactylus acutirostris*, *Notaden bennettii*, *Mixophyes balbus*.  
505  
506

507 Supplementary Materials

508

509 Data available from the Dryad Digital Repository:

510 [http://dx.doi.org/10.5061/dryad.\[NNNN\]](http://dx.doi.org/10.5061/dryad.[NNNN])

511 and from the GitHub repository: [https://github.com/IanGBrennan/Crown\\_Frogs](https://github.com/IanGBrennan/Crown_Frogs)

512

513 Table S1. Taxon sampling for this project.

Geography	Superfamily/Clade	Family	Subfamily	Genus species	Registration
Outgroup	Pipoidea	Pipidae	—	<i>Xenopus tropicalis</i>	NCBI Genome
Outgroup	Pipoidea	Pipidae	—	<i>Pipidae Pipa pipa</i>	MVZ 247511
Outgroup	Pipoidea	Rhinophrynidiae	—	<i>Rhinophrynus dorsalis</i>	MVZ 164756
Outgroup	Leiopelmatoidae	Ascaphidae	—	<i>Ascaphus montanus</i>	REF AscMon
Outgroup	Discoglossoidea	Bombinatoridae	—	<i>Bombina microdelinqitora</i>	CAS 242112
Outgroup	Discoglossoidea	Alytidae	—	<i>Alytes obstetricans</i>	MVZ 231914
Outgroup	Pelobatoidea	Scaphiopodidae	—	<i>Spea hammondii</i>	MVZ 145187
Outgroup	Pelobatoidea	Pelodrytidae	—	<i>Pelodytes ibericus</i>	MVZ 186009
Outgroup	Pelobatoidea	Megophryidae	—	<i>Leptolalax bourreti</i>	AMCC 106489
Outgroup	Pelobatoidea	Pelobatidae	—	<i>Pelobates syriacus</i>	MVZ 234650
Outgroup	—	Heleophrynidiae	—	<i>Heleophryne purcelli</i>	SANBI 1954
Outgroup	Ranoidea	Ptychadenidae	—	<i>Ptychadena mascareniensis</i>	ESP/CJR R1068
Outgroup	Ranoidea	Phrynobatrachidae	—	<i>Phrynobatrachus keniensis</i>	MVZ 226261
Outgroup	Ranoidea	Microhylidae	Phrynomatiniae	<i>Phrynomantis annectens</i>	ESP/CJR R1330
Outgroup	Ranoidea	Microhylidae	Otophryinae	<i>Otophryne robusta</i>	PLVP PT459
Outgroup	Ranoidea	Microhylidae	Gastrophryinae	<i>Stereocyclops incrassatus</i>	PLVP PT273
Outgroup	Ranoidea	Microhylidae	Scaphiophryinae	<i>Scaphiophryne brevis</i>	PLVP PT312
Outgroup	Ranoidea	Microhylidae	Cophylinae	<i>Plethodontohyla notosticta</i>	AMCC 128714
Outgroup	Ranoidea	Microhylidae	Kalophryinae	<i>Kalophrynus interlineatus</i>	ABTC 105933
Outgroup	Ranoidea	Microhylidae	Dyscophinae	<i>Dyscophus quinetti</i>	MVZ 238744
Outgroup	Ranoidea	Microhylidae	Microhylinae	<i>Kaloula picta</i>	ABTC 76311
Outgroup	Ranoidea	Microhylidae	Microhylinae	<i>Microhyla berdmorei</i>	ABTC 106005
Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Liophryne rhododactyla</i>	ABTC 49542
Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Callulops doriae</i>	ABTC 98415
Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Hylophorbus rainierguntheri</i>	ABTC 98304
Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Genyophryne thomsoni</i>	PLVP PT452
Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Barygenys flavigularis</i>	PLVP PT439
Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Copula pipilans</i>	ABTC 114698
Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Austrochaperina guttata</i>	ABTC 141506
Australian Clade	Ranoidea	Microhylidae	Asterophryinae	<i>Austrochaperina gracilipes</i>	ABTC 79186
Australian Clade	Ranoidea	Microhylidae	Asterophryinae	<i>Austrochaperina robusta</i>	conx5153
Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Oreophryne brachypus</i>	ABTC 104804
Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Aphantophryne pansa</i>	ABTC 49605
Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Cophixalus parkeri</i>	ABTC 49557

# AUSTRALIAN FROG PHYLOGENOMICS

Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Cophixalus balbus</i>	ABTC 114884
Outgroup	Ranoidea	Microhylidae	Asterophryinae	<i>Cophixalus bewaniensis</i>	ABTC 112107
Australian Clade	Ranoidea	Microhylidae	Asterophryinae	<i>Cophixalus crepitans</i>	conx1112
Australian Clade	Ranoidea	Microhylidae	Asterophryinae	<i>Cophixalus infacetus</i>	conx5295
Australian Clade	Ranoidea	Microhylidae	Asterophryinae	<i>Cophixalus hosmeri</i>	conx5267
Outgroup	Myobatrachoidea	Calyptocephalellidae	—	<i>Calyptocephalella gayi</i>	PMH 1
Australian Clade	Myobatrachoidea	Rheobatrachidae	—	<i>Rheobatrachus silus</i>	ABTC 7324
Australian Clade	Myobatrachoidea	Rheobatrachidae	—	<i>Rheobatrachus vitellinus</i>	ABTC 105698
Australian Clade	Myobatrachoidea	Mixophyidae	—	<i>Mixophyes balbus</i>	ABTC 25323
Australian Clade	Myobatrachoidea	Mixophyidae	—	<i>Mixophyes hihihorlo</i>	ABTC 45861
Australian Clade	Myobatrachoidea	Limnodynastidae	—	<i>Lechriodus fletcheri</i>	ABTC 24892
Australian Clade	Myobatrachoidea	Limnodynastidae	—	<i>Opisthodon ornatus</i>	ABTC 15543
Australian Clade	Myobatrachoidea	Limnodynastidae	—	<i>Heleioporos australiacus</i>	ABTC 67742
Australian Clade	Myobatrachoidea	Limnodynastidae	—	<i>Neobatrachus albipes</i>	ABTC 15833
Australian Clade	Myobatrachoidea	Limnodynastidae	—	<i>Notaden nichollsi</i>	ABTC 15833
Australian Clade	Myobatrachoidea	Limnodynastidae	—	<i>Limnodynastes dumerilii</i>	ABTC 104299
Australian Clade	Mvobatrachoidea	Limnodynastidae	—	<i>Philaria sphaanicola</i>	ABTC 25832
Australian Clade	Myobatrachoidea	Limnodynastidae	—	<i>Adelotus brevis</i>	ABTC 24210
Australian Clade	Mvobatrachoidea	Mvobatrachidae	—	<i>Taudactylus liemi</i>	ABTC 50947
Australian Clade	Myobatrachoidea	Myobatrachidae	—	<i>Paracrinia haswelli</i>	ABTC 26441
Australian Clade	Myobatrachoidea	Myobatrachidae	—	<i>Geocrinia alba</i>	ABTC 106079
Australian Clade	Myobatrachoidea	Myobatrachidae	—	<i>Assa darlingtoni</i>	ABTC 136278
Australian Clade	Myobatrachoidea	Myobatrachidae	—	<i>Bryobatrachus nimbus</i>	ABTC 25297
Australian Clade	Myobatrachoidea	Myobatrachidae	—	<i>Crinia signifera</i>	ABTC 25676
Australian Clade	Myobatrachoidea	Myobatrachidae	—	<i>Spicospina flammoecaerulea</i>	ABTC 144371
Australian Clade	Myobatrachoidea	Myobatrachidae	—	<i>Uperoleia laevigata</i>	MM 1227
Australian Clade	Myobatrachoidea	Myobatrachidae	—	<i>Pseudophryne major</i>	ABTC 16479
Australian Clade	Mvobatrachoidea	Mvobatrachidae	—	<i>Metacrinia nichollsi</i>	ABTC 17124
Australian Clade	Myobatrachoidea	Myobatrachidae	—	<i>Arenophryne rotunda</i>	ABTC 114066
Australian Clade	Myobatrachoidea	Myobatrachidae	—	<i>Myobatrachus gouldii</i>	WAM R156759
Outgroup	Hyoioidea	Hemiphractidae	—	<i>Stefania evansi</i>	BNP1286
Outgroup	Hyoioidea	Ceratophryidae	—	<i>Ceratophrys cornuta</i>	MVZ 247561
Outgroup	Hyoioidea	Hylidae	Cophomantinae	<i>Hypsiboas crepitans</i>	YPM 10666
Outgroup	Hyoioidea	Hylidae	Lophohylinae	<i>Osteopilus dominicensis</i>	MCZA148702
Outgroup	Hyoioidea	Hylidae	Scinaxinae	<i>Scinax staufferi</i>	MVZ 257781
Outgroup	Hyoioidea	Hylidae	Pseudinae	<i>Pseudis paradoxa</i>	LSUMNS 12511
Outgroup	Hyoioidea	Hylidae	Dendropsophinae	<i>Dendropsophus microcephalus</i>	MVZ 264263
Outgroup	Hyoioidea	Hylidae	Acrisinae	<i>Pseudacris nigrita</i>	REF PseNig
Outgroup	Hyoioidea	Hylidae	Hylinae	<i>Smilisca fodiens</i>	YPM 014191
Outgroup	Hyoioidea	Phyllomedusidae	—	<i>Cruziohyla calcarifer</i>	QCAZ 48552
Outgroup	Hyoioidea	Phyllomedusidae	—	<i>Phyllomedusa vallantii</i>	QCAZ 48818
Australian Clade	Hyoioidea	Pelodryadidae	—	<i>Litoria citropa</i>	ABTC 7146
Australian Clade	Hyoioidea	Pelodryadidae	—	<i>Nyctimystes dayi</i>	ABTC 15997
Australian Clade	Hyoioidea	Pelodryadidae	—	<i>Litoria genimaculata</i>	ABTC 42824
Australian Clade	Hyoioidea	Pelodryadidae	—	<i>Litoria wilcoxii</i>	ABTC 16804
Australian Clade	Hyoioidea	Pelodryadidae	—	<i>Litoria andiirrmalin</i>	ABTC 142651
Australian Clade	Hyoioidea	Pelodryadidae	—	<i>Litoria xanthomera</i>	ABTC 102385
Australian Clade	Hyoioidea	Pelodryadidae	—	<i>Litoria ailleni</i>	ABTC 30786

Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria raniformis</i>	ABTC 12854
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria thesaurensis</i>	ABTC 50489
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria dahlii</i>	ABTC 102434
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Cyclorana cultripes</i>	ABTC 16892
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria infrafrenata</i>	ABTC 86210
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria brevipalmata</i>	ABTC 127632
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Nyctimystes disrupta</i>	ABTC 48225
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria revelata</i>	ABTC 80814
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria burrowsi</i>	ABTC 17631
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria tyleri</i>	ABTC 3925
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria balatus</i>	ABTC 100638
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria dorsalis</i>	ABTC 79181
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria adelaidensis</i>	ABTC 28282
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria anqiana</i>	ABTC 48210
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria fallax</i>	ABTC 102409
Australian Clade	Hyloidea	Pelodryadidae	—	<i>Litoria tornieri</i>	ABTC 11777

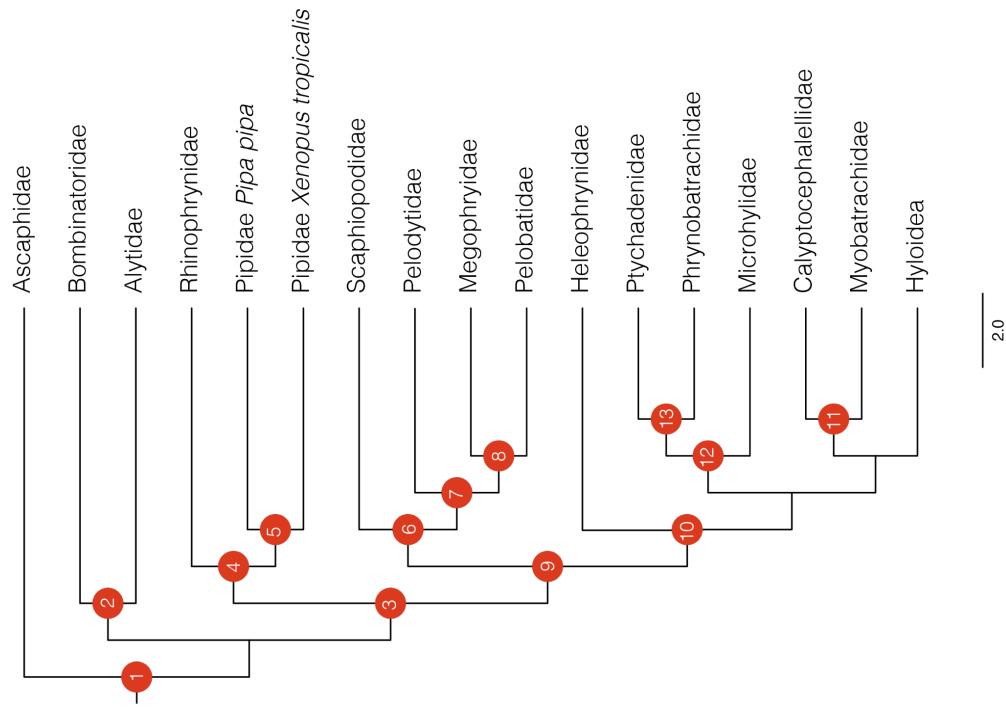
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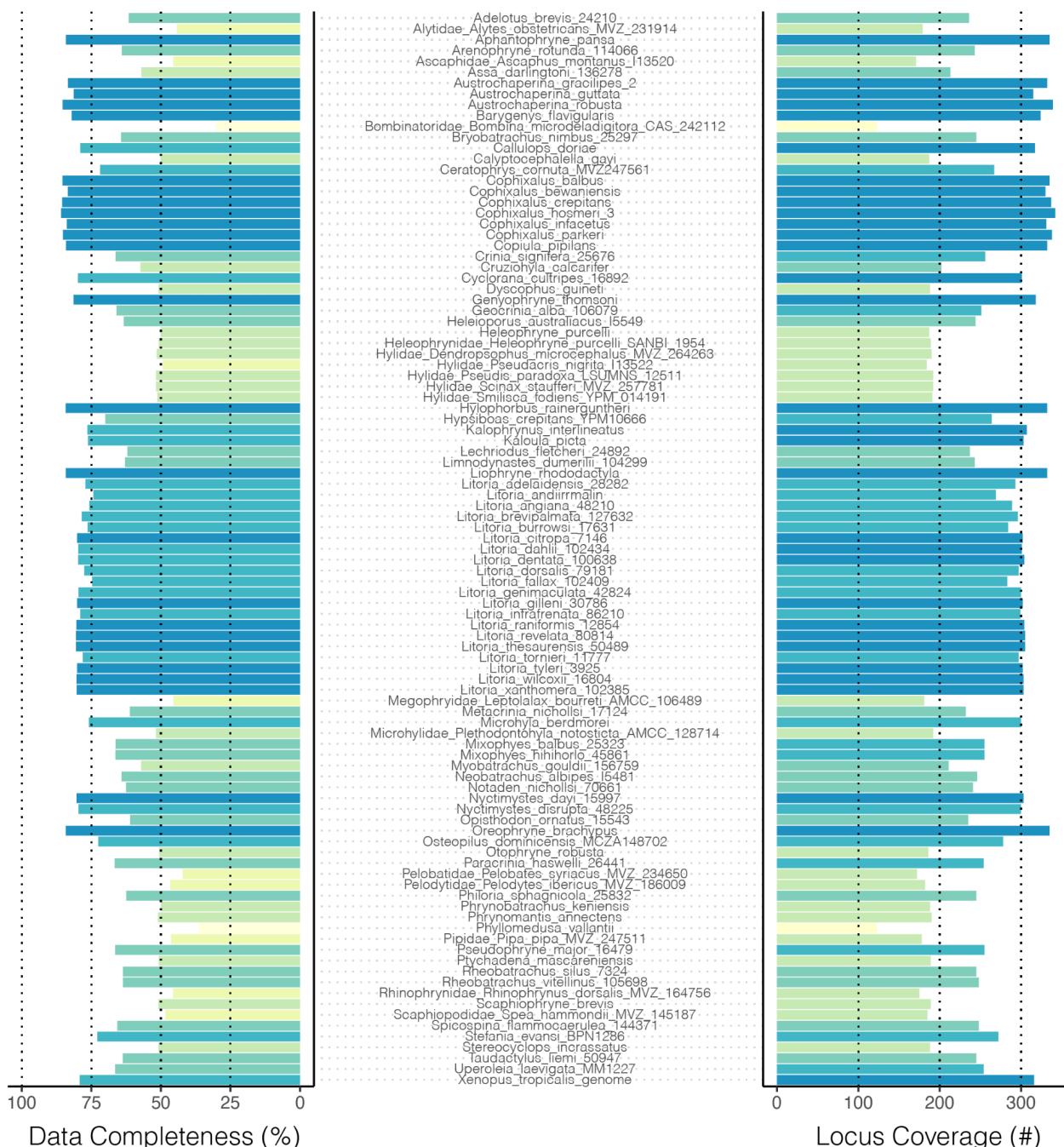
515

516 Table S2. Fossil calibrations implemented in MCMCTree analysis of frog divergence  
 517 dates. Node number (#) corresponds to nodes in supplementary figure below.  
 518

#	Node Calibrated	Fossil	Minimum	Soft Max.	Source (see Feng et al. 2017)
1	Anura	$\dagger$ <i>Liaobatrachus zhaoi</i>	129.7	252	Chang et al. (2009)
2	Alytoidea	$\dagger$ <i>Iberobatrachus angelae</i>	125	252	Gomez et al. (2016)
3	Pipanura	$\dagger$ <i>Rhadinosteus parvus</i>	148.1	252	Cannatella (2015)
4	Pipoidea	$\dagger$ <i>Neusibatrachus wilferti</i>	127.2	52	Gomez et al. (2016)
5	Pipidae	$\dagger$ <i>Pachycentra taquetti</i>	83.6	48.1	Cannatella (2015)
6	Pelobatoidea	$\dagger$ <i>Elkobatrachus brocki</i>	46.1	148.1	Henrici and Haynes (2006)
7	Pelodytes + (Pelobatidae + Megophryidae)	$\dagger$ <i>Miopelodytes gilmorei</i>	38.9	148.1	Henrici and Haynes (2006)
8	Pelobatidae + Megophryidae	$\dagger$ <i>Macropelobates osborni</i>	28.1	148.1	Cohen et al. (2013)
9	Acosmanura	$\dagger$ <i>Eurycephalella alcinae</i>	113	252	Baez (2009)
10	Neobatrachia	$\dagger$ <i>Beelzebufo ampinga</i>	66	148.1	Rogers et al. (2013)
11	Myobatrachoidea	$\dagger$ <i>Calyptocephalella pichileufensis</i>	47.5	48.1	Gomez et al. (2011)
12	Ranoidea	$\dagger$ <i>Thamatosaurus gezei</i>	33.9	148.1	Rage and Rocek (2007)
13	Ptychadenidae + Phrynobatrachus	<i>Ptychadenidae fossil</i>	25	148.1	Blackburn et al. (2015)

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522      Data Completeness (%)

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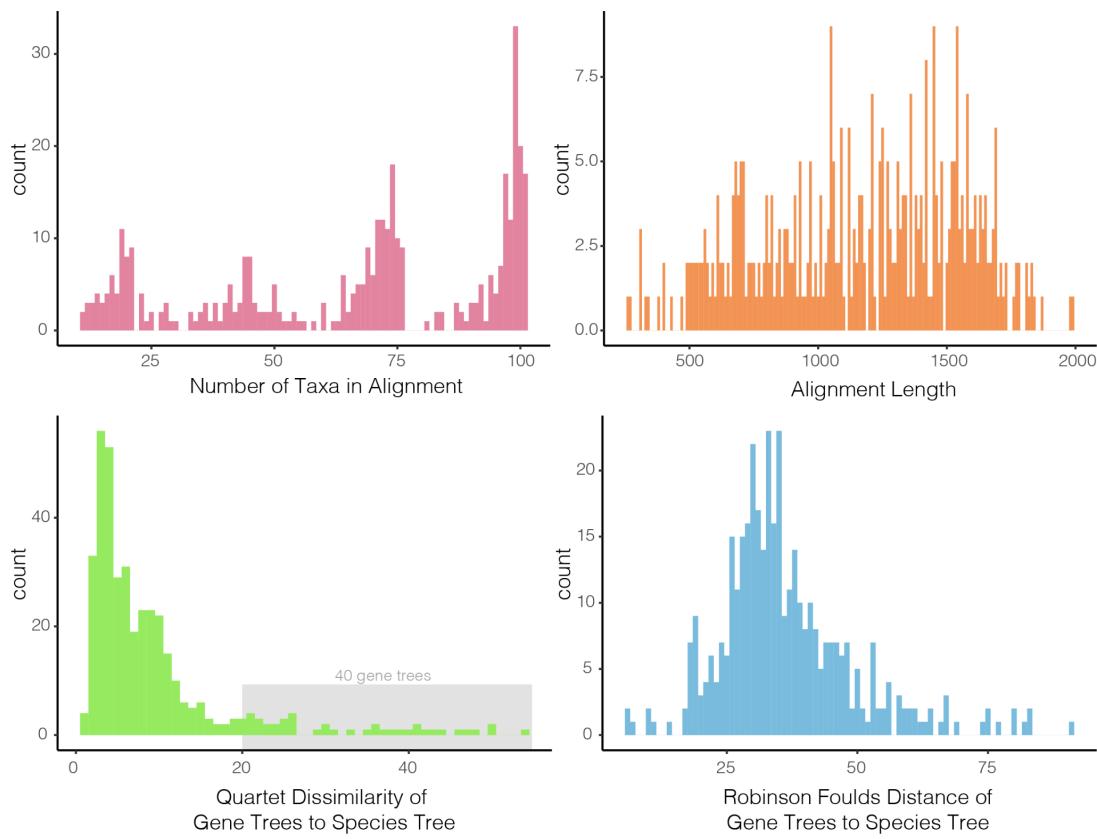
524      Figure S1. Data completeness across all samples. Left histogram shows data

525      completeness as percent of bases in total alignment (concatenated alignment length

526      523,036 bp) exclusive of gaps (-) and missing bases (N). Right histogram shows data

527      completeness as the absolute number of loci included per sample, as a representation of

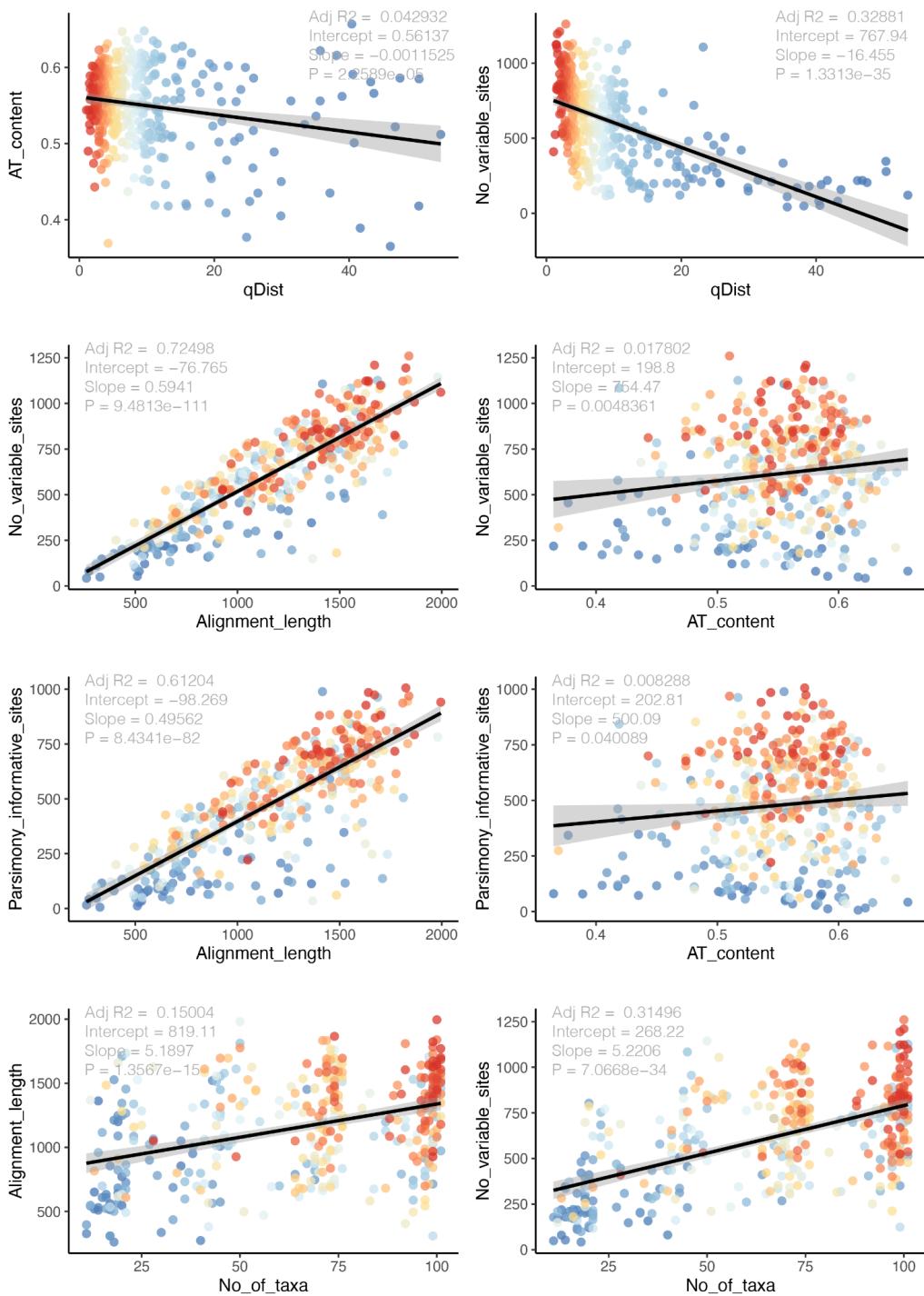
528      the number of gene trees per sample.



529

530 Figure S2. Basic summary statistics of the 450 locus alignments and gene trees. Top row  
 531 shows histograms of the number of taxa in (max=101, min=11) and length of each  
 532 alignment. Bottom row shows gene tree--species tree distances as quartet dissimilarity  
 533 scores and Robinson Foulds distances, two different measures of topological similarity.  
 534 Both quartet dissimilarity and RF scores are estimated by first subsetting the species  
 535 tree to match gene tree sampling.

536

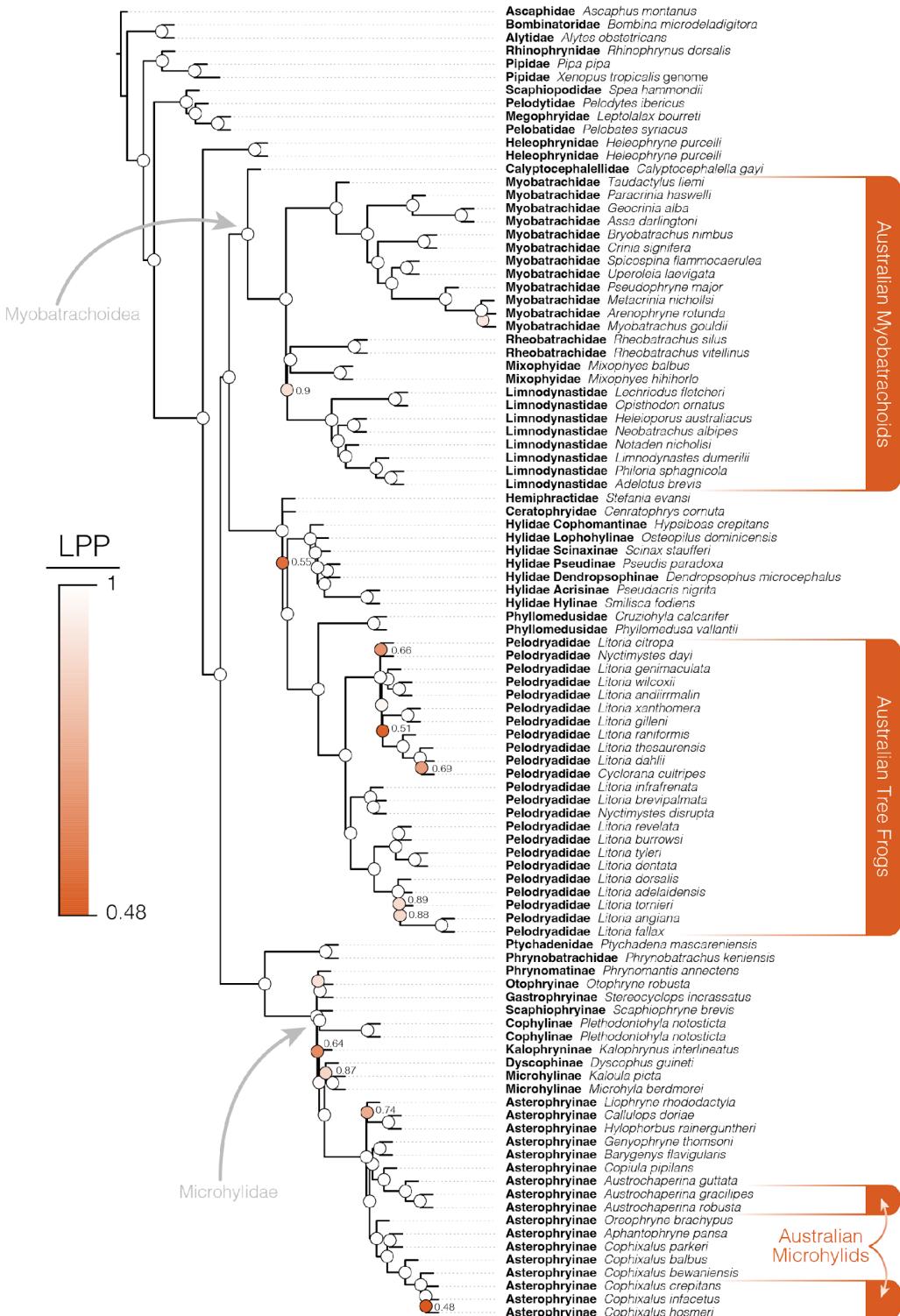


537

538 Figure S3. Detailed summary statistics of the 450 locus alignments and gene trees. Top  
 539 row compares AT content and number of variable sites against quartet distance between  
 540 each gene tree and the species tree (a measure of topological similarity). The second and  
 541 third rows compare measures of locus informativeness (number of variable sites, number

542 of parsimony informative sites) against alignment length and AT content. The bottom  
543 row shows alignment length and number of variable sites as a function of the number of  
544 taxa in the alignment. In all plots points (representing trees or alignments) are colored  
545 according to the quartet distance from the species tree.

546



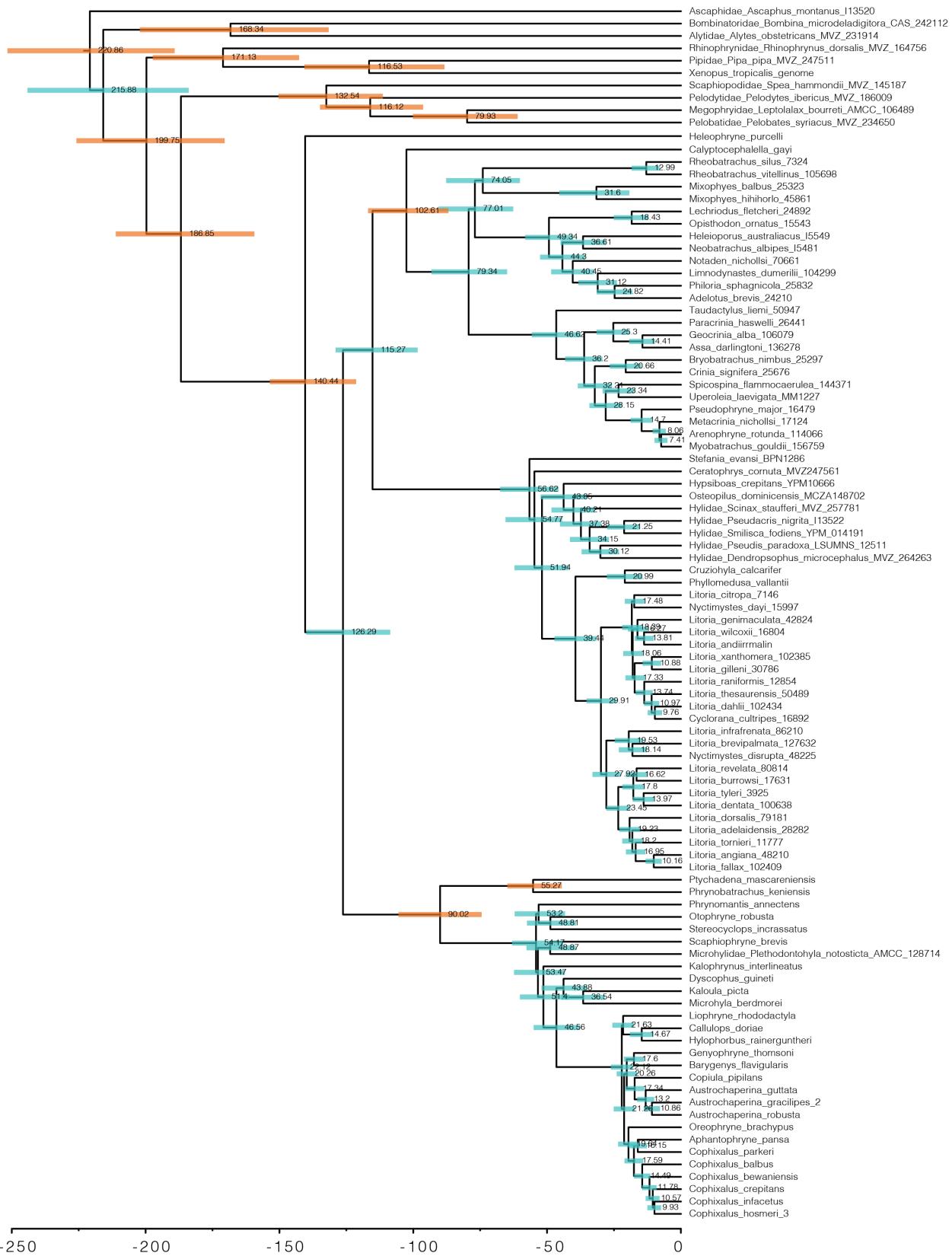
547

548 Figure S4. Species tree of Australian frogs and appropriate outgroup taxa estimated using  
549 ASTRAL with locus trees estimated by IQTREE as input. Phylogenetic resolution among  
550 major frog groups and within Australian frog clades is consistently high. Support values

551 are shown at nodes and colored according to local posterior probabilities (LPP), values

552 >0.9 are considered strongly supported and not indicated at nodes (white circles).

553



555 Figure S5. Species tree of Australian and outgroup frogs estimated with ASTRAL from  
556 IQTREE genetrees and time-calibrated with MCMCTree. Shaded bars at nodes indicate  
557 95% confidence estimates on ages and numbers indicate mean age estimates. Orange  
558 shaded bars indicate nodes which were calibrated with fossil evidence (see Table  
559 S2).