Correlates of eye colour and pattern in mantellid frogs

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Abstract. With more than 250 species, the Mantellidae is the most species-rich family of frogs in Madagascar. These frogs are highly diversified in morphology, ecology and natural history. Based on a molecular phylogeny of 248 mantellids, we here examine the distribution of three characters reflecting the diversity of eye colouration and two characters of head colouration along the mantellid tree, and their correlation with the general ecology and habitat use of these frogs. We use Bayesian stochastic character mapping, character association tests and concentrated changes tests of correlated evolution of these variables. We confirm previously formulated hypotheses of eye colour pattern being significantly correlated with ecology and habits, with three main character associations: many tree frogs of the genus *Boophis* have a bright coloured iris, often with annular elements and a blue-coloured iris periphery (sclera); terrestrial leaf-litter dwellers have an iris horizontally divided into an upper light and lower dark part; and diurnal, terrestrial and aposematic *Mantella* frogs have a uniformly black iris. Furthermore, the presence of a frenal streak and a dark tympanic patch were associated with each other, with horizontally divided iris colour, and with terrestrial habits. Our study is restricted to the mantellid radiation, and the performed tests detect the simultaneous distribution of independent character states in a tree, rather than providing a measure for phylogenetic independent correlation of these character states. The concentrated changes tests suggest that the evolutionary origin of a bright iris might indeed be correlated to arboreal habits. Yet, rather than testing hypotheses of adaptive evolution of eye colour in anurans, our study serves to formulate hypotheses of convergence more precisely and thus to open perspectives for their further testing in a comparative framework along the anuran tree of life. For instance, a brightly coloured iris and sclera might serve mate recognition or as aposematic defensive strategy especially in tree frogs, and a horizontally divided iris colour might constitute a disruptive defensive strategy in frogs inhabiting the leaf litter stratum.

Key words. Amphibia, Anura, Mantellidae, Madagascar, correlated evolution, iris colour, sclera, frenal streak, tympanic patch.

Introduction

The evolution of amphibians is known to be strongly characterized by homoplasy, and convergence has been demonstrated in the evolution of characters of external morphology (e.g., Ohler & Dubois 1989) and skeleton (Kamermans & Vences 2009, Manzano et al. 2007, Fabrezi & Emerson 2003). Convergence has putatively shaped species in multiple unrelated lineages (Emerson 1986) to such similar general external appearances that distantly related species can look virtually identical (e.g., miniaturized frogs, tree frogs, or leaf litter frogs) and their evolutionary relationships could only be reliably deciphered with the aid of molecular phylogenetic tools (e.g., Bossuyt & Milinkovitch 2000, Van der Meijden et al. 2005, Mueller et al. 2004). Similar to the situation in some lizards (Williams 1983, Losos & Thorpe 2004), the putative association between general habits and morphology has led biologists to hypothesize whether so-called "ecomorphs" could also be defined in frogs, referring to forms with similar ecology-morphology relationships that appear repeatedly in the evolution of insular frog radiations (Brown 2009). These similarities among largely unrelated frogs also extend to patterns of colouration, a field that has only recently received increased attention (e.g., Summers 2003, Hagman & Forsman 2003, Siddiqi et al. 2004, Wollenberg et al. 2007, 2008, Ries et al. 2008, Wang & Shaffer 2008, Wollenberg & Measey 2009, Brown et al. 2010, Sztatecsny et al. 2010, de Luna et al. 2010, Santos & Cannatella 2011, O'Neill et al. 2012, Bell & Zamudio 2012).

Frogs show a remarkable diversity in colouration, including instances of colour polymorphism (Hoffmann & Blouin 2000, Bell & Zamudio 2012) and the co-occurrence of skin toxins and bright colours that often qualify as aposematic (Saporito et al. 2007). Convergent evolution of amphibian colour is obvious from the occurrence of very similar patterns in multiple independent clades, e.g., midvertebral stripes or dorsolateral bands that are known to be, in at least some species, inherited by simple Mendelian genetics (reviewed in Hoffmann & Blouin 2000). However, such convergences have so far only been explicitly analysed with respect to aposematic colour patterns of poison frogs (e.g., Symula et al. 2001, Summers 2003, Vences et al. 2003, Chiari et al. 2004). Even less studied is the colouration of anuran eyes. Many species of frogs have a remarkably colourful iris that often is in stark contrast to the colour of the body (e.g., Glaw & Vences 1997).

Madagascar's fauna has been flagged as an excellent model to study evolutionary questions (Vences et al. 2009) as it contains several species-rich endemic radiations. By far the largest endemic frog radiation in Madagascar is the family Mantellidae, which currently contains 141 nominal species in eight genera (Glaw & Vences 2006, 2007) plus a large number of undescribed but already identified candidate species (Vieites et al. 2009), making up a total of over 250 species. Mantellids contain a striking diversity not only of species but also of morphological diversity and adaptations to different habitats, ranging from large (> 100 mm) semiaquatic frogs living in streams to minute (< 15 mm) species that mainly inhabit the leaf litter of rainforests. In the course of their diversification, mantellids have conquered such diverse habitats as high mountains (> 2500 m altitude) and the xeric areas of Madagascar's south-west, but their centre of diversity is in the rainforest where they include arboreal, terrestrial and semiaquatic species, breeding in ponds, streams, or fully independently from open water (Glaw & Vences 2006, 2007). Mantellids are also very diverse in their colouration, including iris colour (Glaw & Vences 2007). Among the most remarkably coloured mantellids are Malagasy poison frogs in the genus *Mantella*, which sequester dietary alkaloids in their skin and have bright, aposematic dorsal colourations, ranging from bright orange to black-yellow-orange or blue (e.g., Daly et al. 1996). Many other mantellids have a brownish, cryptic colour, with or without vertebral or dorsolateral lines. Some mantellid tree frogs in the genus *Boophis* have a bright green dorsal colour with a translucent shade, similar to the unrelated Neotropical tree frogs of the family Centrolenidae. The sister clade to the Mantellidae is the mainly Asian family Rhacophoridae (Van der Meijden et al. 2005, Bossuyt et al. 2006, Frost et al. 2006), which mainly comprises arboreal species that are morphologically convergent with many mantellids (Bossuyt & Milinkovitch 2000).

The diversity of eye colouration in the Mantellidae triggered the informal analysis of Glaw & Vences (1997) who observed that bright iris colouration was found mainly in the largely arboreal genus *Boophis,* and black eyes mainly in the aposematic *Mantella* and proposed some further hypotheses of the possibly causal association of certain anuran colour patterns with their ecology. At the time, however, no reliable phylogeny for the Mantellidae was available, the taxonomy of these frogs was only incompletely known, and no quantitative analysis of character association was carried out. In the meantime the number of new frog species from Madagascar, mostly mantellids, has skyrocketed (Köhler et al. 2005, Vieites et al. 2009), their genus-level classification has been revised (Glaw & Vences 2006), and a comprehensive molecular phylogeny has been published (Wollenberg et al. 2011). In the light of this advanced state of knowledge, we here aim to refine and more precisely formulate the hypotheses of character association of Glaw & Vences (1997) based on explicit Bayesian reconstruction of character evolution along a densely sampled phylogenetic tree of mantellid species.

Materials and methods
Molecular phylogeny

A phylogeny of 138 of the 141 described species in the Mantellidae plus 122 undescribed confirmed candidate species (Vieites et al. 2009) was reconstructed based on 1772 basepairs of mitochondrial DNA (564 bp of 16S rRNA, 583 bp of cytochrome b, and 625 bp of cytochrome oxidase subunit I). The backbone of the phylogeny (i.e., relationships among subfamilies and genera) was constrained on the basis of a combined analysis of 46 species representing all major mantellid lineages, for a total of 3760 basepairs (bp) of fragments of the mitochondrial genes 12S rRNA, (538 bp), 16S rRNA (two fragments of 582 bp and 505 bp), cytochrome b (988 bp), cytochrome oxidase subunit I (625 bp), and of the nuclear genes rhodopsin exon 1 (289 bp) and regulation-activating gene 2 (816 bp). For details of the analyses performed see Wollenberg et al. (2011). From the resulting time-calibrated Bayesian inference tree we pruned those taxa for which no or incomplete ecological and colour data were available, and used this final tree with a total of 248 species for comparative analyses.

Ecological and colour character coding

Data on the natural history, habitat and habits of mantellid frog species, as well as on their head and eye colour patterns, was compiled from a large collection of original live photographs that are to the largest extent reproduced in Glaw & Vences (2007) (see Supplementary Table S1). Translating ecological and morphological traits into categorical character states always requires making uncomfortable decisions because the complexity of nature rarely fits perfectly into human-made categories. This particularly refers to the interpretation of the habits and general ecology of a given species, where these decisions were some-

times difficult to make. However, we are convinced that in general our categorization reflects true ecological differences between species. Another source of uncertainty, the individual variation of colour patterns within species, was of lesser importance. As previously discussed (e.g., GLAW & VENCES 1997), eye colouration appears to be remarkably constant within species, even between geographically distant conspecific populations. The same is true for the frenal streak (e.g., VENCES & GLAW 2004) and to a somewhat lesser degree also for the dark tympanic patch. Coding of ecological and morphological characters was as follows:

General ecology and habits: (0) arboreal, (1) terrestrial, (2) semiarboreal, (3) saxicolous, (4) rheophilous (semi-aquatic), (5) terrestrial to rheophilous (riparian).

Detailed iris pattern: (0) uniform black (also used for taxa with a small amount of light pigment in the upper half of the iris), (1) more or less uniform, any other colour but black, sometimes with reticulation; (2) densely reticulated (dark reticle on a light iris), (3) annular, divided in an outer and inner iris colour (not counting a colourful area around the iris margin, called iris periphery by GLAW & VENCES 1997 and probably constituting the sclera), (4) horizontally striped with central dark stripes on both sides lateral to the pupil, (5) horizontally divided into two halves of different colour, usually an upper light and a lower dark half.

Iris contrast: (0) iris of similar tone as body, (1) iris darker than body, (2) iris distinctly more colourful.

Colour of iris periphery (sclera): (0) indistinct, (1) blue, (2) bluish (including light blue to turquoise), (3) green, (4) yellow, (5) red, (6) white.

Dark tympanic patch on both sides of the head or broad dark longitudinal line behind eyes: (0) present, (1) absent.

Frenal streak (light streak running from below tympanum along upper lip): (0) present, (1) absent.

General dorsal colouration: (0) presumed cryptic, non-aposematic, (1) presumed aposematic.

Reconstruction of character evolution and correlation

We chose Bayesian stochastic character mapping (HUELSENBECK et al. 2003) to reconstruct character evolution instead of parsimony or maximum likelihood for several reasons. First, parsimony is an unrealistic method for fast-changing characters, but also performs poorly on conservative characters evolving across long time trajectories, underestimating the number of changes (RONQUIST 2004). This latter situation is the case in mantellid frogs, which separated from other frog lineages circa 60 mya (ROELANTS et al. 2007). Second, stochastic mapping allows transitions among states of characters along the branches in phylogenetic trees and evaluates character histories based on their posterior probabilities (RONQUIST 2004).

All analyses were performed using SIMMAP 1.5.2 software (BOLLBACK 2006). Because of the large size of the group examined, stochastic mapping on a subset of trees

obtained by Bayesian inference was computationally not feasible. Therefore, we conducted the analyses using our preferred tree (the majority-rule consensus tree from Bayesian analysis). Correlated evolution among morphological characters, and between morphological and ecological characters was examined using the pairwise association value d_{ij} and overall character correlation D_{ij} (see Supplementary Materials for detailed values obtained) as described by HUELSENBECK et al. (2003) and BOLLBACK (2006). Predictive P-values (P) for determining significance of character state associations and posterior probabilities of relevant nodes in the phylogeny were calculated by averaging 100 realizations and 1000 simulations of the null hypothesis as the probability of observing a value larger than expected by the null model of character independence. The same scheme was used to obtain the null distributions for d_{ij} statistics of state association. To be certain to only consider highly significant rather than spurious character state associations, we applied sequential Bonferroni correction, taking into account their total number in all 36 tests performed (considering both the association tests of general ecology vs. colour patterns, and among colour patterns, thus following the most conservative approach possible).

We tested for an evolutionary correlation among ecology and colour pattern with the concentrated-changes test of MADDISON (1990) to assess the association of changes in these two binary characters (see LORCH & EADIE, 1999). This test, as implemented in MacClade 3.0 (MADDISON & MADDISON 1998), uses only binary characters and we therefore performed it on simplified characters of arboreal vs. non-arboreal frogs (counting semi-arboreal species as non-arboreal), and iris contrast as bright vs. dull (species with an iris darker than body counted as dull), as well as the already binary characters "frenal streak" and "dark tympanic patch". This test determines the probability that various numbers of gains and losses of the dependent character state (colour pattern) would occur in certain distinguished areas of the clade selected (defined by ecology – arboreal vs. non-arboreal), given that a certain number of gains and losses occur in the whole clade, and given the null model that changes are randomly distributed among the branches of the clade.

Results
Evolution of ecology, habitat, eye and head colours in the Mantellidae

Bayesian analysis of character evolution indicates a complex history of ecological diversification in mantellid frogs. The ancestral general ecology at the mantellid root could not be reliably resolved; both a saxicolous state (posterior probability of this character state: PP = 0.431; Supplementary Table S2; Fig. 1A) as observed in some deep mantellid clades of low species diversity (*Tsingymantis* and *Boehmantis*), and an arboreal origin (PP = 0.315) received
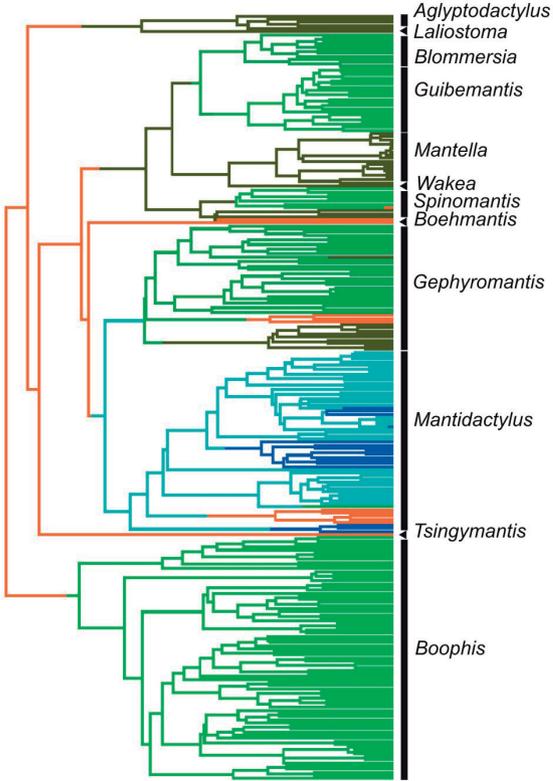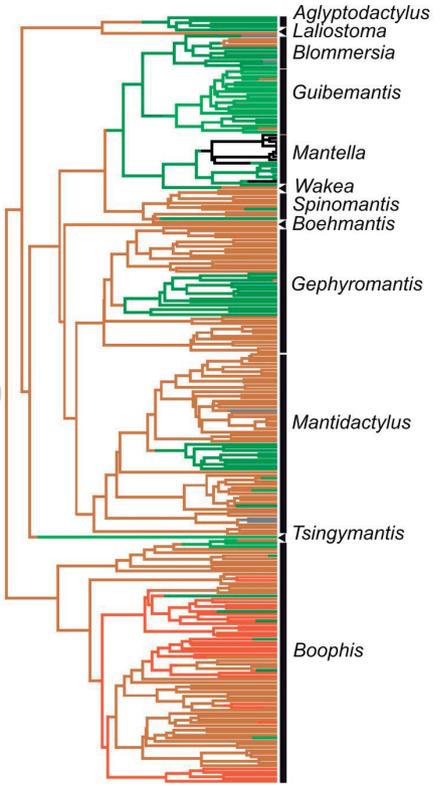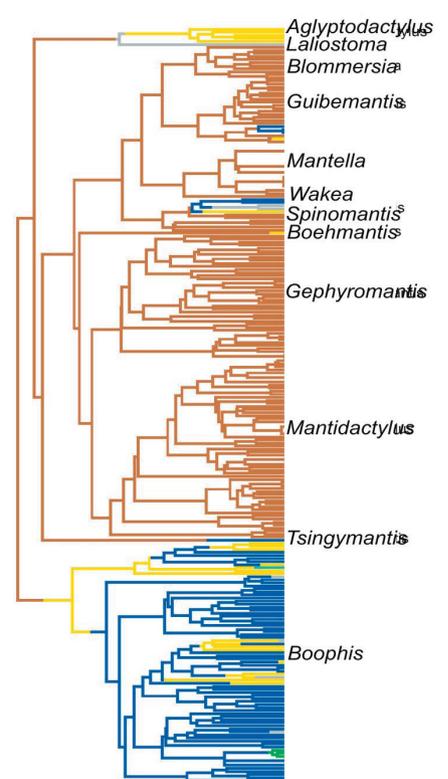
comparable posterior probabilities. In general terms, most mantellid genera are relatively uniform and well-defined regarding their general ecology and habits (Fig. 1A). Several independent evolutionary transitions leading to arboreal, semiarboreal, terrestrial and saxicolous habits are reconstructed within the family (Fig. 1A). For example, arboreality might have evolved directly from saxicolous ancestors in *Boophis*, from terrestrial forms in *Spinomantis*, or through intermediate semiarboreal stages as in *Guibemantis*. Semiarboreal habits evolved from terrestrial ancestors in *Blommersia,* or from terrestrial-rheophilous ones in *Gephyromantis* and *Mantidactylus argenteus*, in this latter case clearly supported by the nested position of the species within its genus. Remarkably, progressive adaptation to streams has occurred from terrestrial-rheophilous generalists to rheophilous specialists four times. Saxicolous habits appear derived from arboreal and terrestrial-rheophilous ancestors in three cases.

All mantellids have horizontal pupils, but iris colour and pattern has been modified multiple times across the mantellid tree (Fig. 1B; Supplementary Table S2). Uniformly black eyes evolved exclusively (and most probably twice convergently) in the genus *Mantella* but this state is not derived from the densely reticulated iris that is found in some *Mantidactylus* and *Blommersia*. Bright iris colour arranged in an annular pattern evolved convergently in various clades of the genus *Boophis*, excluding the pond-breeding subgenus *Sahona*. A contrasted iris colour also originated in two other clades of arboreal and semiarboreal frogs (*Mantidactylus argenteus* and *Guibemantis*), although in these species, the iris is clearly less bright than in most *Boophis* and has no annular pattern (Fig. 1C). All *Boophis* have a brightly coloured iris periphery (sclera) (Fig. 1D), and this character state also evolved in several other, mainly arboreal or saxicolous clades, e.g., *Spinomantis* or *Guibemantis* frogs. Generally, clades with a brightly coloured iris typically contain species with different iris periphery colours (blue, bluish, yellow, and white). Green sclera, however, were only present in one clade of *Boophis*. Of the head colour characters analysed, our reconstruction indicates that a dark tympanic patch and a frenal streak (which might however be weakly expressed) are ancestral in mantellids, and both these characters experienced many independent secondary losses (Fig. 2 and Supplementary Table S2). Aposematic colouration is exclusive to the genus *Mantella* and is reconstructed as having been present in the ancestor of this clade, with two reversals within the clade (Supplementary Table S2).

Correlation between ecology, eye and body colours in the Mantellidae

As summarized in Table 1, our analysis supported with statistical significance an association of several characters of eye and head colours with the general habits and ecology of mantellid frogs. Test statistics are detailed in Supplementary Materials. The largest differences in eye colour were found between arboreal and non-arboreal frogs. A significant tendency of iris colour being brighter than the body was only observed in arboreal frogs whereas in most other ecological clusters, this association was significantly negative. An annular iris pattern was associated with arboreal frogs (only occurring in those of the genus *Boophis*) and negatively associated with terrestrial-rheophilous and semiarboreal habits. In contrast, semiarboreal and rheophilous frogs shared a prevalence of horizontally divided eyes. Arboreality was the only ecological state negatively associated with an indistinctly coloured iris periphery, but it was positively associated with blue iris periphery colour, which in turn was negatively associated with all other habits except the saxicolous one. Dark tympanic patches and a frenal streak were positively associated with terrestriality, but negatively with stream-bank dwellers (terrestrial-rheophilous), and arboreal frogs.

We furthermore identified several instances of association of eye colour and head colour patterns (Supplementary Table S3). Aposematic body colouration was associated with black eyes (only occurring in the *Mantella* clade). Frogs with indistinctly coloured sclera had most often horizontally divided eyes. Blue sclera occurred in frogs whose iris was brighter than the body, while an iris of similar brightness as the body occurred in frogs that had indistinctly coloured sclera. Frenal streak and dark tympanic patch were strongly correlated with each other, and both were more frequently found in frogs with a horizontally divided or striped iris than expected by chance.

To obtain some first indications whether these character associations would also point to a correlated evolutionary origin of the respective character states, we performed concentrated changes tests of character correlation as implemented in MacClade (using 10,000 simulations), which compare the real data against the null hypothesis that gains and losses of a character are randomly distributed across the phylogeny. In this test, only binary characters can be used and tracing is carried out using parsimony criteria. Both ecology and iris contrast were therefore simplified for analysis (see Materials and Methods). Counting only strictly arboreal frogs in the "Arboreal" category, using the
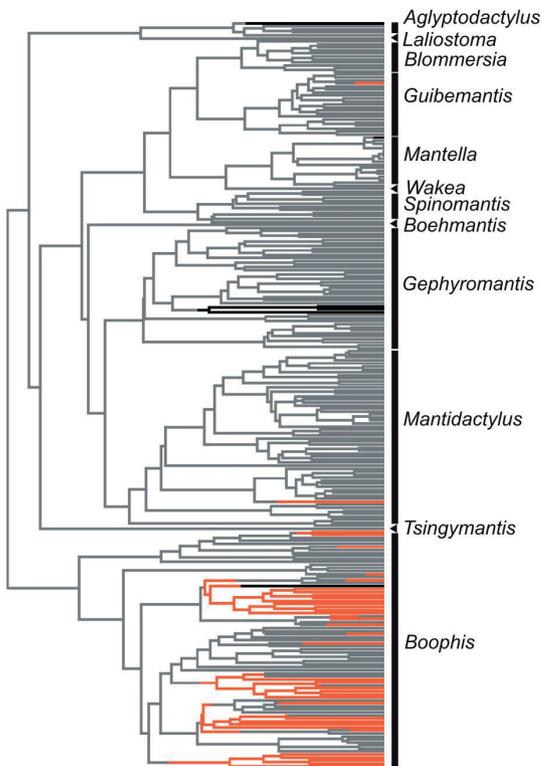
Left page. Figure 1. One-character evolutionary histories reconstructed through Bayesian stochastic character mapping on a phylogeny of mantellid frogs (from WOLLENBERG et al. 2011). Inset photos show exemplary species for the various character states. (A) General ecology and habits in mantellid frogs; (B) Iris pattern in mantellid frogs; (C) Iris contrast; (D) Iris periphery colour (area usually hidden under eyelid, here visible to the right of the iris, probably corresponding to the sclera). Inset photos from top to bottom: (A) *Boophis jaegeri, Gephyromantis cornutus, G. silvanus, Mantidactylus guttulatus, M. femoralis, Aglyptodactylus securifer*; (B) *Boophis luteus, Mantella aurantiaca, Guibemantis liber, G. kathrinae, Mantidactylus madecassus, Boophis majori*; (C) *Mantidactylus betsileanus, Mantella crocea, Boophis miniatus*; (D) *Boophis viridis, B. picturatus, Aglyptodactylus securifer, Boophis praedictus, B. madagascariensis, B. axelmeyeri, Gephyromantis cornutus*.
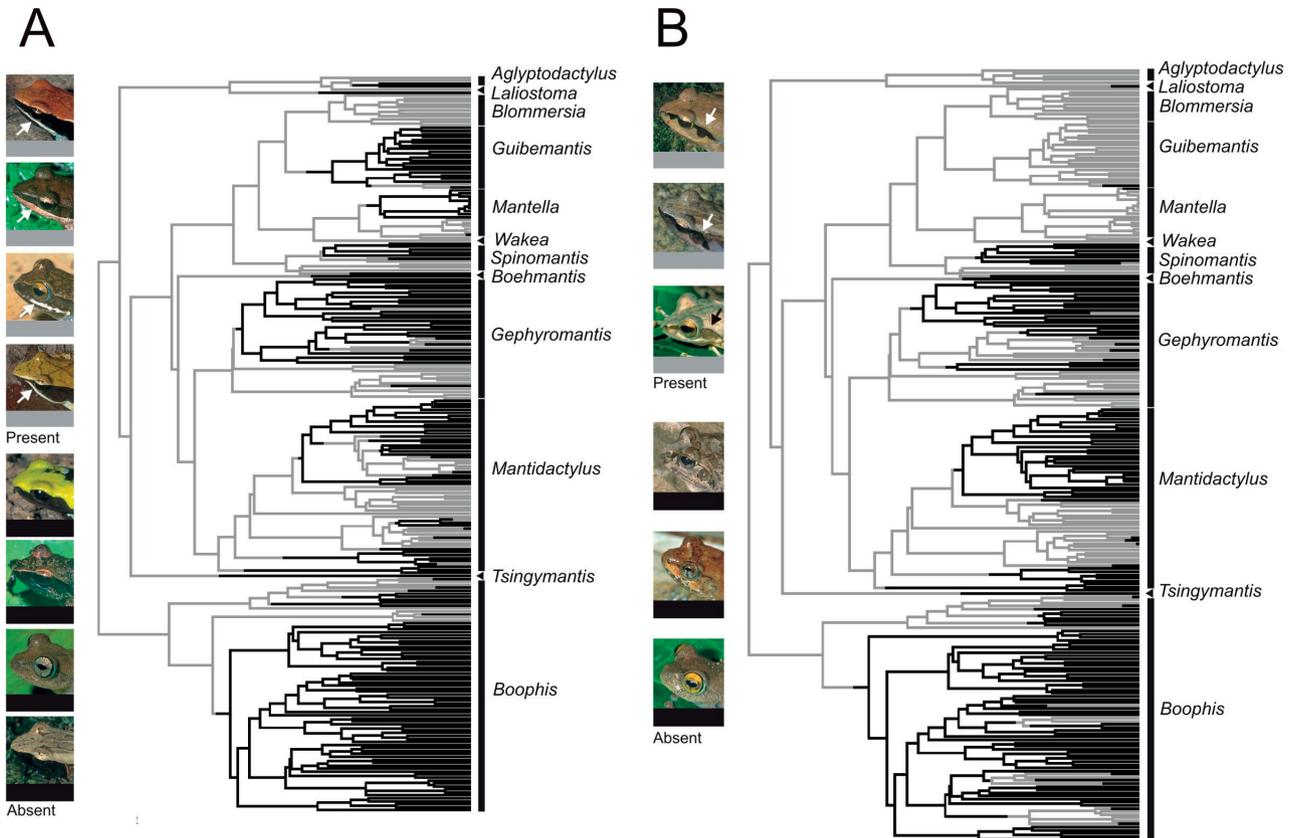
Figure 2. One-character evolutionary histories reconstructed through Bayesian stochastic character mapping on a phylogeny of mantellid frogs (from WOLLENBERG et al. 2011). Inset photos show exemplary species for the various character states. (A) presence/absence of frenal streak (as indicated by arrows in the upper three inset photos); (B) presence/absence of dark tympanic patch (as indicated by arrows in the upper three inset photos). Inset photos from top to bottom: (A) *Mantella betsileo, Gephyromantis granulatus, Boophis rhodoscelis, Mantidactylus melanopleura, Mantella laevigata, Gephyromantis zavona, Boophis arcanus, Mantidactylus aerumnalis;* (B) *Aglyptodactylus madagascariensis, Mantidactylus* sp. aff. *aerumnalis, Boophis doulioti, Laliostoma labrosum, Mantidactylus* sp. aff. *biporus, Boophis majori.*

MINSTATE simulation, the probability of observing, out of 14 gains and 1 loss, of the character state "bright iris", the observed 14 and 1 (defined as more than 13 and fewer than 2), respectively, on branches distinguished by the character state "climbing", was P < 0.01. The evolutionary origin of frenal streak and dark tympanic patch was not significantly correlated with terrestrial habits: 19 gains and 6 losses of the frenal streak were reconstructed of which 13 and 5 occurred in terrestrial frogs (P = 0.20) and 15 gains and 7 losses of the dark tympanic patch of which 11 and 5 occurred in terrestrial frogs (P = 0.17).

Discussion

Among the more than 250 species and candidate species of mantellid frogs (VIEITES et al. 2009, WOLLENBERG et al. 2011), most have arboreal habits. According to the character reconstructions performed herein, this state evolved various times and comprises some variability, such as phyto-telmic breeders adapted to particular plants only or tree dwellers that reproduce in streams or ponds. In contrast, strictly rheophilous frogs evolved in only one mantellid clade (*Mantidactylus*). Moist rocks and slopes are inhabited by only a few clades, which typically are species-poor, and they share morphological adaptations with arboreal species such as terminal toe pads (MANZANO et al. 2007). Their rather isolated phylogenetic position suggests that these saxicolous frogs could be relics of older lineages surviving through competitive exclusion from other frogs in this rare and marginal habitat (*Tsingymantis* and *Boehmantis*), or small, regional radiations in areas where such habitats are more common (some *Gephyromantis,* KAFFENBERGER et al. 2012). This pattern in mantellids agrees with that in other tropical frogs, where arboreal habits are generally more common than truly rheophilous or saxicolous habits (INGER & COLWELL 1977, DUELLMAN 1978, DAS 1996, PARMELEE 1999).

Our study provides evidence for multiple courses of parallel evolution of eye and head colour patterns in mantellid

Table 1. Summary of significant character state associations between general ecology and habits of mantellid species and colour and pattern of eye and head. For each association, the table shows the character states that have a statistically significant association (P = positive or N = negative) with the respective general ecology state after passing a Bonferroni correction over all tests. "Positive" indicates that the two states occur together at a higher frequency than expected by chance, while "negative" indicates they occur together at a lower frequency than expected by chance. For detailed d_{ij} pairwise statistics see Supplementary Materials Table S3.

	Arboreal	Terrestrial	Saxicolous	Semiarboreal	Rheophilous	Terrestrial – rheophilous
Iris contrast	P: Brighter than body N: Similar to body	N: Brighter than body	–	N: Brighter than body	–	P: Similar to body N: Brighter than body
Detailed iris pattern	P: Annular. N: Horizontally divided	–	–	P: Horizontally divided N: Annular	P: Horizontally divided	N: Annular, Horizontally divided
Iris periphery colour	P: Blue N: Indistinct	N: Blue	–	P: Indistinct N: Blue	N: Blue	P: Indistinct N: Blue
Dark tympanic patch	P: Absent N: Present	P: Present N: Absent	–	–	–	P: Absent N: Present
Frenal streak	P: Absent N: Present	P: Present N: Absent	–	–	–	P: Absent N: Present

frogs. These characters are furthermore statistically associated with the general ecology of mantellid frogs, corroborating the informal analysis by GLAW & VENCES (1997). Although we could also show the simultaneous distribution of morphological and ecological states in the phylogeny, it must be emphasized that this analysis is purely correlative and can neither prove any causal relationship between ecology and morphology, nor the convergent evolution of certain eye and head morphological characters with certain ecological states.

The concentrated changes test instead provided evidence that the evolution (not just the occurrence) of bright irises occurred significantly more often, given a background of arboreal vs. non-arboreal habits. This, however, strongly depends on the binary character coding of the test: semi-arboreal frogs such as *Gephyromantis* and *Blommersia* (without bright irises) were scored as terrestrial in this analysis and bright irises arose almost exclusively, yet several times, within a single clade of arboreal frogs (*Boophis*). Although the separate origins of bright iris colouration within distinct clades of *Boophis*, strictly speaking, are phylogenetically independent events, it still is questionable whether they should be really counted as such given that, for instance, a genetic basis for colourful irises might have arisen only once (in the ancestor of *Boophis*) and could then have reversed and re-evolved several times within the genus.

Despite the restrictions of these analyses to (i) mantellid frogs only and (ii) character association rather than convergent evolution, they allow us to formulate and refine hypotheses for further testing (PRUM 1997, EMERSON 2000). In particular the idea that similar processes of natural or sexual selection might have convergently shaped these characters, and that the selective pressures on eye and body colours differ among frogs adapted to different lifestyles, appears attractive for further studies.

Indications that our results might have wider implications derive from the observation that the observed correlations probably also apply beyond the Mantellidae, as was in part already discussed by GLAW & VENCES (1997). (1) Bright iris colours are likewise found in arboreal frogs of numerous unrelated clades, as exemplified by prominent species such as the Neotropical *Agalychnis callidryas* (Hylidae), or African *Leptopelis* (Arthroleptidae) with bright red eyes. An annular iris pattern is found in phylogenetically unrelated tree frogs such as *Rhacophorus baluensis* (Rhacophoridae) or *Litoria chloris* (Hylidae). (2) The presence of uniform black eyes in aposematic species is also repeated in the Neotropical poison frogs (family Dendrobatidae), which exhibit a striking convergence with Malagasy *Mantella* in diet, ecology and colouration (CLARK et al. 2005). (3) Similar to many mantellids, other unrelated frogs living in leaf litter have a horizontally contrasted iris pattern and a large dark tympanic patch (TOLEDO & HADDAD 2006), as is the case with the Asian *Hylarana luctuosa* (Ranidae) or Australian *Mixophyes* (Myobatrachidae). Together with obvious similarities in external body proportions among many of these frogs, this suggests that future attempts to objectively define anuran ecomorphological guilds (as in tadpoles by ALTIG & JOHNSTON 1989) or ecomorphs (as in *Anolis* lizards; WILLIAMS 1983, LOSOS & THORPE 2004, LOSOS 2009) might lead to novel insights into the evolution and macroecology of amphibians.

GLAW & VENCES (1997) proposed three alternative hypotheses for eye colour function in anurans, in addition to the null hypothesis of no function: (1) a physiological role in that it would influence vision, (2) a function as predator deterrent, or (3) a function as mate recognition signal. Furthermore, they mention (4) a possible function of iris colour supporting a generally cryptic colouration, for instance when a horizontal pattern of the iris is associated

with a flank-dorsum colour difference. In the absence of experimental results it is not possible to reliably discriminate among these alternatives, although some appear to be more probable than others at present.

Sexual selection has been hypothesized to influence eye colouration in humans (Frost 2006) and birds (Smith 1967), but these hypotheses have remained little investigated (e.g., Hill & McGraw 2006). A functional association has been presumed with image sharpness: light irises may allow more light to reach the retina, which may reduce the sharpness of images relative to dark irises (Hill & McGraw 2006). We consider it likely that bright iris colours in tree frogs indeed have a function in mate recognition and that they evolve under the influence of sexual selection, which is also supported by the fact that in tree frogs with bright-coloured irises, the eye colour is usually more stable and species-specific than their body colouration (Glaw & Vences 1997). Craig & Hulley (2004) did not find a correlation of bird iris colouration with social behaviour, but these authors emphasized that critical information was missing for many species in their analysis. In arboreal frogs with a bright eye colour, several colours are usually present in different species. Visual signalling is mainly known from frogs living along noisy streams, but also from some tree frogs, and might play a role in individual recognition (Hödl & Amézquita 2001). The conspicuousness of iris colour is magnified by a division into circular areas with different pigmentations in annular-patterned eyes. This might favour species recognition in species-rich frog communities, considering that in Madagascar, around 30 species of *Boophis* are known to co-occur in some areas (Vieites et al. 2009). Assuming a sensory-driven role of iris colour in mantellid speciation as known in cichlid fishes (Maan et al. 2006, Seehausen et al. 2008) appears to be far-fetched. However, such a mechanism, i.e., a divergent evolution of the visual system associated with differences in colour (in this case of the iris) and colour preference biasing mate choice, should not be *a priori* disregarded when designing future studies on anuran eye colouration. A better understanding of the intraspecific variation of iris colour is also necessary. While in birds, some groups such as *Ploceus* weavers with sexually dimorphic iris colour are known (Craig & Hulley 2004), no such pattern has thus far been observed in mantellids or other frogs (Glaw & Vences 1997). On the contrary, ontogenetic changes that are common in birds (Craig & Hulley 2004, Nogueira et al. 2008) are probable (although not studied in detail) in anurans.

Toledo & Haddad (2009) assign an adaptive function as disruptive colouration to the horizontally divided iris pattern and assume that it contributes to breaking up the frog's shape. This hypothesis seems straightforward, also because such a pattern, in Madagascar and elsewhere, is often found in partly diurnal leaf litter frogs, which often are light brown dorsally but dark on the flanks, and in these cases, the upper light iris colour prevents that dark eyes make a frog silhouette stand out in dorsal view. Similar mimetic functions might also be hypothesized for the dark tympanic patch of many terrestrial frogs, while the frenal streak, which we found being statistically associated to this patch, might play a role in intraspecific communication as in some mantellids, it has a divergent expression in closely related sympatric species such as *Mantidactylus melanopleura* and *M. opiparis* (Vences & Glaw 2004).

To better understand selective pressures and the function of eye colour in frogs and other vertebrates, it will also be crucial to understand its genomic and genetic basis. Amphibian pigment cells are located in the epidermis, but are well known not to be ectodermal but derived from the neural crest. In the vertebrate eye, mesenchymal cells (head mesoderm and neural crest cells) form the iris stroma as well as other structures such as the corneal entoderm, structures at the iridocorneal angle, and ciliary body stroma (Soules & Link 2005). Thus, the pigment cells both in the iris and the body skin are derived from the neural crest. However, either the genetic regulation of cell differentiation seems to be different between eye and skin, or the migration of their precursor cells during embryonic development might be differently affected. This is obvious from semialbinistic frogs that often lack pigments in the body but have normally pigmented eyes (Glaw & Vences 1997). Given that iris colour in humans and other primates is influenced by numerous loci (e.g., Bradley et al. 2009, Liu et al. 2009), it is probable that the colours of iris and sclera are determined by a complex interplay of various genes and gene regulatory mechanisms also in amphibians.

Conclusion and outlook

The evolutionary history of ecological diversification in mantellids is complex as indicated by character mapping on a well-resolved phylogeny of these frogs. Also iris contrast and pattern, colour of sclera, and several conspicuous colour patterns on the head have evolved and reversed multiple times within the Mantellidae, and most of these characters have certain states significantly associated both with each other and the general ecology of the frogs. In particular, a brightly coloured iris and iris periphery with annular pattern was mainly observed in *Boophis* tree frogs whereas a frenal streak and dark tympanic patch were associated with terrestrial habits. Experimental behavioural studies are needed to understand the function of these traits. In particular, the role of bright eye colour in either intraspecific communication or predator deterrence is worth further analysis. Similar analyses of character association in other major clades of frogs could clarify whether not only the same character states but also the same character state associations evolved convergently in independent anuran radiations. Additionally, a better understanding of the underlying developmental genetics might allow disentangling the evolutionary processes that influence pigmentation in tree frogs. As a testable hypothesis, natural selection might act more strongly on body colour while sexual selection, at least in some groups, might act more strongly on eye colour.

Acknowledgements

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Online Supplementary Material

3 Supplementary tables
8 Supplementary figures

Supplementary Figure S1. One-character history reconstructed through stochastic character mapping of presumed adaptive functions of colouration: aposematic and cryptic. Reconstruction of cryptic ancestor, PP=0.999.

Supplementary Table S1. Matrix of species, ecology, habitat, eye morphology variables and body colour characters in the mantellid frogs used in this study: ECO, general ecology and habits; DIP, detailed iris pattern; ICB, iris colour brightness; CIP, iris periphery (sclera) colour; FS, frenal streak; TPS, dark tympanic patch or streak; COL, general dorsal colouration. State number follows material and methods definitions. Names of species in second column refer to those used in the supplementary figures S2-S7.

Species name (Wollenberg et al. 2011)	Species name (Glaw & Vences 2007)	ECO	DIP	ICB	CIP	FS	TPS	COL
Aglyptodactylus laticeps	*Aglyptodactylus laticeps*	1	3	1	6	1	1	0
Aglyptodactylus madagascariensis	*Aglyptodactylus madagascariensis*	1	3	0	6	1	1	0
Aglyptodactylus securifer	*Aglyptodactylus securifer*	1	3	0	6	1	1	0
Aglyptodactylus sp 2	*Aglyptodactylus* sp. aff. *madagascariensis* east	1	3	0	6	0	1	0
Aglyptodactylus sp 3	*Aglyptodactylus* sp. aff. *madagascariensis* Ranomafana	1	3	0	6	0	1	0
Blommersia blommersae	*Blommersia blommersae*	3	2	0	3	1	1	0
Blommersia domerguei	*Blommersia domerguei*	3	3	0	3	1	1	0
Blommersia grandisonae	*Blommersia grandisonae*	3	2	0	3	1	1	0
Blommersia kely	*Blommersia kely*	3	4	0	3	1	1	0
Blommersia sarotra	*Blommersia sarotra*	3	3	0	3	1	1	0
Blommersia sp. 2	*Blommersia* sp. aff. *blommersae* Maroantsetra	3	5	0	3	1	1	0
Blommersia sp. 1	*Blommersia* sp. aff. *blommersae* Nosy Boraha	3	5	0	3	1	1	0
Blommersia sp. 3	*Blommersia* sp. aff. *blommersae* Toamasina	3	5	0	3	1	1	0
Blommersia sp. 5	*Blommersia* sp. aff. *wittei* west	3	3	0	3	1	1	0
Blommersia sp. 4	*Blommersia* sp. Comoros	3	3	0	3	1	1	0
Blommersia wittei	*Blommersia wittei*	3	3	0	3	1	1	0
Boehmantis microtympanum	*Boehmantis microtympanum*	2	5	0	6	0	0	0
Boophis albilabris	*Boophis albilabris*	0	5	0	5	1	0	0
Boophis albipunctatus	*Boophis albipunctatus*	0	5	0	0	0	0	0
Boophis andohahela	*Boophis andohahela*	0	3	1	0	0	0	0
Boophis andreonei	*Boophis andreonei*	0	0	2	6	0	0	0
Boophis anjanaharibeensis	*Boophis anjanaharibeensis*	0	0	2	0	0	0	0
Boophis ankaratra	*Boophis ankaratra*	0	0	0	0	0	0	0
Boophis axelmeyeri	*Boophis axelmeyeri*	0	3	0	5	0	0	0
Boophis blommersae	*Boophis blommersae*	0	5	0	6	0	0	0
Boophis boehmei	*Boophis boehmei*	0	0	2	0	0	0	0
Boophis bottae	*Boophis bottae*	0	0	2	0	0	0	0
Boophis brachychir	*Boophis brachychir*	0	5	0	6	0	1	0
Boophis burgeri	*Boophis burgeri*	0	0	0	0	0	0	0
Boophis doulioti	*Boophis doulioti*	0	4	2	6	1	1	0
Boophis elenae	*Boophis elenae*	0	5	2	0	0	0	0
Boophis englaenderi	*Boophis englaenderi*	0	0	2	0	0	0	0
Boophis erythrodactylus	*Boophis erythrodactylus*	0	0	2	0	0	0	0
Boophis feonnyala	*Boophis feonnyala*	0	5	0	0	0	0	0
Boophis goudoti	*Boophis goudoti*	0	5	0	0	0	0	0
Boophis guibei	*Boophis guibei*	0	3	2	0	0	0	0
Boophis haematopus	*Boophis haematopus*	0	5	0	0	0	0	0
Boophis idae	*Boophis idae*	0	5	0	6	0	0	0
Boophis jaegeri	*Boophis jaegeri*	0	0	2	0	0	0	0
Boophis laurenti	*Boophis laurenti*	0	5	0	2	0	0	0
Boophis liami	*Boophis liami*	0	5	2	0	0	0	0
Boophis lichenoides	*Boophis lichenoides*	0	5	0	0	0	0	0
Boophis luteus	*Boophis luteus*	0	0	2	0	0	0	0
Boophis madagascariensis	*Boophis madagascariensis*	0	0	0	6	0	0	0
Boophis majori	*Boophis majori*	0	5	2	0	0	0	0
Boophis mandraka	*Boophis mandraka*	0	5	2	0	0	0	0

Species name (Wollenberg et al. 2011)	Species name (Glaw & Vences 2007)	ECO	DIP	ICB	CIP	FS	TPS	COL
Boophis marojezensis	*Boophis marojezensis*	0	5	2	0	0	0	0
Boophis microtympanum	*Boophis microtympanum*	0	5	0	2	0	1	0
Boophis miniatus	*Boophis miniatus*	0	5	2	0	0	0	0
Boophis occidentalis	*Boophis occidentalis*	0	0	0	0	0	0	0
Boophis opisthodon	*Boophis opisthodon*	0	5	0	6	1	1	0
Boophis pauliani	*Boophis pauliani*	0	5	0	1	0	0	0
Boophis periegetes	*Boophis periegetes*	0	5	0	6	0	0	0
Boophis picturatus	*Boophis picturatus*	0	0	0	0	0	0	0
Boophis pyrrhus	*Boophis pyrrhus*	0	5	2	5	0	0	0
Boophis rappiodes	*Boophis rappiodes*	0	0	2	0	0	0	0
Boophis reticulatus	*Boophis reticulatus*	0	0	0	6	0	1	0
Boophis rhodoscelis	*Boophis rhodoscelis*	0	5	0	0	0	1	0
Boophis rufioculis	*Boophis rufioculis*	0	0	2	6	0	0	0
Boophis sambirano	*Boophis sambirano*	0	5	2	0	0	0	0
Boophis schuboeae	*Boophis schuboeae*	0	0	2	0	0	0	0
Boophis septentrionalis	*Boophis septentrionalis*	0	3	2	0	0	0	0
Boophis sibilans	*Boophis sibilans*	0	5	2	0	0	0	0
Boophis solomaso	*Boophis solomaso*	0	5	2	0	0	0	0
Boophis sp. 5	*Boophis* sp. aff. *albilabris* red eyes	0	5	2	4	1	0	0
Boophis sp. 20	*Boophis* sp. aff. *ankaratra* Andohahela fast	0	0	0	0	0	0	0
Boophis sp. 19	*Boophis* sp. aff. Ankaratra Andohahela slow	0	0	2	0	0	0	0
Boophis sp. 16	*Boophis* sp. aff. *boehmei* Ranomafana	0	5	0	0	0	0	0
Boophis sp. 11	*Boophis* sp. aff. *brachychir* 2	0	5	0	0	0	1	0
Boophis sp. 22	*Boophis* sp. aff. *elenae vigoi*	0	5	2	0	0	0	0
Boophis sp. 15	*Boophis* sp. aff. *lichenoides* Ambatolahy	0	5	0	6	0	0	0
Boophis sp. 12	*Boophis* sp. aff. *madagascariensis* north	0	0	0	5	0	0	0
Boophis sp 35	*Boophis* sp. aff. *majori* Ranomafana long call	0	5	0	0	0	0	0
Boophis sp. 28	*Boophis* sp. aff. *mandraka* Marojejy	0	0	2	0	0	0	0
Boophis sp. 33	*Boophis* sp. aff. *microtympanum* low altitude	0	5	0	2	0	1	0
Boophis sp. 29	*Boophis* sp. aff. *miniatus* Mahakajy	0	5	0	0	0	0	0
Boophis sp. 4	*Boophis* sp. aff. *occidentalis* Berara	0	0	0	0	1	0	0
Boophis sp. *pauliani*	*Boophis* sp. aff. *pauliani* Tolagnaro	0	5	0	6	0	0	0
Boophis sp. 13	*Boophis* sp. aff. *periegetes* Ranomafana	0	3	0	0	0	0	0
Boophis sp. 31	*Boophis* sp. aff. *rappiodes* Ambre	0	5	2	0	0	0	0
Boophis sp. 32	*Boophis* sp. aff. *rappiodes lilianae*	0	5	2	0	0	0	0
Boophis sp. 31	*Boophis* sp. aff. *rappiodes* northeast	0	4	2	6	0	0	0
Boophis sp. 34	*Boophis* sp. aff. *rhodoscelis* Ambohitantely	0	5	0	0	0	1	0
Boophis sp. *rhodoscelis*	*Boophis* sp. aff. *rhodoscelis* Ranomafana	0	5	0	0	0	1	0
Boophis sp. 8	*Boophis* sp. aff. *rufioculis* Ranomafana	0	0	0	0	0	0	0
Boophis sp. 17	*Boophis* sp. aff. *sibilans* trill call	0	5	0	0	0	0	0
Boophis sp. 4	*Boophis* sp. Comoros	0	5	2	6	0	0	0
Boophis sp. 27	*Boophis* sp. n. aff. *mandraka* Andreone 1	0	5	0	0	0	0	0
Boophis sp. 2	*Boophis* sp. *sarotra*	0	5	0	0	0	0	0
Boophis tampoka	*Boophis tampoka*	0	3	2	0	0	0	0
Boophis tasymena	*Boophis tasymena*	0	0	2	0	0	0	0
Boophis tephraeomystax	*Boophis tephraeomystax*	0	4	0	6	1	1	0
Boophis viridis	*Boophis viridis*	0	0	2	0	0	0	0
Boophis vittatus	*Boophis vittatus*	0	5	0	0	0	0	0
Boophis williamsi	*Boophis williamsi*	0	5	0	0	0	0	0
Boophis xerophilus	*Boophis xerophilus*	0	5	0	0	0	0	0
Gephyromantis ambohitra	*Gephyromantis ambohitra*	3	5	0	3	0	0	0

Species name (Wollenberg et al. 2011)	Species name (Glaw & Vences 2007)	ECO	DIP	ICB	CIP	FS	TPS	COL
Gephyromantis asper	*Gephyromantis asper*	3	5	0	3	0	0	0
Gephyromantis azzurae	*Gephyromantis azzurae* Andreone Isalo Andrianamero	3	5	0	3	0	0	0
Gephyromantis blanci	*Gephyromantis blanci*	1	5	0	3	1	1	0
Gephyromantis boulengeri	*Gephyromantis boulengeri*	1	5	0	3	0	0	0
Gephyromantis cornutus	*Gephyromantis cornutus*	3	3	0	3	0	0	0
Gephyromantis corvus	*Gephyromantis corvus*	3	5	0	3	0	0	0
Gephyromantis decaryi	*Gephyromantis decaryi*	1	5	0	3	1	1	0
Gephyromantis eiselti	*Gephyromantis eiselti*	1	5	0	3	1	1	0
Gephyromantis enki	*Gephyromantis enki*	1	5	0	3	1	1	0
Gephyromantis granulatus	*Gephyromantis granulatus*	3	3	0	3	1	1	0
Gephyromantis horridus	*Gephyromantis horridus*	3	5	0	3	0	0	0
Gephyromantis klemmeri	*Gephyromantis klemmeri*	1	5	0	3	1	1	0
Gephyromantis leucocephalus Ste Luce	*Gephyromantis leucocephalus* Ste Luce	1	5	0	3	1	1	0
Gephyromantis leucomaculatus	*Gephyromantis leucomaculatus*	3	3	0	3	0	0	0
Gephyromantis luteus	*Gephyromantis luteus*	3	3	1	3	0	0	0
Gephyromantis malagasius	*Gephyromantis malagasius*	3	5	0	3	0	0	0
Gephyromantis moseri	*Gephyromantis moseri*	3	3	0	3	0	0	0
Gephyromantis plicifer	*Gephyromantis plicifer*	3	3	1	3	0	0	0
Gephyromantis pseudoasper	*Gephyromantis pseudoasper*	3	5	0	3	0	0	0
Gephyromantis redimitus	*Gephyromantis redimitus*	3	5	0	3	0	0	0
Gephyromantis rivicola	*Gephyromantis rivicola*	2	5	0	3	1	1	0
Gephyromantis runewsweeki	*Gephyromantis runewsweeki*	1	5	0	3	1	1	0
Gephyromantis salegy	*Gephyromantis salegy*	3	3	0	3	0	0	0
Gephyromantis schilfi	*Gephyromantis schilfi*	3	3	0	3	1	1	0
Gephyromantis sculpturatus	*Gephyromantis sculpturatus*	3	3	1	3	0	0	0
Gephyromantis silvanus	*Gephyromantis silvanus*	2	5	0	3	1	1	0
Gephyromantis sp. 1	*Gephyromantis* sp. aff. Ambohitra Marojejy	3	5	0	3	0	0	0
Gephyromantis sp. 5	*Gephyromantis* sp. aff. *blanci* Andohahela	1	5	0	3	1	1	0
Gephyromantis sp. 10	*Gephyromantis* sp. aff. *corvus* Bemaraha	3	5	0	3	0	0	0
Gephyromantis sp. 11	*Gephyromantis* sp. aff. *horridus* Marojejy	3	5	0	3	0	0	0
Gephyromantis sp. 17	*Gephyromantis* sp. aff. *leucomaculatus* Marojejy	3	3	0	3	0	1	0
Gephyromantis sp. 13	*Gephyromantis* sp. aff. *malagasius* highlands	3	5	0	3	0	0	0
Gephyromantis spinifer	*Gephyromantis spinifer*	3	5	0	3	0	0	0
Gephyromantis striatus	*Gephyromantis striatus*	3	5	0	3	0	0	0
Gephyromantis tandroka	*Gephyromantis tandroka*	3	3	0	3	0	0	0
Gephyromantis thelenae	*Gephyromantis thelenae*	1	5	0	3	1	1	0
Gephyromantis tschenki	*Gephyromantis tschenki*	3	3	0	3	0	0	0
Gephyromantis ventrimaculatus	*Gephyromantis ventrimaculatus*	3	5	0	3	0	0	0
Gephyromantis webbi	*Gephyromantis webbi*	2	5	0	3	1	1	0
Gephyromantis zavona	*Gephyromantis zavona*	3	3	0	3	0	1	0
Guibemantis albolineatus	*Guibemantis albolineatus*	0	4	0	3	0	1	0
Guibemantis bicalcaratus	*Guibemantis bicalcaratus*	0	4	0	3	0	1	0
Guibemantis depressiceps	*Guibemantis depressiceps*	0	3	0	0	0	1	0
Guibemantis flavobrunneus	*Guibemantis flavobrunneus*	0	4	0	3	0	1	0
Guibemantis kathrinae	*Guibemantis kathrinae*	0	3	0	0	0	1	0
Guibemantis liber	*Guibemantis liber*	0	4	0	3	0	1	0
Guibemantis pulcher	*Guibemantis pulcher*	0	5	2	3	0	1	0
Guibemantis punctatus	*Guibemantis punctatus*	0	4	2	3	0	1	0
Guibemantis sp. 3	*Guibemantis* sp. aff. *albolineatus* Andasibe	0	4	0	3	0	1	0
Guibemantis sp. 8	*Guibemantis* sp. aff. *bicalcaratus* Besariaka	0	4	0	3	0	1	0

Species name (Wollenberg et al. 2011)	Species name (Glaw & Vences 2007)	ECO	DIP	ICB	CIP	FS	TPS	COL
Guibemantis sp. 14	*Guibemantis* sp. aff .*bicalcaratus* Fierenana	0	4	0	3	0	1	0
Guibemantis sp. 12	*Guibemantis* sp. aff. *bicalcaratus* Manongarivo	0	4	0	3	0	1	0
Guibemantis sp. 9	*Guibemantis* sp. aff. *bicalcaratus* Nosy boraha 2	0	4	0	3	0	1	0
Guibemantis sp. 7	*Guibemantis* sp. aff. *bicalcaratus* Tolagnaro	0	4	0	3	0	1	0
Guibemantis sp. 19	*Guibemantis* sp. aff. *depressiceps* Andohahela	0	4	0	3	0	1	0
Guibemantis sp. 10	*Guibemantis* sp. aff. *flavobrunneus* Manombo	0	4	0	3	0	1	0
Guibemantis sp. 20	*Guibemantis* sp. aff. *liber* giant	0	4	0	3	0	0	0
Guibemantis sp. 5	*Guibemantis* sp. aff. *liber* Vevembe	0	4	0	3	0	1	0
Guibemantis sp. 6	*Guibemantis* sp. aff. *punctatus* south	0	4	0	3	0	1	0
Guibemantis timidus	*Guibemantis timidus*	0	5	0	6	1	1	0
Guibemantis tornieri	*Guibemantis tornieri*	0	3	0	0	0	1	0
Laliostoma labrosum	*Laliostoma labrosum*	1	5	0	5	0	0	0
Mantella aurantiaca	*Mantella aurantiaca*	1	1	1	3	0	0	1
Mantella baroni	*Mantella baroni*	1	1	0	3	0	1	1
Mantella bernhardi	*Mantella bernhardi*	1	3	0	3	0	1	1
Mantella betsileo	*Mantella betsileo*	1	3	0	3	1	1	0
Mantella cowani	*Mantella cowani*	1	1	0	3	0	1	1
Mantella crocea	*Mantella crocea*	1	1	0	3	0	1	0
Mantella ebenaui	*Mantella ebenaui*	1	3	0	3	1	1	0
Mantella expectata	*Mantella expectata*	1	3	0	3	1	1	0
Mantella haraldmeieri	*Mantella haraldmeieri*	1	3	0	3	0	1	0
Mantella laevigata	*Mantella laevigata*	1	1	0	3	0	1	0
Mantella madagascariensis	*Mantella madagascariensis*	1	1	0	3	0	1	1
Mantella manery	*Mantella manery*	1	3	0	3	1	1	0
Mantella milotympanum	*Mantella milotympanum*	1	1	0	3	0	0	1
Mantella nigricans	*Mantella nigricans*	1	1	0	3	0	1	1
Mantella pulchra	*Mantella pulchra*	1	1	0	3	0	1	0
Mantella sp. 1	*Mantella* sp. aff. *expectata* Tranomaro	1	3	0	3	1	1	0
Mantella viridis	*Mantella viridis*	1	3	0	3	1	1	0
Mantidactylus aerumnalis	*Mantidactylus aerumnalis*	4	3	0	3	1	0	0
Mantidactylus albofrenatus	*Mantidactylus albofrenatus*	4	3	0	3	1	1	0
Mantidactylus alutus	*Mantidactylus alutus*	5	5	0	3	0	0	0
Mantidactylus ambreensis	*Mantidactylus ambreensis*	5	5	0	3	1	1	0
Mantidactylus argenteus	*Mantidactylus argenteus*	3	5	2	3	0	0	0
Mantidactylus bellyi	*Mantidactylus bellyi*	5	5	0	3	0	0	0
Mantidactylus betsileanus	*Mantidactylus betsileanus*	5	5	0	3	0	0	0
Mantidactylus biporus	*Mantidactylus biporus*	5	5	0	3	0	0	0
Mantidactylus bourgati	*Mantidactylus bourgati*	5	5	0	3	0	0	0
Mantidactylus brevipalmatus	*Mantidactylus brevipalmatus*	4	3	0	3	1	1	0
Mantidactylus charlotteae	*Mantidactylus charlotteae*	4	3	0	3	1	1	0
Mantidactylus cowanii	*Mantidactylus cowanii*	2	2	0	3	0	0	0
Mantidactylus curtus Antoetra	*Mantidactylus curtus* Antoetra	4	5	0	3	1	0	0
Mantidactylus delormei	*Mantidactylus delormei*	4	3	0	3	1	1	0
Mantidactylus femoralis	*Mantidactylus femoralis*	5	4	0	3	1	1	0
Mantidactylus guttulatus east	*Mantidactylus guttulatus* east	4	5	0	3	0	0	0
Mantidactylus guttulatus north	*Mantidactylus guttulatus* north	4	5	0	3	0	0	0
Mantidactylus lugubris Andasibe	*Mantidactylus lugubris* Andasibe	2	5	0	3	0	0	0
Mantidactylus madecassus	*Mantidactylus madecassus*	4	2	0	3	0	0	0
Mantidactylus majori	*Mantidactylus majori*	5	5	0	3	1	1	0
Mantidactylus melanopleura	*Mantidactylus melanopleura*	4	3	0	3	1	1	0
Mantidactylus mocquardi Andasibe	*Mantidactylus mocquardi* Andasibe	5	5	0	3	0	0	0

Species name (Wollenberg et al. 2011)	Species name (Glaw & Vences 2007)	ECO	DIP	ICB	CIP	FS	TPS	COL
Mantidactylus noralottae Andreone Isalo Andrianamero	*Mantidactylus noralottae* Andreone Isalo Andrianamero	5	5	0	3	0	0	0
Mantidactylus opiparis	*Mantidactylus opiparis*	4	3	0	3	1	1	0
Mantidactylus pauliani	*Mantidactylus pauliani*	4	2	0	3	0	0	0
Mantidactylus sp. 26	*Mantidactylus* sp. aff. *betsileanus* Andranofotsy	5	5	0	3	0	0	0
Mantidactylus sp. 27	*Mantidactylus* sp. aff. *betsileanus* Nosy Boraha	5	5	0	3	0	0	0
Mantidactylus sp. 28	*Mantidactylus* sp. aff. *betsileanus* slow calls	5	5	0	3	0	0	0
Mantidactylus sp. 36	*Mantidactylus* sp. aff. *betsileanus* Toamasina	5	5	0	3	0	0	0
Mantidactylus sp. 29	*Mantidactylus* sp. aff. *betsileanus* Tolagnaro	5	5	0	3	0	0	0
Mantidactylus sp. 17	*Mantidactylus* sp. aff. *biporus* Ambohitantely	5	5	0	3	0	0	0
Mantidactylus sp. 23	*Mantidactylus* sp. aff. *biporus* Andasibe	5	5	0	3	0	0	0
Mantidactylus sp. 26	*Mantidactylus* sp. aff. *biporus* Andranofotsy	5	5	0	3	0	0	0
Mantidactylus sp. 24	*Mantidactylus* sp. aff. *biporus* Ranomafana	5	5	0	3	0	0	0
Mantidactylus sp. 32	*Mantidactylus* sp. aff. *biporus* Tsaratanana camp 0	5	5	0	3	0	0	0
Mantidactylus sp. 33	*Mantidactylus* sp. aff. *biporus* Tsaratanana camp 1	5	5	0	3	0	0	0
Mantidactylus sp. 13	*Mantidactylus* sp. aff. *charlotteae* Ranomafana	4	3	0	3	1	1	0
Mantidactylus sp. 48	*Mantidactylus* sp. aff. *cowanii* small	2	2	0	3	0	0	0
Mantidactylus sp. 18	*Mantidactylus* sp. aff. *curtus* Ambohitantely	5	5	0	3	1	0	0
Mantidactylus sp. 30	*Mantidactylus* sp. aff. *curtus* Andohahela short snout	5	5	0	3	0	0	0
Mantidactylus sp. 19	*Mantidactylus* sp. aff. *curtus* Ankaratra	5	5	0	3	1	0	0
Mantidactylus sp. 44	*Mantidactylus* sp. aff. *femoralis* Ambohitsara	5	5	0	3	0	0	0
Mantidactylus sp. 42	*Mantidactylus* sp. aff. *femoralis* Ambre	5	3	0	3	1	1	0
Mantidactylus sp. 40	*Mantidactylus* sp. aff. *femoralis* Tsaratanana	5	5	0	3	0	1	0
Mantidactylus sp. 57	*Mantidactylus* sp. aff. *grandidieri* north	4	5	0	3	0	0	0
Mantidactylus sp. 52	*Mantidactylus* sp. aff. *lugubris* Marojejy	2	5	0	3	0	0	0
Mantidactylus sp. 49	*Mantidactylus* sp. aff. *lugubris* south	2	5	0	3	0	0	0
Mantidactylus sp. 41	*Mantidactylus* sp. aff. *majori* andapa	5	5	0	3	1	1	0
Mantidactylus sp. 47	*Mantidactylus* sp. aff. *mocquardi* Ambatolahy	5	5	0	3	0	0	0
Mantidactylus sp. 46	*Mantidactylus* sp. aff. *mocquardi* Marojejy	5	5	0	3	1	1	0
Mantidactylus sp. 45	*Mantidactylus* sp. aff. *mocquardi* Tsaratanana	5	4	0	3	1	1	0
Mantidactylus sp. 20	*Mantidactylus* sp. aff. *pauliani* Itremo	4	5	0	3	0	0	0
Mantidactylus tricinctus	*Mantidactylus* sp. aff. *tricinctus* parvus	5	5	0	3	0	0	0
Mantidactylus sp. 14	*Mantidactylus* sp. aff. *ulcerosus* Isalo	5	5	0	3	0	0	0
Mantidactylus sp. 7	*Mantidactylus tricinctus* Manantantely	5	5	0	3	0	0	0
Mantidactylus tricinctus Manombo	*Mantidactylus tricinctus* Manombo	5	5	0	3	0	0	0
Mantidactylus ulcerosus	*Mantidactylus ulcerosus*	5	5	0	3	0	0	0
Mantidactylus zipperi	*Mantidactylus zipperi*	4	3	0	3	1	1	0
Mantidactylus zolitschka	*Mantidactylus zolitschka*	5	5	0	3	1	1	0
Spinomantis aglavei	*Spinomantis aglavei*	0	5	0	0	0	0	0
Spinomantis bertini	*Spinomantis bertini*	1	5	0	3	1	1	0
Spinomantis elegans	*Spinomantis elegans*	2	3	0	3	1	1	0
Spinomantis fimbriatus	*Spinomantis fimbriatus*	0	5	0	0	0	0	0
Spinomantis guibei	*Spinomantis guibei*	1	3	0	3	1	1	0
Spinomantis massorum	*Spinomantis massorum*	0	5	0	5	0	0	0
Spinomantis microtis	*Spinomantis microtis*	2	5	0	3	0	0	0
Spinomantis peraccae	*Spinomantis peraccae*	0	5	0	6	0	0	0
Spinomantis phantasticus	*Spinomantis phantasticus*	0	5	0	5	0	0	0
Spinomantis sp. 6	*Spinomantis* sp. aff. *bertini* Andohahela low altitude	1	5	0	3	1	1	0
Spinomantis sp. 8	*Spinomantis* sp. aff *.bicalcaratus* Maharira	0	5	0	3	0	0	0
Tsingymantis antitra	*Tsingymantis antitra*	2	4	0	0	0	0	0
Wakea madinika	*Wakea madinika*	1	5	0	3	1	1	0

Supplementary Table S2. Posterior probabilities of the character states (in bold) for the eight characters analysed as reconstructed for the following relevant nodes: *Aglyptodactylus, Blommersia, Gephyromantis, Guibemantis, Mantella, Mantidactylus* and *Spinomantis*, nodes representing the most recent common ancestor (MRCA) of all species of each genus; Boophinae, Mantellinae, Laliostominae, nodes of the MRCAs of the mantellid subfamilies according to GLAW & VENCES (2006). ECO, general ecology and habits; DIP, detailed iris pattern; ICB, iris colour brightness; CIP, iris periphery (sclera) colour; FS, frenal streak; TPS, dark tympanic patch or streak; COL, general dorsal colouration. Character state values are detailed in Materials and Methods.

Node	ECO	DIP	ICB	CIP	FS	TPS	COL
Aglyptodactylus	**(1)**1.000	**(4)**1.000	**(0)**0.999	**(6)**1.000	**(1)**0.999	**(1)**0.999	**(0)**0.999
Blommersia	**(3)**1.000	**(4)**0.984	**(1)**1.000	**(4)**1.000	**(1)**1.000	**(1)**1.000	**(0)**1.000
Boophis	**(0)**0.998	**(6)**1.000	**(1)**1.000	**(1)**0.892	**(1)**0.885	**(1)**0.890	**(0)**0.999
Gephyromantis	**(3)**0.729	**(6)**1.000	**(1)**1.000	**(4)**1.000	**(1)**0.933	**(1)**0.938	**(0)**1.000
Guibemantis	**(0)**1.000	**(5)**1.000	**(1)**1.000	**(4)**1.000	**(1)**1.000	**(1)**1.000	**(0)**1.000
Mantella	**(1)**1.000	**(4)**0.522	**(1)**1.000	**(4)**1.000	**(1)**1.000	**(1)**1.000	**(1)**0.879
Mantidactylus	**(2)**0.400	**(6)**1.000	**(1)**1.000	**(4)**1.000	**(1)**0.932	**(1)**0.937	**(0)**1.000
Spinomantis	**(1)**0.884	**(6)**1.000	**(1)**1.000	**(4)**1.000	**(1)**0.932	**(1)**0.937	**(0)**1.000
Mantellinae	**(2)**0.999	**(6)**0.999	**(1)**1.000	**(4)**0.985	**(1)**0.932	**(1)**0.937	**(0)**1.000
Laliostominae	**(1)**1.000	**(6)**0.978	**(1)**1.000	**(6)**0.869	**(1)**0.928	**(1)**0.933	**(0)**0.999
Boophinae	**(0)**0.998	**(6)**1.000	**(1)**1.000	**(1)**0.892	**(1)**0.885	**(1)**0.890	**(0)**0.999
Mantellidae	**(3)**0.431	**(5)**1.000	**(0)**1.000	**(0)**0.847	**(1)**0.999	**(1)**0.897	**(0)**0.999

Supplementary Table S3. Matrix of correlations among eye and body morphology and general ecology and habits in Malagasy mantellid frogs. The upper number gives the statistics of character association d_{ij}, the lower number is predictive of the p-values below. Under each sub-table, D_{ij} values (overall character correlation) and the associated significances are given. Pairwise association values (d_{ij}) that remained significant (P≤0.05) after sequential Bonferroni correction (over the total number of independent tests) are highlighted in bold. Positive values indicate that the two states occur together at a higher frequency than expected by chance, while negative values indicate they occur together at a lower frequency than expected by chance. Negative values indicate a negative correlation among the character states.

Detailed iris pattern / General ecology and habits

	Arboreal	Terrestrial	Semiarboreal	Saxicolous	Rheophilous	Terrestrial – rheophilous
Black eyes	-0.004	0.010	-0.001	-0.001	-0.001	-0.003
	0.124	0.019	0.296	0.550	0.439	0.273
Uniform	-0.015	-0.010	-0.008	0.003	-0.011	0.041
	0.002	0.006	0.013	0.171	0.001	< 0.001
Densely reticulated	-0.003	-0.001	0.001	0.003	0.001	-0.002
	0.200	0.495	0.307	0.173	0.402	0.259
Annular	**0.040**	-0.008	**-0.013**	-0.002	-0.003	**-0.011**
	< 0.0001	0.025	< 0.001	0.201	0.213	0.001
Horizontally divided	**-0.040**	0.014	**0.030**	-0.004	**0.018**	**-0.017**
	< 0.001	0.004	< 0.001	0.151	0.001	< 0.001
Horizontally striped	0.023	-0.005	-0.007	-0.001	-0.002	-0.007
	< 0.001	0.058	0.036	0.509	0.178	0.034

D=0.307 P<0.001

Iris contrast / General ecology and habits

	Arboreal	Terrestrial	Semiarboreal	Saxicolous	Rheophilous	Terrestrial – rheophilous
Similar to body	**-0.049**	0.009	0.012	0.001	0.004	**0.021**
	< 0.001	0.010	0.004	0.324	0.049	< 0.001
Darker than body	0.001	0.001	0.003	0.001	-0.001	-0.005
	0.311	0.316	0.168	0.290	0.348	0.040
Brighter than body	**0.048**	**-0.010**	**-0.015**	-0.001	-0.004	**-0.015**
	< 0.001	0.001	0.001	0.207	0.115	< 0.001

D=0.307 P<0.001

General ecology and habits / Colour of iris periphery (sclera)

	Indistinct	Blue	Bluish	Green	Yellow	Red	White
Arboreal	**-0.143**	**0.120**	0.002	0.003	0.009	0.021	0.005
	< 0.001	< 0.001	0.207	0.121	0.025	0.293	0.085
Terrestrial	0.014	**-0.024**	0.001	-0.001	0.010	-0.001	0.001
	0.002	< 0.001	0.511	0.450	0.013	0.520	0.513
Semiarboreal	**0.059**	**-0.042**	-0.001	-0.001	-0.011	-0.001	-0.003
	< 0.001	< 0.001	0.280	0.421	0.003	0.361	0.243
Saxicolous	0.007	-0.001	0.001	0.001	0.001	0.001	0.001
	0.056	0.005	0.384	0.491	0.504	0.327	0.417
Rheophilous	0.015	**-0.011**	-0.001	-0.001	-0.002	-0.001	-0.001
	0.005	0.001	0.524	0.448	0.254	0.541	0.422
Terrestrial – rheophilous	**0.046**	**-0.032**	-0.001	-0.001	-0.007	-0.001	-0.002
	< 0.001	< 0.001	0.465	0.355	0.018	0.352	0.284

D=0.627 P<0.001

General ecology and habits / Head with dark tympanic patch or streak

	Presence	Absence
Arboreal	**-0.013**	**0.013**
	< 0.001	< 0.001
Terrestrial	**0.023**	**-0.023**
	< 0.001	< 0.001
Semiarboreal	-0.001	0.001
	0.263	0.240
Saxicolous	0.001	-0.001
	0.152	0.162
Rheophilous	0.003	-0.003
	0.025	0.025
Terrestrial – rheophilous	**-0.013**	**0.013**
	< 0.001	< 0.001

D=0.141 P<0.001

General ecology and habits / Head with frenal streak

	Presence	Absence
Arboreal	**-0.014**	**0.014**
	< 0.001	< 0.001
Terrestrial	**0.022**	**-0.022**
	< 0.001	< 0.001
Semiarboreal	0.002	-0.002
	0.041	0.042
Saxicolous	-0.002	0.002
	0.111	0.109
Rheophilous	0.003	-0.003
	0.021	0.021
Terrestrial – rheophilous	-0.013	0.013
	< 0.001	**< 0.001**

D=0.139 P<0.001

General dorsal colouration / Detailed iris pattern

	Black eyes	Uniform	Densely reticulated	Annular	Horizontally divided	Horizontally striped
Cryptic	-0.006	0.002	-0.001	-0.001	0.002	0.004
	0.006	0.062	0.190	0.141	0.102	0.013
Aposematic	**0.006**	-0.002	0.001	0.001	-0.002	-0.004
	0.004	0.062	0.180	0.138	0.103	0.014

D=0.074 P<0.104

Detailed iris pattern / Colour of iris periphery (sclera)

	Indistinct	Blue	Bluish	Green	Yellow	Red	White
Black eyes	0.001	-0.002	0.001	0.001	0.001	0.001	-0.001
	0.325	0.291	0.481	0.461	0.423	0.402	0.464
Uniform	0.009	-0.001	0.001	0.001	**-0.012**	-0.001	0.001
	0.027	0.432	0.352	0.233	< 0.001	0.467	0.304
Densely reticulated	0.001	-0.002	0.001	-0.001	0.001	0.001	0.001
	0.402	0.233	0381	0.501	0.444	0.362	0.397
Annular	**-0.045**	**0.042**	0.001	0.001	0.001	0.001	0.001
	< 0.001	< 0.001	0.486	0.418	0.258	0.473	0.385
Horizontally divided	**0.023**	**-0.025**	-0.001	-0.001	0.007	-0.001	-0.002
	< 0.001	< 0.001	0.368	0.373	0.039	0.390	0.316
Horizontally striped	0.010	-0.012	-0.001	-0.001	0.002	-0.005	-0.005
	0.022	0.002	0.538	0.404	0.234	0.552	0.449

D=0.247 P<0.060

Iris contrast / Colour of iris periphery (sclera)

	Indistinct	Blue	Bluish	Green	Yellow	Red	White
General tones	**0.071**	**-0.055**	-0.002	-0.001	-0.008	-0.002	-0.001
	< 0.001	< 0.001	0.201	0.411	0.009	0.204	0.274
Darker than body	-0.012	0.003	0.001	0.001	0.005	0.001	0.001
	0.003	0.189	0.367	0.361	0.049	0.346	0.247
More colourful	**-0.059**	**0.052**	0.001	-0.001	0.003	0.001	0.001
	< 0.001	< 0.001	0.258	0.459	0.176	0.283	0.434

D=0.311 P<0.001

Detailed iris pattern / Head with dark tympanic patch or streak

	Presence	Absence
Black eyes	0.003	-0.003
	0.028	0.028
Uniform	**-0.026**	**0.026**
	< 0.001	< 0.001
Densely reticulated	-0.001	0.001
	0.343	0.318
Annular	**-0.012**	**0.012**
	< 0.001	< 0.001
Horizontally divided	**0.019**	**-0.019**
	< 0.001	< 0.001
Horizontally striped	**0.016**	**-0.016**
	< 0.001	< 0.001

D=0.166 P<0.001

Frenal streak / Head with dark tympanic patch or streak

	Presence	Absence
Presence	**0.028**	**-0.028**
	< 0.001	< 0.001
Absence	**-0.028**	**0.028**
	< 0.001	< 0.001

D=0.122 P<0.001

Supplementary Figure S2 (next 3 pages). One-character history reconstructed through stochastic character mapping of general ecology and habits in mantellid frogs (as in Figure 1 of main paper but including taxon names as in second column of Table S1).

Gephyromantis ambohitra
Gephyromantis sp aff ambohitra Marojejy
Gephyromantis asper
Gephyromantis spinifer
Gephyromantis horridus
Gephyromantis sp aff horridus Marojejy
Gephyromantis striatus
Gephyromantis malagasius
Gephyromantis sp aff malagasius highlands
Gephyromantis ventrimaculatus
Gephyromantis klemmeri
Gephyromantis corvus
Gephyromantis azzurae Andreone Isalo Andrianamero
Gephyromantis sp aff corvus Bemaraha
Gephyromantis pseudoasper
Gephyromantis cornutus
Gephyromantis schenki
Gephyromantis redimitus
Gephyromantis leucomaculatus
Gephyromantis sp aff leucomaculatus Marojejy
Gephyromantis salegy
Gephyromantis schilfy
Gephyromantis tandroka
Gephyromantis granulatus
Gephyromantis zavona
Gephyromantis moseri
Gephyromantis luteus
Gephyromantis sculpturatus
Gephyromantis plicifer
Gephyromantis rivicola
Gephyromantis silvanus
Gephyromantis webbi
Gephyromantis enki
Gephyromantis blanci
Gephyromantis runewsweeki
Gephyromantis sp aff blanci Andohahela
Gephyromantis boulengeri
Gephyromantis decaryi
Gephyromantis leucocephalus Ste Luce
Gephyromantis eiselti
Gephyromantis thelenae
Mantidactylus noralottae Andreone Isalo Andrianamero
Mantidactylus sp aff betsileanus slow calls
Mantidactylus sp aff betseileanus Tolagnaro
Mantidactylus sp aff curtus Andohahela short snout
Mantidactylus betsileanus
Mantidactylus sp aff betsileanus Andranofotsy
Mantidactylus sp aff betsileanus Nosy Borana
Mantidactylus sp aff betsileanus Toamasina
Mantidactylus bellyi
Mantidactylus ulcerosus
Mantidactylus sp aff biporus Tsaratanana camp1
Mantidactylus sp aff biporus Tsaratanana camp0
Mantidactylus alutus
Mantidactylus biporus
Mantidactylus sp aff biporus Ambohitantely
Mantidactylus sp aff biporus Andasibe
Mantidactylus sp aff biporus Andranofotsy
Mantidactylus sp aff biporus Ranomafana
Mantidactylus pauliani
Mantidactylus curtus Antoetra
Mantidactylus bourgati
Mantidactylus sp aff curtus Ankaratra
Mantidactylus sp aff curtus Amponitantely
Mantidactylus sp aff pauliani Itremo
Mantidactylus madecassus
Mantidactylus sp aff ulcerosus Isalo
Mantidactylus tricinctus Manatalteitely
Mantidactylus tricinctus Manompo
Mantidactylus sp aff tricinctus parvus
Mantidactylus aerumnalis
Mantidactylus albofrenatus
Mantidactylus charlotteae
Mantidactylus brevipalmatus
Mantidactylus delormei
Mantidactylus opiparis
Mantidactylus melanopleura
Mantidactylus zipperi
Mantidactylus sp aff charlotteae Ranomafana
Mantidactylus majori
Mantidactylus ambreensis
Mantidactylus femoralis
Mantidactylus mocquardi Andasibe
Mantidactylus sp aff mocquardi Ambatolahy
Mantidactylus sp aff femoralis Ambohitsara
Mantidactylus sp aff mocquardi Tsaratanana
Mantidactylus sp aff mocquardi Marojejy
Mantidactylus sp aff femoralis Tsaratanana
Mantidactylus sp aff majori Andapa
Mantidactylus zolitschka
Mantidactylus sp aff femoralis Ambre
Mantidactylus argenteus
Mantidactylus sp aff lugubris Marojejy
Mantidactylus lugubris Andasibe
Mantidactylus cowani
Mantidactylus sp aff cowani small
Mantidactylus sp aff lugubris south
Mantidactylus guttulatus east
Mantidactylus sp aff grandidieri north
Mantidactylus guttulatus north
Tsingymantis antitra

Boophis sp Comoros
Boophis doulioti
Boophis tephraeomystax
Boophis xerophilus
Boophis lichenoides
Boophis guibei
Boophis sp sarotra
Boophis ideae
Boophis pauliani
Boophis sp aff pauliani Tolagnaro
Boophis opisthodon
Boophis albilabris
Boophis occidentalis
Boophis sp aff occidentalis Berara
Boophis sp aff albilabris red eyes
Boophis albipunctatus
Boophis sibilans
Boophis sp aff sibilans trill call
Boophis andohahela
Boophis andreonei
Boophis elenae
Boophis anjanaharibeensis
Boophis sp aff elenae vigoi
Boophis septentrionalis
Boophis englaenderi
Boophis luteus
Boophis jaegeri
Boophis tandroka
Boophis ankaratra
Boophis sp aff ankaratra Andohahela slow
Boophis sp aff ankaratra Andohahela fast
Boophis schuboeae
Boophis axelmeyeri
Boophis burgeri
Boophis rufioculis
Boophis reticulatus
Boophis sp aff rufioculis Ranomafana
Boophis boehmei
Boophis sp aff boehmei Ranomafana
Boophis brachychir
Boophis sp aff brachychir 2
Boophis goudoti
Boophis sp aff periegetes Ranomafana
Boophis madagascariensis
Boophis sp aff madagascariensis north
Boophis sp lichenoides Ambatolahy
Boophis periegets
Boophis blommersae
Boophis vittatus
Boophis marojezensis
Boophis liami
Boophis sp aff mandraka Andreone 1
Boophis mandraka
Boophis sp aff mandraka Marojejy
Boophis sambirano
Boophis solomaso
Boophis feonnyala
Boophis miniatus
Boophis sp aff rhodoscelis ranomafana
Boophis picturatus
Boophis sp aff miniatus Mahakajy
Boophis haematopus
Boophis pyrrhus
Boophis sp aff rappiodes Ambre
Boophis sp aff rappiodes northeast
Boophis sp aff rappiodes lilianae
Boophis majori
Boophis sp aff majori Ranomafana long call
Boophis laurenti
Boophis microtympanum
Boophis sp aff microtympanum low altitude
Boophis rhodoscelis
Boophis sp aff rhodoscelis Ambohitantely
Boophis williamsi
Boophis bottae
Boophis rappiodes
Boophis erythrodactylus
Boophis tasymena
Boophis viridis

Supplementary Figure S3 (next 3 pages). One character history reconstructed through stochastic character mapping of different character states of iris pattern in mantellid frogs (as in Figure 1 of main paper but including taxon names as in second column of Table S1).

Boehmantis microtympanum
Gephyromantis ambohitra
Gephyromantis sp aff ambohitra Marojejy
Gephyromantis asper
Gephyromantis spinifer
Gephyromantis horridus
Gephyromantis sp aff horridus Marojejy
Gephyromantis striatus
Gephyromantis malagasius
Gephyromantis sp aff malagasius highlands
Gephyromantis ventrimaculatus
Gephyromantis klemmeri
Gephyromantis corvus
Gephyromantis azzurae Andreone Isalo Andrianamero
Gephyromantis sp aff corvus Bemaraha
Gephyromantis pseudoasper
Gephyromantis cornutus
Gephyromantis schenki
Gephyromantis redimitus
Gephyromantis leucomaculatus
Gephyromantis sp aff leucomaculatus Marojejy
Gephyromantis salegy
Gephyromantis schilfy
Gephyromantis tandroka
Gephyromantis granulatus
Gephyromantis zavona
Gephyromantis moseri
Gephyromantis luteus
Gephyromantis sculpturatus
Gephyromantis plicifer
Gephyromantis rivicola
Gephyromantis silvanus
Gephyromantis webbi
Gephyromantis blanci
Gephyromantis enki
Gephyromantis runewsweeki
Gephyromantis sp aff blanci Andohahela
Gephyromantis boulengeri
Gephyromantis decaryi
Gephyromantis leucocephalus Ste Luce
Gephyromantis eiselti
Gephyromantis thelenae
Mantidactylus noralottae Andreone Isalo Andrianamero
Mantidactylus sp aff betsileanus slow calls
Mantidactylus sp aff betseileanus Tolagnaro
Mantidactylus sp aff curtus Andohahela short snout
Mantidactylus betsileanus
Mantidactylus sp aff betsileanus Andranofotsy
Mantidactylus sp aff betsileanus Nosy Borana
Mantidactylus sp aff betsileanus Toamasina
Mantidactylus bellyi
Mantidactylus ulcerosus
Mantidactylus sp aff biporus Tsaratanana camp1
Mantidactylus sp aff biporus Tsaratanana camp0
Mantidactylus alutus
Mantidactylus biporus
Mantidactylus sp aff biporus Ambohitantely
Mantidactylus sp aff biporus Andasibe
Mantidactylus sp aff biporus Andranofotsy
Mantidactylus sp aff biporus Ranomafana
Mantidactylus pauliani
Mantidactylus bourgati
Mantidactylus curtus Antoetra
Mantidactylus sp aff curtus Ankaratra
Mantidactylus sp aff curtus Amponitantely
Mantidactylus sp aff pauliani Itremo
Mantidactylus madecassus
Mantidactylus sp aff ulcerosus Isalo
Mantidactylus tricinctus Manatahtely
Mantidactylus tricinctus Manompo
Mantidactylus sp aff tricinctus parvus
Mantidactylus aerumnalis
Mantidactylus albofrenatus
Mantidactylus charlotteae
Mantidactylus brevipalmatus
Mantidactylus delormei
Mantidactylus opiparis
Mantidactylus melanopleura
Mantidactylus zipperi
Mantidactylus sp aff charlotteae Ranomafana
Mantidactylus majori
Mantidactylus ambreensis
Mantidactylus femoralis
Mantidactylus mocquardi Andasibe
Mantidactylus sp aff mocquardi Ambatolahy
Mantidactylus sp aff femoralis Ambohitsara
Mantidactylus sp aff mocquardi Tsaratanana
Mantidactylus sp aff mocquardi Marojejy
Mantidactylus sp aff femoralis Tsaratanana
Mantidactylus sp aff majori Andapa
Mantidactylus zolitschka
Mantidactylus sp aff femoralis Ambre
Mantidactylus argenteus
Mantidactylus sp aff lugubris Marojejy
Mantidactylus lugubris Andasibe
Mantidactylus cowani
Mantidactylus sp aff cowani small
Mantidactylus sp aff lugubris south
Mantidactylus guttulatus east
Mantidactylus sp aff grandidieri north
Mantidactylus guttulatus north
Tsingymantis antitra

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Boophis sp Comoros
Boophis doulioti
Boophis tephraeomystax
Boophis xerophilus
Boophis lichenoides
Boophis guibei
Boophis sp sarotra
Boophis ideae
Boophis pauliani
Boophis sf aff pauliani Tolagnaro
Boophis obhisthodon
Boophis albilabris
Boophis occidentalis
Boophis sp aff occidentalis Berara
Boophis sp aff albilabris red eyes
Boophis albipunctatus
Boophis sibilans
Boophis sf aff sibilans trill call
Boophis andohahela
Boophis andreonei
Boophis elenae
Boophis anjanaharibeensis
Boophis sp aff elenae vigoi
Boophis septentrionalis
Boophis englaenderi
Boophis luteus
Boophis tandroka
Boophis jaegeri
Boophis ankaratra
Boophis sp aff ankaratra Andohahela slow
Boophis sp aff ankaratra Andohahela fast
Boophis schuboeae
Boophis axelmeyeri
Boophis burgeri
Boophis rufioculis
Boophis reticulatus
Boophis sp aff rufioculis Ranomafana
Boophis boehmei
Boophis sp aff boehmei Ranomafana
Boophis brachychir
Boophis sp aff brachychir 2
Boophis goudoti
Boophis sp aff periegetes Ranomafana
Boophis madagascariensis
Boophis sp aff madagascariensis north
Boophis sp lichenoides Ambatolahy
Boophis periegets
Boophis blommersae
Boophis vittatus
Boophis marojezensis
Boophis liami
Boophis sp aff mandraka Andreone 1
Boophis mandraka
Boophis sp aff mandraka Marojejy
Boophis sambirano
Boophis solomaso
Boophis feonnyala
Boophis miniatus
Boophis sp aff rhodoscelis ranomafana
Boophis picturatus
Boophis sp aff miniatus Mahakajy
Boophis haematopus
Boophis pyrrhus
Boophis sp aff rappiodes Ambre
Boophis sp aff rappiodes northeast
Boophis sp aff rappiodes lilianae
Boophis majori
Boophis sp aff majori Ranomafana long call
Boophis laurenti
Boophis microtympanum
Boophis sp aff microtympanum low altitude
Boophis rhodoscelis
Boophis sp aff rhodoscelis Ambohitantely
Boophis williamsi
Boophis bottae
Boophis rappiodes
Boophis erytrhrodactylus
Boophis tasymena
Boophis viridis

Supplementary Figure S4 (next 3 pages). One character history reconstructed through stochastic character mapping of different character states of iris contrast in mantellid frogs (as in Figure 1 of main paper but including taxon names as in second column of Table S1).

Boehmantis microtympanum
Gephyromantis ambohitra
Gephyromantis sp aff ambohitra Marojejy
Gephyromantis asper
Gephyromantis spinifer
Gephyromantis horridus
Gephyromantis sp aff horridus Marojejy
Gephyromantis striatus
Gephyromantis malagasius
Gephyromantis sp aff malagasius highlands
Gephyromantis ventrimaculatus
Gephyromantis klemmeri
Gephyromantis corvus
Gephyromantis azzurae Andreone Isalo Andrianamero
Gephyromantis sp aff corvus Bemaraha
Gephyromantis pseudoasper
Gephyromantis cornutus
Gephyromantis schenki
Gephyromantis redimitus
Gephyromantis leucomaculatus
Gephyromantis sp aff leucomaculatus Marojejy
Gephyromantis salegy
Gephyromantis schilfy
Gephyromantis tandroka
Gephyromantis granulatus
Gephyromantis zavona
Gephyromantis moseri
Gephyromantis luteus
Gephyromantis sculpturatus
Gephyromantis plicifer
Gephyromantis tivicola
Gephyromantis silvanus
Gephyromantis webbi
Gephyromantis blanci
Gephyromantis enki
Gephyromantis runewsweeki
Gephyromantis sp aff blanci Andohahela
Gephyromantis boulengeri
Gephyromantis decaryi
Gephyromantis leucocephalus Ste Luce
Gephyromantis eiselti
Gephyromantis thelenae
Mantidactylus noralottae Andreone Isalo Andrianamero
Mantidactylus sp aff betsileanus slow calls
Mantidactylus sp aff betseileanus Tolagnaro
Mantidactylus sp aff curtus Andohahela short snout
Mantidactylus betsileanus
Mantidactylus sp aff betsileanus Andranofotsy
Mantidactylus sp aff betsileanus Nosy Borana
Mantidactylus sp aff betsileanus Toamasina
Mantidactylus bellyi
Mantidactylus ulcerosus
Mantidactylus sp aff biporus Tsaratanana camp1
Mantidactylus sp aff biporus Tsaratanana camp0
Mantidactylus alutus
Mantidactylus biporus
Mantidactylus sp aff biporus Ambohitantely
Mantidactylus sp aff biporus Andasibe
Mantidactylus sp aff biporus Andranofotsy
Mantidactylus sp aff biporus Ranomafana
Mantidactylus pauliani
Mantidactylus bourgati
Mantidactylus sp aff curtus Antoetra
Mantidactylus sp aff curtus Ankaratra
Mantidactylus sp aff curtus Amponitantely
Mantidactylus sp aff pauliani Itremo
Mantidactylus madecassus
Mantidactylus sp aff ulcerosus Isalo
Mantidactylus tricinctus Manatahtely
Mantidactylus tricinctus Manompo
Mantidactylus sp aff tricinctus parvus
Mantidactylus aerumnalis
Mantidactylus albofrenatus
Mantidactylus charlotteae
Mantidactylus brevipalmatus
Mantidactylus delormei
Mantidactylus opiparis
Mantidactylus melanopleura
Mantidactylus zipperi
Mantidactylus sp aff charlotteae Ranomafana
Mantidactylus majori
Mantidactylus ambreensis
Mantidactylus femoralis
Mantidactylus mocquardi Andasibe
Mantidactylus sp aff femoralis Ambohitsara
Mantidactylus sp aff mocquardi Ambatolahy
Mantidactylus sp aff mocquardi Tsaratanana
Mantidactylus sp aff mocquardi Marojejy
Mantidactylus sp aff femoralis Tsaratanana
Mantidactylus sp aff majori Andapa
Mantidactylus zolitschka
Mantidactylus sp aff femoralis Ambre
Mantidactylus argenteus
Mantidactylus sp aff lugubris Marojejy
Mantidactylus lugubris Andasibe
Mantidactylus sp aff cowani small
Mantidactylus cowani
Mantidactylus sp aff lugubris south
Mantidactylus guttulatus east
Mantidactylus sp aff grandidieri north
Mantidactylus guttulatus north
Tsingymantis antitra

Boophis sp Comoros
Boophis doulioti
Boophis tephraeomystax
Boophis xerophilus
Boophis lichenoides
Boophis guibei
Boophis sp sarotra
Boophis ideae
Boophis pauliani
Boophis sf aff pauliani Tolagnaro
Boophis obhisthodon
Boophis albilabris
Boophis occidentalis
Boophis sp aff occidentalis Berara
Boophis sp aff albilabris red eyes
Boophis albipunctatus
Boophis sibilans
Boophis sf aff sibilans trill call
Boophis andohahela
Boophis andreonei
Boophis elenae
Boophis anjanaharibeensis
Boophis sp aff elenae vigol
Boophis septentrionalis
Boophis englaenderi
Boophis luteus
Boophis tandroka
Boophis jaegeri
Boophis ankaratra
Boophis sp aff ankaratra Andohahela slow
Boophis sp aff ankaratra Andohahela fast
Boophis schuboeae
Boophis axelmeyeri
Boophis burgeri
Boophis rufioculis
Boophis reticulatus
Boophis sp aff rufioculis Ranomafana
Boophis boehmei
Boophis sp aff boehmei Ranomafana
Boophis brachychir
Boophis sp aff brachychir 2
Boophis goudoti
Boophis sp aff periegetes Ranomafana
Boophis madagascariensis
Boophis sp aff madagascariensis north
Boophis sp lichenoides Ambatolahy
Boophis periegets
Boophis blommersae
Boophis vittatus
Boophis marojezensis
Boophis sp aff mandraka Andreone 1
Boophis liami
Boophis mandraka
Boophis sp aff mandraka Marojely
Boophis sambirano
Boophis solomaso
Boophis feonnyala
Boophis miniatus
Boophis sp aff rhodoscelis ranomafana
Boophis picturatus
Boophis sp aff miniatus Mahakajy
Boophis haematopus
Boophis pyrrhus
Boophis sp aff rappiodes Ambre
Boophis sp aff rappiodes northeast
Boophis sp aff rappiodes lilianae
Boophis majori
Boophis sp aff majori Ranomafana long call
Boophis laurenti
Boophis microtympanum
Boophis sp aff microtympanum low altitude
Boophis rhodoscelis
Boophis sp aff rhodoscelis Ambohitantely
Boophis williamsi
Boophis bottae
Boophis rappiodes
Boophis erythrodactylus
Boophis tasymena
Boophis viridis

Supplementary Figure S5 (next 3 pages). One character history reconstructed through stochastic character mapping of different character states of iris periphery colour in mantellid frogs (as in Figure 1 of main paper but including taxon names as in second column of Table S1).

Boehmantis microtympanum
Gephyromantis ambohitra
Gephyromantis sp aff ambohitra Marojejy
Gephyromantis asper
Gephyromantis spinifer
Gephyromantis horridus
Gephyromantis sp aff horridus Marojejy
Gephyromantis striatus
Gephyromantis malagasius
Gephyromantis sp aff malagasius highlands
Gephyromantis ventrimaculatus
Gephyromantis klemmeri
Gephyromantis corvus
Gephyromantis azzurae Andreone Isalo Andrianamero
Gephyromantis sp aff corvus Bemaraha
Gephyromantis pseudoasper
Gephyromantis cornutus
Gephyromantis schenki
Gephyromantis redimitus
Gephyromantis leucomaculatus
Gephyromantis sp aff leucomaculatus Marojejy
Gephyromantis salegy
Gephyromantis schilfi
Gephyromantis tandroka
Gephyromantis granulatus
Gephyromantis zavona
Gephyromantis moseri
Gephyromantis luteus
Gephyromantis sculpturatus
Gephyromantis plicifer
Gephyromantis rivicola
Gephyromantis silvanus
Gephyromantis webbi
Gephyromantis blanci
Gephyromantis enki
Gephyromantis runewsweeki
Gephyromantis sp aff blanci Andohahela
Gephyromantis boulengeri
Gephyromantis decaryi
Gephyromantis leucocephalus Ste Luce
Gephyromantis eiselti
Gephyromantis thelenae
Mantidactylus noralottae Andreone Isalo Andrianamero
Mantidactylus sp aff betsileanus slow calls
Mantidactylus sp aff betseileanus Tolagnaro
Mantidactylus sp aff curtus Andohahela short snout
Mantidactylus betsileanus
Mantidactylus sp aff betsileanus Andranofotsy
Mantidactylus sp aff betsileanus Nosy Borana
Mantidactylus sp aff betsileanus Toamasina
Mantidactylus bellyi
Mantidactylus ulcerosus
Mantidactylus sp aff biporus Tsaratanana camp1
Mantidactylus sp aff biporus Tsaratanana camp0
Mantidactylus alutus
Mantidactylus biporus
Mantidactylus sp aff biporus Ambohitantely
Mantidactylus sp aff biporus Andasibe
Mantidactylus sp aff biporus Andranofotsy
Mantidactylus sp aff biporus Ranomafana
Mantidactylus pauliani
Mantidactylus bourgati
Mantidactylus curtus Antoetra
Mantidactylus sp aff curtus Ankaratra
Mantidactylus sp aff curtus Amponitantely
Mantidactylus sp aff pauliani Itremo
Mantidactylus madecassus
Mantidactylus sp aff ulcerosus Isalo
Mantidactylus tricinctus Manatahtely
Mantidactylus tricinctus Manompo
Mantidactylus sp aff tricinctus parvus
Mantidactylus aerumnalis
Mantidactylus albofrenatus
Mantidactylus charlotteae
Mantidactylus brevipalmatus
Mantidactylus delormei
Mantidactylus opiparis
Mantidactylus melanopleura
Mantidactylus zipperi
Mantidactylus sp aff charlotteae Ranomafana
Mantidactylus majori
Mantidactylus ambreensis
Mantidactylus femoralis
Mantidactylus mocquardi Andasibe
Mantidactylus sp aff mocquardi Ambatolahy
Mantidactylus sp aff femoralis Ambohitsara
Mantidactylus sp aff mocquardi Tsaratanana
Mantidactylus sp aff mocquardi Marojejy
Mantidactylus sp aff femoralis Tsaratanana
Mantidactylus sp aff majori Andapa
Mantidactylus zolitschka
Mantidactylus sp aff femoralis Ambre
Mantidactylus argenteus
Mantidactylus sp aff lugubris Marojejy
Mantidactylus lugubris Andasibe
Mantidactylus cowani
Mantidactylus sp aff cowani small
Mantidactylus sp aff lugubris south
Mantidactylus guttulatus east
Mantidactylus sp aff grandidieri north
Mantidactylus guttulatus north
Tsingymantis antitra

Boophis sp Comoros
Boophis doulioti
Boophis tephraeomystax
Boophis xerophilus
Boophis lichenoides
Boophis guibei
Boophis sp sarotra
Boophis ideae
Boophis pauliani
Boophis sp aff pauliani Tolagnaro
Boophis obhisthodon
Boophis albilabris
Boophis occidentalis
Boophis sp aff occidentalis Berara
Boophis sp aff albilabris red eyes
Boophis albipunctatus
Boophis sibilans
Boophis sp aff sibilans trill call
Boophis andohahela
Boophis andreonei
Boophis elenae
Boophis anjanaharibeensis
Boophis sp aff elenae vigoi
Boophis septentrionalis
Boophis englaenderi
Boophis luteus
Boophis tandroka
Boophis jaegeri
Boophis anKaratra
Boophis sp aff ankaratra Andohahela slow
Boophis sp aff ankaratra Andohahela fast
Boophis schuboeae
Boophis axelmeyeri
Boophis burgeri
Boophis rufioculis
Boophis reticulatus
Boophis sp aff rufioculis Ranomafana
Boophis boehmei
Boophis sp aff boehmei Ranomafana
Boophis brachychir
Boophis sp aff brachychir 2
Boophis goudoti
Boophis sp aff periegetes Ranomafana
Boophis madagascariensis
Boophis sp aff madagascariensis north
Boophis sp lichenoides Ambatolahy
Boophis periegets
Boophis blommersae
Boophis vittatus
Boophis marojezensis
Boophis liami
Boophis sp aff mandraka Andreone 1
Boophis mandraka
Boophis sp aff mandraka Marojejy
Boophis sambirano
Boophis solomaso
Boophis feonnyala
Boophis miniatus
Boophis sp aff rhodoscelis ranomafana
Boophis picturatus
Boophis sp aff miniatus Mahakajy
Boophis haematopus
Boophis pyrrhus
Boophis sp aff rappiodes Ambre
Boophis sp aff rappiodes northeast
Boophis sp aff rappiodes lilianae
Boophis majori
Boophis sp aff majori Ranomafana long call
Boophis laurenti
Boophis microtympanum
Boophis sp aff microtympanum low altitude
Boophis rhodoscelis
Boophis sp aff rhodoscelis Ambohitantely
Boophis williamsi
Boophis bottae
Boophis rappiodes
Boophis erytrhrodactylus
Boophis tasymena
Boophis viridis

Supplementary Figure S6 (next 3 pages). One character history reconstructed through stochastic character mapping of presence vs. absence of the frenal streak in mantellid frogs (as in Figure 1 of main paper but including taxon names as in second column of Table S1).

Boehmantis microtympanum
Gephyromantis ambohitra
Gephyromantis sp aff ambohitra Marojejy
Gephyromantis asper
Gephyromantis spinifer
Gephyromantis horridus
Gephyromantis sp aff horridus Marojejy
Gephyromantis striatus
Gephyromantis malagasius
Gephyromantis sp aff malagasius highlands
Gephyromantis ventrimaculatus
Gephyromantis klemmeri
Gephyromantis corvus
Gephyromantis azzurae Andreone Isalo Andrianamero
Gephyromantis sp aff corvus Bemaraha
Gephyromantis pseudoasper
Gephyromantis cornutus
Gephyromantis schenki
Gephyromantis leucomaculatus
Gephyromantis redimitus
Gephyromantis sp aff leucomaculatus Marojejy
Gephyromantis salegy
Gephyromantis schilfy
Gephyromantis tandroka
Gephyromantis granulatus
Gephyromantis moseri
Gephyromantis zavona
Gephyromantis luteus
Gephyromantis sculpturatus
Gephyromantis plicifer
Gephyromantis rivicola
Gephyromantis silvanus
Gephyromantis webbi
Gephyromantis blanci
Gephyromantis enki
Gephyromantis runewsweeki
Gephyromantis sp aff blanci Andohahela
Gephyromantis boulengeri
Gephyromantis decaryi
Gephyromantis leucocephalus Ste Luce
Gephyromantis eiselti
Gephyromantis thelenae
Mantidactylus noralottae Andreone Isalo Andrianamero
Mantidactylus sp aff betsileanus slow calls
Mantidactylus sp aff betsileanus Tolagnaro
Mantidactylus sp aff curtus Andohahela short snout
Mantidactylus betsileanus
Mantidactylus sp aff betsileanus Andranofotsy
Mantidactylus sp aff betsileanus Nosy Borana
Mantidactylus sp aff betsileanus Toamasina
Mantidactylus bellyi
Mantidactylus ulcerosus
Mantidactylus sp aff biporus Tsaratanana camp1
Mantidactylus sp aff biporus Tsaratanana camp0
Mantidactylus alutus
Mantidactylus biporus
Mantidactylus sp aff biporus Ambohitantely
Mantidactylus sp aff biporus Andasibe
Mantidactylus sp aff biporus Andranofotsy
Mantidactylus sp aff biporus Ranomafana
Mantidactylus pauliani
Mantidactylus bourgati
Mantidactylus curtus Antoetra
Mantidactylus sp aff curtus Ankaratra
Mantidactylus sp aff curtus Amponitantely
Mantidactylus sp aff pauliani Itremo
Mantidactylus madecassus
Mantidactylus sp aff ulcerosus Isalo
Mantidactylus tricinctus Manatahtely
Mantidactylus tricinctus Manompo
Mantidactylus sp aff tricinctus parvus
Mantidactylus aerumnalis
Mantidactylus albofrenatus
Mantidactylus charlotteae
Mantidactylus brevipalmatus
Mantidactylus delormei
Mantidactylus opiparis
Mantidactylus melanopleura
Mantidactylus zipperi
Mantidactylus sp aff cf charlotteae Ranomafana
Mantidactylus majori
Mantidactylus ambreensis
Mantidactylus femoralis
Mantidactylus mocquardi Andasibe
Mantidactylus sp aff femoralis Ambohitsara
Mantidactylus sp aff mocquardi Ambatolahy
Mantidactylus sp aff mocquardi Tsaratanana
Mantidactylus sp aff mocquardi Marojejy
Mantidactylus sp aff femoralis Tsaratanana
Mantidactylus sp aff majori Andapa
Mantidactylus zolitschka
Mantidactylus sp aff femoralis Ambre
Mantidactylus argenteus
Mantidactylus sp aff lugubris Marojejy
Mantidactylus lugubris Andasibe
Mantidactylus cowani
Mantidactylus sp aff cowani small
Mantidactylus sp aff lugubris south
Mantidactylus guttulatus east
Mantidactylus sp aff grandidieri north
Mantidactylus guttulatus north
Tsingymantis antitra

Boophis sp Comoros
Boophis doulioti
Boophis tephraeomystax
Boophis xerophilus
Boophis lichenoides
Boophis guibei
Boophis sp sarotra
Boophis ideae
Boophis pauliani
Boophis sp aff pauliani Tolagnaro
Boophis obhisthodon
Boophis albilabris
Boophis occidentalis
Boophis sp aff occidentalis Berara
Boophis sp aff albilabris red eyes
Boophis albipunctatus
Boophis sibilans
Boophis sp aff sibilans trill call
Boophis ahdohahela
Boophis andreonei
Boophis elenae
Boophis anjanaharibeensis
Boophis sp aff elenae vigoi
Boophis septentrionalis
Boophis englaenderi
Boophis luteus
Boophis tandroka
Boophis jaegeri
Boophis ankaratra
Boophis sp aff ankaratra Andohahela slow
Boophis sp aff ankaratra Andohahela fast
Boophis schuboeae
Boophis axelmeyeri
Boophis burgeri
Boophis rufioculis
Boophis reticulatus
Boophis sp rufioculis Ranomafana
Boophis boehmei
Boophis sp aff boehmei Ranomafana
Boophis brachychir
Boophis sp aff brachychir 2
Boophis goudoti
Boophis sp aff periegetes Ranomafana
Boophis madagascariensis
Boophis sp aff madagascariensis north
Boophis sp lichenoides Ambatolahy
Boophis periegets
Boophis blommersae
Boophis vittatus
Boophis marojezensis
Boophis liani
Boophis sp aff mandraka Andreone 1
Boophis mandraka
Boophis sp aff mandraka Marojejy
Boophis sambirano
Boophis solomaso
Boophis feonnyala
Boophis miniatus
Boophis sp aff rhodoscelis ranomafana
Boophis picturatus
Boophis sp aff miniatus Mahakajy
Boophis haematopus
Boophis pyrrhus
Boophis sp aff rappiodes Ambre
Boophis sp aff rappiodes northeast
Boophis sp aff rappiodes lilianae
Boophis majori
Boophis sp aff majori Ranomafana long call
Boophis laurenti
Boophis microtympanum
Boophis sp aff microtympanum low altitude
Boophis rhodoscelis
Boophis sp aff rhodoscelis Ambohitantely
Boophis williamsi
Boophis bottae
Boophis rappiodes
Boophis erythrhrodactylus
Boophis tasymena
Boophis viridis

Supplementary Figure S7 (next 3 pages). One character history reconstructed through stochastic character mapping of presence vs. absence of the dark tympanic patch in mantellid frogs (as in Figure 1 of main paper but including taxon names as in second column of Table S1).

Boehmantis microtympanum
Gephyromantis ambohitra
Gephyromantis sp aff ambohitra Marojejy
Gephyromantis asper
Gephyromantis spinifer
Gephyromantis horridus
Gephyromantis sp aff horridus Marojejy
Gephyromantis striatus
Gephyromantis malagasius
Gephyromantis sp aff malagasius highlands
Gephyromantis ventrimaculatus
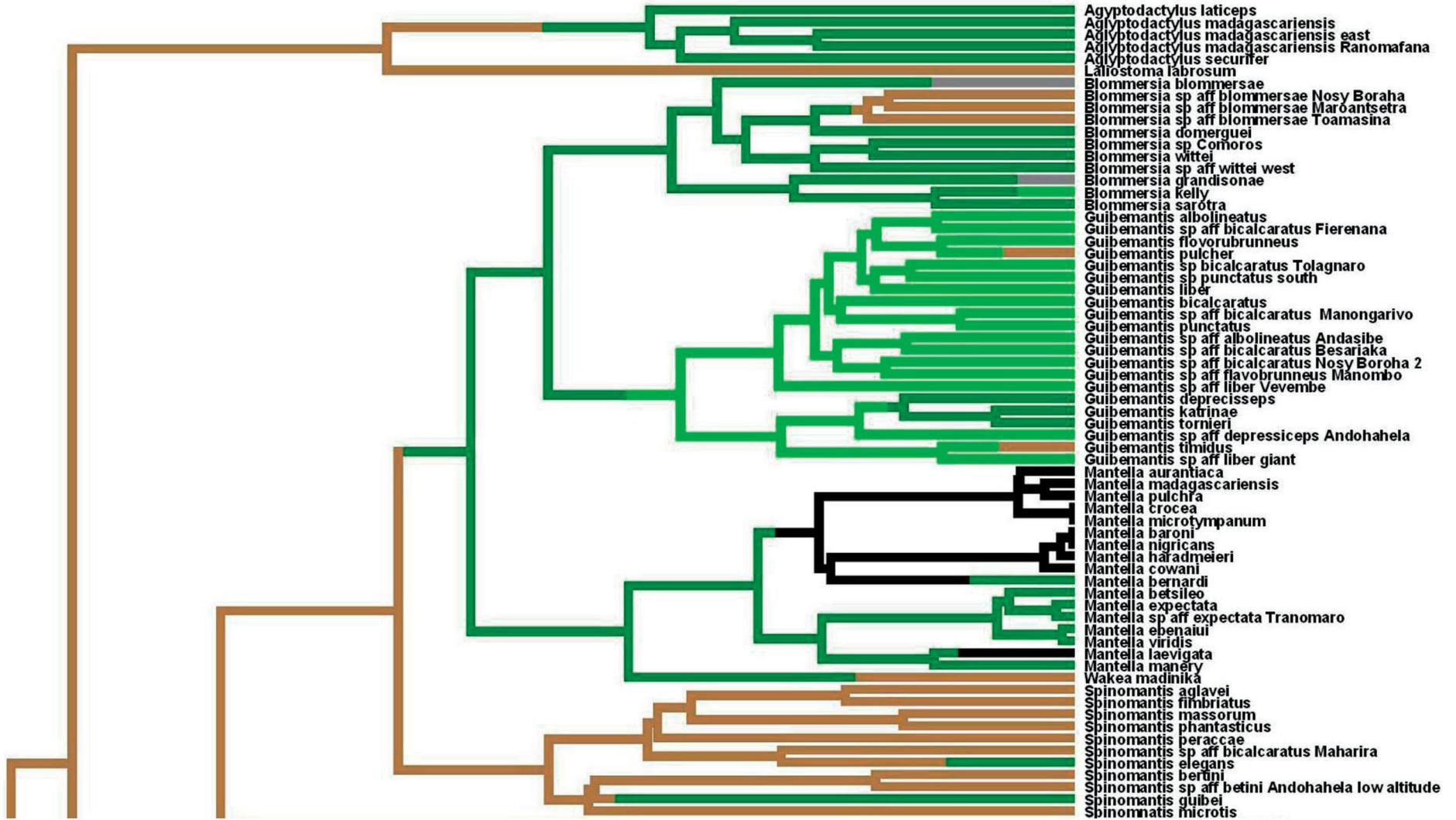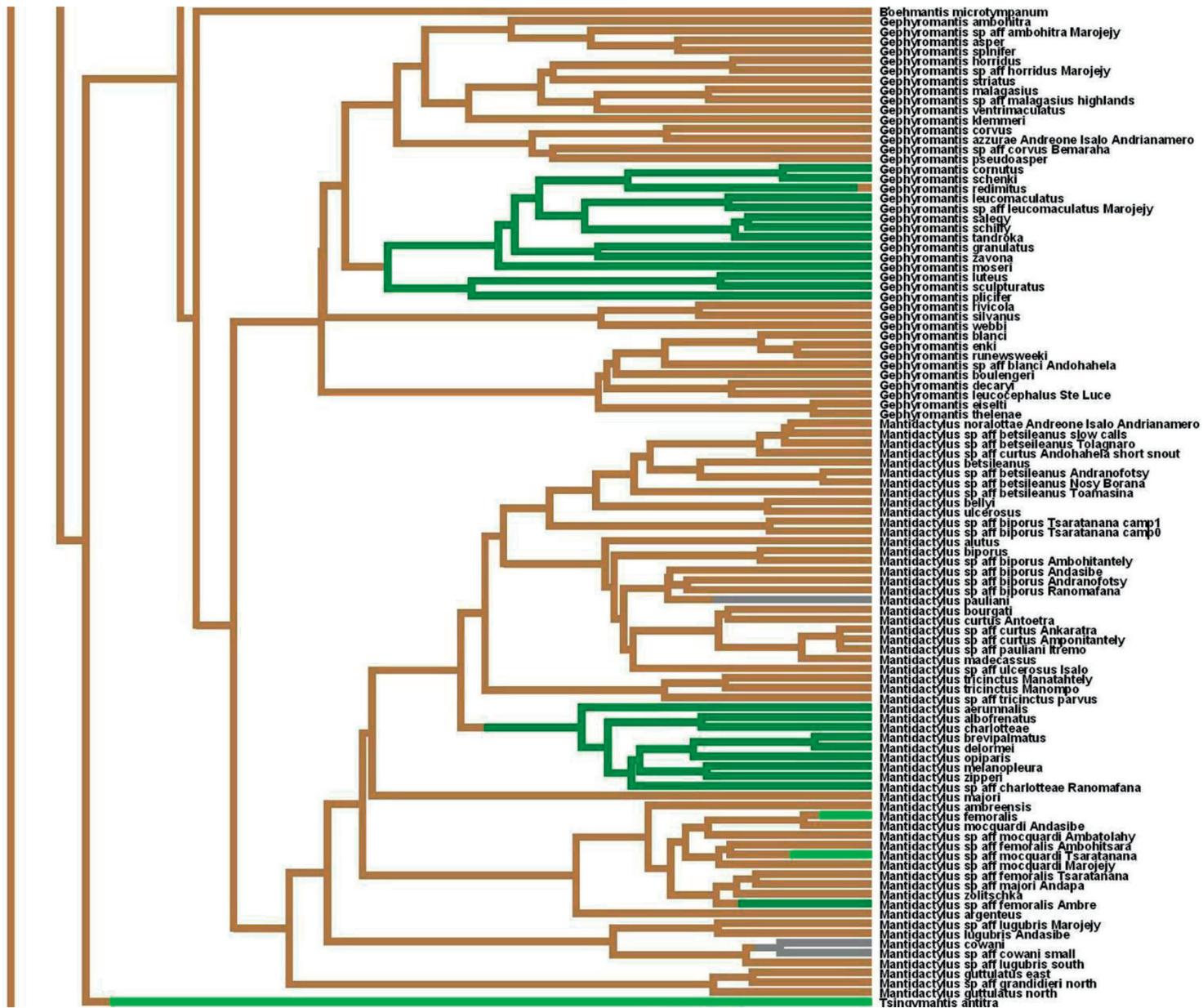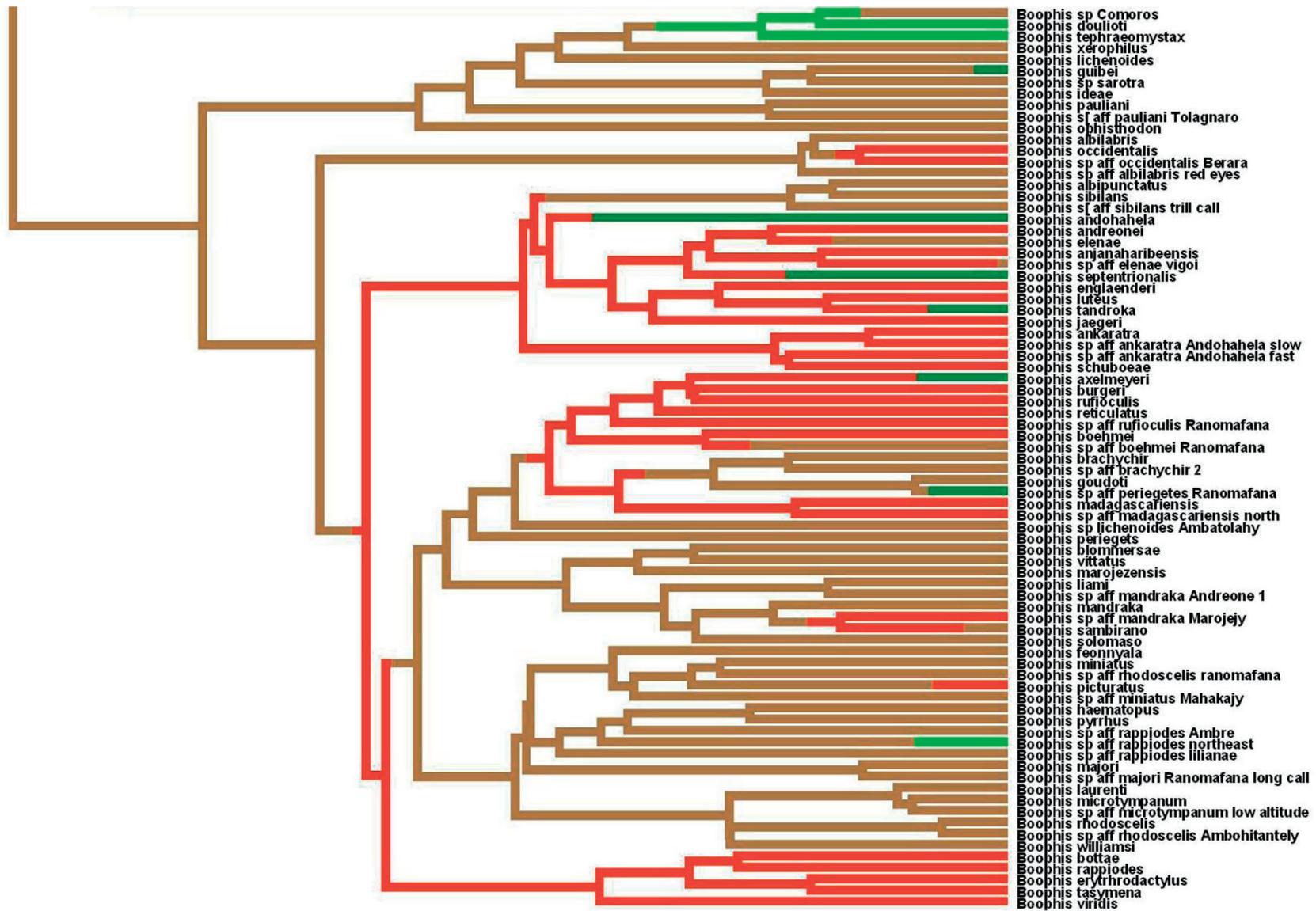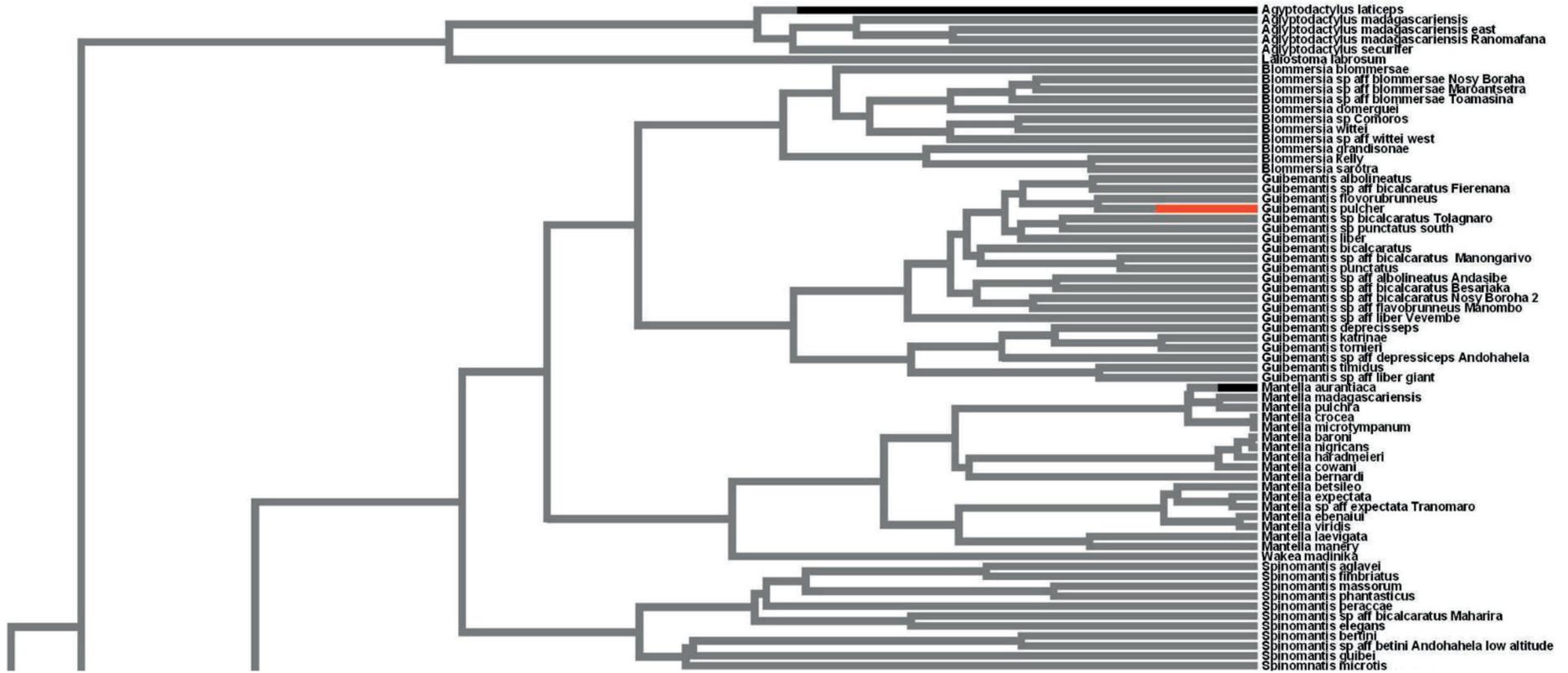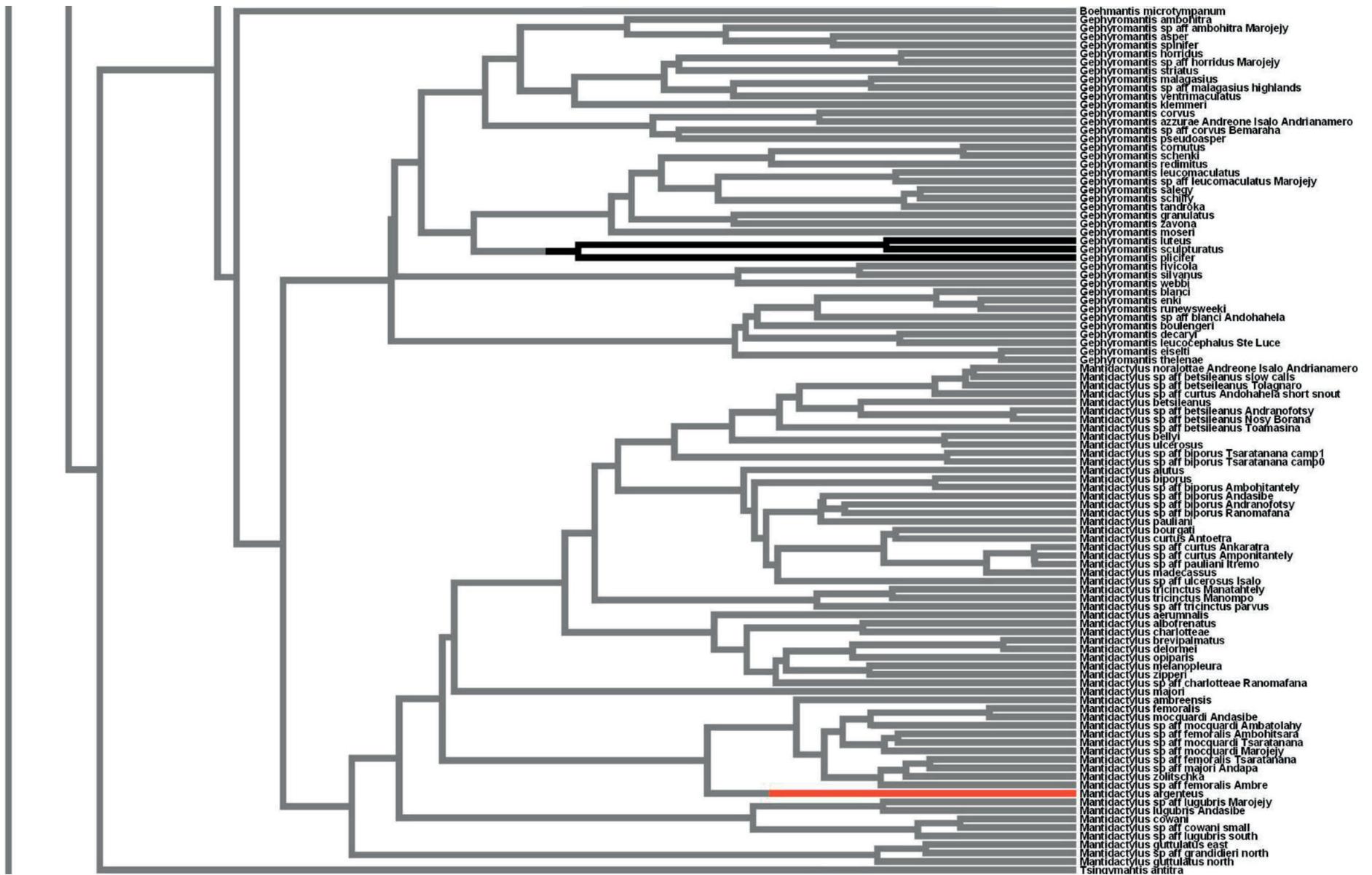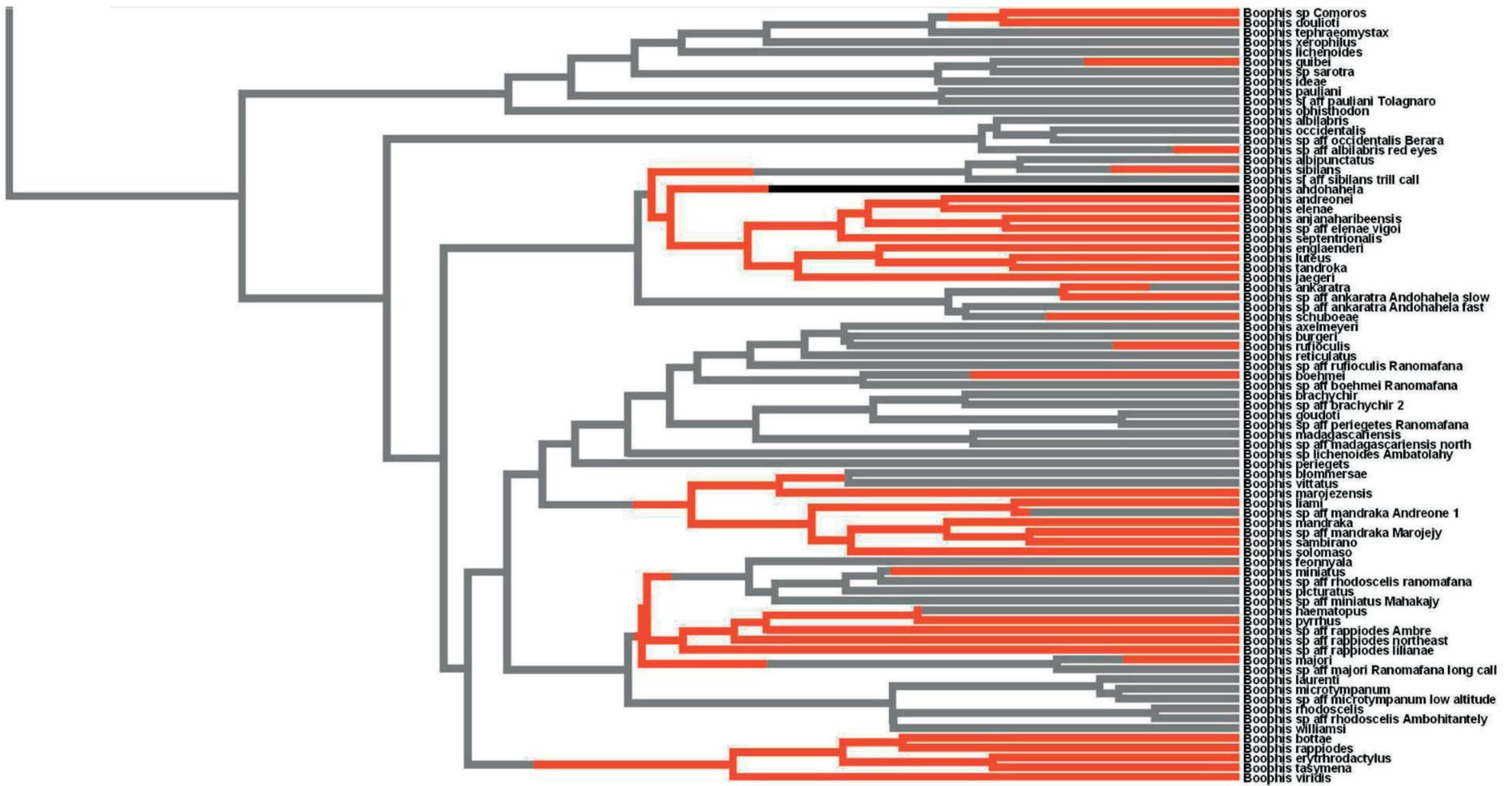Gephyromantis klemmeri
Gephyromantis corvus
Gephyromantis azzurae Andreone Isalo Andrianamero
Gephyromantis sp aff corvus Bemaraha
Gephyromantis pseudoasper
Gephyromantis cornutus
Gephyromantis schenki
Gephyromantis redimitus
Gephyromantis leucomaculatus
Gephyromantis sp aff leucomaculatus Marojejy
Gephyromantis salegy
Gephyromantis schilfy
Gephyromantis tandroka
Gephyromantis granulatus
Gephyromantis moseri
Gephyromantis zavona
Gephyromantis luteus
Gephyromantis sculpturatus
Gephyromantis plicifer
Gephyromantis rivicola
Gephyromantis silvanus
Gephyromantis webbi
Gephyromantis blanci
Gephyromantis enki
Gephyromantis runewsweeki
Gephyromantis sp aff blanci Andohahela
Gephyromantis boulengeri
Gephyromantis decaryi
Gephyromantis leucocephalus Ste Luce
Gephyromantis eiselti
Gephyromantis thelenae
Mantidactylus noralottae Andreone Isalo Andrianamero
Mantidactylus sp aff betsileanus slow calls
Mantidactylus sp aff betsileanus Tolagnaro
Mantidactylus sp aff curtus Andohahela short snout
Mantidactylus betsileanus
Mantidactylus sp aff betsileanus Andranofotsy
Mantidactylus sp aff betsileanus Nosy Borana
Mantidactylus sp aff betsileanus Toamasina
Mantidactylus bellyi
Mantidactylus ulcerosus
Mantidactylus sp aff biporus Tsaratanana camp1
Mantidactylus sp aff biporus Tsaratanana camp0
Mantidactylus alutus
Mantidactylus biporus
Mantidactylus sp aff biporus Ambohitantely
Mantidactylus sp aff biporus Andasibe
Mantidactylus sp aff biporus Andranofotsy
Mantidactylus sp aff biporus Ranomafana
Mantidactylus pauliani
Mantidactylus bourgati
Mantidactylus sp aff curtus Antoetra
Mantidactylus curtus Ankaratra
Mantidactylus sp aff curtus Amponitantely
Mantidactylus sp aff pauliani Itremo
Mantidactylus madecassus
Mantidactylus sp aff ulcerosus Isalo
Mantidactylus tricinctus Manatahtely
Mantidactylus tricinctus Manompo
Mantidactylus sp aff tricinctus parvus
Mantidactylus aerumnalis
Mantidactylus albofrenatus
Mantidactylus charlotteae
Mantidactylus brevipalmatus
Mantidactylus delormei
Mantidactylus opiparis
Mantidactylus melanopleura
Mantidactylus zipperi
Mantidactylus sp aff charlotteae Ranomafana
Mantidactylus majori
Mantidactylus ambreensis
Mantidactylus femoralis
Mantidactylus mocquardi Andasibe
Mantidactylus sp aff mocquardi Ambatolahy
Mantidactylus sp aff femoralis Ambohitsara
Mantidactylus sp aff mocquardi Tsaratanana
Mantidactylus sp aff mocquardi Marojejy
Mantidactylus sp aff femoralis Tsaratanana
Mantidactylus sp aff majori Andapa
Mantidactylus zolitschka
Mantidactylus sp aff femoralis Ambre
Mantidactylus argenteus
Mantidactylus sp aff lugubris Marojejy
Mantidactylus lugubris Andasibe
Mantidactylus cowani
Mantidactylus sp aff cowani small
Mantidactylus sp aff lugubris south
Mantidactylus guttulatus east
Mantidactylus sp aff grandidieri north
Mantidactylus guttulatus north
Tsingymantis antitra

Boophis sp Comoros
Boophis doulioti
Boophis tephraeomystax
Boophis xerophilus
Boophis lichenoides
Boophis guibei
Boophis sp sarotra
Boophis ideae
Boophis pauliani
Boophis sf aff pauliani Tolagnaro
Boophis obtusirostrodon
Boophis albilabris
Boophis occidentalis
Boophis sp aff occidentalis Berara
Boophis sp aff albilabris red eyes
Boophis albipunctatus
Boophis sibilans
Boophis sf aff sibilans trill call
Boophis andohahela
Boophis andreonei
Boophis elenae
Boophis anjanaharibeensis
Boophis sp aff elenae vigoi
Boophis septentrionalis
Boophis englaenderi
Boophis luteus
Boophis tandroka
Boophis jaegeri
Boophis ankaratra
Boophis sp aff ankaratra Andohahela slow
Boophis sp aff ankaratra Andohahela fast
Boophis schuboeae
Boophis axelmeyeri
Boophis burgeri
Boophis rufioculis
Boophis reticulatus
Boophis sp aff rufioculis Ranomafana
Boophis boehmei
Boophis sp aff boehmei Ranomafana
Boophis brachychir
Boophis sp aff brachychir 2
Boophis sp aff periegetes Ranomafana
Boophis goudoti
Boophis sp aff madagascariensis north
Boophis madagascariensis
Boophis sp lichenoides Ambatolahy
Boophis periegets
Boophis blommersae
Boophis vittatus
Boophis marojezensis
Boophis liami
Boophis sp aff mandraka Andreone 1
Boophis mandraka
Boophis sp aff mandraka Marojejy
Boophis sambirano
Boophis solomaso
Boophis feonnyala
Boophis miniatus
Boophis sp aff rhodoscelis ranomafana
Boophis picturatus
Boophis sp aff miniatus Mahakajy
Boophis haematopus
Boophis pyrrhus
Boophis sp aff rappiodes Ambre
Boophis sp aff rappiodes northeast
Boophis sp aff rappiodes lilianae
Boophis majori
Boophis sp aff majori Ranomafana long call
Boophis laurenti
Boophis microtympanum
Boophis sp aff microtympanum low altitude
Boophis rhodoscelis
Boophis sp aff rhodoscelis Ambohitantely
Boophis williamsi
Boophis bottae
Boophis rappiodes
Boophis erythrodactylus
Boophis tasymena
Boophis viridis
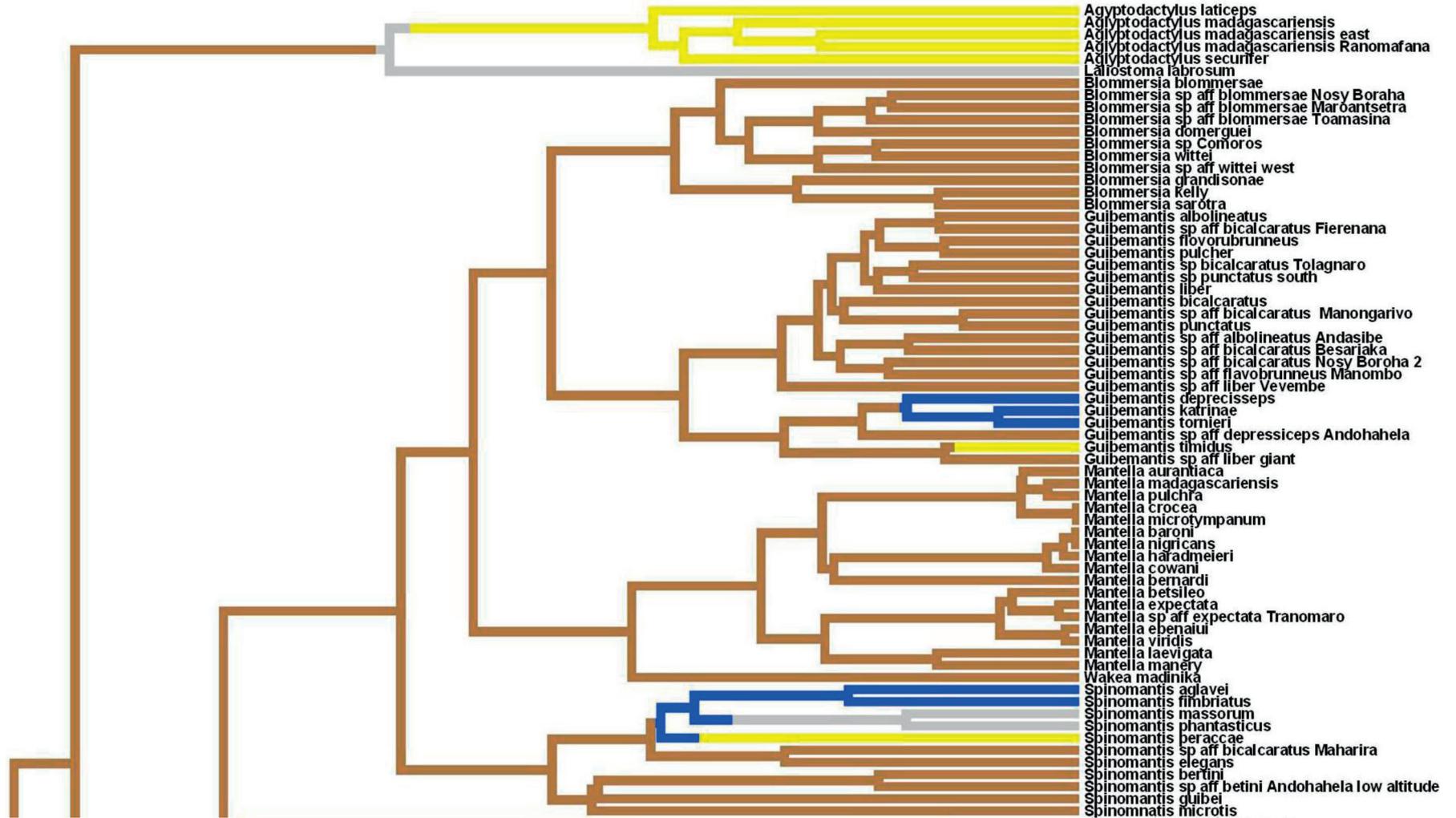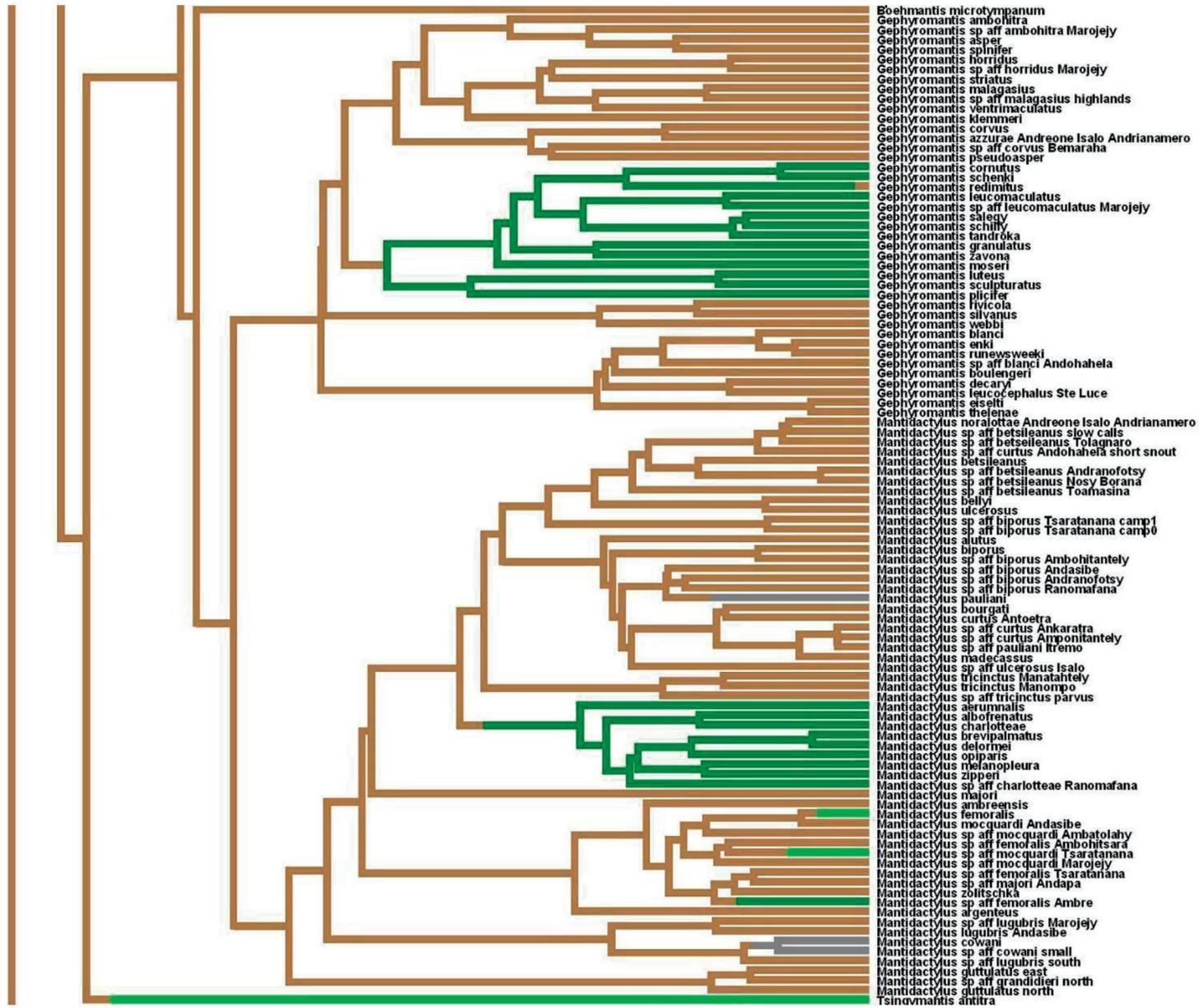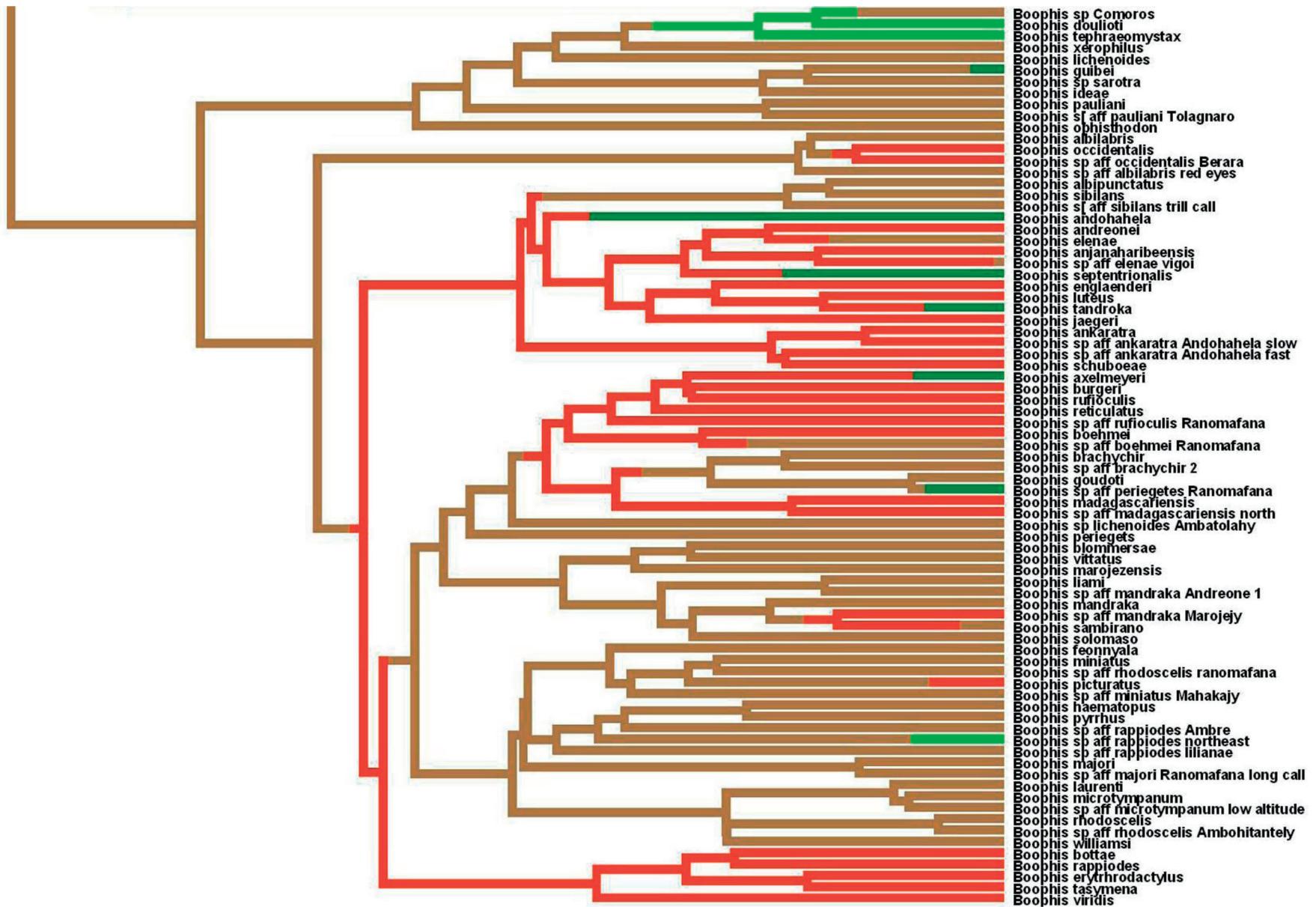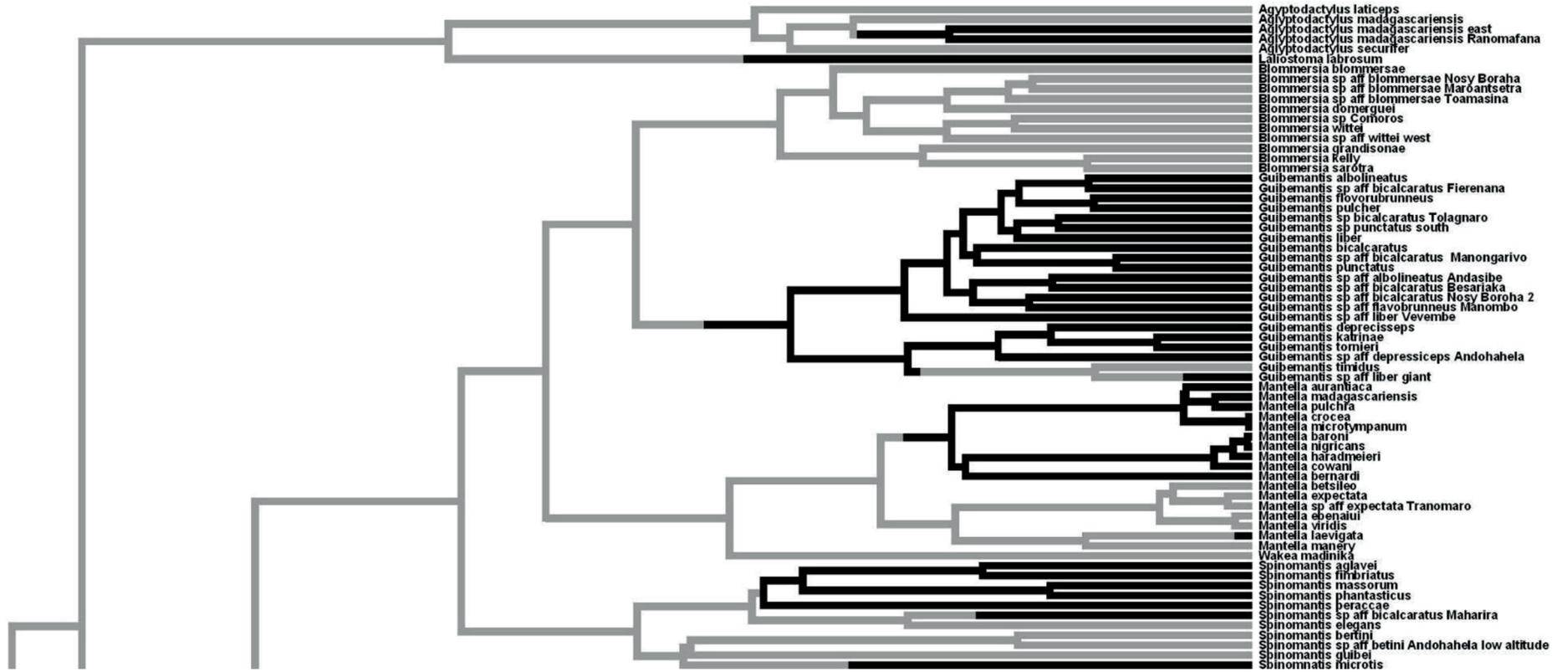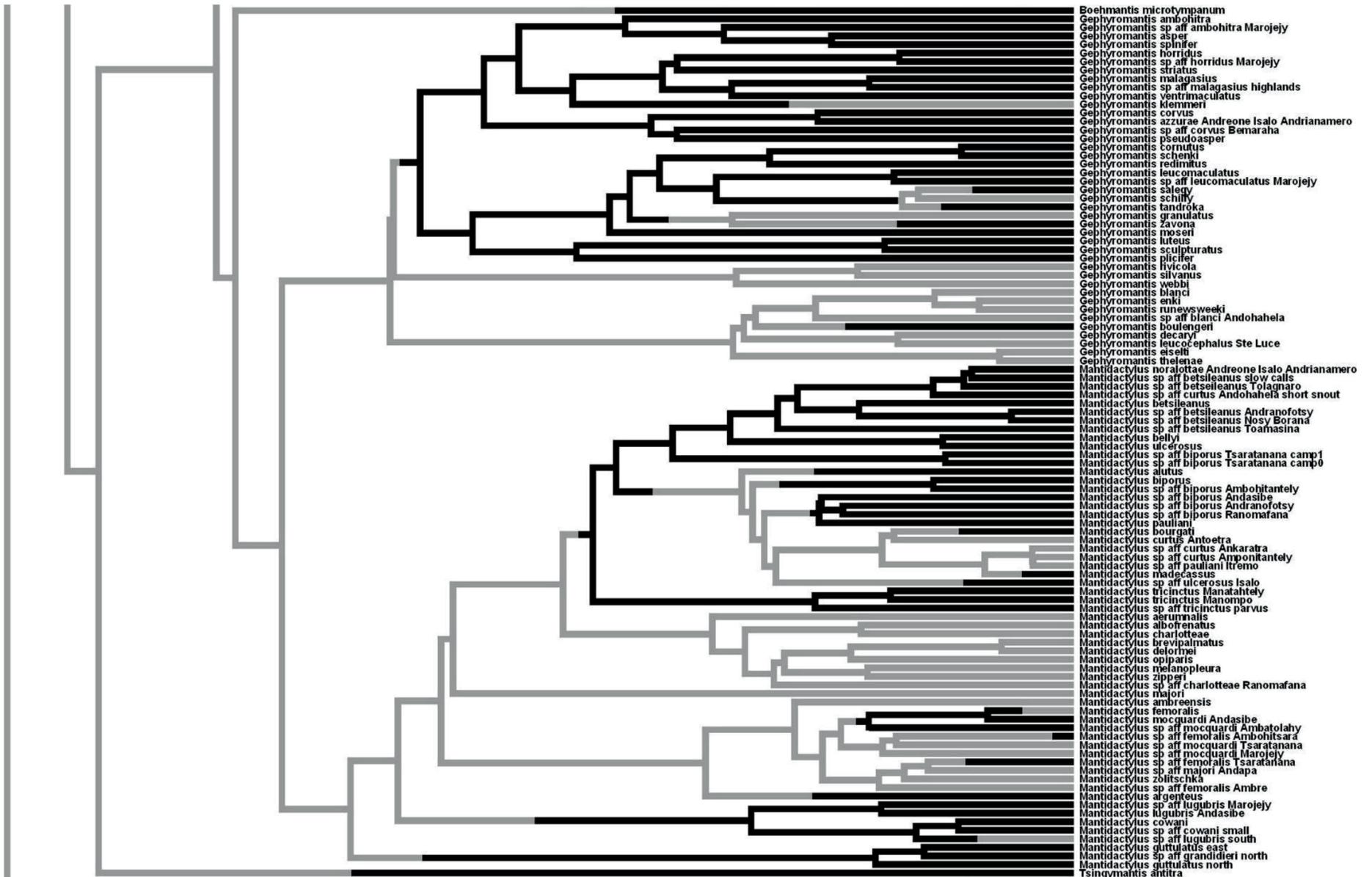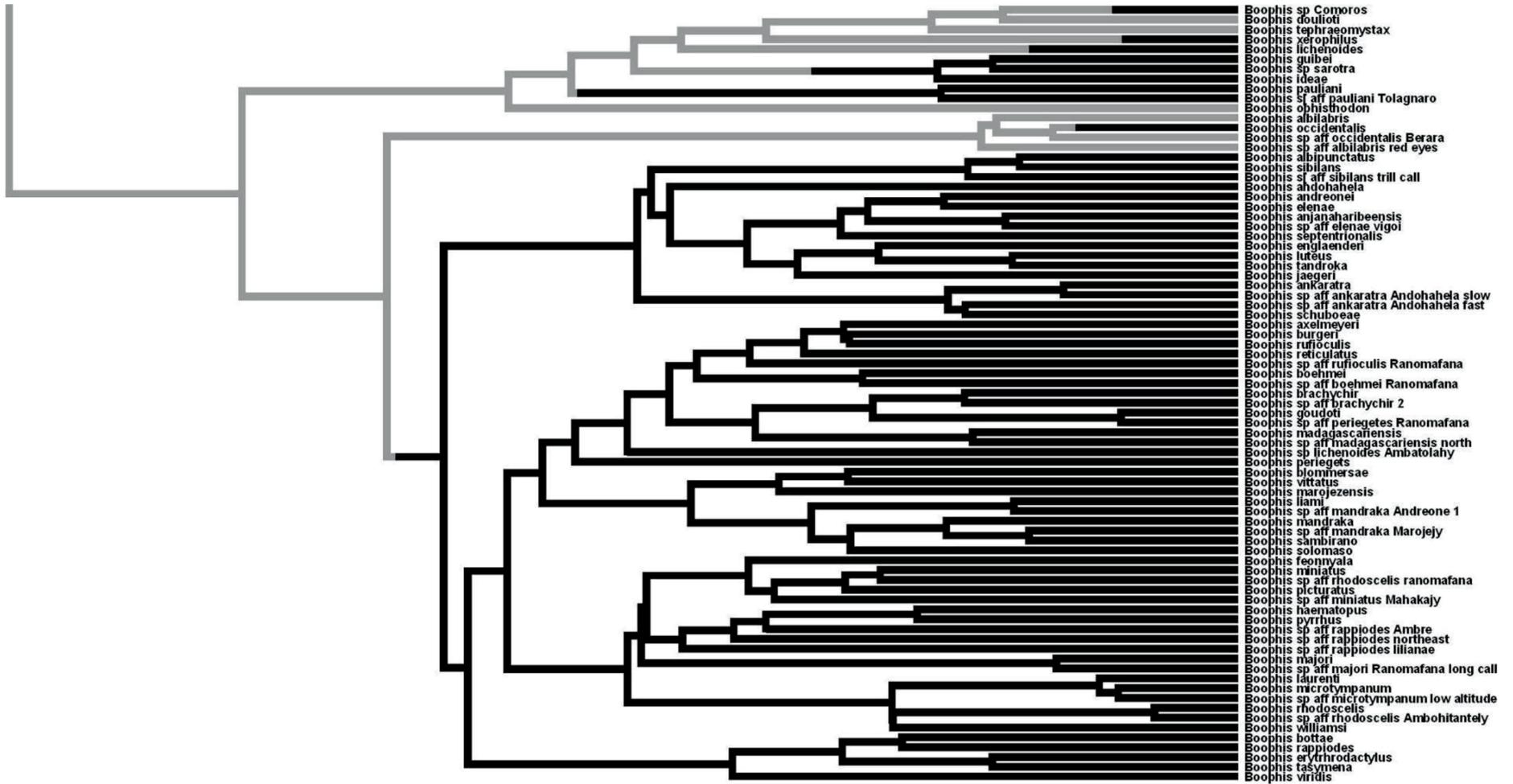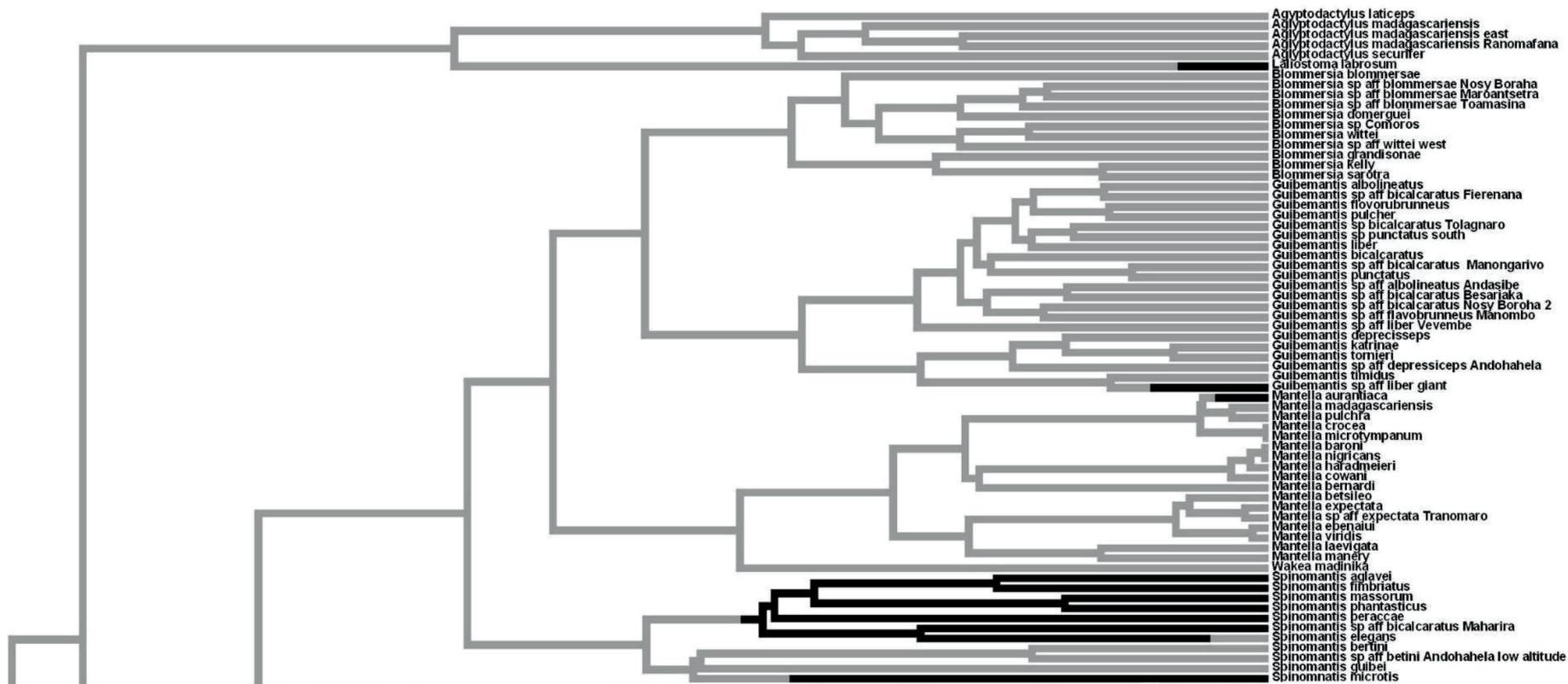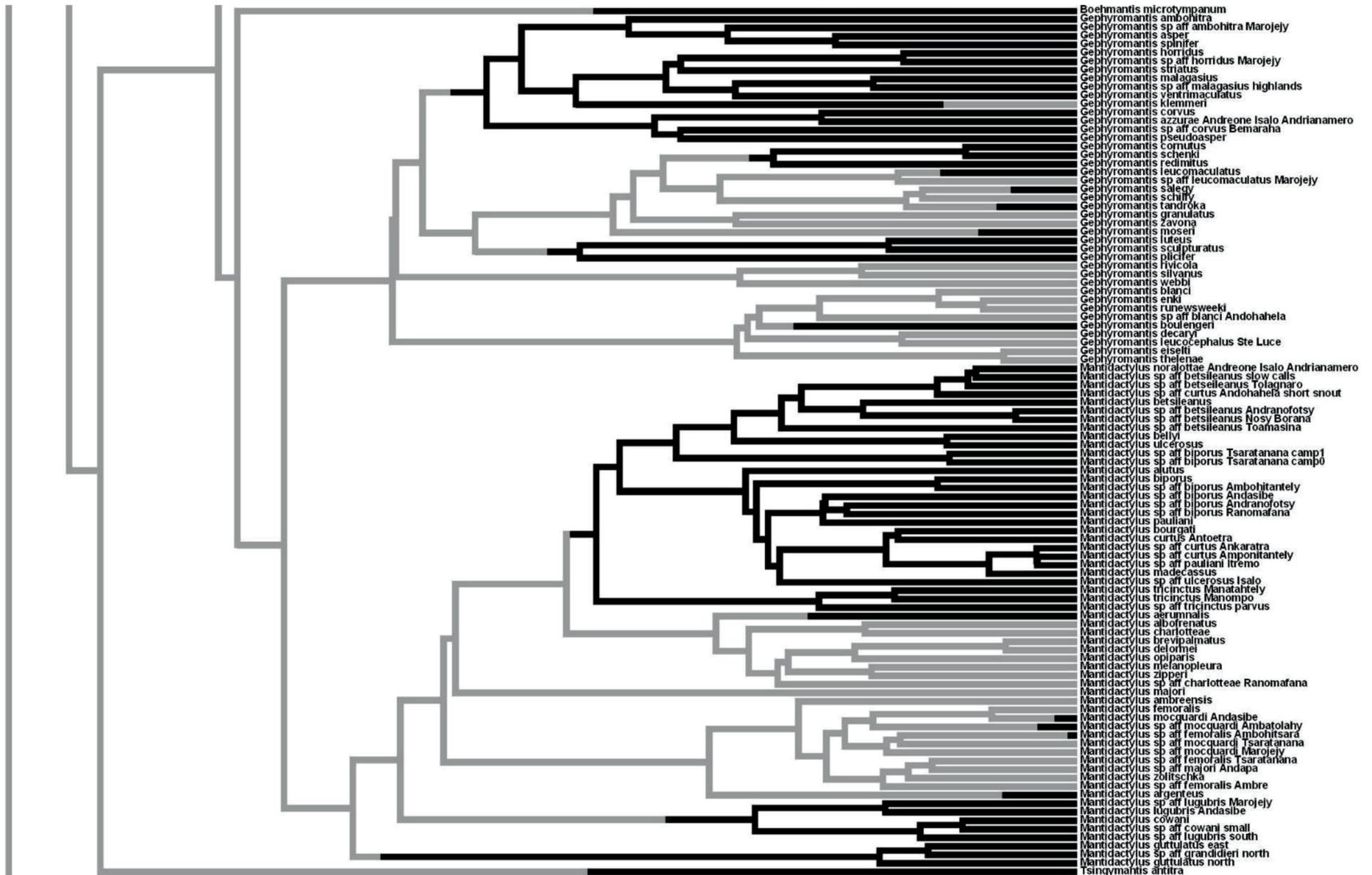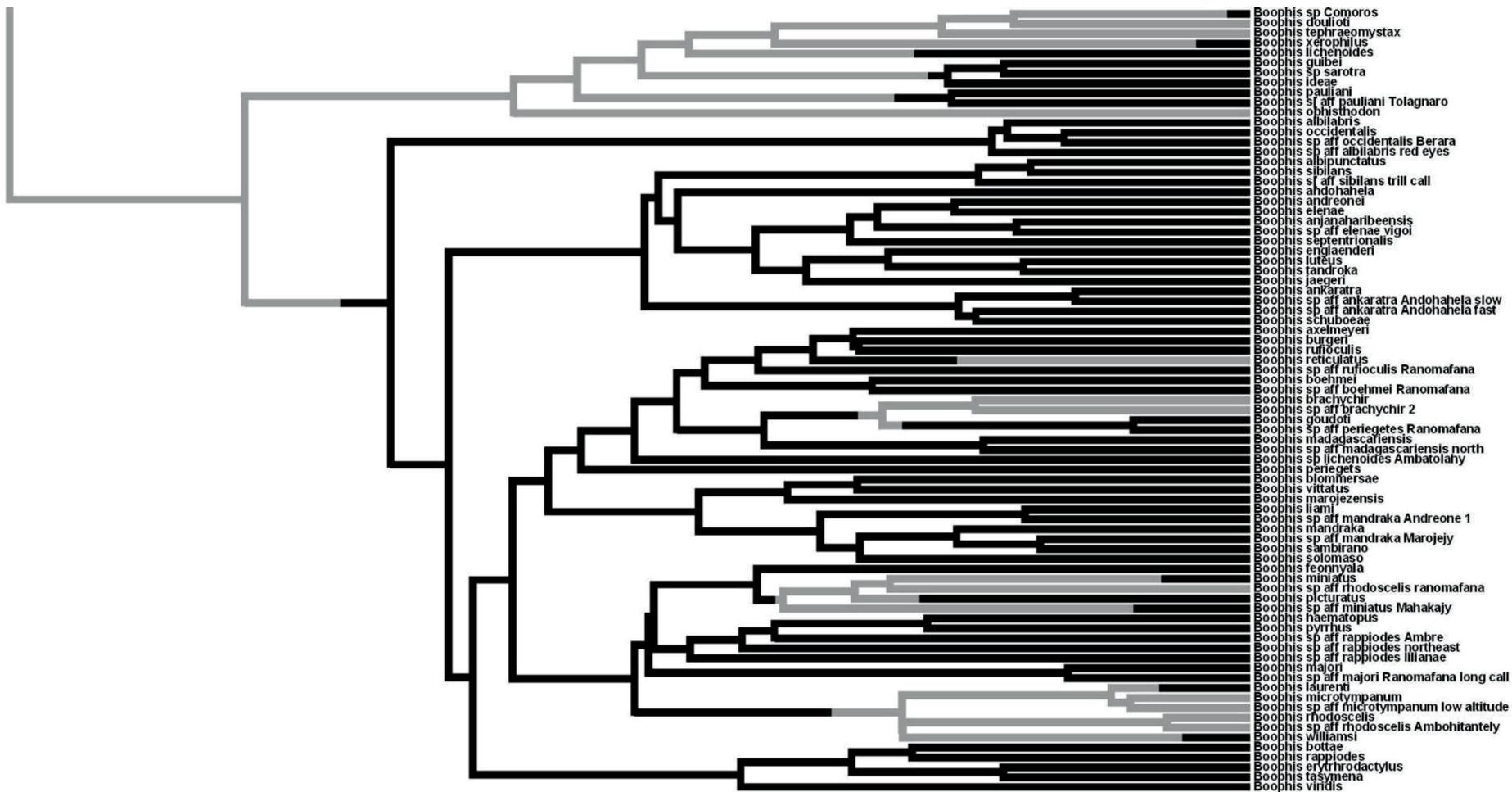
Supplementary Figure S8 (next 3 pages). One character history reconstructed through stochastic character mapping of function of body colouration in mantellid frogs (as in Figure 1 of main paper but including taxon names as in second column of Table S1).

Boophis sp Comoros
Boophis doulioti
Boophis tephraeomystax
Boophis xerophilus
Boophis lichenoides
Boophis guibei
Boophis sp sarotra
Boophis ideae
Boophis pauliani
Boophis sp aff pauliani Tolagnaro
Boophis ophisthodon
Boophis albilabris
Boophis occidentalis
Boophis sp aff occidentalis Berara
Boophis sp aff albilabris red eyes
Boophis albipunctatus
Boophis sibilans
Boophis sp aff sibilans trill call
Boophis andohahela
Boophis andreonei
Boophis elenae
Boophis anjanaharibeensis
Boophis sp aff elenae vigoi
Boophis septentrionalis
Boophis englaenderi
Boophis luteus
Boophis tandroka
Boophis jaegeri
Boophis ankaratra
Boophis sp aff ankaratra Andohahela slow
Boophis sp aff ankaratra Andohahela fast
Boophis schuboeae
Boophis axelmeyeri
Boophis burgeri
Boophis rufioculis
Boophis reticulatus
Boophis sp aff rufioculis Ranomafana
Boophis boehmei
Boophis sp aff boehmei Ranomafana
Boophis brachychir
Boophis sp aff brachychir 2
Boophis goudoti
Boophis sp aff periegetes Ranomafana
Boophis madagascariensis
Boophis sp aff madagascariensis north
Boophis sp lichenoides Ambatolahy
Boophis periegets
Boophis blommersae
Boophis vittatus
Boophis marojezensis
Boophis liami
Boophis sp aff mandraka Andreone 1
Boophis mandraka
Boophis sp aff mandraka Marojejy
Boophis sambirano
Boophis solomaso
Boophis feonnyala
Boophis miniatus
Boophis sp aff rhodoscelis ranomafana
Boophis picturatus
Boophis sp aff miniatus Mahakajy
Boophis haematopus
Boophis pyrrhus
Boophis sp aff rappiodes Ambre
Boophis sp aff rappiodes northeast
Boophis sp aff rappiodes lilianae
Boophis majori
Boophis sp aff majori Ranomafana long call
Boophis laurenti
Boophis microtympanum
Boophis sp aff microtympanum low altitude
Boophis rhodoscelis
Boophis sp aff rhodoscelis Ambohitantely
Boophis williamsi
Boophis bottae
Boophis rappiodes
Boophis erythrodactylus
Boophis tasymena
Boophis viridis