Molecular phylogenetics and Grinnellian niche conservatism within the genus *Brachycephalus* (Anura: Brachycephalidade)

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Abstract

Brachycephalus is a miniaturized toadlets genus endemic from the Brazilian Atlantic Forest (BAF). Almost half of its currently known species have been described in the last five years and are microendemic to mountaintops. Despite the growing taxonomic knowledge about the genus, few studies focused on the phylogenetic relationships among species and the conditions of the ecological niche envelope which they inhabit. This study aimed on the reconstruction of phylogenetic hypothesis from multilocus data (three mitochondrial and four nuclear loci), providing the most comprehensive phylogenetic reconstruction to date. It allows the recognition of the main evolutionary lineages within the group. Additionally it focused on the reconstruction of the ecological envelope and Grinnellian niche requirements for the species and lineages, ascertaining the degree of phylogenetic niche conservatism in the genus. Four main evolutionary lineages were reconstructed. Three of them restricted to the southern BAF and another one widely ranging from north Paraná to Espírito Santo. The southern lineages showed significant niche overlap between each other, but very little overlap with the northern lineage, evidencing two main Grinnellian niche usage profiles in the genus. Mantel tests evidenced the presence of low-moderate levels of niche conservatism within the genus. Species of the southern clades tend to use more thermally variable and drier environments with its precipitation evenly distributed throughout the year. Whereas the northern lineage tolerates less temperature seasonality and inhabits wetter and with summer concentrated rains habitats.

Key-words: Brazilian Atlantic Forest; diversification; evolution; Principal Component Analysis; Schoener's D; Warren's I; Mantel test; niche overlap; Ecological Niche Modeling; MaxEnt; molecular phylogeny; *BEAST2; MrBayes; Predicted Niche Occupancy Profile.

Introduction

The pumpkin toadlets and flea-toadlets genus *Brachycephalus* Fitzinger comprises 35 currently described species. They are characterized by miniaturized body size (snout-vent length usually smaller than 2.5 cm), being among the smallest known terrestrial vertebrates (Estrada & Hedges 1996; Pires et al. 2005). Their diminished size is supposed to be associated with a variety of biological modifications including reduction of fertility, direct development and some morphological aspects (Hanken and Wake, 1993; Pombal Jr., 1999; Yeh, 2002) such as the reduction of toes, fingers and phalangeal elements (Yeh 2002; Hedges et al. 2008; Clemente-Carvalho et al. 2011) and the lack of some cranial bones (e. g. columella and neopalatine) (Trueb & Alberch 1985; Hanken & Wake 1993; Yeh 2002). Most *Brachycephalus* species present conspicuous aposematic yellow-orange skin coloration associated with the secretion of tetrotoxins and other toxic substances (Sebben et al. 1986; Pires et al. 2002, 2005; Hanifin 2010; Arcanjo et al. 2015).

Regardless taxonomical debate currently being conducted (Condez et al 2017; Pie et al 2017), 15 of the 35 *Brachycephalus* species had been described during the last 5 years. Some studies reconstructed phylogenetic relationships (Clemente-Carvalho et al 2011; Padial et al 2014) prior to the recent burst of *Brachycephalus* species description and some studies reconstructed phylogenetic hypothesis (Firkowski et al 2016) of species restricted to the southern range of the genus. Nonetheless an up to date comprehensive phylogenetic relationship reconstruction comprising a relevant number of elements of *Brachycephalus* is still lacking (Gruimarães et al 2017).

Species in this genus occur from Espírito Santo and south Bahia to Santa Catarina and Paraná in its southern distribution, being endemic to the Brazilian Atlantic Forest (Pombal Jr. et al.

1998; Dayrell et al. 2006; Napoli et al. 2011; Ribeiro et al. 2015). However some species occur in very restricted mountain ranges, being known only from its type locality and being supposed to be microendemic from these regions (Ribeiro et al 2015; Bornschein et al 2016; Firkowski et al 2016). Despite the absence of phylogenetic hypothesis for the genus comprising all the species currently recognized, morphological information along with geographic distribution records for the species led some authors (Pie et al 2013; Ribeiro et al 2015; Bornschein et al 2016) to the proposal of three classical morphological groups, following the results from Clemente-Carvalho et al (2011). The Pernix group is the largest group in number of species and comprises *B. pernix* (the oldest element of the group), *B. olivaceus*, *B. mariaeterezae*, *B. verrucosus*, *B. fuscolineatus*, *B. albolineatus*, *B. boticario*, *B. pombali*, *B. ferruginus*, *B. quiririensis*, *B. auroguttatus*, *B. actaeus*, *B. izecksohni*, *B. curupira*, *B. brunneus*, *B. leopardus*, *B. tridactylus* and the three unidentified species *B.* sp.4 and *B.* sp.5 (Bornschein et al 2016). The Ephippium group comprises the species *B. ephippium*, *B. vertebralis*, *B. pitanga*, *B. toby*, *B. nodoterga*, *B. alipioi* and *B. garbeanus*. The Didactylus group is the most controversial group and has not been reconstructed as monophyletic in the studies of Clemente-Carvalho et al (2011) and Padial et al (2014). It comprises *B. didactylus, B. sulfuratus, B. hermogenesi* and *B.* sp.1 (Bornschein et al 2016) and widely varies in geographic distribution (from 15°S in Bahia to 26ºS in Santa Catarina).

Ecological Niche Models with suitability probabilities for the different groups reconstructed areas of high occurrence probabilities aiming future surveys in search for new species and populations (Pie et al 2013). However these studies were conducted prior to the recent species description boom that took place in the last five years. Besides that, Pie et al (2013) did not aimed specifically in the reconstruction of the bioclimatic conditions underlying the occurrence of the species and groups and did not aimed the overlap and phylogenetic conservation of environmental niche (Grinnellian niche) between *Brachycephalus* species and its lineages.

The Brazilian Atlantic Forest (BAF) is one of the most diverse ecosystems in the world (Galindo-Leal & Câmara, 2005). Despite its huge biodiversity it is one of the most severely impacted ecosystems in the world, granting it the status of biodiversity hotspot (Myers et al; 2000. Garlindo-Leal & Câmara, 2005). Its rich biota is considered to comprise between 1 and 8% of the biological diversity in the world (Silva & Casteleti, 2003). This huge amount of species diversity may be explained by its latitudinal and longitudinal variation, ranging from 1º to 30º south and from 35º to 60º west. Along with its vastness there is its huge elevation range, extending from sea level to 2,700 m (Silva & Casteleti, 2003). All this variation grants the BAF with an immense variation of habitats, making an ideal setting of environmental conditions to the diversification of biological lineages. Nonetheless the BAF is severely threatened and quickly being devastated, undergoing an accentuated process of fragmentation and deforestation leading to the disappearing of species, populations and ecosystems (Garlindo-Leal & Câmara, 2005; Tabarelli et al., 2005; Ribeiro et al., 2009)). The comprehension of evolutionary patterns and processes driving the diversification of the BAF is capital to better protect it in a climate changing world (Moritz et al., 2000; Moritz, 2002; Turchetto-Zolet et al., 2013).

Some recent studies focused on the species delimitation and evolution of *Brachycephalus* genus in its southern distribution (Firkowski et al 2016) and provided a scenario of climatic evolution but did not explicitly tested niche conservation, position and overlap between species and lineages. Considering the recent description of a large number of species, the lack of information of some ecological aspects of *Brachycephalus* lineages and the importance of a more complete understanding of the BAF fauna, this study had three main goals: (i) to reconstruct a molecular phylogenetic relationship between *Brachycephalus* species recognizing its main evolutionary lineages and providing a phylogenetic hypothesis including most of its extant taxa; (ii) to ascertain the degree of phylogenetic Grinnellian niche conservatism between lineages and species of the genus; and (iii) the reconstruction of the predicted bioclimatic conditions profiles underlying the distribution of the species and lineages of *Brachycephalus* genus, providing crucial information to better understand and predict the evolution of the genus in a changing world.

Materials and Methods

Geographic and genetic data compilation and preparation

Data used in this study were compiled from publicly available information in the GenBank database. I looked for genetic loci that had information for several species, supporting the conduction of a molecular phylogenetic analysis. In total there were three mitochondrial (12S, 16S and cytb) and four nuclear loci (Bfibr, RAG-1, RPL3 and Tyr) available in GenBank. The most complete loci in terms of number of species was the mitochondrial 16S ribosomal subunit. Sequences were separately aligned using the ClustalW algorithm as implemented in MEGA7. Further visual inspection were conducted to ensure the quality of the alignments. This phylogenetic reconstruction took into account 29 of the 35 currently described species in the genus plus three non-indentified species (*Brachycephalus* sp.1, *B.* sp.4 and *B.* sp.5 *sensu* Bornschein et al 2016). This makes this effort to the phylogenetic history reconstruction of the genus, the most taxonomically comprising study to date.

Geographical occurrence data were compiled from the study of Bornschein et al (2016), which conducted a vast revision and compilation of record locations and geographical occurrences of the different species within the *Brachycephalus* genus, assigning each species to its purposed morphological group. Species described after Bornschein et al (2016) published their study, were incorporated to this study and its occurrence data were assessed from the description paper of each species. Data available in the GBIF database were also incorporated to the data set, being previously screened for errors and cleaned up. Eight different occurrence records were too discrepant from the rest of the distribution range for the species they represent and were closely investigated. Four for *Brachycephalus nodoterga* (catalogue numbers USNM 266187, 266188, 266189, 266190), which may have been misspelled in the GBIF data input have its coordinate assigned to 23°37'48"S 54°49'48"W, despite its locality is Salesópolis, near Estação Ecológica Boraceia. The other four discrepant occurrence records were assigned to the species *Brachycephalus ephippium* (catalogue identifier numbers MCZ:Herp:A-427, MCZ:Herp:A-98559, MCZ:Herp:A-98560 and UNICAMP:ZUEC-AMP:0000011478). Three of them were assigned to the coordinates 24°30'00"S 54°19'58"W, which are in the border with Paraguay, far from the actual species distribution range. As far as these records had no more detailed information about its collecting location, they had to be removed from the analysis. Another record for *B. ephippium* were assigned to the coordinates 22°39'36"S 50°24'35"W, but did not match with the locality description (Estação Ecológica de Itapetininga). For this reason the record was also removed from the analysis.

Phylogenetic relationship

The phylogenetic reconstruction for the *Brachycephalus* genus were conducted in a Bayesian inference framework as implemented in the *BEAST2 software (Bouckaert et al, 2014). The best substitution models for each loci were calculated in R using the *phangorn* package (Schliep, 2011). They resulted in GTR+G for the 12S locus, JC for the 16S, GTR+G+I for cytb, JC for Bfibr, HKY for RAG-1, JC for the RPL3 and K80 + G for the Tyr locus. They were used to perform five independent runs of a partitioned Yule multispecies coalescent model with a lognormal prior in *BEAST2 using 100 million generation chain and a pre-burnin of 100 thousand generations, computing every 5,000 generations. The log file generated in the analyses were combined with LogCombiner (Bouckaert et al, 2014) and investigated in Tracer 1.5 (Rambaut & Drummond, 2009) to ascertain the congruence of chains by an ESS value of 200 or greater to every attribute. TreeAnnotator 2.5.0 (Bouckaert et al, 2014) was used to search for the maximum clade credibility tree with 10% burnin. The resulting tree was visualized in FigTree 1.4.3 and the R package ggtree (Yu et al, 2017). As outgroup I used available sequences for the *Ischnocnema* genus, namely the species *I. parva* and *I. guentheri*.

To estimate the divergence times within the genus *Brachycephalus* a node calibrated phylogenetic analysis in MrBayes 3.2.6 (Ronquist et al, 2012)was performed. The splitting events of Brachycephalidae and Bufonidae was set to 70 to 60 mya and the splitting event of

Eleutherodactylidae and Brachycephalidae was set to 55 to 45 mya, according to Feng et al (2017). Sequences belonging to the family Dendrobatidae were used as outgroups. To perform this analysis only the mitochondrial genes were used (i.e. 12S, 16S and cytb). Dating was performed under a relaxed clock prior with GTR + Γ substitution rate. Four chains in two independent runs were performed for 5 million generations, sampling every 5000 generations with 25% for burnin.

Environmental data and Ecological Niche Modeling

To conduct the Ecological Niche Modeling I used 19 bioclimatic variables from the WorldClim 1.4 website (Hijmans et al., 2005) in a 2.5 arc-min resolution. After trimming the variables for the region of interest in this study, a correlation test was conducted with the *raster* package in R (Hijmans & Van Etten, 2014) aiming to avoid the bias of overestimation of highly correlated variables. Variables with a Pearson correlation value higher then 0.8 were excluded from the analysis. The remaining 10 variables (i.e. Bio1, Bio2, Bio3, Bio4, Bio7, Bio12, Bio13, Bio14, Bio15, Bio18) were used to perform the Ecological Niche Modeling and the extraction of environmental values as predictor variables for the model construction.

To build the Ecological Niche Models I used the software MaxEnt 3.4.1 (Phillips et al 2006), which is a machine-learning framework that builds models of predicted species occurrence from presence-only data. The models generated this way were then used to compute niche overlap metrics using the software ENMTools 1.4.4 (Warren et al, 2010) and predicted niche occupancy profiles. Only species with publicly available genetic information and which had more than three occurrence records were used in this per species analysis, because the Schoener's D and Warren's I metrics of niche overlap were later used to be compared with phylogenetic distances between species to assess phylogenetic niche conservatism (see section *Niche conservatism inference* bellow). After the results from the phylogenetic reconstruction, occurrence records were combined for each one of the subclades recovered by *BEAST2 and a second MaxEnt run were performed.

This step aimed to build ENMs for each one of the main lineages within *Brachycephalus* genus and assess its required climatic conditions and geographic extent.

With clades occurrences, the niche breadth and niche overlap metrics between them were analyzed in NicheAnalyst 3.0 (Qiao et al 2016). This software uses bioclimatic variables to perform a Principal Component Analysis, and uses the first three Principal Components to build a tridimensional environmental background cloud. The occurrence records are then accommodated in this ecological space and plotted as Minimum Volume Ellipsoids (MVE). The occurrence records for the clades were used to build these ellipsoids and to compute niche position, breadth and overlap, characterizing the clades in a Grinnellian ecological space.

Niche conservatism inference and niche occupancy profile

The environmental values for each non-duplicated occurrence point were extracted from the variable files using the *raster* package in R for all the species with any occurrence record. Each point generated a set of values for the bioclimatic variables, resulting in a matrix containing environmental data for the occurrence records for each species. This matrix was used to compute z-scores, aiming to standardize the data set previous to the performance of a Principal Component Analysis multivariate ordination. Afterwards the matrix was averaged per species, retrieving a z-score per variable per species. This matrix was used to perform a PCA based on the covariance matrix for the visualization of the mean values per species in a bidimensional environmental space.

The raw values extracted from the bioclimatic variables were used to the computation of a Mahalanobis distance matrix between species, using the *HDMD* package in R (McFerrin, 2013), to be compared with a patristic phylogenetic distance matrix drawn from the phylogenetic tree reconstructed in this study by means of the *adephylo* package in R (Jombart et al., 2008). Species which had environmental information but lacked the genetic data to be included in the phylogeny were excluded from this analysis once its phylogenetic positioning could not be infered (i.e *B. pulex*, *B. bufonoides*, *B. coloratus*, *B. crispus*, *B. darkside and B. margaritatus*). A Mantel test with

9,999 permutations was used to compare the Mahalanobis distance and the phylogenetic distance matrices. In a Mantel test, the null hypothesis is that there is no correlation between the compared distance matrices. So if the null hypothesis could be rejected ($p=<0.05$), it would mean that there is some correlation between the matrices. In this case, if there is a positive correlation between the distances, it means that as the phylogenetic distance between species increases, the environmental distance between them increases concomitantly, pointing to phylogenetic niche conservatism.

Additionally to the environmental distance, I compared via Mantel test the correlation between the phylogenetic distance and the niche overlap between species (both Schoener's D and Warren's I metrics). If the correlation between these matrices is statistically significant and negative, it means that as the phylogenetic distance increases, the amount of niche overlap between species decreases, meaning that there is some degree of phylogenetic niche conservatism between *Brachycephalus* species. This test was performed with the Schoener's D and Warren's I metrics obtained in the ENM step. All mantel tests were performed using the *ade4* package in R (Dray & Dufour, 2007).

In a further step, to combine the ENMs with the climatic layers and assess the conditions of each variable for each species the predicted niche occupancy profiles (PNO) were estimated for those species that had more then three occurrence records according to the methods proposed by Evans et al (2009). This method was implemented with *phyloclim* package (Heibl & Calenge, 2018) and uses the predictions from the ENM to extracted the environmental requirements to the bioclimatic variables, weighting by the suitability of each cell.

Lastly Niche Identity Tests (Warren et al, 2008) between the four main lineages were conducted to ascertain for the possibility of niche identity between different *Brachycephalus* subclades. This test generates a null distribution of niche overlap values between two species via randomization of pseudoreplicates of the occurrence records. If the overlaps between two species differ substantially from the values drawn from the pseudoreplicates, it means that there is significant differences between their niche conformation, rejecting the niche identity hypothesis.

This test was implemented using the ENMTools 1.4.4 software and was conducted for 100 pseudoreplicates (Warren et al, 2010).

Results

Phylogenetic relationship

Four distinct clades were reconstructed by *BEAST2 (Fig. 1). One containing *B. pernix*, which was named after this species. The sister groups to the Pernix clade is the Brunneus clade, containing *B. brunneus*. These two clades together constitute the Pernix morphologic group, evidencing the monophyletic origin of the group. As sister clade to these two clades is the Sulfuratus clade, which includes *B. sulfuratus* and the unidentified *B.* sp1. These two species are thought to belong to the Didactylus morphologic group, that was not reconstructed as monophyletic in this analysis. Lastly there is the Ephippium clade, which contains *B. ephippium*, the other species of the Ephippium morphologic group and the remaining species of the Didactylus group that were included in these phylogenetic reconstruction. This phylogenetic hypothesis reconstructed the Pernix group as monophyletic with two subclades within it (i.e. Pernix and Brunneus clades). It also reconstructs the Ephippium group as a paraphyletic group because of the exclusion of *B. hermogenesi* and *B. didactylus* from it, making the Didactylus group polyphyletic.

The node dated tree reconstructed by MrBayes (Fig. 2) recovered the splitting event between *Brachycephalus* and *Ischnocnema* approximately at 45 million years ago (between 52.5mya and 38mya). This analysis did not recovered the Sulfuratus clade, placing it within the Ephippium clade and positioning *B.* sp.1 in a polytomy with Ephippium clade and the lineage containing Pernix and Brunneus clades. The origin of this lineage seems to have happened at approximately 40 mya (between 49 mya and 31 mya) while the split between the two lineages comprised by the Pernix group occurred at 30 mya (between 40 mya and 20 mya).

Ecological Niche Modeling

MVE for the four main lineages within *Brachycephalus* showed relevant overlap between the Pernix, Brunneus and Sulfuratus clades. Brunneus lineage showed the smallest MVE (MVE formula = 0.470) among these three lineages, while Sulfuratus and Pernix clades presented similar niche breadth (MVE formula = 6.309 and 8.368 respectively). Nonetheless the Ephippium clade showed the wider MVE (MVE formula = 59.341) among the four lineages of *Brachycephalus*, showing a wide range of bioclimatic occupancy among its species (Fig. 3). The highest proportion of niche overlap was between Sulfuratus and Pernix clades (MVE overlap = 3.290041) followed by Ephippium and Pernix (MVE overlap = 2.245898).

MaxEnt prediction models for the lineages showed similar results, with significant overlap between predicted range for Pernix, Brunneus and Sulfuratus lineages. Suitability predictions attribute the Ephippium clade to a more northerly distributed lineage, while the other three lineages tend to occur in the southern region of the Brazilian Atlantic Forest (Fig. 3). The Schoener's D and Warren's I metrics for niche overlap between the lineages show that there is little overlap between the Ephippium clade and the other three lineages, while there is significant overlap between the three southern lineages and its species (Table 1 and Fig. 4).

Niche conservatism inference and niche occupancy profile

Multivariate ordination by PCA shows that there is some degree of clustering of the species in an environmental space, being in concordance with the MaxEnt and NicheAnalyst results. The PC1 alone accounts for more than 91% of the data variation, with predominance of Temperature Seasonality (Bio4), Annual Precipitation (Bio12) and Precipitation of the Warmest Quarter (Bio18) in its composition. Ephippium clade shows little overlap with other clades (Fig. 5). Species assigned to that clade tend to be less tolerant in relation to thermal variation during the year and to inhabit more humid environments. Species which were not included in the phylogenetic hypothesis in this study, but which had geographic information are showed as "Unknown clade relationship". Nonetheless the proximity of certain species assigned to the Ephippium group to the Ephippium clade (i.e. *B. darkside*, *B. guarani*, *B. crispus*, *B. vertebralis* and *B. bufonoides*) may be suggestive of their belonging to this clade. However further analysis may be conducted to ascertain this possibility. The most distant point in the PCAs is *B. pulex*, whose environmental niche requirements may point to a distinct evolutionary lineage not accounted by this study by lack of genetic information. Pernix, Brunneus and Sulfuratus clades are all clustered together in the left-hand portion of the graph. These clades tend to be more tolerant to thermal variation along the year and tend to inhabit drier habitats than Ephippium clade.

Results from the different Mantel tests are very concordant between each other (Fig. 6). The correlation between the environmental Mahalanobis distance and the phylogenetic distance between species was positive and with low-moderate intensity ($r = 0.40$, $p = 0.0004$). It evidences some degree of correlation between the phylogenetic distance and the environmental distance, despite not very strong. Phylogenetic distances and niche overlap tend to be negatively correlated. Both tests using Schoener's D and Warren's I metrics showed a significant negative correlation with phylogenetic distance ($r = -0.43$ with $p = 0.026$ for Schoener's D test and $r = -0.046$ with $p = 0.0042$ for Warren's I test), evidencing that closely related species tend to share more environmental requirements (Fig. 4).

All four *Brachycephalus* lineages showed relatively high annual precipitation indexes (Bio12), ranging from 1696.98 mm for the Sulfuratus clade to 1796.64 mm to Brunneus clade (Table 1). This variation in variable Bio12 was one of the most important variables to explain the variation in climatic conditions of the *Brachycephalus* species, along with precipitation of warmest quarter (Bio18) and temperature seasonality (Bio4). This latter variable means the coefficient of temperature variation and ranged from 212.05% in the Ephippium clade to 291.96% in the Sulfuratus clade. On average the Ephippium clade tends to occupy more thermally stable and wet environments, with most precipitation concentrated in the warmest quarter of the year (Table 2 and Fig. 1). However the species of this lineage present a wide range of PNO profiles. For instance *B. alipioi* presents a low acceptance to temperature variation (Bio4 = 182.52%) and lower annual precipitation indexes (Bio12 = 1369.22 mm and Bio18 = 419.42 mm), while *B. hermogenesi* accepts higher degrees of temperature seasonality (Bio4 = 230.65) and needs wetter environmental conditions (Bio12 = 2466.91 and Bio18 = 912.30).

Niche Identity Test showed similar overlap values between the pseudoreplicates and the observed overlap values between the three southern lineages (Table 1), hence the niche identity hypothesis could not be reject for these three subclades. However the overlap between Ephippium clade and the other three lineages was significantly higher in the niche identity test in comparison to the observed overlap (Fig. 7), amounting to the rejection of the hypothesis of niche identity between these clades.

Discussion

There are four main lineages within the genus *Brachycephalus*. Three of them are nested within a larger southerly occurring clade (Pernix, Brunneus and Sulfuratus) and another one (Ephippium clade) occurring in a northern region. Classical morphological groups were partially reconstructed by this phylogenetic hypothesis. The Pernix group matches precisely with the clades Brunneus and Pernix, presenting a monophyletic origin, insofar the paraphyletic Ephippium group lies within the Ephippium clade, but does not correspond entirely to it. The Didactylus group is reconstructed as polyphyletic with its members belonging to the Ephippium clade (*B. hermogenesi* and *B. didactylus*) and to the Sulfuratus clade (*B. sulfuratus* and *B.* sp.1), sister-group to the clade formed by Brunneus and Pernix clades. These results are highly concordant with those presented in Clemente-Carvalho et al (2011) and Padial et al (2014), showing a southern diverse lineage occurring in Paraná and a northern lineage with more extensive range, occurring from north Paraná to Espírito Santo.

The Grinnellian ecological niche overlap pattern between clades suggests that the Ephippium clade has dissimilar environmental requirements in relation to the other three *Brachycephalus* lineages. There is a substantial amount of niche overlap between Pernix, Brunneus and Sulfuratus clades, reflecting their common origin. Whilst there is very little overlap between these clades and the Ephippium lineage, which is the most environmentally diversified clade, presenting the largest MVE in the environmental space (Fig. 3) and the wider occurrences and 95% CI interval in the PCA (Fig. 5). The most influential bioclimatic variables to the ENMs were temperature seasonality (Bio4), annual precipitation (Bio12) and precipitation of the warmest quarter (Bio18). *Brachycephalus* species varied in terms of their tolerance to high temperature seasonality and low precipitation indexes (left-hand side of Fig. 5) to low tolerance to temperature seasonality and high precipitation indexes (right-hand side of Fig. 5). The variation in the multivariate ordination grouped species of the Ephippium clade at the right-hand side, while species belonging to the other three clades were grouped at the left-hand side, once again reflecting their common ancestrality. Although some species figured in the PCA but wasn't included in the phylogenetic reconstruction, their probable relationship could be suggested by its environmental conditions usage (i. e. *B. darkside*, *B. crispus*, *B. bufonoides* and *B. guarani*). *B. coloratus* has an environmental positioning shared by different clades, making it very hard to infer its relationship from its environmental configuration. The most discrepant species in terms of used environmental conditions is *B. pulex*, which occurs in south Bahia, suggesting a possible discrepant lineage from the other *Brachycephalus* species. Because this species could not be included in the phylogenetic reconstruction, very little further considerations can be done about it from the results here presented.

Mantel tests considering the phylogenetic distances between species against environmental distances and niche overlap metrics suggest that there is a low-moderate degree of niche conservatism between the lineages of the genus. Niche identity tests show that the amount of niche overlap between the three southern lineages does not differ significantly from the observed when the occurrence records are randomized. For this reason the null hypothesis of niche identity could not be reject between these clades. However these clades showed significant more overlap with Ephippium clade in the pseudoreplicates randomization, amounting to the rejection of the null hypothesis, meaning that there is identity of niche for the Ephippium clade in comparison with the three other *Brachycephalus* lineages (Fig. 7 and Table 1).

Species belonging to the Ephippium lineage tend to use more wet and thermally stable environments while species belonging to the other lineages tend to use drier and thermally variable habitats (Table 2 and Fig. 1). This ecological conditions may have led to the diversification of the main lineages within the genus, with southern species occupying drier and more thermally unstable niches and northern species occupying wetter and more thermally stable habitats. According to the evolutionary scenario proposed by Firkowski et al (2016), a widely distributed ancestral followed its climatic conditions upward into mountaintops with posterior speciation events. These events may have gradually led to the accumulation of small amounts of variation between the southern and northern lineages, resulting in slightly different climatic envelopes for its descendants. Yet altitudinal migration could have provided a buffer against climatic instability during certain periods of BAF history, this seems to be less effective in southern BAF in comparison to other regions (Carnaval and Moritz, 2008; Carnaval et al., 2014).

Conclusions

Classical morphological groups are, in general, monophyletic and well supported by molecular data. However there are more lineages within the genus than the proposed groups. The four main lineages of the genus are nested within two main larger lineages, one occurring in the southern region and the other occurring in the northern region. These lineages are well supported by Grinnellian niche conditions with northern lineages submitted to more humid and thermally stable environments and southern lineages to drier and thermally variable habitats. Despite with low-moderate intensity, niche conservatism was detected to these lineages. Therefore the environmental alterations caused by climate change may impact *Brachycephalus* species in the BAF, leading to its extinctions and disappearance. Further studies considering the historical evolution of the genus within an ecological and environmental framework could allude the diversification drivers and conditions of this genus endemic to one of the most diverse and endangered ecosystems of the world.

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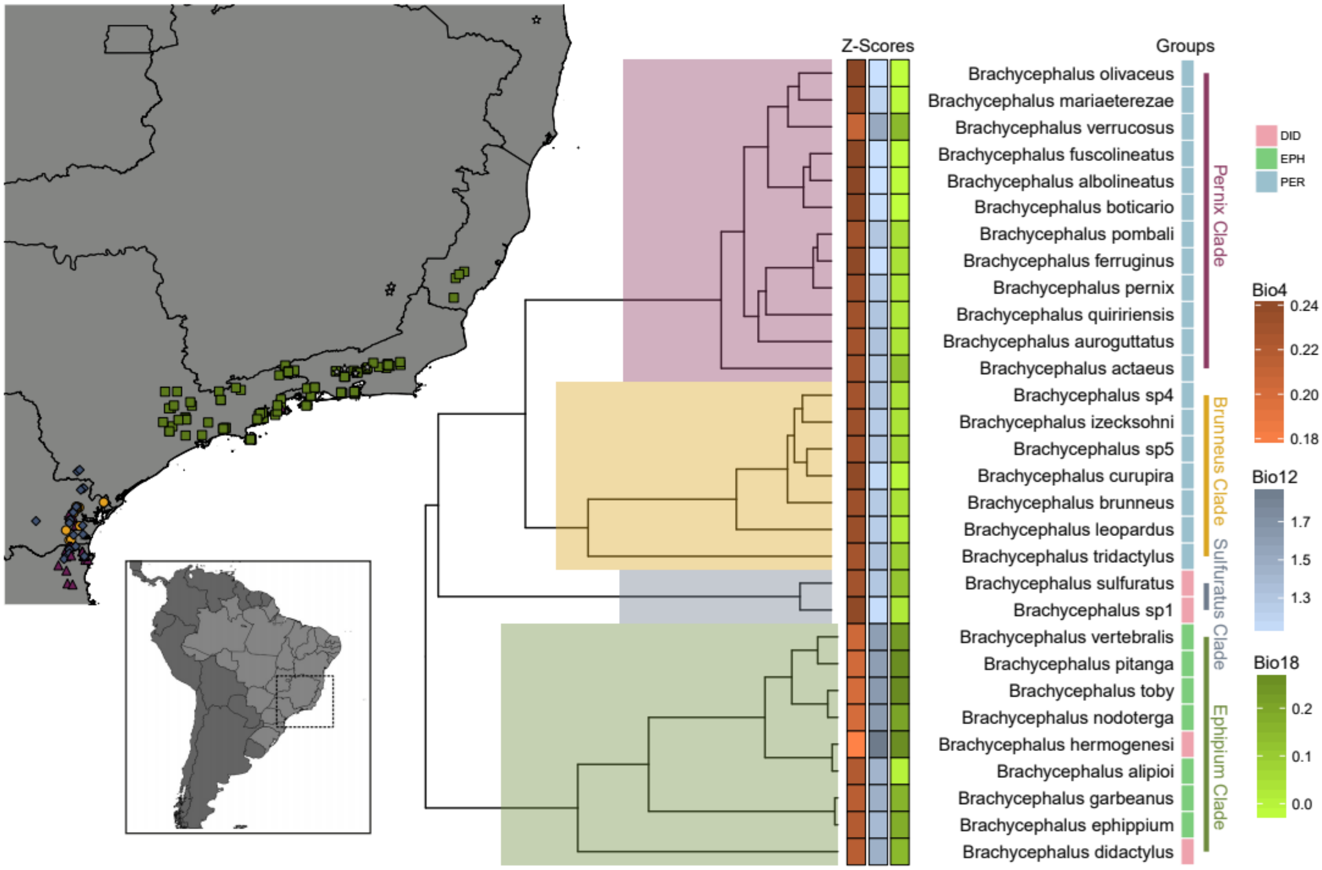

Figure 1. Phylogenetic relationship between *Brachycephalus* species as reconstructed by the partitioned analysis in *BEAST2. Boxes at the right-hand side of species names are the purposed morphological groups to which they are assigned to (DID: Didactylus group; EPH: Ephippium group; and PER: Pernix group). Boxes at the left-hand side of species names are the z-score values for the three most influential bioclimatic variables (Bio4, Bio12 and Bio18). The map shows the occurrence records of each one of the main *Brachycephalus* lineages. In dark green in the Ephippium clade; in dark blue is the Sulfuratus clade; in yellow is the Brunneus clade; and in purple is the Pernix clade, following colors in the cladogram.

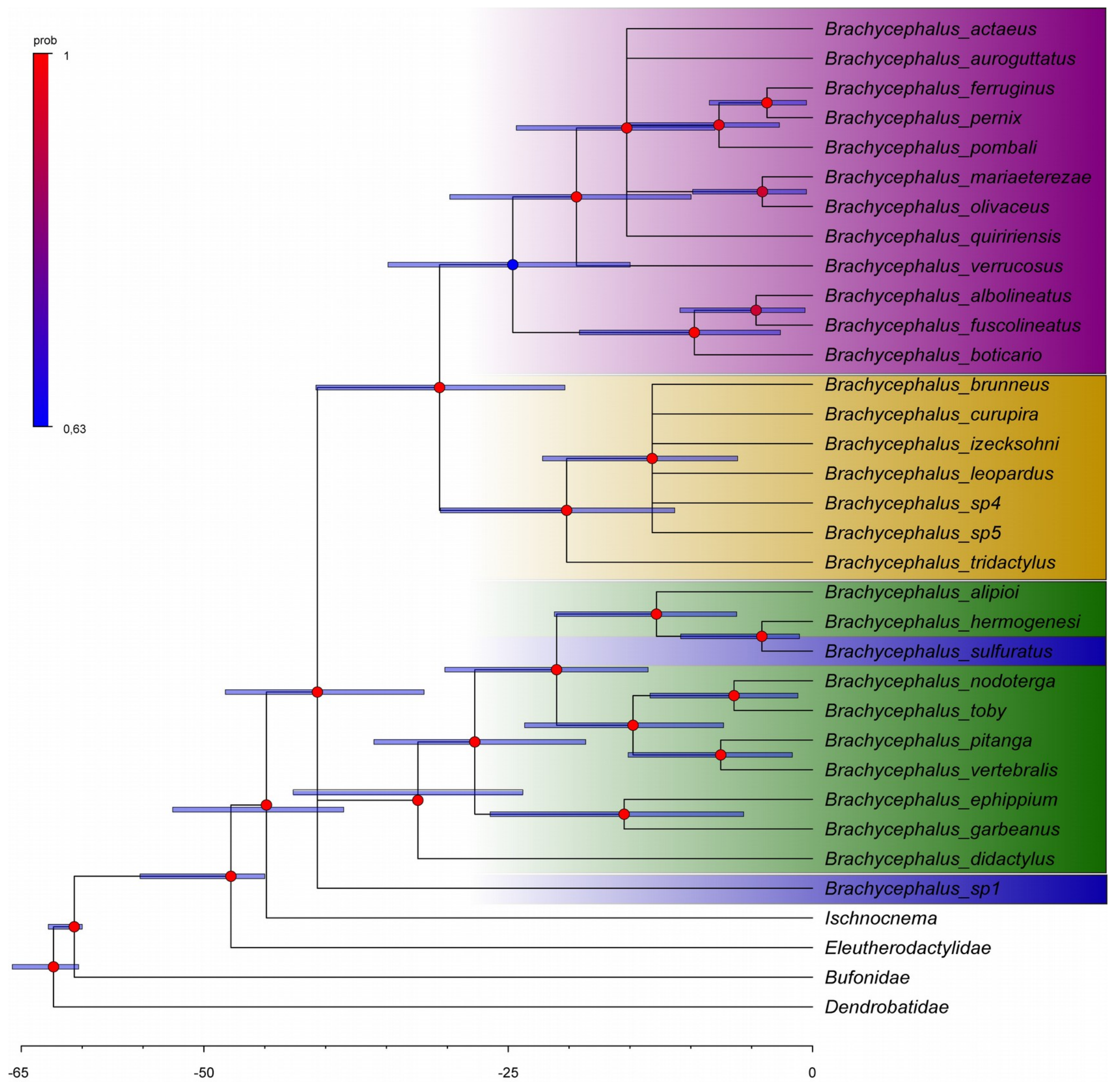

Figure 2. Molecular node dating according to the MrBayes analysis for mitochondrial data. The origin of the *Brachycephalus* genus was estimated to have occurred approximately at 45 mya, while the polytomous split between the Ephippium clade, *B.* sp1 and Pernix and Brunneus clades occurred at 40 mya. The split between the Pernix and Brunneus clade occurred at 30 mya.

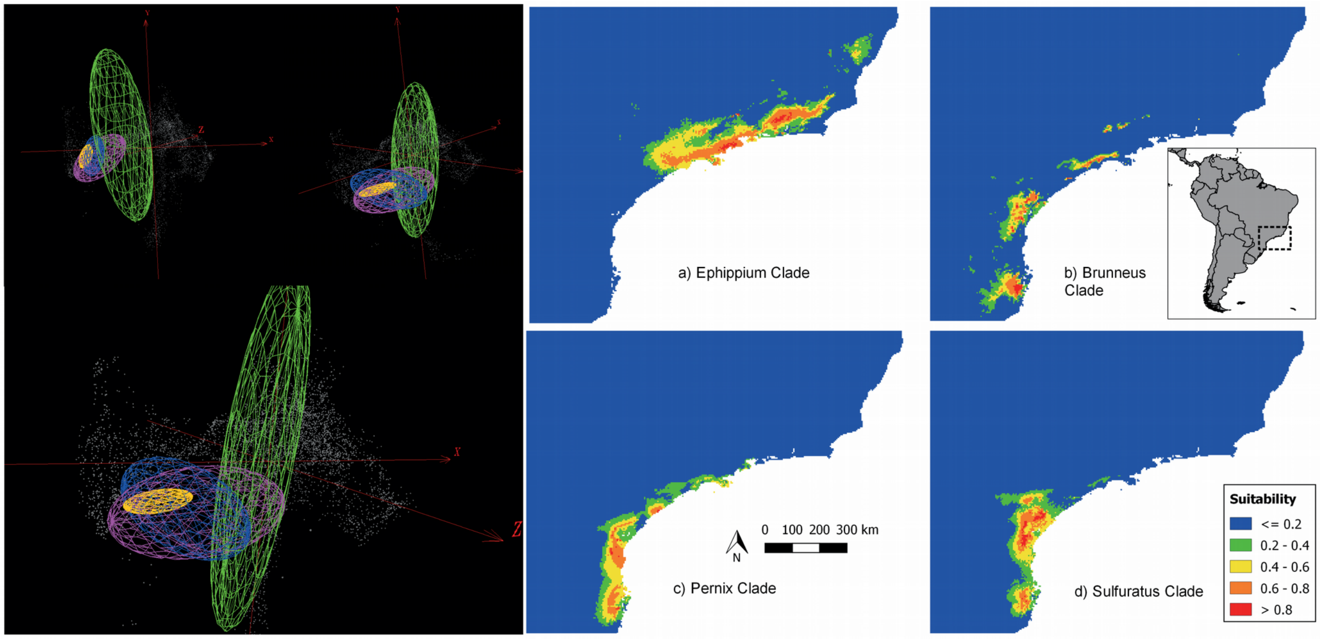

Figure 3. Ecological Niche Models for the four main lineages within *Brachycephalus* genus. NicheAnalyst (left-hand side) shows the MVE representing niche breadth and overlap between clades in an environmental tridimensional space, where the X-axis is PC1, Y-axis is PC2 and Z-axis is PC3. MaxEnt predictive models for the four clades showing their occurrence probability.

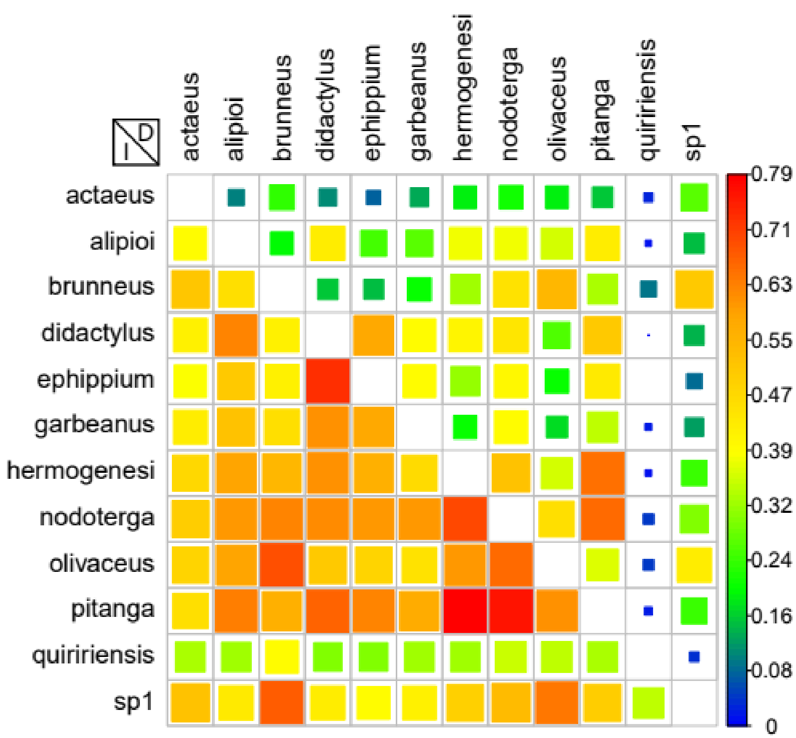

Figure 4. Niche overlap between *Brachycephalus* species. Bellow the diagonals are the Warren's I metric values. Above the diagonal are the Schoener's D metric values.

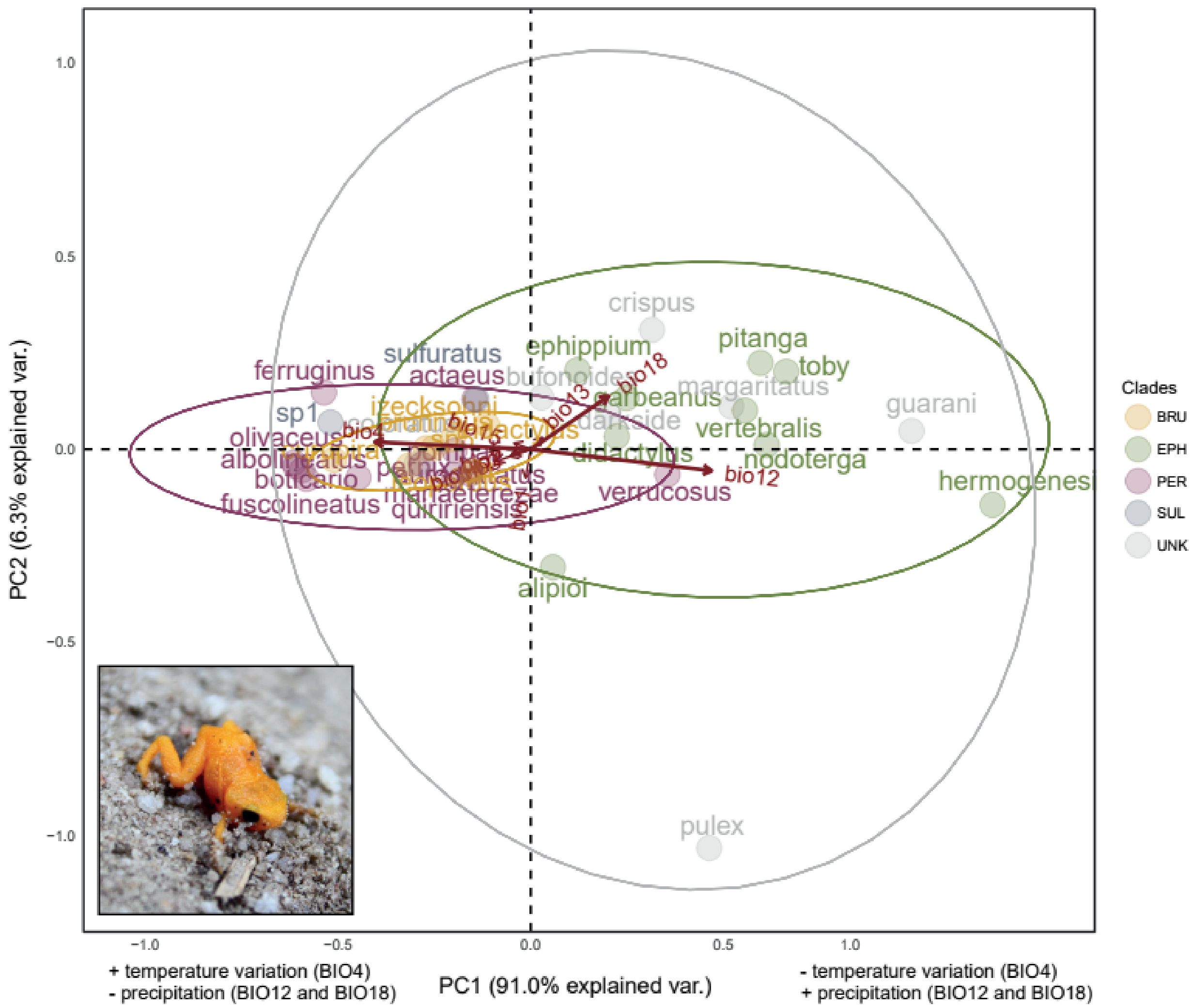

Figure 5. PCA with the mean z-scores for each species. The PC1 is responsible for 91% of the data variation, being composed mainly by Bio4 (Temperature Seasonality), Bio12 (Annual Precipitation) and Bio18 (Precipitation of the Warmest Quarter). Species situated at the right-hand side of the graph tend to require more thermally stable and wet environments, while species at the left-hand side of the graph tend to require more thermally variable and drier environments. Species are colored according to the clades they were assigned to in this study (BRU: Brunneus clade; EPH: Ephippium clade; PER: Perix clade; SUL: Sulfuratus clade; and UNK: species not included in the phylogenetic reconstruction.

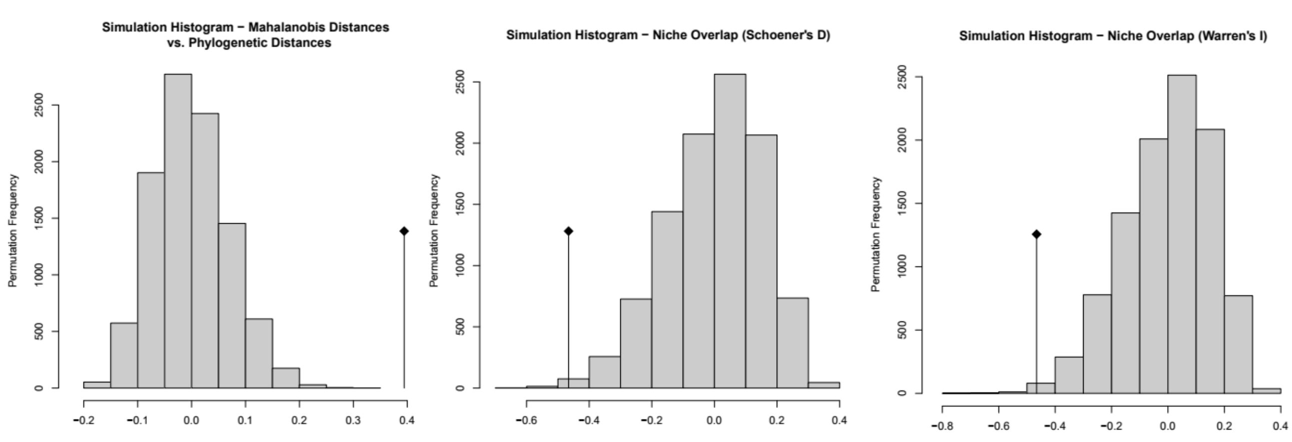

Figure 6. Mantel test histograms showing the permutation frequency of different r-values between matrices. Statistically significant positive values for the correlation between Mahalanobis and phylogenetic distance between species may indicate niche conservatism. Additionally statistically significant negative for the correlations between niche overlap (Schoener's D and Warren's I) and phylogenetic distance corroborate the results of the first Mantel test.

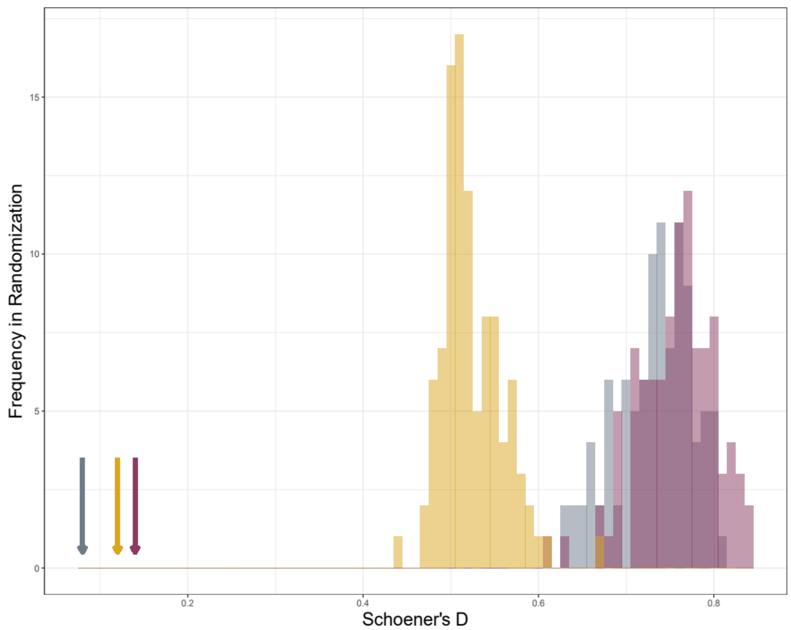

Figure 7. Histogram showing the distribution of the Niche Identity Test randomization for the comparison between the Ephippium clade with Brunneus clade (yellow), Pernix clade (purple) and Sulfuratus clade (blue). Arrows show the observed overlap (Shoener's D) between these clades (Table 2).

	Niche Id. Test I	Niche Id. Test D	Observed I	Observed D
PER – SUL	0.84	0.77	0.77	0.68
PER – BRU	0.73	0.58	0.67	0.54
BRU – SUL	0.77	0.64	0.71	0.59
EPH – BRU	0.69	0.52	0.39	0.12
EPH – SUL	0.81	0.73	0.38	0.08
EPH – PER	0.83	0.76	0.41	0.14

Table 1. Niche Identity Test between the four main lineages of *Brachycephalus*. PER: Pernix clade; SUL: Sulfuratus clade; BRU: Brunneus clade; and EPH: Ephippium clade.

	WorldClim variables									
	Bio1	Bio2	Bio3	Bio4	Bio7	Bio12	Bio13	Bio14	Bio15	Bio18
B. darkside	16.28	11.98	6.55	186.58	18.17	1559.25	268.93	27.08	66.43	614.90
B. margaritatus	19.71	9.99	5.88	216.22	16.77	1796.75	282.51	50.24	56.78	702.93
Brunneus clade	17.19	9.32	5.22	282.48	17.64	1796.64	234.68	86.05	31.02	633.49
B. brunneus	17.06	9.42	5.28	277.00	17.62	1864.97	243.27	88.64	31.88	655.56
Ephippium clade	18.57	10.26	5.99	212.05	16.96	1669.72	261.71	44.99	56.16	671.27
B. alipioi	21.47	10.81	6.36	182.52	16.90	1369.22	219.53	38.37	56.76	419.42
B. didactylus	20.80	10.00	5.94	208.06	16.67	1524.74	244.19	38.65	56.49	599.06
B. ephippium	18.64	10.48	6.01	216.92	17.24	1573.55	257.76	37.76	59.31	657.86
B. garbeanus	18.37	9.85	5.94	201.16	16.42	1483.29	259.34	32.44	62.54	572.19
B. hermogenesi	19.73	9.24	5.62	230.65	16.20	2466.91	326.46	91.72	43.45	912.30
B. nodoterga	18.31	9.51	5.80	223.07	16.26	1967.63	274.95	72.36	44.80	735.06
B. pitanga	18.37	10.47	5.98	221.92	17.27	1980.47	300.86	57.35	55.66	791.31
Pernix clade	19.10	8.87	5.12	279.28	17.16	1765.65	236.23	83.00	32.88	645.48
B. actaeus	20.80	7.65	4.80	275.16	15.81	1916.27	279.61	81.84	38.99	765.60
B. olivaceus	18.76	9.68	5.30	283.24	18.03	1663.63	208.47	86.50	27.75	559.14
B. quiririensis	13.32	9.32	5.37	260.10	17.16	1755.51	197.73	111.64	18.13	538.28
Sulfuratus clade	18.59	9.21	5.12	291.96	17.77	1696.98	231.04	75.97	34.54	629.65
B. sp1	18.50	9.287	5.160	292.82	17.87	1688.60	229.37	75.69	34.33	624.46

Table 2. Predicted Niche Occupancy profiles for the thirteen species with more than three occurrence records and for the four main lineages within *Brachycephalus*. Variables related to temperature (Bio1 – Bio7) are in ºC and precipitation variables (Bio12 – Bio18) are in millimeters.

Locus	Sequences	Length
12S	83	830
16S	280	532
Bfibr	173	407
cytb	74	836
RAG1	79	569
RPL3	165	389
tyr	194	568
TOTAL	1048	4131

Counting per species

	12S	16S	Bfibr	COI	cytb	RAG-1	RPL3	Tyr	TOTAL
B_actaeus	0	16	0	0	0	0	0	0	1
B_albolineatus	0	1	0	0	0	0	0	0	1
B_alipioi	1	2	0	0	1	1	0	1	5
B_auroguttatus	0	16	13	0	0	0	14	16	4
B_boticario	0	8	8	0	0	0	8	8	4
B_brunneus	1	32	31	0	1	1	31	32	7
B_curupira	0	5	5	0	0	0	5	5	4
B_didactylus	2	3	0	0	1	2	0	2	5
B_ephippium	43	36	1	40	42	44	1	2	8
B_ferruginus	1	5	3	0	1	1	0	4	6
B_fuscolineatus	0	8	8	0	0	0	8	8	4
B_garbeanus	1	1	0	0	1	1	0	1	5
B_hermogenesi	1	2	0	0	1	1	0	1	5
B_izecksohni	1	12	11	0	1	1	11	12	7
B_leopardus	0	15	15	0	0	0	15	15	4
B_mariaeterezae	0	11	11	0	0	0	5	11	4
B_nodoterga	20	20	0	22	19	19	0	2	6
B_olivaceus	0	7	5	0	0	0	5	5	4
B_pernix	1	8	7	0	1	1	7	8	7
B_pitanga	1	1	0	0	1	1	0	1	5
B_pombali	1	12	11		1	1	11	12	7
B_quiririensis	0	6	6	0	0	0	6	6	4
B_sp1	0	14	14	0	0	0	14	14	4
B_sp4	0	4	4	0	0	0	4	4	4
B_sp5	0	2	2	0	0	0	2	2	4
B_sulfuratus	4	7	0	0	0	0	0	0	2
B_toby	1	1	0	0	1	1	0	1	5
B_tridactylus	0	8	5	0	0	0	5	5	4
B_verrucosus	0	12	12	0	0	0	12	12	4
B_vertebralis	1	1	0	0	1	1	0	1	5
Ischnocnema	3	4	1	0	1	3	1	3	7
Species total	15	30	19	2	14	14	18	27	
Sequences total	83	280	173	62	74	79	165	194	

HQ435676.1	Brachycephalus_alipioi
HQ435677.1	Brachycephalus_brunneus
HQ435678.1	Brachycephalus_didactylus
JX267389.1	Brachycephalus_didactylus
AF375484.1	Brachycephalus_ephippium
AY326008.1	Brachycephalus_ephippium
DQ283091.1	Brachycephalus_ephippium
HM208305.1	Brachycephalus_ephippium
HM216360.1	Brachycephalus_ephippium
HM216364.1	Brachycephalus_ephippium
HM216368.1	Brachycephalus_ephippium
HQ435679.1	Brachycephalus_ephippium
KP999150.1	Brachycephalus_ephippium
KP999151.1	Brachycephalus_ephippium
KP999152.1	Brachycephalus_ephippium
KP999153.1	Brachycephalus_ephippium
KP999154.1	Brachycephalus_ephippium
KP999155.1	Brachycephalus_ephippium
KP999156.1	Brachycephalus_ephippium
KP999157.1	Brachycephalus_ephippium
KP999158.1	Brachycephalus_ephippium
KP999159.1	Brachycephalus_ephippium
KP999160.1	Brachycephalus_ephippium
KP999161.1	Brachycephalus_ephippium
KP999162.1	Brachycephalus_ephippium
KP999163.1	Brachycephalus_ephippium
KP999164.1	Brachycephalus_ephippium
KP999165.1	Brachycephalus_ephippium
KP999166.1	Brachycephalus_ephippium
KP999167.1	Brachycephalus_ephippium
KP999168.1	Brachycephalus_ephippium
KP999169.1	Brachycephalus_ephippium
KP999170.1	Brachycephalus_ephippium
KP999171.1	Brachycephalus_ephippium
KP999172.1	Brachycephalus_ephippium
KP999173.1	Brachycephalus_ephippium
KP999174.1	Brachycephalus_ephippium
KP999175.1	Brachycephalus_ephippium
KP999176.1	Brachycephalus_ephippium
KP999177.1	Brachycephalus_ephippium
KP999178.1	Brachycephalus_ephippium
KP999179.1	Brachycephalus_ephippium
KP999180.1	Brachycephalus_ephippium
KP999181.1	Brachycephalus_ephippium
KP999182.1	Brachycephalus_ephippium
KP999183.1	Brachycephalus_ephippium
KP999184.1	Brachycephalus_ephippium
HQ435681.1	Brachycephalus_ferruginus
HQ435680.1	Brachycephalus_garbeanus
HQ435682.1	Brachycephalus_hermogenesi
HQ435683.1	Brachycephalus_izecksohni
HQ435684.1	Brachycephalus_nodoterga
KJ649752.1	Brachycephalus_nodoterga
KJ649753.1	Brachycephalus_nodoterga
KJ649754.1	Brachycephalus_nodoterga
KJ649755.1	Brachycephalus_nodoterga
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KJ649762.1	Brachycephalus_nodoterga
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KJ649768.1	Brachycephalus_nodoterga
KJ649769.1	Brachycephalus_nodoterga
KJ649770.1	Brachycephalus_nodoterga
HQ435685.1	Brachycephalus_pernix
HQ435686.1	Brachycephalus_pitanga
HQ435687.1	Brachycephalus_pombali
KX198030.1	Brachycephalus_sulfuratus
KX198031.1	Brachycephalus_sulfuratus
KX198032.1	Brachycephalus_sulfuratus
KX198033.1	Brachycephalus_sulfuratus
HQ435688.1	Brachycephalus_toby
HQ435689.1	Brachycephalus_vertebralis
JX267435.1	Ischnocnema_parva
JX267436.1	Ischnocnema_parva
JX267437.1	Ischnocnema_parva

16s

MG889439.1	Brachycephalus_actaeus	KX025371.1	Brachycephalus_boticario	KX025266.1	Brachycephalus_brunneus
MG889440.1	Brachycephalus_actaeus	KX025372.1	Brachycephalus_boticario	KX025267.1	Brachycephalus_brunneus
MG889441.1	Brachycephalus_actaeus	KX025373.1	Brachycephalus_boticario	KX025268.1	Brachycephalus_brunneus
MG889442.1	Brachycephalus_actaeus	KX025374.1	Brachycephalus_boticario	KX025269.1	Brachycephalus_brunneus
MG889443.1	Brachycephalus_actaeus	KX025375.1	Brachycephalus_boticario	KX025378.1	Brachycephalus_curupira
MG889444.1	Brachycephalus_actaeus	KX025376.1	Brachycephalus_boticario	KX025379.1	Brachycephalus_curupira
MG889445.1	Brachycephalus_actaeus	KX025377.1	Brachycephalus_boticario	KX025380.1	Brachycephalus_curupira
MG889446.1	Brachycephalus_actaeus	HQ435691.1	Brachycephalus_brunneus	KX025381.1	Brachycephalus_curupira
MG889447.1	Brachycephalus_actaeus	KX025284.1	Brachycephalus_brunneus	KX025382.1	Brachycephalus_curupira
MG889448.1	Brachycephalus_actaeus	KX025285.1	Brachycephalus_brunneus	MG889427.1	Brachycephalus_didactylus
MG889449.1	Brachycephalus_actaeus	KX025286.1	Brachycephalus_brunneus	HQ435692.1	Brachycephalus_didactylus
MG889450.1	Brachycephalus_actaeus	KX025287.1	Brachycephalus_brunneus	JX267467.1	Brachycephalus_didactylus
MG889451.1	Brachycephalus_actaeus	KX025288.1	Brachycephalus_brunneus	GQ345243.1	Brachycephalus_ephippium
MG889452.1	Brachycephalus_actaeus	KX025289.1	Brachycephalus_brunneus	HM208306.1	Brachycephalus_ephippium
MG889453.1	Brachycephalus_actaeus	KX025290.1	Brachycephalus_brunneus	HM216361.1	Brachycephalus_ephippium
MG889454.1	Brachycephalus_actaeus	KX025291.1	Brachycephalus_brunneus	HM216365.1	Brachycephalus_ephippium
MG889434.1	Brachycephalus_albolineatus	KX025292.1	Brachycephalus_brunneus	HM216369.1	Brachycephalus_ephippium
HQ435690.1	Brachycephalus_alipioi	KX025293.1	Brachycephalus_brunneus	HQ435693.1	Brachycephalus_ephippium
KX025354.1	Brachycephalus_auroguttatus	KX025294.1	Brachycephalus_brunneus	KP999185.1	Brachycephalus_ephippium
KX025355.1	Brachycephalus_auroguttatus	KX025295.1	Brachycephalus_brunneus	KP999186.1	Brachycephalus_ephippium
KX025356.1	Brachycephalus_auroguttatus	KX025273.1	Brachycephalus_brunneus	KP999187.1	Brachycephalus_ephippium
KX025357.1	Brachycephalus_auroguttatus	KX025274.1	Brachycephalus_brunneus	KP999188.1	Brachycephalus_ephippium
KX025358.1	Brachycephalus_auroguttatus	KX025275.1	Brachycephalus_brunneus	KP999189.1	Brachycephalus_ephippium
KX025359.1	Brachycephalus_auroguttatus	KX025276.1	Brachycephalus_brunneus	KP999190.1	Brachycephalus_ephippium
KX025360.1	Brachycephalus_auroguttatus	KX025277.1	Brachycephalus_brunneus	KP999191.1	Brachycephalus_ephippium
KX025361.1	Brachycephalus_auroguttatus	KX025278.1	Brachycephalus_brunneus	KP999192.1	Brachycephalus_ephippium
KX025362.1	Brachycephalus_auroguttatus	KX025279.1	Brachycephalus_brunneus	KP999193.1	Brachycephalus_ephippium
KX025363.1	Brachycephalus_auroguttatus	KX025280.1	Brachycephalus_brunneus	KP999194.1	Brachycephalus_ephippium
KX025364.1	Brachycephalus_auroguttatus	KX025281.1	Brachycephalus_brunneus	KP999195.1	Brachycephalus_ephippium
KX025365.1	Brachycephalus_auroguttatus	KX025282.1	Brachycephalus_brunneus	KP999196.1	Brachycephalus_ephippium
KX025366.1	Brachycephalus_auroguttatus	KX025283.1	Brachycephalus_brunneus	KP999197.1	Brachycephalus_ephippium
KX025367.1	Brachycephalus_auroguttatus	KX025304.1	Brachycephalus_brunneus	KP999198.1	Brachycephalus_ephippium
KX025368.1	Brachycephalus_auroguttatus	KX025305.1	Brachycephalus_brunneus	KP999199.1	Brachycephalus_ephippium
KX025369.1	Brachycephalus_auroguttatus	KX025306.1	Brachycephalus_brunneus	KP999200.1	Brachycephalus_ephippium
KX025370.1	Brachycephalus_boticario	KX025265.1	Brachycephalus_brunneus	KP999201.1	Brachycephalus_ephippium

KP999202.1	Brachycephalus_ephippium
KP999203.1	Brachycephalus_ephippium
KP999204.1	Brachycephalus_ephippium
KP999205.1	Brachycephalus_ephippium
KP999206.1	Brachycephalus_ephippium
KP999207.1	Brachycephalus_ephippium
KP999208.1	Brachycephalus_ephippium
KP999209.1	Brachycephalus_ephippium
KX025517.1	Brachycephalus_ephippium
KU495162.1	Brachycephalus_ephippium
KU495163.1	Brachycephalus_ephippium
KU495164.1	Brachycephalus_ephippium
KU495165.1	Brachycephalus_ephippium
MG889438.1	Brachycephalus_ferruginus
HQ435695.1	Brachycephalus_ferruginus
KX025236.1	Brachycephalus_ferruginus
KX025237.1	Brachycephalus_ferruginus
KX025238.1	Brachycephalus_ferruginus
KX025296.1	Brachycephalus_fuscolineatus
KX025297.1	Brachycephalus_fuscolineatus
KX025298.1	Brachycephalus_fuscolineatus
KX025339.1	Brachycephalus_fuscolineatus
KX025340.1	Brachycephalus_fuscolineatus
KX025341.1	Brachycephalus_fuscolineatus
KX025342.1	Brachycephalus_fuscolineatus
KX025343.1	Brachycephalus_fuscolineatus
HQ435694.1	Brachycephalus_garbeanus
MG889426.1	Brachycephalus_hermogenesi
KU321531.1	Brachycephalus_hermogenesi
HQ435696.1	Brachycephalus_izecksohni
KX025254.1	Brachycephalus_izecksohni
KX025255.1	Brachycephalus_izecksohni
KX025256.1	Brachycephalus_izecksohni
KX025257.1	Brachycephalus_izecksohni
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KX025262.1	Brachycephalus_izecksohni
KX025263.1	Brachycephalus_izecksohni
KX025264.1	Brachycephalus_izecksohni
KX025239.1	Brachycephalus_leopardus
KX025240.1	Brachycephalus_leopardus
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KX025253.1	Brachycephalus_leopardus
KX025316.1	Brachycephalus_mariaeterezae
KX025344.1	Brachycephalus_mariaeterezae
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KX025346.1	Brachycephalus_mariaeterezae
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KX025352.1	Brachycephalus_mariaeterezae
KX025353.1	Brachycephalus_mariaeterezae
MG889425.1	Brachycephalus_nodoterga
HQ435697.1	Brachycephalus_nodoterga
KJ649771.1	Brachycephalus_nodoterga
KJ649772.1	Brachycephalus_nodoterga
KJ649773.1	Brachycephalus_nodoterga
KJ649774.1	Brachycephalus_nodoterga
KJ649775.1	Brachycephalus_nodoterga
KJ649776.1	Brachycephalus_nodoterga
KJ649777.1	Brachycephalus_nodoterga
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KJ649780.1	Brachycephalus_nodoterga
KJ649781.1	Brachycephalus_nodoterga
KJ649782.1	Brachycephalus_nodoterga
KJ649783.1	Brachycephalus_nodoterga
KJ649784.1	Brachycephalus_nodoterga
KJ649785.1	Brachycephalus_nodoterga
KJ649786.1	Brachycephalus_nodoterga
KJ649787.1	Brachycephalus_nodoterga
KJ649788.1	Brachycephalus_nodoterga
MG889435.1	Brachycephalus_olivaceus
MG889436.1	Brachycephalus_olivaceus
KX025300.1	Brachycephalus_olivaceus
KX025301.1	Brachycephalus_olivaceus
KX025302.1	Brachycephalus_olivaceus
KX025303.1	Brachycephalus_olivaceus
KX025325.1	Brachycephalus_olivaceus
HQ435698.1	Brachycephalus_pernix
KX025218.1	Brachycephalus_pernix
KX025219.1	Brachycephalus_pernix
KX025220.1	Brachycephalus_pernix
KX025221.1	Brachycephalus_pernix
KX025222.1	Brachycephalus_pernix
KX025383.1	Brachycephalus_pernix
KX025384.1	Brachycephalus_pernix
HQ435699.1	Brachycephalus_pitanga
HQ435700.1	Brachycephalus_pombali
KX025223.1	Brachycephalus_pombali

KX025224.1	Brachycephalus_pombali	KX025386.1	Brachycephalus_sp.5
KX025225.1	Brachycephalus_pombali	KX025333.1	Brachycephalus_sp1
KX025308.1	Brachycephalus_pombali	MG889428.1	Brachycephalus_sulfuratus
KX025309.1	Brachycephalus_pombali	MG889429.1	Brachycephalus_sulfuratus
KX025310.1	Brachycephalus_pombali	MG889430.1	Brachycephalus_sulfuratus
KX025311.1	Brachycephalus_pombali	KU321532.1	Brachycephalus_sulfuratus
KX025312.1	Brachycephalus_pombali	KU321533.1	Brachycephalus_sulfuratus
KX025313.1	Brachycephalus_pombali	KU321534.1	Brachycephalus_sulfuratus
KX025314.1	Brachycephalus_pombali	KU321535.1	Brachycephalus_sulfuratus
KX025315.1	Brachycephalus_pombali	HQ435701.1	Brachycephalus_toby
MG889437.1	Brachycephalus_quiririensis	MG889431.1	Brachycephalus_tridactylus
KX025317.1	Brachycephalus_quiririensis	MG889432.1	Brachycephalus_tridactylus
KX025318.1	Brachycephalus_quiririensis	MG889433.1	Brachycephalus_tridactylus
KX025319.1	Brachycephalus_quiririensis	KX025387.1	Brachycephalus_tridactylus
KX025320.1	Brachycephalus_quiririensis	KX025388.1	Brachycephalus_tridactylus
KX025321.1	Brachycephalus_quiririensis	KX025389.1	Brachycephalus_tridactylus
KX025322.1	Brachycephalus_quiririensis	KX025390.1	Brachycephalus_tridactylus
KX025338.1	Brachycephalus_sp.1	KX025391.1	Brachycephalus_tridactylus
KX025307.1	Brachycephalus_sp.1	KX025226.1	Brachycephalus_verrucosus
KX025330.1	Brachycephalus_sp.1	KX025227.1	Brachycephalus_verrucosus
KX025331.1	Brachycephalus_sp.1	KX025228.1	Brachycephalus_verrucosus
KX025332.1	Brachycephalus_sp.1	KX025229.1	Brachycephalus_verrucosus
KX025334.1	Brachycephalus_sp.1	KX025230.1	Brachycephalus_verrucosus
KX025335.1	Brachycephalus_sp.1	KX025231.1	Brachycephalus_verrucosus
KX025337.1	Brachycephalus_sp.1	KX025232.1	Brachycephalus_verrucosus
KX025336.1	Brachycephalus_sp.1	KX025233.1	Brachycephalus_verrucosus
KX025326.1	Brachycephalus_sp.1	KX025234.1	Brachycephalus_verrucosus
KX025327.1	Brachycephalus_sp.1	KX025235.1	Brachycephalus_verrucosus
KX025328.1	Brachycephalus_sp.1	KX025323.1	Brachycephalus_verrucosus
KX025329.1	Brachycephalus_sp.1	KX025324.1	Brachycephalus_verrucosus
KX025270.1	Brachycephalus_sp.4	HQ435702.1	Brachycephalus_vertebralis
KX025271.1	Brachycephalus_sp.4	MG889424.1	Ischnocnema_parva
KX025272.1	Brachycephalus_sp.4	JX267522.1	Ischnocnema_parva
KX025299.1	Brachycephalus_sp.4	JX267523.1	Ischnocnema_parva
KX025385.1	Brachycephalus_sp.5	JX267524.1	Ischnocnema_parva

KX025895.1	Brachycephalus_auroguttatus	KX025816.1	Brachycephalus_brunneus	KX025796.1	Brachycephalus_izecksohni
KX025896.1	Brachycephalus_auroguttatus	KX025817.1	Brachycephalus_brunneus	KX025797.1	Brachycephalus_izecksohni
KX025897.1	Brachycephalus_auroguttatus	KX025818.1	Brachycephalus_brunneus	KX025798.1	Brachycephalus_izecksohni
KX025898.1	Brachycephalus_auroguttatus	KX025819.1	Brachycephalus_brunneus	KX025799.1	Brachycephalus_izecksohni
KX025899.1	Brachycephalus_auroguttatus	KX025820.1	Brachycephalus_brunneus	KX025800.1	Brachycephalus_izecksohni
KX025900.1	Brachycephalus_auroguttatus	KX025821.1	Brachycephalus_brunneus	KX025801.1	Brachycephalus_izecksohni
KX025901.1	Brachycephalus_auroguttatus	KX025822.1	Brachycephalus_brunneus	KX025802.1	Brachycephalus_izecksohni
KX025902.1	Brachycephalus_auroguttatus	KX025823.1	Brachycephalus_brunneus	KX025803.1	Brachycephalus_izecksohni
KX025904.1	Brachycephalus_auroguttatus	KX025824.1	Brachycephalus_brunneus	KX025804.1	Brachycephalus_izecksohni
KX025906.1	Brachycephalus_auroguttatus	KX025845.1	Brachycephalus_brunneus	KX025805.1	Brachycephalus_izecksohni
KX025907.1	Brachycephalus_auroguttatus	KX025846.1	Brachycephalus_brunneus	KX025780.1	Brachycephalus_leopardus
KX025908.1	Brachycephalus_auroguttatus	KX025847.1	Brachycephalus_brunneus	KX025781.1	Brachycephalus_leopardus
KX025909.1	Brachycephalus_auroguttatus	KX025806.1	Brachycephalus_brunneus	KX025782.1	Brachycephalus_leopardus
KX025910.1	Brachycephalus_boticario	KX025807.1	Brachycephalus_brunneus	KX025783.1	Brachycephalus_leopardus
KX025911.1	Brachycephalus_boticario	KX025808.1	Brachycephalus_brunneus	KX025784.1	Brachycephalus_leopardus
KX025912.1	Brachycephalus_boticario	KX025809.1	Brachycephalus_brunneus	KX025785.1	Brachycephalus_leopardus
KX025913.1	Brachycephalus_boticario	KX025810.1	Brachycephalus_brunneus	KX025786.1	Brachycephalus_leopardus
KX025914.1	Brachycephalus_boticario	KX025918.1	Brachycephalus_curupira	KX025787.1	Brachycephalus_leopardus
KX025915.1	Brachycephalus_boticario	KX025919.1	Brachycephalus_curupira	KX025788.1	Brachycephalus_leopardus
KX025916.1	Brachycephalus_boticario	KX025920.1	Brachycephalus_curupira	KX025789.1	Brachycephalus_leopardus
KX025917.1	Brachycephalus_boticario	KX025921.1	Brachycephalus_curupira	KX025790.1	Brachycephalus_leopardus
KX025825.1	Brachycephalus_brunneus	KX025922.1	Brachycephalus_curupira	KX025791.1	Brachycephalus_leopardus
KX025826.1	Brachycephalus_brunneus	KX026057.1	Brachycephalus_ephippium	KX025792.1	Brachycephalus_leopardus
KX025827.1	Brachycephalus_brunneus	KX025777.1	Brachycephalus_ferruginus	KX025793.1	Brachycephalus_leopardus
KX025828.1	Brachycephalus_brunneus	KX025778.1	Brachycephalus_ferruginus	KX025794.1	Brachycephalus_leopardus
KX025829.1	Brachycephalus_brunneus	KX025779.1	Brachycephalus_ferruginus	KX025857.1	Brachycephalus_mariaeterezae
KX025830.1	Brachycephalus_brunneus	KX025837.1	Brachycephalus_fuscolineatus	KX025885.1	Brachycephalus_mariaeterezae
KX025831.1	Brachycephalus_brunneus	KX025838.1	Brachycephalus_fuscolineatus	KX025886.1	Brachycephalus_mariaeterezae
KX025832.1	Brachycephalus_brunneus	KX025839.1	Brachycephalus_fuscolineatus	KX025887.1	Brachycephalus_mariaeterezae
KX025833.1	Brachycephalus_brunneus	KX025880.1	Brachycephalus_fuscolineatus	KX025888.1	Brachycephalus_mariaeterezae
KX025834.1	Brachycephalus_brunneus	KX025881.1	Brachycephalus_fuscolineatus	KX025889.1	Brachycephalus_mariaeterezae
KX025835.1	Brachycephalus_brunneus	KX025882.1	Brachycephalus_fuscolineatus	KX025890.1	Brachycephalus_mariaeterezae
KX025836.1	Brachycephalus_brunneus	KX025883.1	Brachycephalus_fuscolineatus	KX025891.1	Brachycephalus_mariaeterezae
KX025814.1	Brachycephalus_brunneus	KX025884.1	Brachycephalus_fuscolineatus	KX025892.1	Brachycephalus_mariaeterezae
KX025815.1	Brachycephalus_brunneus	KX025795.1	Brachycephalus_izecksohni	KX025893.1	Brachycephalus_mariaeterezae

KX025894.1	Brachycephalus_mariaeterezae
KX025841.1	Brachycephalus_olivaceus
KX025842.1	Brachycephalus_olivaceus
KX025843.1	Brachycephalus_olivaceus
KX025844.1	Brachycephalus_olivaceus
KX025866.1	Brachycephalus_olivaceus
KX025759.1	Brachycephalus_pernix
KX025760.1	Brachycephalus_pernix
KX025761.1	Brachycephalus_pernix
KX025762.1	Brachycephalus_pernix
KX025763.1	Brachycephalus_pernix
KX025923.1	Brachycephalus_pernix
KX025924.1	Brachycephalus_pernix
KX025764.1	Brachycephalus_pombali
KX025765.1	Brachycephalus_pombali
KX025766.1	Brachycephalus_pombali
KX025849.1	Brachycephalus_pombali
KX025850.1	Brachycephalus_pombali
KX025851.1	Brachycephalus_pombali
KX025852.1	Brachycephalus_pombali
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KX025854.1	Brachycephalus_pombali
KX025855.1	Brachycephalus_pombali
KX025856.1	Brachycephalus_pombali
KX025858.1	Brachycephalus_quiririensis
KX025859.1	Brachycephalus_quiririensis
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KX025862.1	Brachycephalus_quiririensis
KX025863.1	Brachycephalus_quiririensis
KX025879.1	Brachycephalus_sp.1
KX025848.1	Brachycephalus_sp.1
KX025871.1	Brachycephalus_sp.1
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KX025868.1	Brachycephalus_sp.1
KX025869.1	Brachycephalus_sp.1
KX025870.1	Brachycephalus_sp.1
KX025811.1	Brachycephalus_sp.4
KX025812.1	Brachycephalus_sp.4
KX025813.1	Brachycephalus_sp.4
KX025840.1	Brachycephalus_sp.4
KX025925.1	Brachycephalus_sp.5
KX025926.1	Brachycephalus_sp.5
KX025927.1	Brachycephalus_tridactylus
KX025928.1	Brachycephalus_tridactylus
KX025929.1	Brachycephalus_tridactylus
KX025930.1	Brachycephalus_tridactylus
KX025931.1	Brachycephalus_tridactylus
KX025767.1	Brachycephalus_verrucosus
KX025768.1	Brachycephalus_verrucosus
KX025769.1	Brachycephalus_verrucosus
KX025770.1	Brachycephalus_verrucosus
KX025771.1	Brachycephalus_verrucosus
KX025772.1	Brachycephalus_verrucosus
KX025773.1	Brachycephalus_verrucosus
KX025774.1	Brachycephalus_verrucosus
KX025775.1	Brachycephalus_verrucosus
KX025776.1	Brachycephalus_verrucosus
KX025864.1	Brachycephalus_verrucosus
KX025865.1	Brachycephalus_verrucosus
KX026058.1	Ischnocnema_guentheri

HQ435703.1	Brachycephalus_alipioi
HQ435704.1	Brachycephalus_brunneus
HQ435705.1	Brachycephalus_didactylus
GQ345195.1	Brachycephalus_ephippium
HM208304.1	Brachycephalus_ephippium
HM216359.1	Brachycephalus_ephippium
HM216363.1	Brachycephalus_ephippium
HM216367.1	Brachycephalus_ephippium
HQ435706.1	Brachycephalus_ephippium
KP999250.1	Brachycephalus_ephippium
KP999251.1	Brachycephalus_ephippium
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KP999253.1	Brachycephalus_ephippium
KP999254.1	Brachycephalus_ephippium
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KP999256.1	Brachycephalus_ephippium
KP999257.1	Brachycephalus_ephippium
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KP999260.1	Brachycephalus_ephippium
KP999261.1	Brachycephalus_ephippium
KP999262.1	Brachycephalus_ephippium
KP999263.1	Brachycephalus_ephippium
KP999264.1	Brachycephalus_ephippium
KP999265.1	Brachycephalus_ephippium
KP999266.1	Brachycephalus_ephippium
KP999267.1	Brachycephalus_ephippium
KP999268.1	Brachycephalus_ephippium
KP999269.1	Brachycephalus_ephippium
KP999270.1	Brachycephalus_ephippium
KP999271.1	Brachycephalus_ephippium
KP999272.1	Brachycephalus_ephippium
KP999273.1	Brachycephalus_ephippium
KP999274.1	Brachycephalus_ephippium
KP999275.1	Brachycephalus_ephippium
KP999276.1	Brachycephalus_ephippium
KP999277.1	Brachycephalus_ephippium
KP999278.1	Brachycephalus_ephippium
KP999279.1	Brachycephalus_ephippium
KP999280.1	Brachycephalus_ephippium
KP999281.1	Brachycephalus_ephippium
KP999282.1	Brachycephalus_ephippium
KP999283.1	Brachycephalus_ephippium
KP999284.1	Brachycephalus_ephippium
KP999285.1	Brachycephalus_ephippium
HQ435708.1	Brachycephalus_ferruginus
HQ435707.1	Brachycephalus_garbeanus
HQ435709.1	Brachycephalus_hermogenesi
HQ435710.1	Brachycephalus_izecksohni
HQ435711.1	Brachycephalus_nodoterga
KJ649810.1	Brachycephalus_nodoterga
KJ649811.1	Brachycephalus_nodoterga
KJ649812.1	Brachycephalus_nodoterga
KJ649813.1	Brachycephalus_nodoterga
KJ649814.1	Brachycephalus_nodoterga
KJ649815.1	Brachycephalus_nodoterga
KJ649816.1	Brachycephalus_nodoterga
KJ649817.1	Brachycephalus_nodoterga
KJ649818.1	Brachycephalus_nodoterga
KJ649819.1	Brachycephalus_nodoterga
KJ649820.1	Brachycephalus_nodoterga
KJ649821.1	Brachycephalus_nodoterga
KJ649822.1	Brachycephalus_nodoterga
KJ649823.1	Brachycephalus_nodoterga
KJ649824.1	Brachycephalus_nodoterga
KJ649825.1	Brachycephalus_nodoterga
KJ649826.1	Brachycephalus_nodoterga
KJ649827.1	Brachycephalus_nodoterga
HQ435712.1	Brachycephalus_pernix
HQ435713.1	Brachycephalus_pitanga
HQ435714.1	Brachycephalus_pombali
HQ435715.1	Brachycephalus_toby
HQ435716.1	Brachycephalus_vertebralis
HQ435717.1	Ischnocnema_parva

HQ435718.1	Brachycephalus_alipioi
HQ435719.1	Brachycephalus_brunneus
HQ435720.1	Brachycephalus_didactylus
JX267544.1	Brachycephalus_didactylus
EU186761.1	Brachycephalus_ephippium
GQ345275.1	Brachycephalus_ephippium
GQ345290.1	Brachycephalus_ephippium
HM208307.1	Brachycephalus_ephippium
HM216362.1	Brachycephalus_ephippium
HM216366.1	Brachycephalus_ephippium
HM216370.1	Brachycephalus_ephippium
HQ435721.1	Brachycephalus_ephippium
KP999286.1	Brachycephalus_ephippium
KP999287.1	Brachycephalus_ephippium
KP999288.1	Brachycephalus_ephippium
KP999289.1	Brachycephalus_ephippium
KP999290.1	Brachycephalus_ephippium
KP999291.1	Brachycephalus_ephippium
KP999292.1	Brachycephalus_ephippium
KP999293.1	Brachycephalus_ephippium
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KP999299.1	Brachycephalus_ephippium
KP999300.1	Brachycephalus_ephippium
KP999301.1	Brachycephalus_ephippium
KP999302.1	Brachycephalus_ephippium
KP999303.1	Brachycephalus_ephippium
KP999304.1	Brachycephalus_ephippium
KP999305.1	Brachycephalus_ephippium
KP999306.1	Brachycephalus_ephippium
KP999307.1	Brachycephalus_ephippium
KP999308.1	Brachycephalus_ephippium
KP999309.1	Brachycephalus_ephippium
KP999310.1	Brachycephalus_ephippium
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KP999318.1	Brachycephalus_ephippium
KP999319.1	Brachycephalus_ephippium
KP999320.1	Brachycephalus_ephippium
KP999321.1	Brachycephalus_ephippium
HQ435723.1	Brachycephalus_ferruginus
HQ435722.1	Brachycephalus_garbeanus
HQ435724.1	Brachycephalus_hermogenesi
HQ435725.1	Brachycephalus_izecksohni
HQ435726.1	Brachycephalus_nodoterga
KJ649828.1	Brachycephalus_nodoterga
KJ649829.1	Brachycephalus_nodoterga
KJ649830.1	Brachycephalus_nodoterga
KJ649831.1	Brachycephalus_nodoterga
KJ649832.1	Brachycephalus_nodoterga
KJ649833.1	Brachycephalus_nodoterga
KJ649834.1	Brachycephalus_nodoterga
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KJ649836.1	Brachycephalus_nodoterga
KJ649837.1	Brachycephalus_nodoterga
KJ649838.1	Brachycephalus_nodoterga
KJ649839.1	Brachycephalus_nodoterga
KJ649840.1	Brachycephalus_nodoterga
KJ649841.1	Brachycephalus_nodoterga
KJ649842.1	Brachycephalus_nodoterga
KJ649843.1	Brachycephalus_nodoterga
KJ649844.1	Brachycephalus_nodoterga
KJ649845.1	Brachycephalus_nodoterga
HQ435727.1	Brachycephalus_pernix
HQ435728.1	Brachycephalus_pitanga
HQ435729.1	Brachycephalus_pombali
HQ435730.1	Brachycephalus_toby
HQ435731.1	Brachycephalus_vertebralis
JX267642.1	Ischnocnema_parva
JX267644.1	Ischnocnema_parva
JX267645.1	Ischnocnema_parva

RPL3

KX026492.1	Brachycephalus_auroguttatus	KX026418.1	Brachycephalus_brunneus	KX026401.1	Brachycephalus_izecksohni
KX026493.1	Brachycephalus_auroguttatus	KX026419.1	Brachycephalus_brunneus	KX026402.1	Brachycephalus_izecksohni
KX026494.1	Brachycephalus_auroguttatus	KX026420.1	Brachycephalus_brunneus	KX026403.1	Brachycephalus_izecksohni
KX026495.1	Brachycephalus_auroguttatus	KX026421.1	Brachycephalus_brunneus	KX026404.1	Brachycephalus_izecksohni
KX026496.1	Brachycephalus_auroguttatus	KX026422.1	Brachycephalus_brunneus	KX026405.1	Brachycephalus_izecksohni
KX026497.1	Brachycephalus_auroguttatus	KX026423.1	Brachycephalus_brunneus	KX026406.1	Brachycephalus_izecksohni
KX026498.1	Brachycephalus_auroguttatus	KX026424.1	Brachycephalus_brunneus	KX026407.1	Brachycephalus_izecksohni
KX026499.1	Brachycephalus_auroguttatus	KX026425.1	Brachycephalus_brunneus	KX026408.1	Brachycephalus_izecksohni
KX026500.1	Brachycephalus_auroguttatus	KX026426.1	Brachycephalus_brunneus	KX026383.1	Brachycephalus_leopardus
KX026501.1	Brachycephalus_auroguttatus	KX026427.1	Brachycephalus_brunneus	KX026384.1	Brachycephalus_leopardus
KX026502.1	Brachycephalus_auroguttatus	KX026448.1	Brachycephalus_brunneus	KX026385.1	Brachycephalus_leopardus
KX026503.1	Brachycephalus_auroguttatus	KX026449.1	Brachycephalus_brunneus	KX026386.1	Brachycephalus_leopardus
KX026504.1	Brachycephalus_auroguttatus	KX026450.1	Brachycephalus_brunneus	KX026387.1	Brachycephalus_leopardus
KX026505.1	Brachycephalus_auroguttatus	KX026409.1	Brachycephalus_brunneus	KX026388.1	Brachycephalus_leopardus
KX026506.1	Brachycephalus_boticario	KX026410.1	Brachycephalus_brunneus	KX026389.1	Brachycephalus_leopardus
KX026507.1	Brachycephalus_boticario	KX026411.1	Brachycephalus_brunneus	KX026390.1	Brachycephalus_leopardus
KX026508.1	Brachycephalus_boticario	KX026412.1	Brachycephalus_brunneus	KX026391.1	Brachycephalus_leopardus
KX026509.1	Brachycephalus_boticario	KX026413.1	Brachycephalus_brunneus	KX026392.1	Brachycephalus_leopardus
KX026510.1	Brachycephalus_boticario	KX026514.1	Brachycephalus_curupira	KX026393.1	Brachycephalus_leopardus
KX026511.1	Brachycephalus_boticario	KX026515.1	Brachycephalus_curupira	KX026394.1	Brachycephalus_leopardus
KX026512.1	Brachycephalus_boticario	KX026516.1	Brachycephalus_curupira	KX026395.1	Brachycephalus_leopardus
KX026513.1	Brachycephalus_boticario	KX026517.1	Brachycephalus_curupira	KX026396.1	Brachycephalus_leopardus
KX026428.1	Brachycephalus_brunneus	KX026518.1	Brachycephalus_curupira	KX026397.1	Brachycephalus_leopardus
KX026429.1	Brachycephalus_brunneus	KX026653.1	Brachycephalus_ephippium	KX026460.1	Brachycephalus_mariaeterezae
KX026430.1	Brachycephalus_brunneus	KX026440.1	Brachycephalus_fuscolineatus	KX026488.1	Brachycephalus_mariaeterezae
KX026431.1	Brachycephalus_brunneus	KX026441.1	Brachycephalus_fuscolineatus	KX026489.1	Brachycephalus_mariaeterezae
KX026432.1	Brachycephalus_brunneus	KX026442.1	Brachycephalus_fuscolineatus	KX026490.1	Brachycephalus_mariaeterezae
KX026433.1	Brachycephalus_brunneus	KX026483.1	Brachycephalus_fuscolineatus	KX026491.1	Brachycephalus_mariaeterezae
KX026434.1	Brachycephalus_brunneus	KX026484.1	Brachycephalus_fuscolineatus	KX026444.1	Brachycephalus_olivaceus
KX026435.1	Brachycephalus_brunneus	KX026485.1	Brachycephalus_fuscolineatus	KX026445.1	Brachycephalus_olivaceus
KX026436.1	Brachycephalus_brunneus	KX026486.1	Brachycephalus_fuscolineatus	KX026446.1	Brachycephalus_olivaceus
KX026437.1	Brachycephalus_brunneus	KX026487.1	Brachycephalus_fuscolineatus	KX026447.1	Brachycephalus_olivaceus
KX026438.1	Brachycephalus_brunneus	KX026398.1	Brachycephalus_izecksohni	KX026469.1	Brachycephalus_olivaceus
KX026439.1	Brachycephalus_brunneus	KX026399.1	Brachycephalus_izecksohni	KX026365.1	Brachycephalus_pernix
KX026417.1	Brachycephalus_brunneus	KX026400.1	Brachycephalus_izecksohni	KX026366.1	Brachycephalus_pernix

KX026367.1	Brachycephalus_pernix	KX026473.1	Brachycephalus_sp.1
KX026368.1	Brachycephalus_pernix	KX026414.1	Brachycephalus_sp.4
KX026369.1	Brachycephalus_pernix	KX026415.1	Brachycephalus_sp.4
KX026519.1	Brachycephalus_pernix	KX026416.1	Brachycephalus_sp.4
KX026520.1	Brachycephalus_pernix	KX026443.1	Brachycephalus_sp.4
KX026370.1	Brachycephalus_pombali	KX026521.1	Brachycephalus_sp.5
KX026371.1	Brachycephalus_pombali	KX026522.1	Brachycephalus_sp.5
KX026372.1	Brachycephalus_pombali	KX026523.1	Brachycephalus_tridactylus
KX026452.1	Brachycephalus_pombali	KX026524.1	Brachycephalus_tridactylus
KX026453.1	Brachycephalus_pombali	KX026525.1	Brachycephalus_tridactylus
KX026454.1	Brachycephalus_pombali	KX026526.1	Brachycephalus_tridactylus
KX026455.1	Brachycephalus_pombali	KX026527.1	Brachycephalus_tridactylus
KX026456.1	Brachycephalus_pombali	KX026373.1	Brachycephalus_verrucosus
KX026457.1	Brachycephalus_pombali	KX026374.1	Brachycephalus_verrucosus
KX026458.1	Brachycephalus_pombali	KX026375.1	Brachycephalus_verrucosus
KX026459.1	Brachycephalus_pombali	KX026376.1	Brachycephalus_verrucosus
KX026461.1	Brachycephalus_quiririensis	KX026377.1	Brachycephalus_verrucosus
KX026462.1	Brachycephalus_quiririensis	KX026378.1	Brachycephalus_verrucosus
KX026463.1	Brachycephalus_quiririensis	KX026379.1	Brachycephalus_verrucosus
KX026464.1	Brachycephalus_quiririensis	KX026380.1	Brachycephalus_verrucosus
KX026465.1	Brachycephalus_quiririensis	KX026381.1	Brachycephalus_verrucosus
KX026466.1	Brachycephalus_quiririensis	KX026382.1	Brachycephalus_verrucosus
KX026482.1	Brachycephalus_sp.1	KX026467.1	Brachycephalus_verrucosus
KX026451.1	Brachycephalus_sp.1	KX026468.1	Brachycephalus_verrucosus
KX026474.1	Brachycephalus_sp.1	KX026654.1	Ischnocnema_guentheri
KX026475.1	Brachycephalus_sp.1		
KX026476.1	Brachycephalus_sp.1		
KX026477.1	Brachycephalus_sp.1		
KX026478.1	Brachycephalus_sp.1		
KX026479.1	Brachycephalus_sp.1		
KX026480.1	Brachycephalus_sp.1		
KX026481.1	Brachycephalus_sp.1		
KX026470.1	Brachycephalus_sp.1		
KX026471.1	Brachycephalus_sp.1		
KX026472.1	Brachycephalus_sp.1		

HQ435732.1	Brachycephalus_alipioi
KX026200.1	Brachycephalus_auroguttatus
KX026201.1	Brachycephalus_auroguttatus
KX026202.1	Brachycephalus_auroguttatus
KX026203.1	Brachycephalus_auroguttatus
KX026204.1	Brachycephalus_auroguttatus
KX026205.1	Brachycephalus_auroguttatus
KX026206.1	Brachycephalus_auroguttatus
KX026207.1	Brachycephalus_auroguttatus
KX026208.1	Brachycephalus_auroguttatus
KX026209.1	Brachycephalus_auroguttatus
KX026210.1	Brachycephalus_auroguttatus
KX026211.1	Brachycephalus_auroguttatus
KX026212.1	Brachycephalus_auroguttatus
KX026213.1	Brachycephalus_auroguttatus
KX026214.1	Brachycephalus_auroguttatus
KX026215.1	Brachycephalus_auroguttatus
KX026216.1	Brachycephalus_boticario
KX026217.1	Brachycephalus_boticario
KX026218.1	Brachycephalus_boticario
KX026219.1	Brachycephalus_boticario
KX026220.1	Brachycephalus_boticario
KX026221.1	Brachycephalus_boticario
KX026222.1	Brachycephalus_boticario
KX026223.1	Brachycephalus_boticario
HQ435733.1	Brachycephalus_brunneus
KX026130.1	Brachycephalus_brunneus
KX026131.1	Brachycephalus_brunneus
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KX026150.1	Brachycephalus_brunneus
KX026151.1	Brachycephalus_brunneus
KX026152.1	Brachycephalus_brunneus
KX026111.1	Brachycephalus_brunneus
KX026112.1	Brachycephalus_brunneus
KX026113.1	Brachycephalus_brunneus
KX026114.1	Brachycephalus_brunneus
KX026115.1	Brachycephalus_brunneus
KX026224.1	Brachycephalus_curupira
KX026225.1	Brachycephalus_curupira
KX026226.1	Brachycephalus_curupira
KX026227.1	Brachycephalus_curupira
KX026228.1	Brachycephalus_curupira
HQ435734.1	Brachycephalus_didactylus
JX267681.1	Brachycephalus_didactylus
HQ435735.1	Brachycephalus_ephippium
KX026363.1	Brachycephalus_ephippium
HQ435737.1	Brachycephalus_ferruginus
KX026082.1	Brachycephalus_ferruginus
KX026083.1	Brachycephalus_ferruginus
KX026084.1	Brachycephalus_ferruginus
KX026142.1	Brachycephalus_fuscolineatus
KX026143.1	Brachycephalus_fuscolineatus
KX026144.1	Brachycephalus_fuscolineatus
KX026185.1	Brachycephalus_fuscolineatus
KX026186.1	Brachycephalus_fuscolineatus
KX026187.1	Brachycephalus_fuscolineatus
KX026188.1	Brachycephalus_fuscolineatus
KX026189.1	Brachycephalus_fuscolineatus
HQ435736.1	Brachycephalus_garbeanus
HQ435738.1	Brachycephalus_hermogenesi
HQ435739.1	Brachycephalus_izecksohni
KX026100.1	Brachycephalus_izecksohni
KX026101.1	Brachycephalus_izecksohni
KX026102.1	Brachycephalus_izecksohni
KX026103.1	Brachycephalus_izecksohni
KX026104.1	Brachycephalus_izecksohni
KX026105.1	Brachycephalus_izecksohni
KX026106.1	Brachycephalus_izecksohni
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KX026110.1	Brachycephalus_izecksohni
KX026085.1	Brachycephalus_leopardus
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KX026097.1	Brachycephalus_leopardus

KX026098.1	Brachycephalus_leopardus
KX026099.1	Brachycephalus_leopardus
KX026162.1	Brachycephalus_mariaeterezae
KX026190.1	Brachycephalus_mariaeterezae
KX026191.1	Brachycephalus_mariaeterezae
KX026192.1	Brachycephalus_mariaeterezae
KX026193.1	Brachycephalus_mariaeterezae
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KX026196.1	Brachycephalus_mariaeterezae
KX026197.1	Brachycephalus_mariaeterezae
KX026198.1	Brachycephalus_mariaeterezae
KX026199.1	Brachycephalus_mariaeterezae
HQ435740.1	Brachycephalus_nodoterga
JX298238.1	Brachycephalus_nodoterga
KX026146.1	Brachycephalus_olivaceus
KX026147.1	Brachycephalus_olivaceus
KX026148.1	Brachycephalus_olivaceus
KX026149.1	Brachycephalus_olivaceus
KX026171.1	Brachycephalus_olivaceus
HQ435741.1	Brachycephalus_pernix
KX026064.1	Brachycephalus_pernix
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KX026066.1	Brachycephalus_pernix
KX026067.1	Brachycephalus_pernix
KX026068.1	Brachycephalus_pernix
KX026229.1	Brachycephalus_pernix
KX026230.1	Brachycephalus_pernix
HQ435742.1	Brachycephalus_pitanga
HQ435743.1	Brachycephalus_pombali
KX026069.1	Brachycephalus_pombali
KX026070.1	Brachycephalus_pombali
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KX026159.1	Brachycephalus_pombali
KX026160.1	Brachycephalus_pombali
KX026161.1	Brachycephalus_pombali
KX026163.1	Brachycephalus_quiririensis
KX026164.1	Brachycephalus_quiririensis
KX026165.1	Brachycephalus_quiririensis
KX026166.1	Brachycephalus_quiririensis
KX026167.1	Brachycephalus_quiririensis
KX026168.1	Brachycephalus_quiririensis
KX026184.1	Brachycephalus_sp.1
KX026153.1	Brachycephalus_sp.1
KX026176.1	Brachycephalus_sp.1
KX026177.1	Brachycephalus_sp.1
KX026178.1	Brachycephalus_sp.1
KX026179.1	Brachycephalus_sp.1
KX026180.1	Brachycephalus_sp.1
KX026181.1	Brachycephalus_sp.1
KX026182.1	Brachycephalus_sp.1
KX026183.1	Brachycephalus_sp.1
KX026172.1	Brachycephalus_sp.1
KX026173.1	Brachycephalus_sp.1
KX026174.1	Brachycephalus_sp.1
KX026175.1	Brachycephalus_sp.1
KX026116.1	Brachycephalus_sp.4
KX026117.1	Brachycephalus_sp.4
KX026118.1	Brachycephalus_sp.4
KX026145.1	Brachycephalus_sp.4
KX026231.1	Brachycephalus_sp.5
KX026232.1	Brachycephalus_sp.5
HQ435744.1	Brachycephalus_toby
KX026233.1	Brachycephalus_tridactylus
KX026234.1	Brachycephalus_tridactylus
KX026235.1	Brachycephalus_tridactylus
KX026236.1	Brachycephalus_tridactylus
KX026237.1	Brachycephalus_tridactylus
KX026072.1	Brachycephalus_verrucosus
KX026073.1	Brachycephalus_verrucosus
KX026074.1	Brachycephalus_verrucosus
KX026075.1	Brachycephalus_verrucosus
KX026076.1	Brachycephalus_verrucosus
KX026077.1	Brachycephalus_verrucosus
KX026078.1	Brachycephalus_verrucosus
KX026079.1	Brachycephalus_verrucosus
KX026080.1	Brachycephalus_verrucosus
KX026081.1	Brachycephalus_verrucosus
KX026169.1	Brachycephalus_verrucosus
KX026170.1	Brachycephalus_verrucosus
HQ435745.1	Brachycephalus_vertebralis
JX267782.1	Ischnocnema_parva
JX267783.1	Ischnocnema_parva
JX267784.1	Ischnocnema_parva

GBIF

GBIF Id	Species	GBIF Id	Species	GBIF Id	Species	GBIF Id	Species
1499611458	B. darkside	1838115454	B. ephippium	1321965818	B. ephippium	1320583585	B. ephippium
1499611460	B. darkside	1838115432	B. ephippium	1321895643	B. ephippium	1320577121	B. ephippium
1323981216	B. alipioi	1838115392	B. ephippium	1321875610	B. ephippium	1320534916	B. ephippium
1322440569	B. didactylus	1838115387	B. ephippium	1321857505	B. ephippium	1320522558	B. ephippium
1320911350	B. didactylus	1830940153	B. ephippium	1321796691	B. ephippium	1320506677	B. ephippium
1319740257	B. didactylus	1830940084	B. ephippium	1321790833	B. ephippium	1320402945	B. ephippium
1319180094	B. didactylus	1802704836	B. ephippium	1321680267	B. ephippium	1320277958	B. ephippium
1317741431	B. didactylus	1638365274	B. ephippium	1321593298	B. ephippium	1320249674	B. ephippium
686889450	B. didactylus	1638365262	B. ephippium	1321547915	B. ephippium	1320135452	B. ephippium
686889449	B. didactylus	1322859376	B. ephippium	1321526532	B. ephippium	1320134216	B. ephippium
1321913722	B. hermogenesi	1322835257	B. ephippium	1321472109	B. ephippium	1320090265	B. ephippium
1320837055	B. hermogenesi	1322824244	B. ephippium	1321465275	B. ephippium	1320052591	B. ephippium
1320618965	B. hermogenesi	1322791129	B. ephippium	1321375384	B. ephippium	1320031984	B. ephippium
1318418746	B. hermogenesi	1322683031	B. ephippium	1321366385	B. ephippium	1320022632	B. ephippium
1316246420	B. hermogenesi	1322669904	B. ephippium	1321331257	B. ephippium	1320012713	B. ephippium
1316246416	B. hermogenesi	1322614307	B. ephippium	1321280805	B. ephippium	1319938674	B. ephippium
1316246404	B. hermogenesi	1322561135	B. ephippium	1321261793	B. ephippium	1319823725	B. ephippium
1316246399	B. hermogenesi	1322495507	B. ephippium	1321257456	B. ephippium	1319811300	B. ephippium
1316246398	B. hermogenesi	1322489613	B. ephippium	1321198838	B. ephippium	1319806354	B. ephippium
1316246394	B. hermogenesi	1322479613	B. ephippium	1321119175	B. ephippium	1319772075	B. ephippium
1316246393	B. hermogenesi	1322432692	B. ephippium	1321111717	B. ephippium	1319724489	B. ephippium
1316246390	B. hermogenesi	1322380439	B. ephippium	1320937898	B. ephippium	1319717034	B. ephippium
1316246389	B. hermogenesi	1322377225	B. ephippium	1320877806	B. ephippium	1319526376	B. ephippium
1316246388	B. hermogenesi	1322358014	B. ephippium	1320842167	B. ephippium	1319505747	B. ephippium
1316246381	B. hermogenesi	1322342100	B. ephippium	1320836055	B. ephippium	1319442597	B. ephippium
1300317510	B. hermogenesi	1322337488	B. ephippium	1320808393	B. ephippium	1319434791	B. ephippium
1576195296	B. nodoterga	1322286057	B. ephippium	1320753284	B. ephippium	1319415677	B. ephippium
1322892924	B. nodoterga	1322251345	B. ephippium	1320723587	B. ephippium	1319397564	B. ephippium
1321718426	B. nodoterga	1322198075	B. ephippium	1320684122	B. ephippium	1319397013	B. ephippium
1319815512	B. nodoterga	1322173535	B. ephippium	1320671940	B. ephippium	1319313184	B. ephippium
1318519429	B. nodoterga	1322131136	B. ephippium	1320611972	B. ephippium	1319250480	B. ephippium
1317701593	B. nodoterga	1322043375	B. ephippium	1320606560	B. ephippium	1319185473	B. ephippium
476518559	B. nodoterga	1322031142	B. ephippium	1320587364	B. ephippium	1319163968	B. ephippium

GBIF Id	Species	GBIF Id	Species	GBIF Id	Species	GBIF Id	Species	GBIF Id	Species
1319141648	B. ephippium	1317806154	B. ephippium	1316248186	B. ephippium	1316243820	B. ephippium	1061332587	B. ephippium
1319140716	B. ephippium	1317783521	B. ephippium	1316248182	B. ephippium	1316243817	B. ephippium	1061332585	B. ephippium
1319063689	B. ephippium	1317752534	B. ephippium	1316248178	B. ephippium	1316243563	B. ephippium	1061332577	B. ephippium
1319063562	B. ephippium	1317719477	B. ephippium	1316248174	B. ephippium	1316243549	B. ephippium	1061332573	B. ephippium
1319062526	B. ephippium	1317490654	B. ephippium	1316248165	B. ephippium	1316243536	B. ephippium	1061332559	B. ephippium
1319052414	B. ephippium	1317475818	B. ephippium	1316248163	B. ephippium	1316242675	B. ephippium	1061332548	B. ephippium
1318993823	B. ephippium	1317412412	B. ephippium	1316248155	B. ephippium	1316240809	B. ephippium	686813007	B. ephippium
1318934859	B. ephippium	1317364158	B. ephippium	1316248154	B. ephippium	1316240802	B. ephippium	686813006	B. ephippium
1318822122	B. ephippium	1317329395	B. ephippium	1316248153	B. ephippium	1316238200	B. ephippium	686813005	B. ephippium
1318803391	B. ephippium	1316259931	B. ephippium	1316248151	B. ephippium	1316238184	B. ephippium	686813004	B. ephippium
1318730539	B. ephippium	1316259927	B. ephippium	1316248147	B. ephippium	1316238182	B. ephippium	686813003	B. ephippium
1318700070	B. ephippium	1316259885	B. ephippium	1316246793	B. ephippium	1316238180	B. ephippium	686798422	B. ephippium
1318693266	B. ephippium	1316259446	B. ephippium	1316246555	B. ephippium	1316238177	B. ephippium	686798421	B. ephippium
1318570257	B. ephippium	1316250015	B. ephippium	1316246541	B. ephippium	1316238175	B. ephippium	686798420	B. ephippium
1318524832	B. ephippium	1316249938	B. ephippium	1316246539	B. ephippium	1316238174	B. ephippium	686798419	B. ephippium
1318446963	B. ephippium	1316249936	B. ephippium	1316246528	B. ephippium	1316238170	B. ephippium	686798418	B. ephippium
1318374083	B. ephippium	1316249935	B. ephippium	1316245866	B. ephippium	1316238167	B. ephippium	686798417	B. ephippium
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1318327786	B. ephippium	1316249643	B. ephippium	1316245843	B. ephippium	1316238142	B. ephippium	657384309	B. ephippium
1318316193	B. ephippium	1316249640	B. ephippium	1316245834	B. ephippium	1316238139	B. ephippium	657371249	B. ephippium
1318221757	B. ephippium	1316249637	B. ephippium	1316245827	B. ephippium	1316238120	B. ephippium	657371248	B. ephippium
1318221660	B. ephippium	1316249629	B. ephippium	1316245825	B. ephippium	1316237664	B. ephippium	621071343	B. ephippium
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1318076919	B. ephippium	1316249623	B. ephippium	1316245678	B. ephippium	1078798687	B. ephippium	609482266	B. ephippium
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1317926112	B. ephippium	1316249613	B. ephippium	1316244756	B. ephippium	1061332610	B. ephippium	543694083	B. ephippium
1317924312	B. ephippium	1316248207	B. ephippium	1316243846	B. ephippium	1061332605	B. ephippium	543694082	B. ephippium
1317899499	B. ephippium	1316248193	B. ephippium	1316243833	B. ephippium	1061332604	B. ephippium	543694081	B. ephippium
1317891890	B. ephippium	1316248192	B. ephippium	1316243827	B. ephippium	1061332601	B. ephippium	543694080	B. ephippium
1317891587	B. ephippium	1316248188	B. ephippium	1316243823	B. ephippium	1061332596	B. ephippium	543694079	B. ephippium

GBIF Id	Species	GBIF Id	Species	GBIF Id	Species
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543694076	B. ephippium	476518758	B. ephippium	476517661	B. ephippium
543694075	B. ephippium	476518757	B. ephippium	476517660	B. ephippium
543694074	B. ephippium	476518756	B. ephippium	476517636	B. ephippium
543694073	B. ephippium	476518755	B. ephippium	476517635	B. ephippium
543694072	B. ephippium	476518735	B. ephippium	476517634	B. ephippium
543694071	B. ephippium	476518734	B. ephippium	476517633	B. ephippium
543694070	B. ephippium	476518733	B. ephippium	476517632	B. ephippium
543694069	B. ephippium	476518732	B. ephippium	476517631	B. ephippium
543694068	B. ephippium	476518731	B. ephippium	476513827	B. ephippium
543694066	B. ephippium	476518730	B. ephippium	476513826	B. ephippium
543686590	B. ephippium	476518710	B. ephippium	476513825	B. ephippium
543686589	B. ephippium	476518709	B. ephippium	476471046	B. ephippium
543522808	B. ephippium	476518708	B. ephippium	476471045	B. ephippium
543522807	B. ephippium	476518018	B. ephippium	476471002	B. ephippium
543522806	B. ephippium	476518017	B. ephippium	476470942	B. ephippium
543522804	B. ephippium	476518016	B. ephippium	476470941	B. ephippium
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543522802	B. ephippium	476518014	B. ephippium	476470939	B. ephippium
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476792574	B. ephippium	476517718	B. ephippium		
476637738	B. ephippium	476517717	B. ephippium		
476637635	B. ephippium	476517716	B. ephippium		
476557693	B. ephippium	476517715	B. ephippium		
476518787	B. ephippium	476517714	B. ephippium		
476518786	B. ephippium	476517692	B. ephippium		
476518785	B. ephippium	476517691	B. ephippium		
476518784	B. ephippium	476517690	B. ephippium		
476518783	B. ephippium	476517689	B. ephippium		
476518765	B. ephippium	476517688	B. ephippium		
476518764	B. ephippium	476517665	B. ephippium		
476518763	B. ephippium	476517664	B. ephippium		
476518762	B. ephippium	476517663	B. ephippium		