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A New Species of Phenacosaur *Anolis* (Squamata; Iguanidae) from Peru and a Comprehensive Phylogeny of *Dactyloa*-clade *Anolis* Based on New DNA Sequences and Morphology

Steven Poe[1], Ian Latella[1], Fernando Ayala-Varela[2], Christian Yañez-Miranda[3], and Omar Torres-Carvajal[2]

We describe a new species of *Anolis* from the Andes of northern Peru. This form is similar to species formerly assigned to the genus *Phenacosaurus* and to Ernest Williams' *tigrinus* series. That is, the new species possesses large smooth headscales, cryptic coloration, and short limbs and tail. We present new DNA and morphological data and perform a comprehensive phylogenetic analysis of the *Dactyloa* clade of *Anolis*. The new species is estimated to be close to phenotypically similar species from Peru and Venezuela. We revise the taxonomy of *Dactyloa* based on our estimate. Most previously recognized phylogenetically defined groups are retained with restricted species contents. Several species currently scorable only for morphological data could not be placed in any group with confidence. The species status of the enigmatic mainland form *Anolis deltae* should be re-examined with reference to the *roquet* group of southern Lesser Antillean *Anolis*.

THE *Anolis* formerly assigned to the genus *Phenacosaurus* are known from the tepuis of Venezuela and the Andes as far south as northern Peru. These species have short limbs and tail, large smooth headscales, and apparently cryptic coloration and behavior. What little is known of the ecology of phenacosaur anoles (we here use this term as an informal designation for species in the *Dactyloa* clade that share the above phenotype) suggests that the "twig" anoles of the Caribbean such as *A. insolitus* are strikingly convergent to these forms in ecology and morphology, apparently signaling one of the few cases of mainland-island convergence for the well-studied Caribbean ecomorphs (Lazell, 1969; Miyata, 1983; Schaad and Poe, 2010).

Until the late 1980s the phenacosaur anoles were represented by three forms, *Phenacosaurus heterodermus* Dumeril, 1851; *P. nicefori* Barbour, 1932; and *P. orcesi* Lazell, 1969. The collective distinctiveness of these species allowed Lazell (1969) to cleanly diagnose Barbour's (1920) genus *Phenacosaurus*, although even at that time it was recognized that if this group formed a clade it was likely to be nested within *Anolis* (Etheridge, pers. comm., in Lazell, 1969:4; see Etheridge, 1959:fig. 10). Seven more species of *Phenacosaurus* were described between 1988 and 1996, including five by Ernest Williams and collaborators (e.g., Williams et al., 1996). Among these were small, *Anolis*-like species such as *Phenacosaurus euskalerriari* that blurred the boundaries between *Phenacosaurus* and Ernest Williams' (1976) *tigrinus* group of *Anolis*. The results of phylogenetic analyses necessitated synonymizing *Phenacosaurus* with *Anolis* (Etheridge, 1959; Poe, 1998). Recent descriptions of large smooth headscaled, short-limbed Andean *Anolis* have simply compared the described species to both *tigrinus*- and phenacosaur-group *Anolis* (e.g., Ugueto et al., 2007).

Phylogenetic analyses have included some species from the *tigrinus* and *Phenacosurus* groups. Poe (2004) included two species described as *Phenacosaurus* (*nicefori, heterodermus*), which formed a clade in his analyses, and two species from Williams' (1976) *tigrinus* group (*solitarius, ruizii*) that formed part of a larger sister clade to the *Phenacosaurus* plus *A. proboscis*. Castañeda and de Queiroz (2011) analyzed six species described as *Phenacosaurus* (*heterodermus, inderenae, vanzolinii, euskalerriari, nicefori, neblininus*) and *tigrinus*-group anoles *A. tigrinus* and *A. anatoloros*. They found five of their six *Phenacosaurus* to be monophyletic, with *A.* (*Phenacosaurus*) *neblininus*, *A. tigrinus*, and *A. anatoloros* placed elsewhere within the *Dactyloa* clade, and named a *Phenacosaurus* clade for their five monophyletic species. Most species archetypically at the *tigrinus*/*Phenacosaurus* group boundary (e.g., *A. orcesi, A. lamari, A. menta*) have not been included in phylogenetic analyses. A phylogenetic description of phenacosaur anoles remains elusive (but see Castañeda and de Queiroz, 2013), and new species descriptions of Andean *Anolis* with large smooth head scales must take account of all species that fit the phenotypic profile of phenacosaur species.

The *Phenacosaurus*/*tigrinus* group was documented in Peru by Williams and Mittermeier in 1991. Poe and Yañez-Miranda (2007) subsequently described this population as a new species, *A. williamsmittermeierorum*. Here we describe a second Peruvian phenacosaur *Anolis* from near the type locality of *A. williamsmittermeierorum*. We estimate the evolutionary placement of this new species in the *Dactyloa* clade of *Anolis* via a phylogenetic analysis of all species in this clade.

MATERIALS AND METHODS

Species description.—We adopt the evolutionary species concept (Simpson, 1961; Wiley, 1978) and operationalize this concept by identifying species based on consistent differences between populations. That is, we hypothesize that populations that are diagnosable by major differences in the frequencies of traits are distinct evolutionary lineages or species.

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Measurements were made with digital calipers on preserved specimens and are given in millimeters (mm), usually to the nearest 0.1 mm. Snout–vent length (SVL) was measured from tip of snout to anterior margin of cloaca. Head length was measured from tip of snout to anterior margin of ear opening. Femoral length was measured from midline of venter to knee, with limb bent at a 90-degree angle. Head width was measured at the broadest part of the head, between the posterolateral corners of the orbits. Comparisons were made with preserved material of species that are phenetically similar to the new species (Appendix 1). Scale terminology and characters used mainly follow standards established by Ernest Williams for species descriptions of anoline lizards (e.g., Williams et al., 1995). Type specimens were deposited in the Museum of Southwestern Biology (MSB) and the Universidad Nacional de la Amazonía Peruana (UNAP).

Phylogenetics.—We endeavored to obtain a phylogenetic estimate for all *Dactyloa* (content hypothesized by Etheridge [1959; as his *latifrons* series], Nicholson et al. [2012], and others; we adopt the definition of Castañeda and de Queiroz [2011, 2013] for this clade name for this group of *Anolis*), but viable tissues still are not available for several forms. Thus we attempted to obtain morphological data for all species of *Dactyloa* so that a preliminary comprehensive phylogenetic estimate was possible. We were able to examine specimens or detailed drawings of several poorly known forms, including *Anolis deltae* (TCWC 58522, the second known specimen of this species), *A. dissimilis* (USNM 538280, the first known female of this species), *A. parilis* (our collections; previously known from only the holotype), *A. antioquiae* (our collections), *A. pseudotigrinus* (ZMH RO1153), and *A. nasofrontalis* (ZMH RO4117; head scale drawings discovered at MCZ commissioned by Ernest Williams). Specimens, photographs, or useful drawings of some species (*Anolis laevis, A. paravertebralis*) were not available to us. These species were scored for a few characters based mainly on original descriptions.

We scored the new species, all other species of *Dactyloa* anoles except *Anolis poei*, and six undescribed species and seven outgroups for a maximum of 34 phylogenetic characters of external morphology (Appendix 2). These characters mostly comprise a subset of those morphological characters used by previous students of phylogenetics of this group (Etheridge, 1959; Poe, 2004; Castañeda and de Queiroz, 2013). We used this subset because we found these characters to be informatively variable and unambiguously scorable in most species of this clade. Continuous variation was coded using Thiele's (1993) approach, intraspecific variation was coded with Wiens' (1995) frequency coding with six states (i.e., 0–5). The final morphological matrix included 90 species of *Dactyloa* (including six undescribed forms) and seven outgroups. Our analysis allows only limited testing of the monophyly of the *Dactyloa* group due to the inclusion of few non-*Dactyloa* anoles and no non-anoles. We make this assumption of the likely monophyly of *Dactyloa* without complete confidence, but believe it reasonable based on previous work (e.g., Castañeda and de Queiroz, 2011) and our own unpublished analyses using much larger samples of *Anolis*.

We combined the morphological data with DNA sequence data from Jackman et al. (1999; ND2), Castañeda and de Queiroz (2011; ND2, RAG1, COI), Lotzkat et al. (2013; 16S), additional GenBank sequences of *Anolis* for these genes, and newly collected data from our labs (51 new sequences among ND2, COI, and ECEL; Table 1). This sample includes nine recognized species of *Dactyloa* never before scored for DNA sequence data (*Anolis anchicayae, A. apollinaris, A. eulaemus, A. fasciatus, A. megalopithecus, A. orcesi, A. otongae, A. parilis, A. proboscis)* and 24 additional recognized species of the *Dactyloa* clade beyond the previous largest estimate (Castañeda and de Queiroz, 2013). Sixty-one species were scored for at least one gene. One species included by Castañeda and de Queiroz (2013), *A. purpurescens*, is excluded by us because we believe it to be a junior synonym of *A. frenatus*. Genes were aligned using the ClustalW algorithm defaults in MEGA (Tamura et al., 2013), then altered manually with reference to amino acid codon position.

We first used PartitionFinder (Lanfear et al., 2012) to explore different partitioning strategies for the DNA data. This program tests for optimal data partitions and models under the Bayesian Information Criterion (BIC; among other options) given some set of genes and some hypothesized maximum number of partitions. We hypothesized that each codon position for the protein coding genes (COI, ND2, ECEL, RAG1) and the 16S gene may warrant separate models, for a maximum of 13 potential partitions.

Phylogenetic matrices like ours that include both complex morphological and DNA characters are limited to a few programs, and to our knowledge only MrBayes (Ronquist et al., 2012) allows integration of morphological and DNA data relatively equally in a model-based framework (RaxML allows model-based incorporation of morphological data but tests characters for congruence with a tree based on DNA). We ran a concatenated partitioned analysis in MrBayes, with one partition for the morphology (including ordered and unordered characters) and other partitions decreed by PartitionFinder. Morphology was analyzed with the Mk model and each DNA partition was analyzed with the 'mixed' model, which allows for all GTR class models to be considered. Rate variation among characters was allowed to be independent for each partition using the gamma distribution, with topology and branchlength parameters 'linked' across partitions. Unlinking of the branchlength parameter may be realistic, but our attempts at analyses with this parameter unlinked failed to converge. This nonconvergence result may be due to strong incongruence between the two largest datasets, morphology and ND2 (e.g., $P = 0.001$; PAUP's [Swofford, 2003] incongruence length difference test), manifest in greatly differing branchlengths for shared topologies.

We ran a Markov-Chain Monte Carlo Bayesian analysis under the above parameters and default priors (i.e., Symmetric Dirichlet with fixed variance parameter for state frequencies of morphology, Dirichlet for DNA state frequencies; equal probability for all GTR DNA models; exponential for gamma distributed site rates) for 25,000,000 generations with two runs of one cold and three heated chains with heating temp of 0.03, sampling trees every 1,000 generations.

Anolis peruensis, new species

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Figures 1–3, Tables 1–2

Table 1. Data coverage for phylogenetic analysis. J = Jackman et al. (1999); C = Castañeda and de Queiroz (2011); N^1= Nicholson et al. (2005); N^2 = Nicholson et al. (2012); H = Hass et al. (1993); A = Alföldi et al. (2011); L = Lotzkat et al. (2013); CR = Creer et al. (2001); HN = Harmon et al. (2003); CE = Castoe et al. (2008); S = Schulte and Cartwright (2009); K = Köhler et al. (2012); * = this paper.

Species	morphology	ND2	COI	16S	RAG1	ECEL
aeneus	*	J	C	A	C	
aequatorialis	*	C	C		C	
agassizi	*	C	C		C	
anatoloros	*	C	C		C	
anchicayae	*					*
anoriensis	*	C	C		C	
antioquiae	*					
apollinaris	*					*
bellipeniculus	*					
blanquillanus	*					
boettgeri	*			H		
bonairensis	*	CR				
calimae	*	C	C		C	
caquetae	*					
carlostoddi	*					
casildae	*	N^1	C	L	C	*
chloris	*	*	C		C	*
chocorum	*	C	C		C	*
cuscoensis	*					
danieli	*	C	C		C	
deltae	*					
dissimilis	*					
eulaemus	*					*
euskalerriari	*	C	C		C	
extremus	*	CR	C	A	C	*
fasciatus	*	*	*			*
festae	*	C	C		C	
fitchi	*	C	C		C	*
fraseri	*	*	C		C	*
frenatus	*	C	C	L	C	*
gemmosus	*	C	C		C	
ginaelisae	*			L		
gorgonae	*	N^2				
griseus	*	HN	C	H	C	
heterodermus	*	C	C		C	
huilae	*	C	C		C	
ibanezi	*		*	L		*
inderenae	*	HN	C		C	
insignis	*					
jacare	*	C	C		C	
kunayalae	*	N^1	*	L		
laevis	*					
lamari	*					
latifrons	*		*			
limon	*					
luciae	*	C	C		C	
maculigula	*	C	C		C	
megalopithecus	*					*
menta	*					
microtus	*	J	*	L		*
mirus	*					
nasofrontalis	*					
neblininus	*	C	C		C	
nicefori	*	J				
NSP.E	*			L		
NSP.F	*	*	C	L		*
NSP.L	*					
NSP.R	*	*	*			*
NSP.W	*	*	*			
NSP.Z	*	*	*			
orcesi	*	*	*			
otongae	*	*	*			
paravertebralis	*					
parilis	*	*	*			*
peraccae	*	*	C		C	*
peruensis	*					
philopunctatus	*					
phyllorhinus	*					
podocarpus	*	C	C			
princeps	*	*	C		C	*
proboscis	*	*	*			*
propinquus	*					
pseudotigrinus	*					
punctatus	*	C	C	A	C	*
richardii	*	C	C		C	
roquet	*	C	C	A	C	
ruizii	*					
santamartae	*					
soinii	*	*				
solitarius	*					
squamulatus	*					
tetarii	*					
tigrinus	*	C	C		C	
transversalis	*	C	C	A	C	
trinitatus	*	HN	C		C	
umbrivagus	*					
vanzolini	*	*	C			
vaupesianus	*					
ventrimaculatus	*	C	C		C	
williamsmittermeierorum	*					
bimaculatus	*	J	C		C	
carolinensis	*	CE	CE	CE	S	CE
cupreus	*	C	C	K	C	*
cuvieri	*	J	C	A	C	*
equestris	*	J	C	A	C	*
lucius	*	J	C	H	C	
marcanoi	*	J	C		C	*

Holotype.—MSB 72521, adult male, 2.4 km west of Esperanza, Amazonas Province, Peru, 05°43.553′S, 77°54.328′W, 1857 m, Steven Poe, Christian Yañez-Miranda, and Jenny Hollis, 25 April 2005.

Paratypes.—MSB 72522, adult female, MZUNAP 2.000188, hatchling female, same locality and collectors as holotype, 24 April 2005.

Diagnosis.—We compare the new species to all recognized species of *Anolis* in Ecuador and Peru that display large smooth headscales and short limbs and tail. *Anolis peruensis* may be differentiated from *A. heterodermus* and *A. vanzolinii* by its smaller body size (SVL to 104 mm in *A. vanzolinii*, 73 mm in *A. heterodermus*; 56 mm in *A. peruensis*) and homogeneous lateral scutellation (heterogeneous in *A. heterodermus* and *A. vanzolinii*). *Anolis peruensis* differs from *A. orcesi* in possessing smaller headscales (Table 2) and differently colored male and female dewlaps (*A. orcesi* male: yellow with greenish blue at base, female: orange;

Fig. 1. Holotype of *Anolis peruensis*, new species (MSB 72521).

A. peruensis male: solid yellow, female: black). *Anolis peruensis* differs from *A. williamsmittermeierorum* in male dewlap color (solid yellow in *A. peruensis*; tan and peach-orange in *A. williamsmittermeierorum*), female dewlap pattern (solid black in *A. peruensis*; black and white in *A. williamsmittermeierorum*), internal throat coloration (gray in new species, black throat with bright yellow-orange at hinges of mouth in *A. williamsmittermeierorum*), larger size of dewlap scales, and smaller male and female dewlap (Fig. 2). *Anolis peruensis* differs from *Anolis laevis* in the anterior extent of the rostral scale (slight overlap of mental in *A. peruensis*; significant anterior extent in ''proboscis anole'' *A. laevis* [see Williams, 1979:fig. 1]), the number of dorsal midcaudal scale rows (one in *A. peruensis*, two in *A. laevis*) and the number of rows of loreal scales anterior to the orbit (three or four in *A. peruensis*, two in *A. laevis*). *Anolis peruensis* is most likely to be confused with *A. orcesi* and *A. williamsmittermeierorum*. Table 2 summarizes characteristics for these species.

External description of holotype.—Paratype variation in parentheses. Variation in scalation is recorded for both paratypes; measurement variation is recorded only for the adult female paratype. Snout to vent length 56.0 mm (51.0 mm); head length 15.2 mm (0.27 SVL; 13.4, 0.26 SVL), width 7.7 mm (0.14 SVL; 7.4, 0.15 SVL); ear height 0.9 mm (0.02 SVL; 1.1, 0.02 SVL); femoral length 11.9 mm (0.21 SVL; 9.6, 0.19 SVL). Tail length 78 mm (1.39 SVL; 68 mm, 1.33 SVL).

Dorsal head scales smooth; no frontal depression; rostral strongly (slightly) overlaps mental; four (4–5) scales across snout between second canthals; supraorbital semicircles in contact; no elongate supraciliary scales, only one or two slightly enlarged scales anteriorly; three or four loreal rows; circumnasal in contact with rostral; interparietal length 2.4 mm (1.9 mm); interparietal and supraorbital semicircles in contact; seven supralabials to center of eye; four (6) postmentals; five (5–6) postrostrals; some enlarged scales present in supraocular disc, decreasing gradually in size (or 3 abruptly enlarged scales), bordered medially by a partial row of small scales; mental extends deep posteriorly, indented slightly (or pronounced) posteromedially, partially divided, extending posterolaterally beyond rostral; sublabial rows strongly enlarged, with first three (4–5) scales in contact with infralabials, gradually decreasing in size posteriorly; dewlap reaches posterior to axillae in males (length of dewlap fold = 15.1 mm), with large scales in approximately five rows of single scales separated by naked skin, slightly smaller in the adult female (to axillae; length of dewlap fold = 13.4 mm); no axillary pocket; pair of enlarged postcloacal scales separated by a single scale (absent in female paratypes).

Dorsal scales smooth, with no enlarged middorsal rows, 10 (9) longitudinal rows in 5% of SVL; ventral scales slightly imbricate, smooth, 7 (6) scales in 5% of SVL, in transverse or diagonal rows.

Dorsal limb scales smooth, largest anteriorly; supradigitals smooth; toepads expanded; 18 (19) lamellae under second and third phalanges of fourth toe; tail with a single middorsal scale row.

Coloration in life.—(Adapted from field notes and color photos of holotype) Overall dorsum tan-gray, lichenous with faint diagonal lines of spots; limbs as dorsum; head tan-gray above and laterally, except white below eye extending back from lips to arch over ear, white bordered above by a poorly defined black-green line extending back from eye; venter cream; tail with faint broad bands.

Dewlap in male solid yellow with white scales. Female dewlap solid black with white scales.

Tongue tan, edges of mouth gray, throat gray. Iris reddish-tan.

Habitat and natural history.—*Anolis peruensis* currently is known only from its type locality (Fig. 4). This area is cultivated land with several small houses and other buildings. Vegetation includes ferns and bushes, with few trees and no large trees. The three specimens were collected sleeping at night on narrow perches 1.5 to 2 m up with limbs flexed. No other herpetological specimens were collected at the type locality. The type locality of *A. williamsmittermeierorum* and *A. soinii* is 34 km by road to the east. Near that site we also collected a species of *Anolis* similar to *A. fuscoauratus*. We searched briefly at sites between these localities but failed to find anoles. The disturbed nature of the type locality makes characterization difficult, but we could detect no obvious biogeographic break between the type localities of *A. williamsmittermeierorum* (described in Poe and Yañez-Miranda [2007]) and *A. peruensis*.

Phylogenetics.—The PartitionFinder analysis estimated three partitions for the DNA data (1: 16S, COI positions 1 and 2, ND2 positions 1 and 2; 2: COI position 3, ND2 position 3; 3:

Fig. 2. Dewlaps of male holotype of *A. peruensis* (A); female paratype of *Anolis peruensis* (B); male holotype of *A. williamsmittermeierorum* (C); female paratype of *A. williamsmittermeierorum* (D).

all ECEL, RAG1 positions). Phylogenetic results are summarized in Figure 5. Clades appearing in 50% or more of postburnin trees are shown. We accept this tree as the current best estimate of the phylogeny for the *Dactyloa* clade, with uncertainty represented by unresolved branches.

Anolis peruensis was found to be monophyletic with *A. williamsmittermeierorum* and some of the small Venezuelan *Phenacosaurus*/*tigrinus*-group anoles, *A. carlostoddi, A. bellipeniculus,* and *A. neblininus*. This group is part of a larger unresolved clade that includes most *Dactyloa* separate from the *roquet* group. This group is morphologically and probably ecologically uniform—all are small, high-elevation species with large smooth head scales and short limbs and tail. However, this gestalt is shared with other species found elsewhere in the tree (e.g., *A. orcesi*). The evolutionary origin of this apparent mainland ''twig'' ecomorph is not clear (see below).

The *Dactyloa* group was recovered as monophyletic. The southern Lesser Antillean *roquet* group is sister to the remaining dactyloids. This remaining group includes some well-supported clades as well as several species of unresolved relationships. The inclusion of a large number of poorly scored species (i.e., for just morphology; Table 1) more or less precludes the possibility of strong support throughout the tree (Sanderson and Shaffer, 2002), but allows at least a preliminary hypothesis of relationship for all species of *Dactyloa*.

DISCUSSION

The description of *Anolis peruensis* brings the number of currently valid species of *Anolis* in Peru to 15–17, depending on the status of *A. bocourti* and *A. scapularis* (Poe and Yañez-Miranda, 2008). We discovered at least four new species of *Anolis* (Poe and Yañez-Miranda, 2007, 2008; Poe et al., 2008; this paper) during a brief visit to 34 kilometers of northern Peruvian road in 2005. Many areas of Peru are similarly underexplored herpetologically, and we expect the anole (and reptile and amphibian) species count to increase substantially in the coming years.

Dactyloa ***clade phylogeny and taxonomy.***—Castañeda and de Queiroz (2013; hereafter CDQ) presented the most comprehensive phylogenetic estimate of the *Dactyloa* clade to date (but see Velasco and Hurtado-Gómez [2014] for an analysis of nearly as many species of *Dactyloa*) and modernized the taxonomy of the *Dactyloa* clade by erecting testable, phylogenetically defined groups based on previous names suggested by Etheridge (1959) and others. Other recent

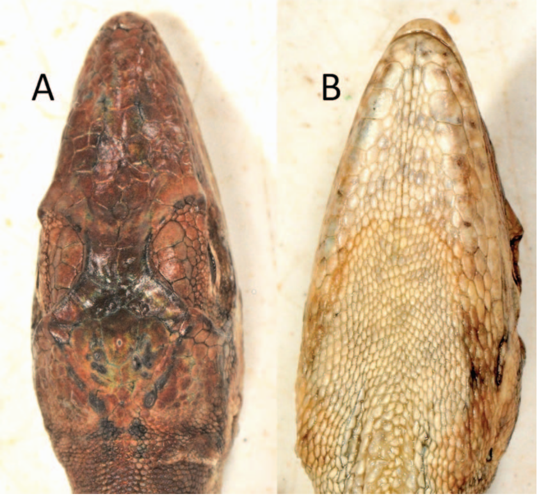

Fig. 3. Dorsal (A) and ventral (B) views of head of the holotype of *Anolis peruensis*, new species (MSB 72521).

Table 2. Comparison of species similar to *Anolis peruensis*. Mean and range are shown for measurements and counts.

	A. orcesi	*A. williamsmittermeierorum*	*A. peruensis*
Ear height/head length	0.09 (0.07–0.10)	0.09 (0.08–0.11)	0.07 (0.06–0.08)
No. scales across snout between second canthals	3.8 (3–5)	5.3 (5–6, one juvenile with 3)	4.3 (4–5)
No. loreals	7.3 (6–8)	15.1 (10–21)	18.7 (17–21)
Color of male dewlap skin	dull yellow, bluish at base	tan with peach edge	yellow
Color of female dewlap skin	yellow-orange	black and white	black
Color of throat	black	black, edges of mouth yellow-orange	gray
Enlarged middorsal crest scales	present	absent	absent
Length of dewlap fold/snout to vent length			
males	0.30 (0.27–0.33)	0.37 (0.34–0.40)	0.27
females	0.25 (0.23–0.26)	0.29 (0.27–0.31)	0.26

treatments (Vargas-Ramírez and Moreno-Arias, 2014; Prates et al., 2015) produced results largely compatible with our tree and those of CDQ; the generally lower support values in our tree relative to Prates et al. (2015) are likely attributable to our attempt to be comprehensive in taxonomic coverage (see above; Sanderson and Shaffer, 2002). The CDQ groups are not straightforwardly interpretable relative to our Figure 5 due to our increased taxon sampling within *Dactyloa* (*n* = 60 vs. *n* = 84). Below we discuss their groups relative to our recovered clades, with reference to their included species and content altered to allow for our additional species (most of which were discussed by CDQ). Castañeda and de Queiroz (2013) applied the following phylogenetically defined names to clades in their recovered trees: *aequatorialis* series (informal clade name; group name originally used by Williams, 1976), *latifrons* series (informal clade name; group name originally used by Etheridge, 1959), *Megaloa* (clade name; Castañeda and de Queiroz [2013]), *punctatus* series (informal clade name; group name first used by Williams [1976]), *roquet* series (informal clade name; group name first used by Underwood [1959]), *heterodermus* series (informal clade name; group name first used by Nicholson et al. [2012]), and *Phenacosaurus* (clade name; genus name erected by Barbour [1920]).

The listed members of the *aequatorialis* series of CDQ are not monophyletic in our optimal tree. This group was defined to include species more closely related to *A. aequatorialis* than to *A. latifrons*, *A. roquet*, and *A. heterodermus*, but some listed members of this group may be more closely related to *A. latifrons* than to *A. aequatorialis* (Fig. 5). The group name may be retained as defined if membership is restricted to the following subset: *A. anoriensis, A. eulaemus, A. aequatorialis, A. megalopithecus, A. gemmosus, A. otongae, A. ventrimaculatus*. *Anolis poei,* the one species of *Dactyloa* not included in our analyses, presumably is part of this group (see relationships in Ayala-Varela et al. [2014]).

The members of the *latifrons* series as defined by CDQ are nearly monophyletic in our tree, lacking only *A. squamulatus* (which is part of an unresolved clade including *aequatorialis*- and *latifrons*-series species) and *A. philopunctatus* (which groups with *A. punctatus* and similar species) and including *A. mirus* and *A. parilis* (''tentatively'' assigned by CDQ to their *aequatorialis* group). This group name was defined to include species more closely related to *A. latifrons* than to *A. aequatorialis, A. roquet*, and *A. heterodermus*. In light of our tree, the *latifrons*-series definition of CDQ indicates the following content: *A. fraseri, A. parilis, A. kunayalae, A. mirus, A. ibanezi, A. limon, A. chocorum, A. apollinaris, A. propinquus, A. danieli, A. latifrons, A. princeps, A. frenatus, A. casildae, A. maculigula, A. insignis, A. ginaelisae, A. microtus, A. agassizi*.

Megaloa was defined by CDQ as ''The clade originating in the ancestor in which a maximum SVL of 100 mm in males,

Fig. 4. Map of Peru. Dot shows type locality of *Anolis peruensis,* new species.

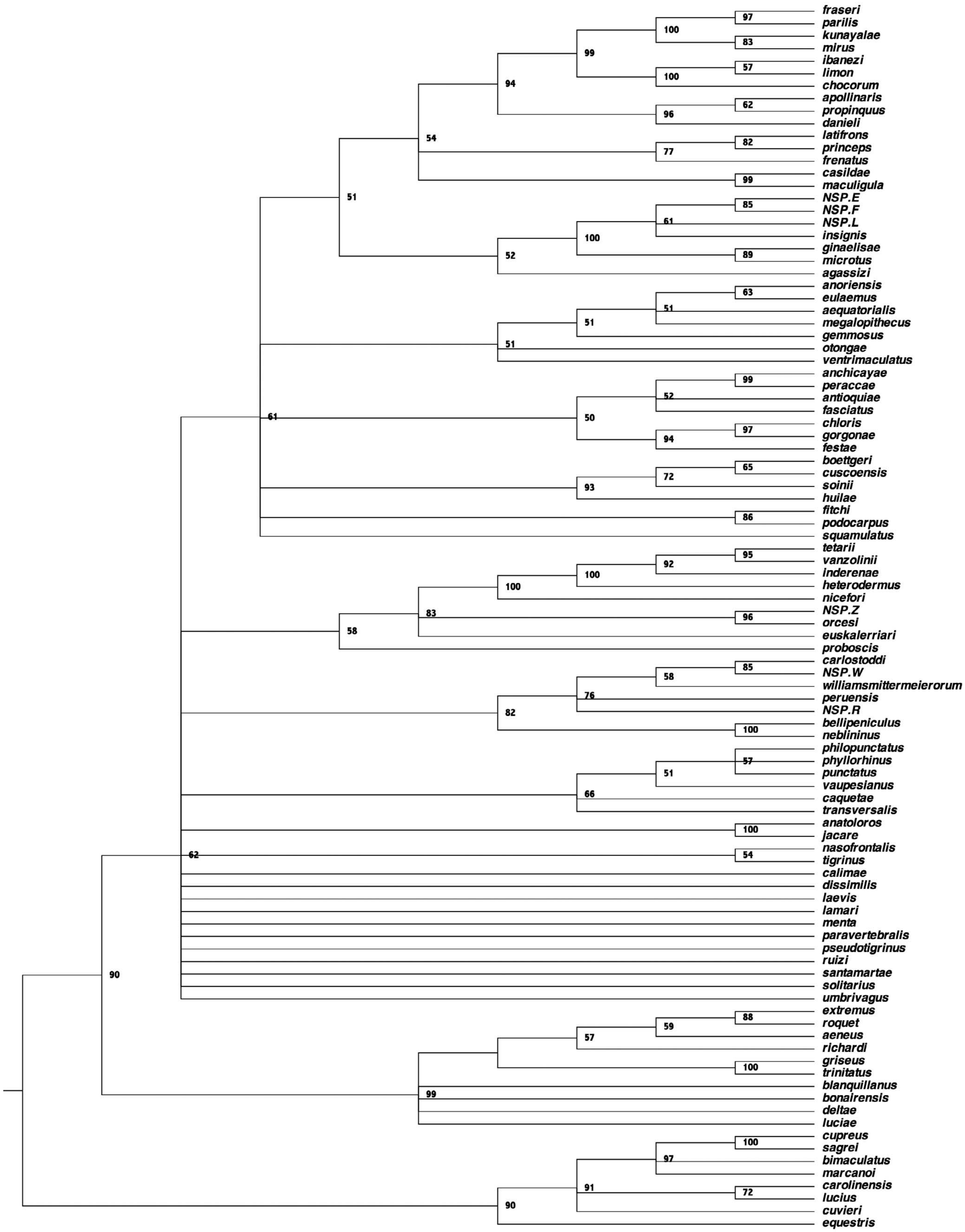

Fig. 5. Estimate of phylogenetic relationships of the *Dactyloa* clade of *Anolis*. Tree is a 50% majority-rule consensus tree of post-burnin trees from Bayesian MCMC analysis. Node labels are posterior probabilities for clades.

synapomorphic with that of *Anolis latifrons* originated.'' In our results, this definition suggests the same content as their *latifrons* series, although the content hinges somewhat on the hypothesized maximum length of some species and the phylogenetic placement of those species.

Their *punctatus* series is defined to include species more closely related to *A. punctatus* than to *A. heterodermus, A. latifrons,* and *A. roquet*. Several of the species assigned to this series, many of which are scored only for morphological data, are members of an unresolved clade that is separate from the *roquet* series. A *punctatus* series may be recognized in a restricted sense (content: *A. philopunctatus, A. phyllorhinus, A. punctatus, A. vaupesianus, A. caquetae, A. transversalis*), with the other members listed by CDQ considered incertae sedis within the large clade that is separate from the *roquet* series. The heterodermus series of CDQ is monophyletic in our preferred tree.

Phenacosaurus was defined by CDQ as ''The clade originating in the ancestor in which the combination of morphological characters of the twig ecomorph (long pointed snout; forelimbs, hindlimbs, and tail short in proportion to body size), synapomorphic with that in *Anolis heterodermus* originated.'' This definition is problematic in that several species found in separate clades from their species of *Phenacosaurus* and/or of uncertain relationship share traits of the twig ecomorph (e.g., *A. bellipeniculus*, originally described as genus *Phenacosaurus*; *A. williamsmittermeierorum*, listed by CDQ as a potential *heterodermus*-series form; both of these are outside of the *heterodermus* clade; Fig. 5). Thus the evolution of the ancestral appearance of the twig morphology—an inference upon which this definition, and associated species content, depends—is not clear. That is, according to our tree, twig morphology may be the ancestral condition for all *Dactyloa* that are not *roquet*-series species, or it may have evolved ancestrally in the *heterodermus* series, to name just two of several possibilities that signal vastly different species contents for this name as defined. We suggest refrainment from use of this name, as defined by CDQ, until further clarification of the relationships of South American phenacosaur anoles is possible.

The *roquet* series of CDQ is monophyletic but for *A. deltae*. *Anolis deltae*, a poorly known Venezuelan form described from one specimen, is unambiguously placed with the southern Lesser Antillean *roquet* group based on morphological data. Its conditions of interparietal-supraorbital scale contact, lack of postcloacal scales in males, and large numbers of toe lamellae are characteristic of the *roquet* group among *Dactyloa*. The species was considered distinctive when described (Williams, 1974), but was not compared to members of the *roquet* group, probably because of its collection on the mainland. The species may represent an interesting biogeographic component as a sister species to or back-invasion from the island *roquet* group lineage. Alternatively, considering the recent invasion of the *roquet* group to Venezuela and Trinidad and Tobago by *A. extremus* (Schwartz and Henderson, 1991; Lever, 2003) and the coastal type locality of *A. deltae* near a widely used shipping channel close to these localities, the species status of *Anolis deltae* should be reinvestigated. We have not examined the type specimen of *A. deltae*, but we are unable to distinguish *A. deltae* from *A. extremus* based on our morphological data.

Below we define one additional clade name following the template of Castañeda and de Queiroz (2013). This clade includes morphologically diverse species that nevertheless are geographically coherent.

Continenteloa Poe et al., new clade name

Definition.—All extant species of *Dactyloa* more closely related to *Anolis latifrons* than to *Anolis roquet*.

Reference phylogeny.—Figure 5, this study.

Inferred composition.—*A. aequatorialis, A. agassizi, A. anatoloros, A. anchicayae, A. anoriensis, A. antioquiae, A. apollinaris, A. bellipeniculus, A. blanquillanus, A. boettgeri, A. calimae, A. caquetae, A. carlostoddi, A. casildae, A. chloris, A. chocorum, A. cuscoensis, A. danieli, A. dissimilis, A. eulaemus, A. euskalerriari, A. fasciatus, A. festae, A. fitchi, A. fraseri, A. frenatus, A. gemmosus, A. ginaelisae, A. gorgonae, A. heterodermus, A. huilae, A. ibanezi, A. inderenae, A. insignis, A. jacare, A. kunayalae, A. laevis, A. lamari, A. latifrons, A. limon, A. maculigula, A. megalopithecus, A. menta, A. microtus, A. mirus, A. nasofrontalis, A. neblininus, A. nicefori, A. orcesi, A. otongae, A. paravertebralis, A. parilis, A. peraccae, A. peruensis, A. philopunctatus, A. phyllorhinus, A. podocarpus, A. poei, A. princeps, A. proboscis, A. propinquus, A. pseudotigrinus, A. punctatus, A. ruizii, A. santamartae, A. soinii, A. solitarius, A. squamulatus, A. tetarii, A. tigrinus, A. transversalis, A. umbrivagus, A. vanzolini, A. vaupesianus, A. ventrimaculatus, A. williamsmittermeierorum.*

Etymology.—Derived from the Latin *continente* (mainland) + *loa* (the last part of the name *Dactyloa*) in reference to the mainland ranges of almost all species in this clade in contrast to the native island ranges of species in the *roquet* series.

MATERIAL EXAMINED

Institutional abbreviations follow Sabaj Pérez (2014).

Anolis carlostoddi: SCN 10351, holotype, Venezuela, Estado Bolivar, the southern high plateau of Abacapa-tepui.

A. euskalleriari: MCZ 176475, Venezuela, Zulia.

A. heterodermus: MCZ 78519, Colombia, Tena; MCZ 78522, Usaquen; MCZ 104409, 110133–8, 145325, Chia; USNM 95922, Bogota; USNM 127100–1, Fusagasuga.

A. nicefori: MCZ 67929, Colombia, Norte de Santander.

A. orcesi: MCZ 38937, holotype, Ecuador, Mt. Sumaco; QCAZ 4502, Ecuador, Napo, Baeza-Borja road, near Hosteria Cumanda; QCAZ 4642, Tungurahua, 4.8 km S of Rio Negro; QCAZ 9692–93, Napo, 2.3 km N of bypassing to Baeza; QCAZ 9697, Napo, Rio Quijos, 15.7 km N of bypassing to Baeza; QCAZ 9705, Napo, 30 km N of bypassing to Baeza; QCAZ 9713, Napo, 44.1 km N of bypassing to Baeza; QCAZ 10156, Tungurahua, Rio Verde; QCAZ 10160, Tungurahua, tunnel Puyo-Baños.

A. tetarii: MCZ 176474, Venezuela, Zulia.

A. vanzolinii: MCZ 175159, 175167, Ecuador, Sucumbios.

A. williamsmittermeierorum: MSB 72521–3, UNAP 2.000181 (holotype), 2.000180, 2.000189–90, Peru, San Martin Province, Venceremos, approximately 94 km west of Rioja (between old kilometer markers 390–1, near new kilometer marker 380), 05°40.405′S, 77°45.310′W, 1739 meters.

See Poe (2004) for additional specimens examined.

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APPENDIX 1
MORPHOLOGICAL CHARACTERS

1. Maximum snout to vent length (mm; ordered). 0: –60; 1: 61–86; 2: 87–112; 3: 113–138; 4: 139–164; 5:165+.

2. Maximum female SVL/maximum SVL (ordered). 0: –0.59; 1: 0.60–0.69; 2: 0.70–79; 3: 0.80–0.89; 4: 0.90–0.99; 5: 1.00+.

3. Femoral length/SVL (ordered). 0: –0.19; 1: 0.20–0.22; 2: 0.23–0.25; 3: 0.26–0.28; 4: 0.29–0.31; 5: 0.32+.

4. Head length/SVL (ordered). 0: –0.22; 1: 0.23–0.24; 2: 0.25–0.26; 3: 0.27–0.28; 4: 0.29–0.30; 5: 0.31+.

5. Ear height/SVL (ordered). 0: –0.017; 1: 0.018–0.025; 2: 0.026–0.033; 3: 0.034–0.041; 4: 0.042–0.048; 5: 0.049+.

6. Toe length/SVL (ordered). 0: –0.13; 1: 0.14–0.16; 2: 0.17–0.19; 3: 0.20–0.22; 4: 0.23–0.25; 5: 0.26+.

7. Tail length/SVL (ordered). 0: –1.29; 1: 1.30–1.59; 2: 1.60–1.89; 3: 1.90–2.19; 4: 2.20–2.49; 5: 2.50+.

8. Female dewlap (ordered). 0: extends posteriorly past arms; 1: to arms or shorter; 2: absent.

9. Head scales (frequency coded). 0: keeled; 5: smooth.

10. Subocular scales (frequency coded). 0: in contact with supralabials; 5: separated from supralabials by a row of scales.

11. Mean number of scales across the snout at the second canthals (ordered). 0: –4; 1: 5–7; 2: 8–10; 3: 11–13; 4: 14–16; 5: 17+.

12. Mean number of supralabial scales from rostral to center of eye (ordered). 0: –5; 1: 6; 2: 7; 3: 8; 4: 9; 5: 10+.

13. Supraorbital semicircles (frequency coded). 0: separated by one or more rows of scales; 5: in contact.

14. Interparietal scale (frequency coded). 0: separated from supraorbital semicircles by at least one scale; 1: in contact with supraorbital semicircles.

15. Length of interparietal scale/length of scale lateral to interparietal (ordered). 0: –1.24; 1: 1.25–2.24; 2: 2.25–3.24; 3: 3.25–4.24; 4: 4.25–5.24; 5: 5.25+.

16. Elongate superciliary scale (longer than first canthal; frequency coded). 0: absent; 5: present.

17. Scales in supraocular disc (unordered). 0: some enlarged, gradually decreasing in size; 1: 2–4 abruptly enlarged, at least 2X larger than other supraocular scales; 2: all scales approximately equal in size.

18. Mean number of postmental scales (ordered). 0: –4.4; 1: 4.5–5.4; 2: 5.5–6.4; 3: 6.5–7.4; 4: 7.5–8.4; 5: 8.5+.

19. Modal nasal scale type (unordered). 0: anterior nasal in contact with rostral; 1: circumnasal separated from rostral by

one scale, not in contact with supralabial; 2: external naris separated from rostral by two scales, not in contact with supralabial; 3: external naris separated from rostral by three or more scales, not in contact with supralabial; 4: circumnasal in contact with rostral; 5: circumnasal in contact with supralabial, separated from rostral by 1–2 scales.

20. Modal number of abruptly enlarged sublabial scales (ordered). 0: zero; 1: one; 2: two.

21. Ventral scales (frequency coded). 0: keeled; 5: smooth.

22. Mean number of longitudinal ventral scales in 5% of SVL (ordered). 0: 3.0–4.4; 1: 4.5–5.9; 2: 6.0–7.4; 3: 7.5–8.9; 4: 9.0–10.4; 5: 10.5+.

23. Mean number of longitudinal dorsal scales in 5% of SVL (ordered). 0: –4.9; 1: 5.0–7.4; 2: 7.5–9.9; 3: 10.0–12.4; 4: 12.5–14.9; 5: 15.0+.

24. Middorsal crest (frequency coded). 0: absent; 5: present.

25. Lateral scales (frequency coded). 0: homogeneous; 5: heterogeneous.

26. Middorsal caudal scales (frequency coded). 0: single row; 5: double row.

27. Scales on dewlap (unordered). 0: in rows of single scales; 1: in rows of multiple scales; 2: scattered.

28. Enlarged postcloacal scales (frequency coded). 0: present in males; 5: absent in males.

29. Mean number of expanded lamellae on toe IV (ordered). 0: <14.9; 1: 15.0–20.9; 2: 21.0–26.9; 3: 27.0–32.9; 4: 33.0–38.9; 5: 39.0+.

30. Discrete expanded toepad on toe IV (frequency coded). 0: present; 5: absent.

31. Modal dominant dorsal color when sleeping (unordered). 0: brown; 1: green; 2: gray/white; 3: blue.

32. Modal lateral pattern when sleeping (unordered). 0: solid; 1: stripe along body; 2: bands; 3: ocelli/spots; 4: speckled; 5: jumbled, lichenous.

33. Tail pattern (frequency coded). 0: solid; 5: banded.

34. Color of iris (unordered). 0: brown; 1: yellow; 2: blue or gray; 3: green; 4: red.

APPENDIX 2
MORPHOLOGICAL CHARACTER CODES

aeneus	122221{10}15021552503025230000 5200?50
aequatorialis	245125500531001524025430051025{10}{32}52
agassizi	32422421501220151502043 00{23}{10}140{20}450
anatoloros	14?31?41{23}022{23}10502{14}25210050020{10}{245}50
anchicayae	1331233200310035030253100 51010{10}{10}52
anoriensis	244{123}244105310015{20}50055300?1020{10}{23}50
antioquiae	1?21244{10}0051000{23}05{10}2544005{20}?20105{10}
apollinaris	23240352053200150 3{12}0{23}43000{12}0201{20}50
bellipeniculus	1?131111501255151042521500002 00?50
blanquillanus	1331222150125525010 2{23}1200005300{10}??
boettgeri	14312352002254250202523005101013?0
bonairensis	1232223150215525050252300005200250
calimae	041221115022200 0{20}2125430050010{210}{25}5{10}
caquetae	0?32123?5022052502120330050020?35?
carlostoddi	0?1221115012501010425 11{23}000?10??5?
casildae	2?4224510441 0015{20}4{410}{12}55200?1020{10}{23}5{30}
chloris	143212325031001 5{20}2{10}20440050010100{20}
chocorum	1441124150330025 02{12}054300510101300
cuscoensis	05312252{23}02240250102523005101 01350
danieli	33331342052300 05040{10}5410052020{10}{23}50
deltae	0?2222?25022552502{10}25210000520????
dissimilis	05130121{23}01555250052032000 00101{20}0?
eulaemus	23323431054300 2525{10}05530051020{20}{235}50
euskalerriari	0?{10}{234}{10}{10}{21}{10}50025500{10}1525??0000020{10}?5?
extremus	12222311{23}021552502025220000 5201?00
fasciatus	1430244200311025{20}4025430051020{10}{23}52
festae	041311325023{23}0350202542005{20}0101{23}0{23}
fitchi	234125400554003522215430 05{20}520{10}{32}52
fraseri	3522114050230 01{23}{20}212{23}3300110201250
frenatus	4341233104350025 25{10}054300510201350
gemmosus	143134520141002522 0{21}55300510101{23}52
ginaelisae	2422023{10}5012001001{21}25420051020{10}252
gorgonae	143113325031002502{10}2{23}2300500103002
griseus	31323431{23}0220025040212300005 30010{30}
heterodermus	141300115013441011{15}25205500020{20}250
huilae	1322124250225425000254200510201350
ibanezi	1451025150330025 02{12}054200510101200
inderenae	2?{10}{234}{210}{10}{21}15003541000525??550{10}0300?5?

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jacare	1422033150122015024252300500200450
kunayalae	23321131{23}2440010{20}3{12}{210}54300510051{230}5{40}
laevis	0?????1?500355????5???005????????
lamari	0?????3?5022551502025??00{23}0010{10}{245}50
latifrons	334234410435001023{10}155300510201350
limon	15?2?24{10}50230025035054200510201{20}{23}0
luciae	21213311{23}0215525030252300005201{10}0{20}
maculigula	2242233205430025{20}5{23}{10}{23}5100010100{31}50
megalopithecus	2?411352054300?5{20}4025530051020{10}{32}5{410}
menta	0?1301215012551{23}120252300500101{25}5?
microtus	3322023{10}5012001002{12}25220051020{10}25{20}
mirus	3??30{12}3101350010{20}4200??00?1005??5?
nasofrontalis	0??1{10}?105012552003425??0????20????
neblininus	1?14111150125315{10}1{45}252250000100?50
nicefori	1?030001501350000052521550{10}010????
NSP.E	4?22213050230010{20}2115330051020{10}{23}5{40}
NSP.F	4?22213050220010{20}1115420051020{10}25{40}
NSP.L	4?11112050220010{20}3125320051030{10}{23}50
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NSP.W	0?1321{10}05012501{10}11525210000020{10}{25}50
NSP.Z	0?021001501255100052522000{10}?100550
orcesi	0502100150025510{10}1525335000010{210}55{40}
otongae	14{2345}32{2345}42{23}042001502{410}254300?1010{10}{23}52
paravertebralis	0???????501355?5{10}0??5??00?0?10??5?
parilis	??32113?00540025241054200510151350
peraccae	042223420021103503025430051010{20}{23}5{20}
peruensis	0413101150125510{10}1425230000010{20}{520}50
philopunctatus	1?33124150320025020253400?0020100{40}
phyllorhinus	23?{23}1{123}415024002502125??00500?0100{40}
podocarpus	24{2345}32{2345}400{23}54002523{410}{10}5??00?1{23}20{10}{23}52
princeps	345133410545002524{10}054200510201350
proboscis	1404101150250020{20}052523500{20}010{210}{25}50
propinquus	??33044?05320015021053300510201??0
pseudotigrinus	0??2{10}?015003551500425??0???010????
punctatus	23231241{23}03320250102{23}340050030100{40}
richardii	40314321{23}0223025040213300005201{10}0{10}
roquet	12322221{23}021553503025230000520{10}3?0
ruizii	0?2312215022552502{10}25240000010??5?
santamartae	0?1{23}32{234}{21}5012551500{40}2{23}210050010??5?
soinii	144113525032403501025330051010135{40}
solitarius	041212315022551{23}00025230050010{10}{25}5?
squamulatus	253324410534003{23}21{10}{012}5440051?201{24}{23}0
tetarii	1?{10}{234}{10}{10}{21}150043{23}0000525??5500?20{210}?5?
tigrinus	0?12101{12}5012551000{14}25320050010{10}{25}50
transversalis	142112315013402503025440051020{10}{32}52
trinitatus	12212111{23}0215435030254300005201000
umbrivagus	0????42501355?5{10}2{14}?5??00??010????
vanzolinii	2?1211115004{23}{23}00{10}0{45}2520550{10}0200{20}5{10}
vaupesianus	1?12124{21}5023002503{14}202400500201???
ventrimaculatus	125235320541003523{10}05430051010{10}{23}{23}0
williamsmittermeierorum	1413211050125510{10}0425220000010{20}{25}50
bimaculatus	303323220012402504025210000030{10}10?
carolinensis	1224122{21}00140015033202100000201000
cupreus	04322332022100350211021000051001?0
cuvieri	3434324002233010{20}1{10}253140010301000
equestris	542411305013001{10}21{12}252155000301000
lucius	134342325012504504025350001020{20}{12}50
marcanoi	0344223204213035020250100000100{12}50