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Taxonomic review of the genus *Cyclopes* Gray, 1821 (Xenarthra: Pilosa), with the revalidation and description of new species

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The taxonomy of *Cyclopes didactylus* is marked by a confusing history of new names, with few or no references to types, and new subspecies without any verified geographic correspondence. Here, we review the taxonomy of the genus *Cyclopes* using an integrative approach that combines morphological, morphometric and molecular data. We, therefore, aim to clarify many issues concerning the taxonomy, distribution and conservation status of the valid taxa and describe new previously unrecognized species for the genus. We examined a total of 287 specimens of *Cyclopes*, including skins and skulls, housed in 20 natural history collections and 33 samples for molecular analyses. Based on evidence provided by molecular phylogenetics using mitochondrial and nuclear DNA, allied with coalescent species delimitation analyses, diagnostic characters of the skull, colour patterns and structures of pelage, we suggest that the genus *Cyclopes* comprises at least seven species. Four previous species designations are considered valid here: *Cyclopes didactylus* (Linnaeus, 1758); *Cyclopes ida* Thomas, 1900; *Cyclopes catellus* Thomas, 1928; and *Cyclopes dorsalis* (Gray, 1865). In addition, three new species are described. The results presented here have large implications for the conservation status and management practices of silky anteaters.

ADDITIONAL KEYWORDS: biogeography – Neotropics – phylogenetic systematics – silky anteater – species delimitation.

INTRODUCTION

Silky anteaters (genus *Cyclopes* Gray, 1821) are the smallest extant anteaters, with a body length of *c*. 35 cm, a tail length of 20 cm and a weight of *c*. 300 g (Miranda *et al.*, 2009). They probably feed predominantly on ants, as no termites have so far been identified as food items (Lubin, 1983; Best & Harada, 1985; Montgomery, 1985a; Miranda *et al.*, 2009). They have exclusively arboreal and nocturnal habits (Montgomery, 1985b), resting in a curled ball during the day in the shade of vines or the tree canopy (Sunquist & Montgomery, 1973), which may explain why they are among the least-studied xenarthrans. Currently, only a single species is recognized for the genus *Cyclopes*

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didactylus (Linnaeus 1758), although a remarkable genetic diversity was recently described for the group (Coimbra *et al.*, 2017). Its range includes the tropical forests of South and Central America towards southern Mexico. Low metabolic rate, low body temperature (around 33 °C) and reduced thermoregulatory abilities of the species are thought to limit its distribution to forests below 1500 m (McNab, 1984), including semideciduous and evergreen tropical moist lowland, gallery and mangrove forests (Miranda & Meritt, 2011).

Cyclopes is included in the family Cyclopedidae Pocock, 1924, within the suborder Vermilingua Illiger, 1811 (Pilosa, Xenarthra), which also contains the giant anteaters (*Myrmecophaga* Linnaeus, 1758) and tamanduas (*Tamandua* Gray, 1825), both in the family Myrmecophagidae Gray, 1825 (Gardner, 2005, 2007). The taxonomic diversity of vermilinguans is considered low and includes, besides the four extant species, three undisputed extinct genera, including an early Cyclopedidae, *Palaeomyrmidon* Rovereto, 1914, from the Huayquerian, Miocene of Argentina (McKenna & Bell, 1997; Gaudin & Branham, 1998). Molecular and morphological analyses suggest an early emergence of Cyclopedidae (Gaudin & Branham, 1998; Delsuc, Vizcaino & Douzery, 2004; Gibb *et al.*, 2016), which is morphologically very divergent from other vermilinguans (Engelmann, 1985; Reiss, 1997; Gaudin & Branham, 1998). Three morphological synapomorphies separate Cyclopedidae from Myrmecophagidae: a glenoid fossa that is well separated from the porus acousticus, a strongly recurved basicranial-basifacial axis and a skull that is strongly tapered anteriorly in lateral view (Gaudin & Branham, 1998).

The genus *Cyclopes* has a convoluted nomenclatural history, with *Cyclopes didactylus* being originally described as *Myrmecophaga didactyla* by Linnaeus (1758). Brongniart (1792) misspelled the name as *Mirmecophaga*, while Gray (1821) was the first to use the current name for the genus, *Cyclopes*, indicating *Myrmecophaga didactyla* Linnaeus, 1758 as the type. However, in 1825, Gray refers to the genus as *Cyclothurus*, in an unjustified change and with no species formally assigned to it, being now considered a *nomen nudum* (Gray, 1825). Cuvier (1829) proposed the generic name *Didactyles* ('Les Didactyles'), which he considered distinct from *Tamanduas* in that the former has two fingers on the front paw, instead of four, as in the latter, although no species are assigned to the genus. Other names that appear subsequently in the literature are *Myrmydon* (Wagler, 1830), *Myrmecolichnus* (Reichenbach, 1836) and *Eurypterna* (Gloger, 1841), all of them referring to the original species described by Linnaeus (1758). Lesson (1842) reused the name *Cyclothurus* given by Gray (1825), but this time indicating that the name referred to the same species of Linnaeus (1758). Sclater (1871) proposed an emendation *Cyclothurus* Lesson, 1842 to *Cycloturus*, based on a linguistic preference. Many other authors used *Cyclothurus* or *Cycloturus* (e.g. Macalister, 1875; Flower, 1882; Forbes, 1882; Trouessart, 1899; Windle & Parsons, 1899; Goeldi & Hagmann, 1904; Edgeworth, 1914; Sonntag, 1923). *Didactyles* of Cuvier (1829) was also used occasionally, sometimes misspelled, as in the case of Liais (1872), who used the spelling *Didactyla*. Cabrera (1958) attributed the usage of the name *Mirmydon* to Wagner (1844), although in this last study, Wagner used *Myrmecophaga didactyla* in the illustration of *Cyclopes*. Despite the many names applied throughout taxonomic history, no change to the taxonomic concept has been made since Gray (1821) established *Cyclopes*, always referring to silky anteaters.

Cyclopes is currently considered a monotypic genus, but with many subspecies recognized besides the nominal *C. didactylus didactylus* (Wetzel, 1982; Gardner, 2007). However, throughout its taxonomic history, different species have also been attributed to *Cyclopes*. Gray (1865) described *Cyclothurus dorsalis* as a new species based on the golden yellow back, an always present, broad, dorsal black stripe and the yellow feet and tail, differing from *Cyclothurus* (*Cyclopes*) *didactylus*, which possessed fulvous back and grey feet and tail. Trouessart (1899) considered *Cyclothurus dorsalis* as a subspecies (var. *dorsalis*) of *Cycloturus* [sic] *didactylus*. Bangs (1902) used the genus *Cyclopes* for *Cyclopes dorsalis*, retaining it as a different species, while Trouessart (1905) considered it a subspecies, being the first to use the current name combination. Gray (1865) defined the type location of *Cyclopes didactylus dorsalis* as Costa Rica, and Goodwin (1946) fixed it in Orosi, near Cartago, based on the area where the type was collected. Oldfield Thomas (1900) described the subspecies *Cyclopes didactylus ida* from Pastaza, Ecuador, differentiating it from *C. d. didactylus* and *C. d. dorsalis* based on different colorations, lack of the sternal stripes and minor skull characteristics. Lönnberg described *Cyclopes juruanus* in 1942, which Cabrera (1958) lowered to subspecies status as *Cyclopes didactylus jurnanus*. However, Gardner (2007) considered it synonymous with *Cyclopes didactylus ida*. Thomas (1902) also described *Cyclopes didactylus eva*, also from Ecuador (west of the Andes), which he considered an intermediate between *C. d. dorsalis* on one hand and *C. d. didactylus* and *C. d. ida* on the other hand. Oldfield Thomas (1928) described one last subspecies, *Cyclopes didactylus catellus*, from Santa Cruz, Bolivia. Lönnberg described another two subspecies from Amazonas, Brazil: *Cyclopes didactylus melini*, in 1928, and *Cyclopes didactylus codajazensis*, in 1942. However, *C. didactylus codajazensis* was treated as a

synonym of *C. didactylus ida* by Cabrera (1958) and as a synonym of *C. didactylus catellus* by Gardner (2007). Finally, Hollister (1914) described a new species of *Cyclopes*, *Cyclopes mexicanus*, from Southern Mexico, which was lowered to subspecies level by Krumbiegel (1940).

More recent compilations (Gardner, 2007; Hayssen, Miranda & Pasch, 2012) recognize seven subspecies for *C. didactylus*: *C. d. didactylus* (Linnaeus, 1758); *C. d. catellus* Thomas, 1928; *C. d. dorsalis* (Gray 1865); *C. d. eva* Thomas, 1902; *C. d. ida* Thomas, 1900; *C. d. melini* Lönnberg, 1928; and *C. d. mexicanus* Hollister, 1914. Despite this recognition of the variation within the genus, and the occasional description of different species, *Cyclopes* has been composed of a single species for most of its taxonomic history. The taxonomy of *C. didactylus* is also marked by a confusing history of new names and combinations, with few or no reference to types, and new subspecies without any verified geographic correspondence. *C. didactylus* is also relatively rare in scientific collections, possibly because of the difficulty involved in its capture given its small size and discrete habits. Consequently, the genus has never been the subject of a major taxonomic revision that addressed adequately, and in a comparative way, the genetic and morphological variation found within the group. New methodological techniques have allowed a more integrative approach to the taxonomy of mammals, demonstrating that much of what was known of the diversity of various groups is underestimated (e.g. Helgen *et al.*, 2013; Reardon *et al.*, 2014; D'Elía, Hurtado & D'Anatro, 2016; Hotaling *et al.*, 2016). Adequate taxonomic knowledge is essential for the clarification of the diversity and geographic distribution of a taxon and, consequently, provides a basis for the implementation of conservation measures.

Here, we review the taxonomy of the genus *Cyclopes* using an integrative approach that combines morphological, morphometric and molecular data. We, therefore, aim to clarify many issues concerning the taxonomy, distribution and conservation status of the valid forms and describe new previously unrecognized species for the genus.

MATERIAL AND METHODS

Molecular analyses

Seventeen samples were obtained during ten expeditions conducted in Brazil and Suriname from 2007 to 2016 in Santa Isabel do Rio Negro (CD015) and Manaus (CD032 and CD033), Amazonas State; Oriximiná (CD007, CD008 and CD009), Pará State; Recife (CD003, CD004, CD005 and CD006), Pernambuco State; Delta do Parnaíba (CD027, CD028 and CD029), Piauí State; São Luis (CD001 and CD002), Maranhão State; Macapá (CD016), Amapá State; and Suriname (CD023) (Fig. 1). Individuals were anaesthetized using 8 mg/kg ketamine chloride (Ketalar, Laboratorios Pfizer, São Paulo, Brazil) with 0.5 mg/kg midazolam (Dormonid, Roche). Sex and geographic location were recorded, and age was determined based on body mass, density of hair and size. Blood was collected into sterile test tubes by puncturing the cephalic or inner femoral vein. Serum was separated with a portable centrifuge, then aliquoted in eppendorf tubes and stored in liquid nitrogen or absolute alcohol. Permits to capture and sample were granted by the Instituto Chico Mendes

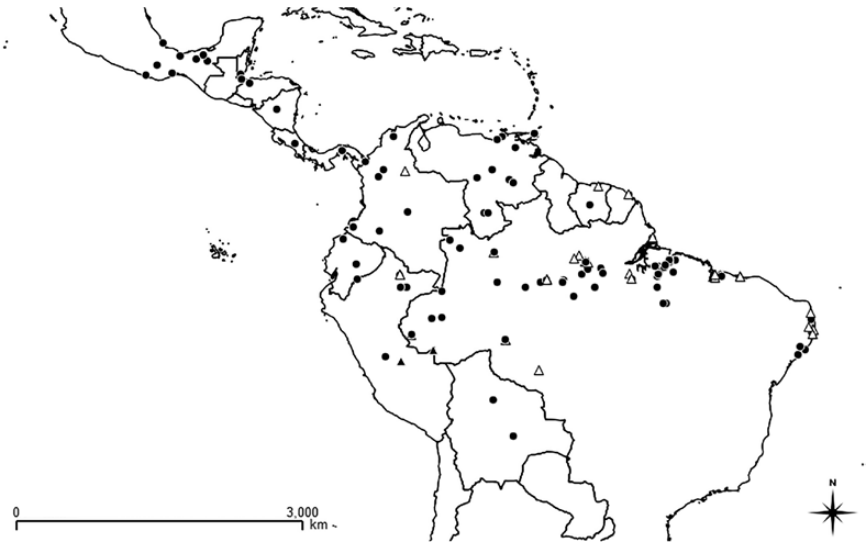

Figure 1. Geographic distribution of sampled data for *Cyclopes* (Gray, 1821) based on museum specimens (black circles), genetic samples (black triangles) and genetic and morphological samples (white triangles).

de Biodiversidade (SisBio: permit numbers 125811, 125813 and 133813). Another 15 tissue samples were obtained from donations by Pontifícia Universidade Católica (PUC-MG) (CD021), Instituto Brasileiro de Meio Ambiente e Recursos Renováveis (IBAMA) (CD010/Goianinha, Rio Grande do Norte State, Brazil), by Universidade Federal de Minas Gerais (UFMG 6015/Porto Velho, Rondônia State, Brazil; CD022/Rosário, Maranhão State/Brazil and CD024 and CD025/Xingu, Pará State, Brazil), Universidade Federal de Rondônia (UFRO) (CD026/Espigão D'oeste, Rondônia State, Brazil), Zoológico de Huachipa, Lima, Peru (CD011 and CD012/Ucayali; Peru, CD017 and CD018/Maynas, Loreto, Peru), by Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil (CD019 and CD031/Manaus, Amazonas State, Brazil), by Museo de Zoologia da USP (MZUSP), São Paulo, Brazil (CD030/Porto Walter, Acre State, Brazil) and by Cunaguaro Biodiversidad y Cultura (CD034/Santander, Colombia).

DNA extraction and sequencing

Total genomic DNA from 33 specimens was extracted from liver, muscle, blood and hair samples using a standard phenol-chloroform protocol (Sambrook & Russell, 2001) or using the DNeasy Blood & Tissue Kit (QIAGEN) following the manufacturer's instructions. For amplification and sequencing, PCRs were carried out in a final volume of 10 µl containing 10 ng of DNA, 1× reaction buffer (Invitrogen), 1.5 mM $MgCl_2$ (Invitrogen), 100 µM deoxynucleotide triphosphates, 0.2 µM of each primer (forward and reverse), 0.5 mg/ml of bovine serum albumin as coadjuvant and 0.2 U of Platinum Taq DNA Polymerase (Invitrogen). Cycling reactions for each fragment are described in Supporting Information, File 1. PCR efficiency was assessed by electrophoresis on 1% agarose gel, and the amplicons were submitted to purification protocol by polyethylene glycol 20% (described in Santos Júnior, Santos & Silveira, 2015). Purified amplicons were sequenced in a MegaBACE 1000 DNA Sequencing System (Amersham-Biosciences) or in an ABI 3130xl Genetic Analyzer (Applied Biosystems). Fragments of the mitochondrial control region (*CR*) (339 bp), the cytochrome *c* oxidase subunit I (*COI*) (676 bp) and cytochrome *b* (*Cyt-b*) (678 bp) genes were amplified with primers L15445 (Douzery & Randi, 1997) and H15978 (Arnason, Gullberg & Janke, 1997), LCO 1490 and HCO 2198 (Folmer *et al.*, 1994) and CYTB-L and CYTB-H (Lara-Ruiz, Chiarello & Santos, 2008). All mtDNA sequences were published elsewhere – KU596973–KU597000, KU597001–KU597027, KU597028–KU59705 (Coimbra *et al.*, 2017) and KT818539 (T1631) (Gibb *et al.*, 2016) – except for the sequences of the specimen UFMG 6015. For nuclear DNA (nDNA), an 843 bp of Von Willebrand factor (*VWF*) and 674 bp of adrenoceptor Beta 2 (ADRB) genes were sequenced. Consensus sequences were generated with either Phred v. 0.20425 (Ewing & Green, 1998; Ewing *et al.*, 1998), Phrap v. 0.990319 (Green, 1994–1999), Consed 19.0 (Gordon, Abajian & Green, 1998) or SeqScape v. 2.6 (Applied Biosystems) and aligned in MEGA 6 using the ClustalW algorithm (Tamura *et al.*, 2013). Single-nucleotide heterozygotes in nDNA sequences were coded with IUPAC ambiguity symbols. The accession numbers for sequences generated in this work are as follows: MF966945, MF966946 and MG252553–MG252583.

Haplotype network

COI sequences were used to construct a median-joining haplotype network (Bandelt, Forster & Röhl, 1999) using the software POPART (http://popart.otago.ac.nz) to visualize the parsimony relationships between haplotypes.

Phylogenetic analyses and divergence-time estimations

For phylogenetic analyses, we chose the models of nucleotide substitution using corrected Akaike information criterion, implemented in jModeltest version 2.1.6 (Darriba *et al.*, 2012). The suggested models were adjusted to the main options available in MrBayes 3.2 (Ronquist & Huelsenbeck, 2003) and BEAST2 (Drummond *et al.*, 2006; Bouckaert *et al.*, 2014). All analyses used four outgroup taxa: the anteaters *Tamandua tetradactyla* and *Myrmecophaga tridactyla* and the sloths *Bradypus tridactylus* and *Choloepus didactylus*. For the nucleotide sequence alignment, specific nucleotide substitution models applied to each marker, and accession numbers for the outgroup sequences, see Supporting Information, Files 2 and 3.

Two analyses were conducted, the first with all five concatenated markers (*COI*, *Cyt-b*, *CR*, *VWF* and *ADRB2*) and the second using only *COI*, to obtain trees to be submitted to a unilocus species delimitation approach. The *COI* mtDNA locus was chosen due to its potential for wide compatibility since it is the most used gene in unilocus species delimitation (Hebert, Ratnasingham & de Waard, 2003).

Bayesian phylogenetic analyses were performed in MrBayes 3.2 with two independent runs, with four chains each, through one million generations, sampling every 100. Each marker was established as an independent partition in the analysis of the complete data set and had its parameters estimated independently, except for branch lengths. A burn-in of the initial 25%

of the samples was conducted before the summary of parameters and trees. Convergence between the two independent runs was checked using MrBayes metrics (PSRF and ESS), and in Tracer 1.6 (Rambaut *et al.*, 2014), checking ESS and trace. Support was verified through posterior probabilities (PP) exhibited in the 50% majority-rule tree (Huelsenbeck & Ronquist, 2001), visualized with FigTree 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree).

The dated phylogenetic analysis was conducted in BEAST2, in CIPRES gateway (Miller, Pfeiffer & Schwartz, 2010), using the Beagle library. Two runs were performed, with 50 million generations each, sampling every 5000. The five partitions were unlinked, but the tree and clock models were maintained linked. A relaxed lognormal clock model and a birth–death tree model were applied. Two calibrations were specified, fixing the clades as monophyletic and applying a lognormal distribution to model the prior information about the ages of calibration, as this assigns higher probabilities to ages somewhat older than the fossil age, which is appropriate for fossil-based calibrations (Ho & Phillips, 2009), and even more so when the age of the fossil can be much more recent than the true divergence. The root was calibrated with the oldest available and securely dated Pilosa (Folivora), *Pseudoglyptodon chilensis* (31.5 Myr) (Engelmann, 1987; McKenna, Wyss & Flynn, 2006; Pujos, De Iuliis & Cartelle, 2016). To define the minimum age of the divergence of Vermilingua and Folivora, the value was applied as an offset. For the anteater clade, the offset (21 Myr) was defined using the maximum bound of the temporal range of the oldest, and so far unnamed, fossil Vermilingua (21–17.5 Myr) (Carlini *et al.*, 1992; McDonald, Vizcaino & Bargo, 2008). Since the available fossils are probably much younger than the true age of divergence and their ages were applied as offsets, we also used the oldest bound of the estimates in Gibb *et al.* (2016) as the mean value of the lognormal prior distribution for both calibrations, allowing the proper exploration of older estimates. The prior distribution for the nucleotide substitution rates was made less informative ($\alpha = 2$, $\beta = 0.5$) than the default, and the mean and SE clock priors were modelled with an exponential distribution, with mean 10 and 1, respectively. In the analysis with *COI* alone, a coalescent constant population tree model was applied instead of the birth–death model. This assures the consistency between the tree model that generates the topology and the methods for delimitations to which it will be submitted. The remaining priors and parameters are the same as in the full data set dating analysis. Convergence was checked in Tracer 1.6, visualizing ESS and trace. Support was verified through posterior probabilities in FigTree, plotted in a major clade credibility tree, which was obtained with TreeAnotator, after combining the tree files with LogCombiner, using a burn-in of 25% (Drummond *et al.*, 2006).

Single locus species delimitation approach

Unilocus species delimitation was performed using two different models: generalized mixed Yule coalescent (GMYC; Fujisawa & Barraclough, 2013) and Bayesian implementation of Poisson tree processes (bPTP; Zhang *et al.*, 2013). Both analyses were performed in the Exelixis Lab's web server (GMYC – http://species.h-its.org/gmyc/; bPTP – http://species.h-its.org/ptp/). The input topologies contained only a singleton sample (CD034).

For GMYC, the ultrametric tree obtained from *COI* sequences was submitted to single and multiple threshold analyses, checking the significance of the delimitation model with respect to the null hypothesis of a single species. The approach using bPTP was applied to the non-dated tree, also obtained from *COI* sequences. The delimitation search was performed for 500 000 Markov chain Monte Carlo (MCMC) generations, with thinning set to 100 and a burn-in of 25% initial samples. The convergence of bPTP analysis was visually checked in the trace plot. Maximum likelihood and Bayesian solutions for bPTP delimitation were considered.

Multilocus species delimitation approach

We tested the delimitation of a maximum of ten species, as recovered by GMYC, which also allows support for the nested hypotheses of seven species recovered by bPTP (see Results) to be evaluated. For that, we used the joint species delimitation and species tree analysis implemented in Bayesian Phylogenetics and Phylogeography – BPP 3.3 (Yang, 2015). This algorithm considers the possibility of occurrence of incomplete lineage sorting and other gene tree/species tree conflicts (Yang & Rannala, 2010; Rannala & Yang, 2013). We used the reversible-jump MCMC (rjMCMC) option (species delimitation model 1), with RJ algorithm = 0 and e = 2 (speciesdelimitation = 1 0 2), inferring the species tree (speciestree = 1) and assuming equal prior probability for each topology (speciesmodelprior = 1). The analysis was performed for 500 000 generations, with a sampling interval of five, and a burn-in of 50 000. We tested different combinations of ancestral population size and divergence time priors, to assure these priors had no influence in the results (Yang, 2015). We considered relatively large (θ~G (1, 10)) and small (θ~G(2, 2000)) ancestral population sizes, and shallow (τ~G(2, 2000)) and deep (τ~G(1, 10)) divergence times. Each analysis

was run twice to confirm consistency of the results. Other divergence-time parameters were assigned to the default Dirichlet prior (Yang & Rannala, 2010). Locus rates were estimated during the analysis, and a heredity file was input to account for the different inheritance patterns in the data set. *ADRB2* locus sequences were excluded to minimize missing data effect.

Specimens examined

We examined a total of 287 specimens of *Cyclopes*, covering the entire known distribution of the genus (Fig. 1) and including skins and skulls, housed in 20 natural history collections: Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (INPA); Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Centro de Coleções Taxonômicas da Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (UFMG); Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil (PUC-MG); Universidade Federal da Paraíba, João Pessoa, Brazil (UFPB); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Universidade Federal de Rondônia, Porto Velho, Brazil (UNIR); Universidade Federal do Piauí, Piauí, Brazil (UFPI); American Museum of Natural History, New York, USA (AMNH); Field Museum of Natural History, Chicago, USA (FMNH); Los Angeles County Museum, Los Angeles, USA (LACM); University of California Museum of Vertebrate Zoology, Berkeley, USA (MVZ); United States National Museum of Natural History, Washington, DC, USA (USNM); British Museum of Natural History, London, UK (BMNH); Naturhistoriska riksmuseet, Stockholm, Sweden (NRM); Museo de Historia Natural 'Noel Kempff Mercado', Santa Cruz de la Sierra, Bolivia (MNK); Museo de Historia Natural 'Gustavo Orcés V', Quito, Ecuador (MHNGO); Museo de Historia Natural da Universidad Nacional Mayor de San Marcos, Lima, Peru (UNMSM) and Institute Pasteur of Cayenne, French Guiana. A complete list of specimens is presented in the species accounts below. The examined specimens include the holotypes of *Cyclopes didactylus mexicanus* (USNM 11137/38534), *Cyclopes didactylus eva* (BMNH 2.7.26.3), *Cyclopes didactylus dorsalis* (BMNH 65.5.18.14), *Cyclopes didactylus juruanus* (NRM 2389), *Cyclopes didactylus codajazensis* (NRM 1089), *Cyclopes didactylus melini* (NRM 14), *Cyclopes didactylus catellus* (BMNH 26.1.12.17) and *Cyclopes didactylus ida* (BMNH 80.5.6.67). All the type specimens were examined through photographs, except *C. d. mexicanus*, for which the specimen was examined directly. Given the rarity of *Cyclopes* in collections, we believe that our sample includes a large proportion of the specimens available in museums worldwide.

Discrete characters

The variation in discrete characters was evaluated focusing on the grouping hypotheses suggested by our genetic results (see below), searching patterns of congruency with these putative delimitations. Discrete morphological variation was also evaluated for specimens that could not be associated a priori with one of our genetic or geographic putative groups, such as those from Bolivia, to perform a complete survey of the variation throughout the distribution of *Cyclopes*.

Eighty-six specimens were evaluated for qualitative characters of the skull. We surveyed the previous discrete morphological characters used to discriminate between species and subspecies of *Cyclopes* (Gray, 1865; Thomas, 1902, 1911, 1928; Lönnberg, 1928, 1942; Wetzel, 1985), in addition to new characters that showed geographical and/or taxonomic congruence. Cranial morphology terminology follows Gaudin & Branham (1998). We also analysed 268 museum skins and 36 live captures to observe variation in colour pattern. Coloration has previously been used to separate subspecies of *Cyclopes* (Gray, 1865; Thomas, 1900, 1902, 1928; Hollister, 1914; Lönnberg, 1928, 1942). The colour pattern of anterior and posterior limbs, tail, back, rump, abdomen and face was analysed in search of possible geographic and taxonomic correspondences. The presence and absence of dorsal and ventral stripes were also evaluated (Fig. 2).

Multivariate geometric morphometrics

We recorded, using an MX or MLX Microscribe digitizer, three-dimensional coordinates using 31 established landmarks (seven on the midline and 24 bilateral) (Fig. 3) from the skull of 118 adult specimens of *Cyclopes*, for geometric morphometric analysis. The landmarks and age determination were based on Hubbe, Melo & Marroig (2016). Asymmetric variation was removed from the sample by superimposing each configuration on its mirror reflection and averaging both (Klingenberg, Barluenga & Meyer, 2002). This procedure was also used to reconstruct missing landmarks based on the reflection from the other side. The resulting landmark configurations were subjected to a generalized Procrustes analysis where the information about position, rotation and scale were removed iteratively (Rohlf & Slice, 1990; Rohlf, 1999). The resulting 96 Procrustes residuals (differences between each dimension of the superimposed configurations and the multivariate average) were subjected to a principal component analysis to reduce the dimensionality of the data to account for the loss of degrees of freedom due to the superimposition and removal of asymmetric variation (Klingenberg *et al.*, 2002), and to improve signal-to-noise ratio (Strauss, 2010; Mitteroecker &

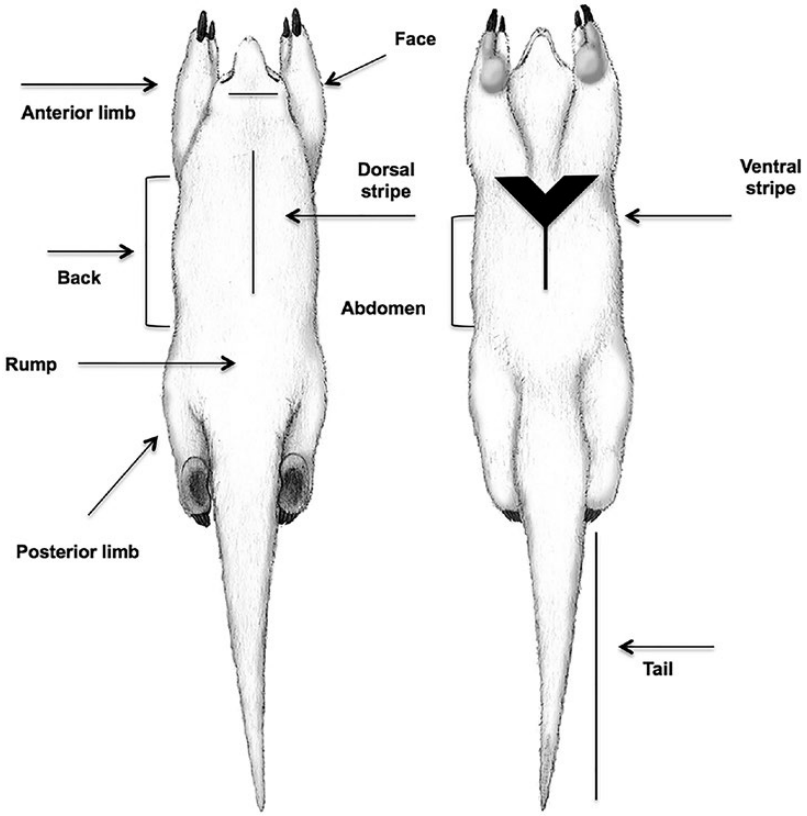

Figure 2. Schematic drawing indicating the regions for which pelage patterns were evaluated.

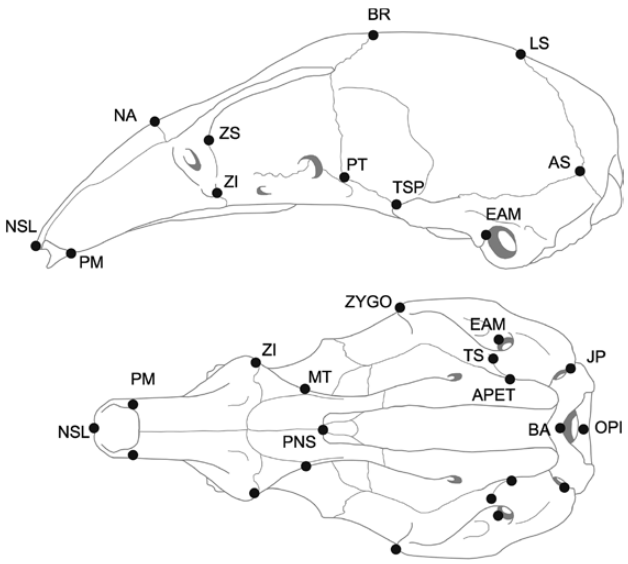

Figure 3. Landmarks on lateral and ventral view of *Cyclopes* skull used for morphometric analyses. Landmark descriptions can be seen in Hubbe *et al.* (2016).

Bookstein, 2011; Marroig, Melo & Garcia, 2012). The logarithm of the centroid size (logCS) was stored for each configuration as a measure of size. To investigate shape differences between units suggested by genetic analyses, specimens were assigned to groups based on geographic proximity to samples with known identity and distribution of geographical barriers. This resulted in a total of 114 skulls assigned to a putative taxon. Multivariate normality of morphometric variables was tested using Mardia's test for skewness and kurtosis (Mardia, 1970). Differences between groups were evaluated through multivariate analysis of variance (MANOVA) and linear discriminant analysis (LDA) on shape (principal components of Procrustes residuals; PCs) and form (shape + size). LDA was calculated on the full sample and with a leave-one-out cross-validation procedure. Visualization of the shape associated with each linear discriminant (LD) axis was obtained through multivariate regression of shape onto the scores of the specimens on each LD (e.g. Rohlf, Loy & Corti, 1996).

Size differences between groups were investigated separately with an analysis of variance (ANOVA) on logCS. To evaluate whether the variation among groups could be explained by allometric variation alone (e.g. Monteiro-Filho, Monteiro & dos Reis, 2002), we first tested whether groups differed in allometric

slope through a multivariate analysis of covariance (MANCOVA) between logCS and shape PCs. In addition, we inspected allometric differences between groups by calculating the common allometric component (CAC) for *Cyclopes* (Mitteroecker *et al.*, 2004). CAC is the shape axis that accounts for the variation in size (logCS) that is common to all groups. If shape differences can be attributed to allometry, then we expect the CACxlogCS relationship among all groups to be the same (e.g. Prevosti, Segura & Cassini, 2013). Multivariate morphometric analyses were performed on R programming environment (R Core Team, 2016) using the GeoMorph package (Adams & Otárola-Castillo, 2013). Symmetrization of configurations used the Osymm function provided by Annat Haber (available at http://life.bio.sunysb.edu/morph/).

Hair ultrastructure analysis

Hair samples of seven specimens of *Cyclopes* from São Luis, Maranhão; Santa Izabel do Rio Negro, Amazonas; Parnaíba, Piauí (Brazil); Santander (Colombia); Loreto (Peru); and Paramaribo (Suriname) were analysed histologically using the technique described by Quadros & Monteiro-Filho (2006). As mammalian hair varies widely in structure over different body parts, all samples were removed from the dorsum, between the scapulae. For the cuticle analysis, the application of a thin colourless layer of glaze on a clean glass slide was made. For observation of the medulla, hairs were diaphonized with creamy hydrogen peroxide 40 volumes for 80 min. After preparation, the slides were photographed under an optical microscope equipped with image capture system. The photographs were taken at a magnification of 400 times.

RESULTS

Haplotype network

The median-joining haplotype network revealed seven genetic clusters separated by at least 13 mutational steps. These clusters correspond to 17 mitochondrial haplotypes found in Nordeste, Guiana, Inambari, Napo, Xingu, Rondônia and Mesoamerica (Fig. 4), highlighting a phylogenetic grouping mostly in agreement with the geographic structure of these populations.

The population of 'Guiana' occurs in northern Amazon Forest, from the left margins of Negro, Orinoco and Amazon Rivers, and 'Nordeste' population occurs, probably, in the right margin of the Amazonas River towards Maranhão and Piauí states, with a disjunct population in northeastern Atlantic Forest. The population 'Napo' occurs throughout the western Amazon drainage of Brazil and adjacent Colombia, Ecuador and Peru (Uaupés and Napo River). 'Inambari' occurs from western Amazon to Acre in Brazil and southwest below the Ucayali River in Peru. The population 'Rondonia' occurs in the interfluve between Madeira and Aripuanã Rivers, and 'Xingu' is located in the northern region of Madeira/Xingu interfluve. 'Mesoamerica' occurs along the Pacific coast of northwestern Colombia, extending throughout Mesoamerica to southern Mexico.

Phylogenetic analyses and divergence-time estimations

Our clock and non-clock Bayesian phylogenetic analyses recovered very similar topologies, recovering the seven clusters found in the haplotype network as distinct clades, well supported in both analyses (PP = 1.0), just like the major clades that unite them. One exception is the clade uniting individuals from 'Napo' (PP = 0.94) in the non-clock analysis, although it is also strongly supported (PP = 1.0) in the analysis with BEAST. The two topologies obtained (clock and non-clock analyses) differ only among minor internal relations of two clades we nominated 'Guiana' and 'Nordeste' (see Supporting Information, Files 4–9 for support values and convergence of the analyses).

In our clock analysis (Fig. 5), *Cyclopes* was estimated to diverge from the remaining anteaters in early Oligocene, at 30 Myr, and the first internal divergence in the genus was estimated to occur in the late Miocene, at 10.3 Myr. The divergence times for the nodes can be found in Table 1. The *COI* trees (and parameter's outputs) used in GMYC and bPTP analyses are available in Supporting Information, Files 10–12, 13–15, respectively.

Species delimitation

The GMYC model delimited ten *Cyclopes* entities (likely species), being nine clusters and a singleton (Fig. 5). Both single and multiple threshold analyses returned the same number of delimited species, and in both, the model was significantly better than the null hypothesis in the likelihood ratio test (LR = 10.82073, LRT results = 0.004470017, threshold time = −0.4265402) (Supporting Information, Files 16–19). This agreement between single and multi-threshold results supports that a single threshold was preferred even in the multi-analysis. Five of those ten delimited entities are the clusters and clades previously recovered in the phylogenetic and haplotype analyses. The other two, 'Nordeste' and 'Guiana', had two and three internal clades, respectively, delimited as separate entities as well.

The bPTP model was somewhat more conservative, delimiting seven entities (Fig. 5) (the seven cluster/

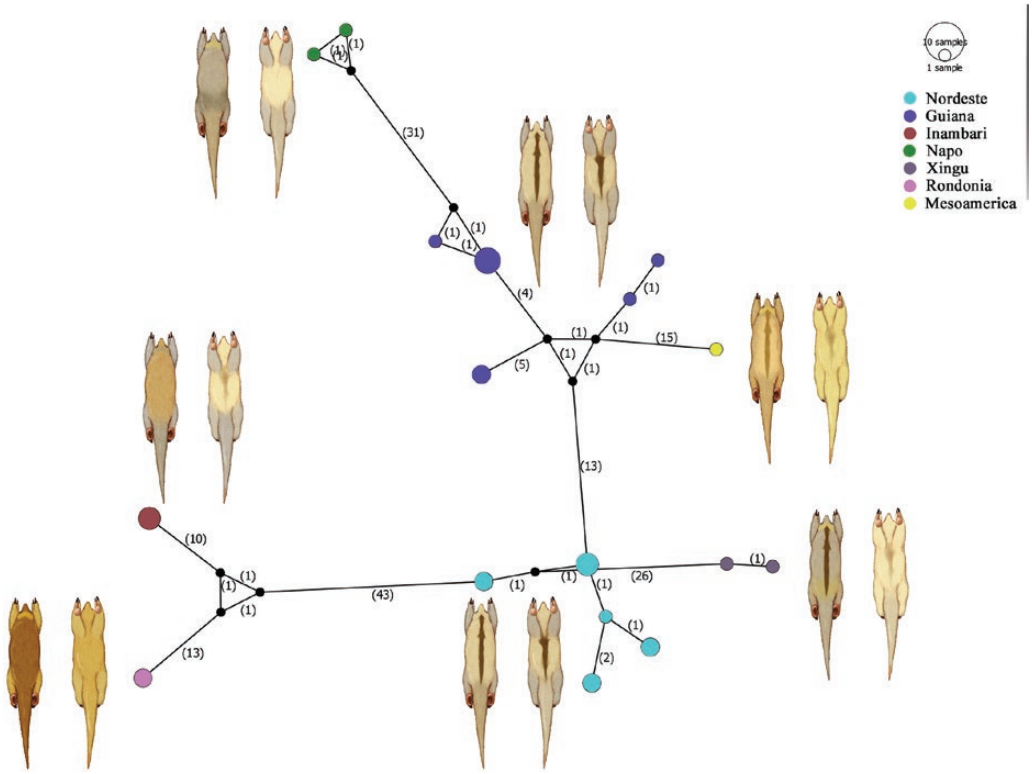

Figure 4. Haplotype network of *COI* with nodes proportional to frequency of individuals carrying the allele, coloured according to the cluster in which it occurs: 'Nordeste' (light blue), 'Guiana' (dark blue), 'Inambari' (brown), 'Napo' (green), 'Xingu' (purple), 'Rondonia' (lilac) and 'Mesoamerica' (yellow). Mutational steps are shown as numbers.

clades obtained in the above-mentioned analyses) using maximum likelihood and Bayesian solutions. Nevertheless, only five of these seven entities received posterior probabilities above 0.95. The other two clades, 'Nordeste' and 'Guiana', received 0.79 and 0.49, respectively, which suggests that we should be cautious interpreting these two clades as independent species (Supporting Information, Files 20–24). Moreover, the bPTP delimitation also attributes low probabilities to species inside these two clades, in contrast with GMYC results.

In BPP, two of the four prior combinations (θ~G(1,10), τ~G(2,2000)) and (θ~G(1,10), τ~G(1,10)) used in the species delimitation analysis, supported ten independent lineages and rejected the hypothesis of seven lineages (Table 2, Fig. 5). The other two analyses (θ~G(2,2000), τ~G(1,0)) and (θ~G(2,2000), τ~G(2,2000)) suffered from problems of convergence, and the two independent runs returned different delimitations (ten or three lineages). Therefore, these results are not reliable and are not further considered here. All outputs are available in Supporting Information, Files 25–32.

DISCRETE CHARACTERS

Cranial analyses allowed the identification of five discrete characters that showed variation within *Cyclopes*. The skull has a depression in the region of the naso-frontal contact, giving a concave profile for the skull in some specimens, while in others, there is no depression and the skull has a straighter profile (Fig. 6A). The aperture of the external auditory meatus also shows variation, with the meatus opening anteriorly in some specimens, while in others, it opens laterally (Fig. 6A). The coronoid (fronto-parietal) suture can have different shapes, being triangular, trapezoidal or horseshoe shaped (Fig. 6B). At the proximal portion of the nasals, the naso-frontal suture could be narrow, resulting in a wide contact between the maxilla and the frontal, or wide, with limited contact between the maxilla and the frontals (Fig. 6B). Finally, the extension of the pterygoid also shows variation since it could overlap the tympanic bullae or just go around the bullae proximal rim (Fig. 6C). This variation is somewhat consistent with the geographical distribution of *Cyclopes*, and different combinations of characters mostly correspond

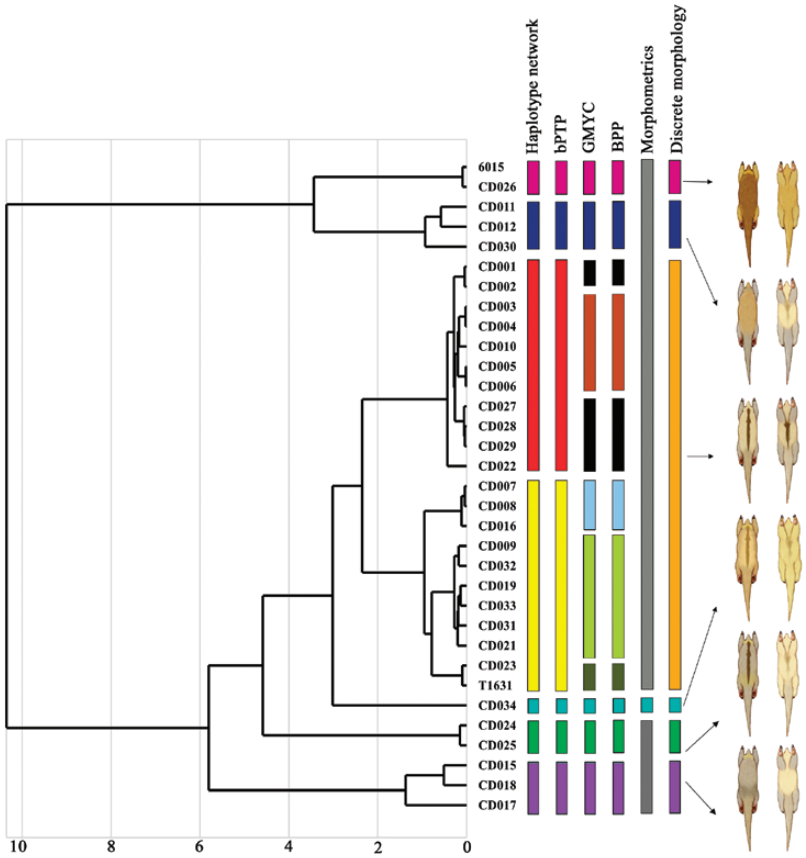

Figure 5. Bayesian chronogram (MCC tree) obtained with a relaxed lognormal clock model and a birth–death diversification model in BEAST2, using five unlinked partitions, each corresponding to a molecular marker. Scale in Myr. Coloured bars represent different delimitation schemes obtained with haplotype network, bPTP, GMYC, BPP, morphometric and morphological data. At the right end, schematic illustrations represent the external morphology of *Cyclopes* species considered after this study, for which we sampled molecular data (six of seven).

Table 1. Divergence-time estimates for each node and the 95% HPD, as recovered in out clock analysis

Divergence	Time (Myr)	95% HPD (Myr)
Pilosa	42.1	32.2–56.8
Bradypus/Choloepus	16.6	9.3–25.2
Vermilingua	30.0	22.0–40.9
Myrmecophaga/Tamandua	12.5	7.0–18.8
Cyclopes	10.3	6.6–15.1
Rondonia/Inambari	3.4	1.9–5.3
Napo/Xingu + Colombia + Nordeste + Guiana	5.8	3.7–8.6
Xingu/Colombia + Nordeste + Guiana	4.6	2.9–6.7
Colombia/Nordeste + Guiana	3.0	1.8–4.5
Nordeste + Guiana	2.3	1.4–3.5

HPD, highest posterior density.

to the taxonomic groups recovered in other analyses, although there are some variations (see below and Supporting Information, File 33).

Colour pattern also showed variation throughout the distribution of *Cyclopes* and, in general, showed even more consistency with genetic characteristics of the evolutionary units proposed below (defined in the Haplotype network section) than the cranial characters (Supporting Information, File 33). Populations that occur in areas of Northern South America ('Nordeste' and 'Guiana') usually have a brown-yellowish general colour, with rump, legs and tail greyish. The dorsal stripe is irregular, but distinctive, and both dorsal and ventral dark stripes are evident. Specimens from western Amazon ('Napo') have rump, legs and tail completely grey, with no ventral stripe and the dorsal one absent or, when present, indistinct and irregular, barely visible among the dorsal fur. The population of the Xingu region ('Xingu') has dorsal fur grey, with the

rump and ventral fur yellowish. No ventral stripe is present, but a dorsal stripe is apparent. In specimens from South America west of the Andes and Central America and Southern Mexico ('Mesoamerica'), we observe a general colour of body, limbs and tail bright yellow, with dorsal stripe present and instinct or no ventral stripe. Specimens of *Cyclopes* from Bolivia have a body with a brown-yellowish tone, with a lighter venter and more yellowish legs and tail. There is no dorsal stripe, but the ventral stripe is well developed. In the population of southwestern Amazon, through the Brazilian state of Acre to the Andean foothills ('Inambari'), the body colour is strikingly orange to reddish-brown, with grey legs and tail. There is no dorsal stripe, and the ventral stripe is little developed. Finally, the population from the interfluve between the Madeira and Aripuanã Rivers ('Rondonia') has a unique coloration, with its body, tail and limbs of a bright reddish tone and without both ventral and dorsal stripes. For detailed information on each observed specimen, see Supporting Information, File 33.

Table 2. Summary of posterior probabilities assigned to the ten- and seven-species hypotheses, according to the multilocus species delimitation analysis of BPP, for tested prior combinations in which the analyses achieved convergence

Prior combinations	10 species	7 species
θ~G(1,10); τ~G(2,2000)	0.99	0.00
θ~G(1,10); τ~G(1,10)	0.99	0.00

MULTIVARIATE GEOMETRIC MORPHOMETRICS

The first ten PCs of Procrustes residuals explained more than 3% of the total variance each, summing up

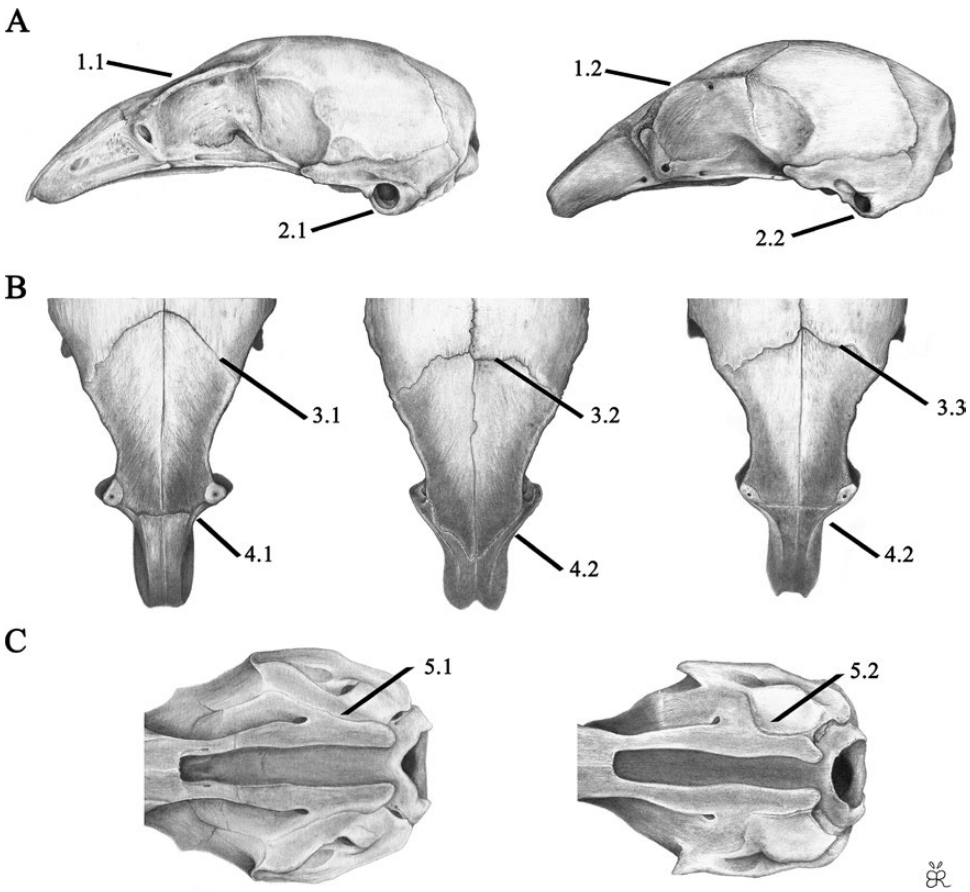

Figure 6. Variation in discrete characters, observed in the skull of *Cyclopes*, exhibited in lateral (A), dorsal (B) and ventral (C) views, in schematic drawings. 1. Naso-frontal depression: 1.1 – depression (concave profile); 1.2 – no depression. 2. Aperture of the external auditory meatus: 2.1 – meatus opens laterally; 2.2 – meatus opens anteriorly. 3. Shape of fronto-parietal suture: 3.1 – horseshoe shaped; 3.2 – trapezoidal; 3.3 – triangular. 4. Naso-frontal suture width: 4.1 – narrow; 4.2 – wide. 5. Pterygoid extension: 5.1 – overlap the tympanic bullae; 5.2 – does not overlap the tympanic bullae.

to 71.84% of the total variation, and were retained for subsequent shape analysis. Multivariate normality of the first ten PCs + logCS were evaluated for the largest groups ('Nordeste + Guiana' and 'Mesoamerica') and for the within-group pooled sample. Kurtosis and skewness tests were non-significant ($P > 0.05$) in all cases, and multivariate QQ plots showed no deviation from multivariate normality.

The ANOVA on logCS shows that there is a significant difference between genetic groups (Supporting Information, File 34). The inspection of the CACxlogCS plot reveals that, even though groups seem to share a similar allometric relationship, shape variation between groups does not follow the intragroup allometric trend (Fig. 7). The MANCOVA using logCS as a covariate shows that both the relationship between size and shape and the difference between groups were significant, even when the influence of the other factor was controlled (see Supporting Information, File 34). This suggests the presence of a similar intraspecific allometric relationship and that the shape difference between groups cannot be explained by allometry alone.

The results for the MANOVA and LDA were nearly identical with and without the inclusion of logCS. For that reason, we focus on the analysis based only on the shape variation (PCs). The MANOVA shows that shape differences among groups are highly significant (see Supporting Information, File 34). The LDA for the full sample, produced high rates of correct reclassification (> 0.7) for most groups, except for 'Napo' (0.62). Cross-validation analysis drastically dropped correct classification rates, apart from the best-sampled groups 'Guiana + Nordeste' and 'Mesoamerica' (Supporting Information, File 35). An inspection of the first two discriminant functions shows that the first axis (LD1) explains 73.80% of the between-group variation and differentiates Mesoamerica from the other units, while the second function (LD2) explains only 14.19% of the between-group variation and separates 'Napo', 'Inambari', 'Bolivia', 'Mesoamerica' and 'Xingu' (Fig. 8).

Shape differences represented by CAC, LD1 and PC1 were very similar. Indeed, a vector correlation between these vectors reveals that CAC and PC1 are 0.99 similar, while the correlation of both to LD1 is 0.97. Figure 8 shows the shape differences associated with LD1, which describes the contrast between individuals with relatively bigger braincases, shorter snouts and greater flexion of the rostrum on positive values and individuals with a relatively smaller brain, longer snouts and a smaller flexion on the negative values. Shape variation associated with CAC and PC1 were similar, but slightly less pronounced than those depicted by LD1.

Hair ultrastructure analysis

In six of the seven samples examined, the patterns of cuticle and medulla found were similar to those described for *C. didactylus* by Miranda, Rodrigues & Paglia (2013). The cuticle is wave shaped and arranged longitudinally along the axis of the hair. The medulla is absent (Fig. 9A), and the cuticle has scales of elongated petal form (Fig. 9B) as found in most Vermilingua. However, the Colombia (Mesoamerica) individual does have a medulla (Fig. 9C). This pattern has not been described before for Pilosa.

Integration of the available evidence and classification

Our unilocus delimitation analyses (GMYC and bPTP) returned slightly divergent results, with GMYC suggesting ten species and bPTP suggesting seven species

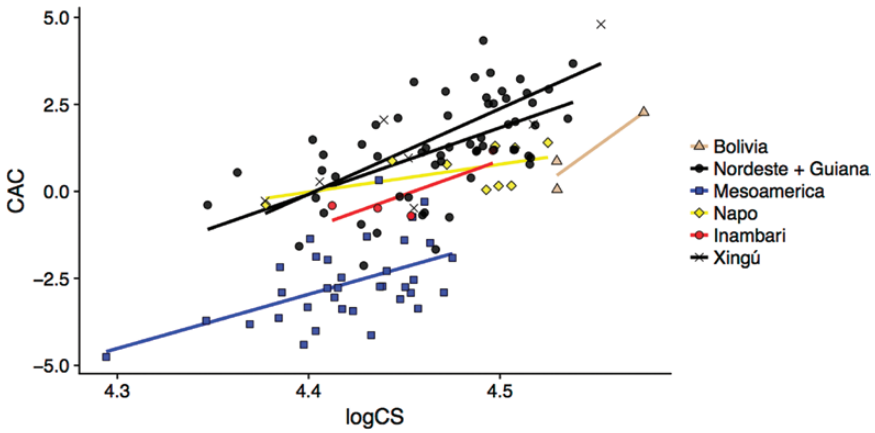

Figure 7. Relationship between the common allometric component (CAC) and the logarithm of the centroid size (logCS). Lines represent the least-squares linear regression for each group.

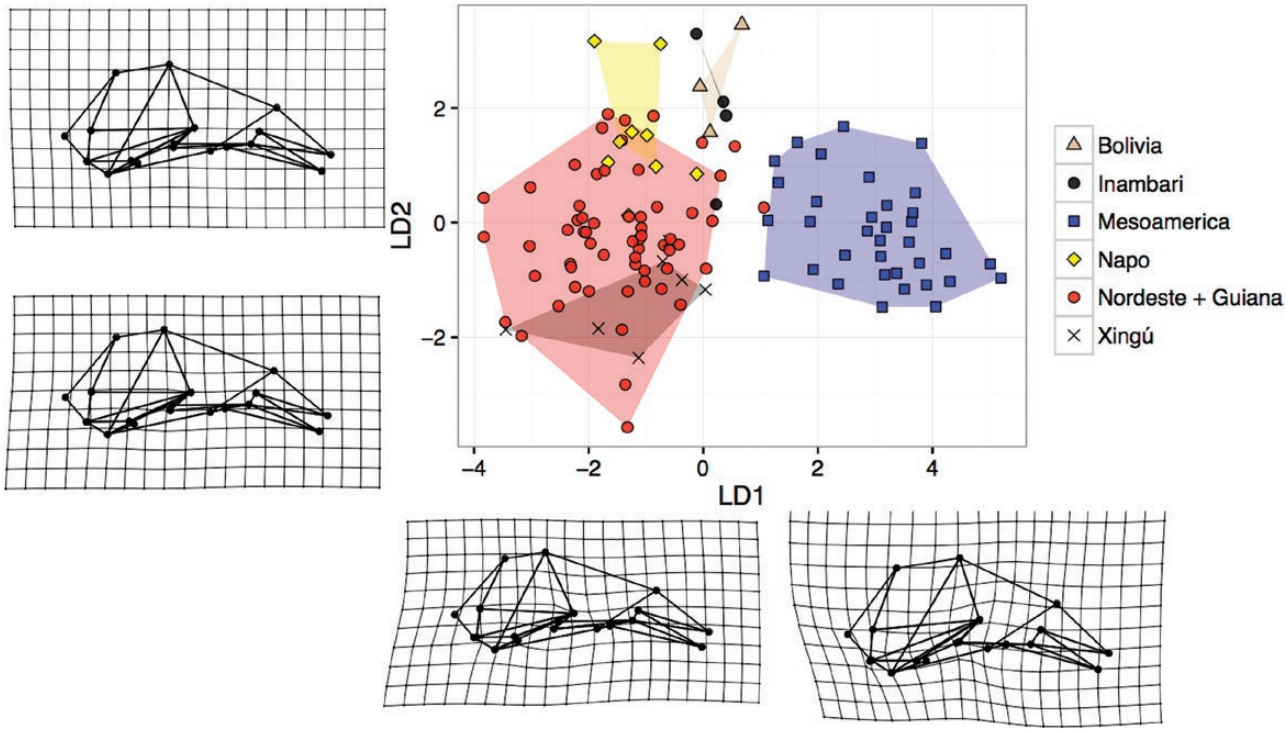

Figure 8. Linear discriminant axes 1 and 2 of *Cyclopes* cranial shape variation. Splines along the axis are the deformation grids of the lateral views of the skull. Each deformation grid represents the difference between the mean shape and extreme values for each axis.

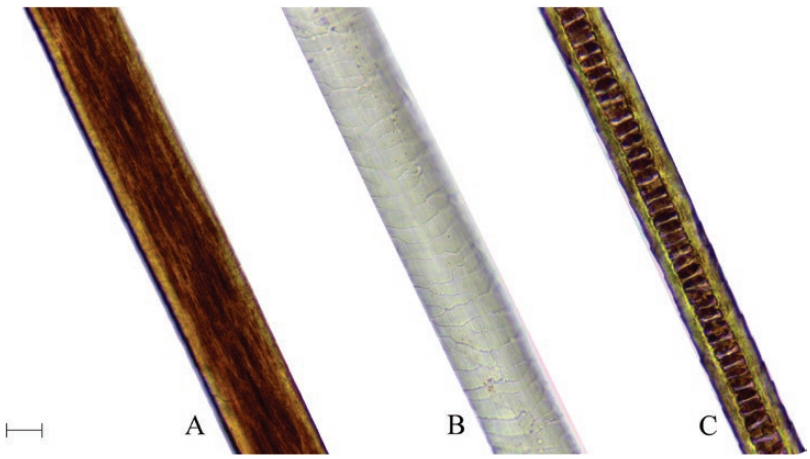

Figure 9. Ultrastructure of hair in *Cyclopes*. A, medulla absent, as usually observed in Xenarthra. B, cuticle arranged transversely to the longitudinal axis of the hair, observed in all *Cyclopes*. C, medulla present in *Cyclopes* specimen of Mesoamerica. Scale bar = 20 μm.

(two of them – 'Guiana' and 'Nordeste' – not well supported as independent entities). The discovered delimitations were then submitted to BPP multilocus, which is a validation method. BPP analysis supported the ten-species hypothesis and rejected the seven-species hypothesis. Despite that, the results of the haplotype network suggest seven species and bPTP suggests no more than six species to be considered unambiguously, given the genetic evidence. This led us to accept, by the more conservative criterion of integration by congruence (Padial *et al.*, 2010), that further data (discrete morphology and morphometrics) could

be evaluated considering these six units and their geographic association. Considering the paradigm of integrative taxonomy (Padial *et al.*, 2010; Carstens *et al.*, 2013), congruence was also evaluated between genetic and phenotypic data. The six genetic units also receive support from unique morphological character combinations (which also supports a seven-species division, for one of which we do not have genetic samples). Skull morphometry and hair ultrastructural morphology showed a much-conserved structure and were not considered informative to integrate via congruence, due to the potential to underestimate species differences (Padial *et al.*, 2010). These data also do not contradict the remaining evidence and were applied here as additional evidence to the species status of the Mesoamerican cluster. Despite the low (molecular) sample sizes for some populations, these congruent results, among several integrative approaches and a clear evidence of much larger interpopulation diversity than currently recognized within the genus, compel us to propose here a new taxonomic arrangement for *Cyclopes*.

Based on evidence provided by molecular phylogenetics using mitochondrial DNA and nDNA, biogeographic analyses of molecular and morphological data, allied with coalescent species delimitation analyses, diagnostic characters of the skull, colour patterns and structures of pelage, we conclude that the genus *Cyclopes* comprises at least seven species. Four previous species designations are considered valid here: *Cyclopes didactylus* (Linnaeus, 1758); *Cyclopes ida* Thomas, 1900; *Cyclopes catellus* Thomas, 1928; and *Cyclopes dorsalis* (Gray 1865). In addition, three new species are described below.

TAXONOMIC ACCOUNTS

FAMILY CYCLOPEDIDAE

GENUS *CYCLOPES* GRAY, 1821

Myrmecophaga Linnaeus, 1758: 35. In part.
Mirmecophaga Brongniart, 1792: 115. In part. Incorrect subsequent spelling of *Myrmecophaga* Linnaeus, 1758.
Cyclopes Gray, 1821: 305. Type species *Myrmecophaga didactyla* Linnaeus, 1758, by monotypy.
Cyclothurus Gray, 1825: 343. *Nomen nudum.*
Didactyles F. Cuvier, 1829: 501. Based on 'Les Didactyles'.
Myrmydon Wagler, 1830: 36. Type species *Myrmecophaga didactyla* Linnaeus, 1758, by monotypy.
Myrmecolichnus Reichenbach, 1836: 51. Type species *Myrmecolichnus didactylus* Reichenbach, 1836 (= *Myrmecophaga didactyla* Linnaeus, 1758), by monotypy.
Eurypterna Gloger, 1841: 112. Type species *Eurypterna didactyla* Gloger, 1841 (= *Myrmecophaga didactyla* Linnaeus, 1758), by monotypy.
Cyclothurus Lesson, 1842: 152. Type species *Cyclothurus didactyla* Lesson, 1842 (= *Myrmecophaga didactyla* Linnaeus, 1758), by monotypy.
Myrmidon Cabrera, 1958: 206. Attributed to Wagner 1844: 211. Incorrect subsequent spelling of *Myrmydon* Wagler, 1830.
Cycloturus Sclater, 1871: 546. Unjustified emendation of *Cyclothurus* Lesson, 1842.
Didactyla Liais, 1872: 356. Type species *Myrmecophaga didactyla* Linnaeus, 1758, by monotypy.
Mamcyclothurus Herrera, 1899: 19. Unavailable name (Gardner 2007).
Cycloturus Goeldi & Hagmann, 1904: 97. Incorrect spelling of *Cyclothurus* Lesson.

Type species: Myrmecophaga didactyla Linnaeus, 1758, by monotypy.

Diagnosis: The smallest of vermilinguans, with average length of 430 mm and average mass of 235 g. Skull compact anteroposteriorly, with rostrum relatively short, not extremely elongated as other vermilinguans. Dense, silky pelage, manus with two well-developed digits and only four digits in the pes, presence of a prehensile tail. Jugals absent, zygomatic process of squamosal straight or dorsally inclined (instead of ventrally inclined, as in other vermilinguans), posterior margin of the palate formed by the palatines and not the pterygoids, extremely anteroposteriorly expanded ribs.

Remarks: See *C. didactylus* remarks below.

CYCLOPES DIDACTYLUS (LINNAEUS, 1758)

(FIG. 10)

[*Myrmecophaga*] *didactyla* Linnaeus, 1758: 35. Type locality 'America australi', restricted to Suriname by Thomas (1911).
Mirmecophaga dydactyla Brongniart, 1792: 115. Incorrect subsequent spelling of *didactyla* Linnaeus, 1758.
Myrmecophaga monodactyla Kerr, 1792: 105. Type locality unknown.
Myrmecophaga unicolor Desmarest, 1822: 375, footnote. Type locality unknown. Name attributed to É. Geoffroy St.-Hilaire.
Eurypterna didactyla: Gloger, 1841: 112. Name combination.
Cyclothurus didactyla: Lesson, 1842: 152. Name combination.
Cyclothurus fulvus Macalister, 1875: 492. *Nomen nudum*.

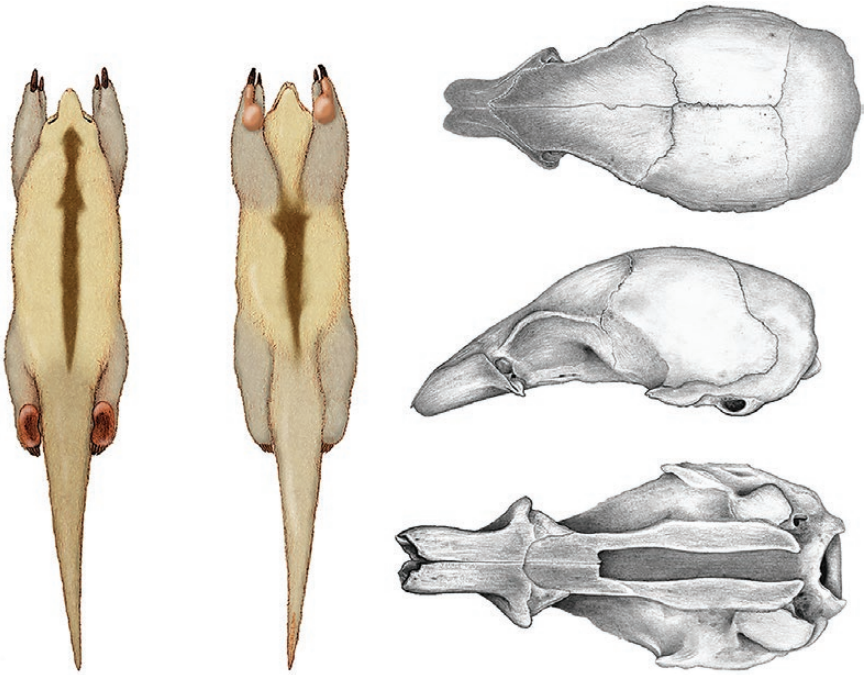

Figure 10. Illustration of *Cyclopes didactylus* (Linnaeus, 1758), pelage and skull.

Mamcyclothurus didactylos Herrera, 1899: 19. Unavailable name (Gardner 2007).
C[*yclopes*]. *didactylus*: Thomas, 1900d: 302. First use of current name combination.
Cyclopes didactylus melini Lönnberg, 1928: 15. Type locality 'S. Gabriel, Rio Negro', Amazonas, Brazil.
Cyclopes pygmaeus Cameron, 1939: 249. *Nomen nudum*.

Holotype: As is usual for many species described by Linnaeus, *C. didactylus* lacks a holotype specimen. It is generally agreed that Linnaeus (1758) based his description on a plate by Albertus Seba (1734–1765), although a specimen of the Museum Adolphi Frederici, described in a published catalogue of the Sweden King's collection, is also referred to (see below). All material in this collection has been transferred to the Naturhistoriska riksmuseet (NRM) in Stockholm, Sweden. An analysis of the skins and skulls of NRM did not locate the referred specimen. Therefore, no name-bearing type specimen is currently known for this species. The type locality assigned by Linnaeus (1758) was *America australi* (South America), but Thomas (1911) restricted it to Suriname. Therefore, we selected a specimen from this locality and designate it a neotype for *C. didactylus*, in accordance with Article 75 of the International Code of Zoological Nomenclature (ICZN, 1999).

Neotype and type locality: Stuffed skin and skull of an adult female, housed at the Field Museum of Natural History, in Chicago, catalogue number 93175, collected by Harry A. Beatty in 29 September 1960, at the Kayser-Gebergte Airstrip, Suriname (Figs 11, 26).

Referred specimens: **Neotype:** FMNH (993175), Suriname; **Brazil:** MNRJ (17294), Maceió, Alagoas, MZUSP (7523, 19942), Manimbu, Alagoas; MNRJ (17295), Rio São Francisco, Alagoas; MNRJ (17293), Viçosa, Alagoas; MNRJ (20593), Ilha do Brigue, Amapá; MZUSP (4679, 4699, 19933), Itacoatiara, Amazonas; MZUSP (7120), Lago do Batista, Amazonas; FMNH (34248, 34249), Manaus, Amazonas; INPA (191, 4075), Manaus, Amazonas; MPEG (1481), Santa Izabel do Rio Negro (left margin of Rio Negro), MZUSP (3176, 3177, 3178), Humberto de Campos, Maranhão; MNRJ (2351, 2352, 2354), Abaeté, Pará; MNRJ (2350), Araguaia River, Pará; AMNH (96470, 96471), Baiao, Pará; MVZ (121210), Belém, Pará; AMHN (37474, 203377), Belém, Pará; MPEG (425, 427, 2333, 2410), Belém, Pará; MZUSP (8680, 8681, 24137), Belém, Pará; MZUSP (4696), Bravo, Pará; AMHN (96444, 96445, 96446, 96448, 96449, 96450, 96451, 96452, 96453, 96454, 96455, 96456, 96457, 96458, 96459, 96460, 96461, 96462, 96463, 96464, 96465, 96466, 96467), Cametá, Pará; FMNH (50907), Cametá, Pará; MNRJ (2349, 5966), Cametá, Pará; MPEG (33940, 33941), Cametá, Pará; MZUSP (4675, 4676, 4677, 4678, 4680, 4681, 4682, 4683, 4684, 4685, 4686, 4687, 4689, 4690, 4691, 4692, 4693, 4694, 4695, 4697, 4698, 4701, 4702, 4703, 19932), Cametá, Pará; MPEG (2335), Castanhal, Pará; AMHN (95506), Igarapé do Amorim, Pará;

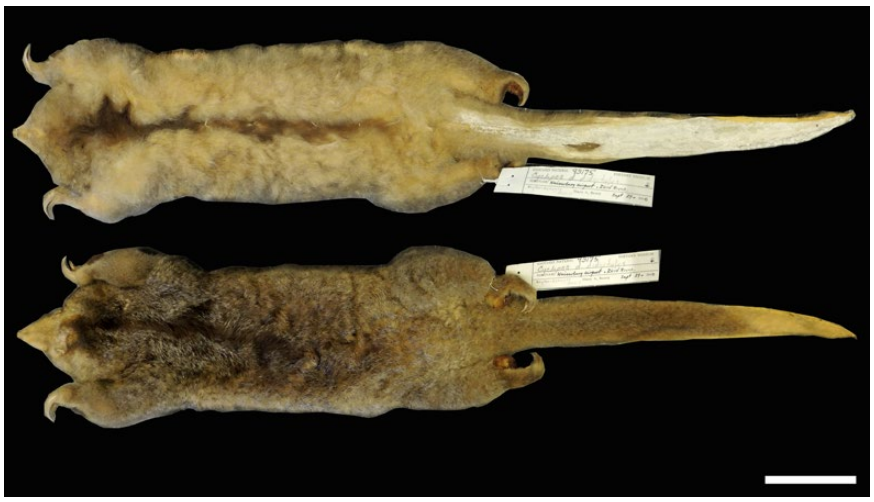

Figure 11. Neotype of *Cyclopes didactylus* – female, FMNH (93175). Ventral view (above) and dorsal view (below). Photograph: Bruce Patterson. Scale bar = 5 cm.

FMNH (24796, 34247), Ilha das Onças, Pará; MNRJ (2345), Ilha das Onças, Pará; AMHN (133505), Ilha de Marajó, Pará; MNRJ (4910), Ilha de Marajó, Pará; MNRJ (2347), Ilha do Mosqueiro; MPEG (38374), Juritί, Pará; AMNH (96468, 96469), Macajuba, Pará; MPEG (38181), Marabá, Pará; MPEG (716, 1190), Marambaia, Pará; MNRJ (23968), Santarém, Pará; MPEG (1955), Tomé-Açu, Pará; INPA (393), Trombetas, Pará; MPEG (12406), Tucuruí, Pará; FMNH (19500), Pará; MNRJ (2346, 2348), Pará; USMN (545910), Pará; MZUSP (8451), Mamanguape, Paraíba; **French Guiana:** FMNH (21719), Cayenne; AMNH (1998, 48388); **Suriname:** FMNH (993175), Zuid River; **Trinidad and Tobago:** AMNH (30744), Aripo; AMNH (186442), Cumana; AMNH (130107); AMNH (174172, 174173, 174183), Ilha de Maingot; FMNH (61853, 61854); USNM (102083, 270995); **Venezuela:** USNM (406494), Acanana; AMNH (77354, 77355), Atabato; AMNH (16129), Bolivar; USNM (296611, 296612), Caicara; AMNH (77356), Esmeralda; USNM (282157), Monagas; AMNH (16956, 16957), Raul Leoni; USNM (143740, 143741), Suapure.

Distribution: Cyclopes didactylus appears to have a disjunct distribution in South America. It occurs in the northern Amazon Forest, left margin of Negro, Uaupés and at both sides of Orinoco Rivers, towards northern Venezuela, and the Guianas, including also the island of Trinidad. It also occurs on the right side of the Amazon River, in northeastern Amazon of Brazil (Pará State) towards the Brazilian states of Maranhão and Piauí, with a disjunct population in the northeastern Atlantic Forest, including the states of Rio Grande do Norte, Paraíba, Pernambuco and Alagoas (Fig. 27).

Diagnosis: General colour brownish-yellow in dorsal and ventral views, rump, legs and tail grey. Dorsal stripe irregular, but distinctive, dorsal and ventral black stripes evident. Fronto-nasal region of the skull is depressed, with a concave profile. External aperture of the ear directed anteriorly. Naso-maxillary sutures divergent proximally, with very short fronto-maxillary suture. Fronto-parietal suture with trapezoidal shape and pterygoid bone partially overlaps tympanic bulla.

Comparisons: Cyclopes didactylus is the only *Cyclopes* species with both dorsal and ventral dark stripes clearly marked. *Cyclopes xinguensis* sp. nov. also have both stripes, but the ventral stripe is faint and irregular. Besides, the coloration of *C. xinguensis* is greyish, in contrast with the yellowish tone of the dorsum and grey limbs of *C. didactylus*. However, some populations of *C. didactylus* may have an indistinct ventral stripe or lack it entirely (see below), which is similar to *C. dorsalis*. However, the dorsal stripe of *C. dorsalis* is paler, and the body coloration is more brightly yellow than *C. didactylus*.

Remarks: The species was described by Linnaeus (1758) as *Myrmecophaga didactyla*, described as '*M[anibus]. palmis didactylis, palmis tetradactylis*', referring to the two digits on the *manus* and four on the *pes*. Linnaeus based his description on a plate by Albertus Seba (1734–1765: pl.XXXVII, fig. 3) (Fig. 12). Linnaeus also refers to a specimen of the Museum Adolphi Frederici, described in a published catalogue of the Sweden King's collection as:

> *{Magnitudo Sciuri aut Felis minoris. Color griseus. Aures parvae. Pedes omnes, ursi instar, talis incedentes. Palmis unguibus duobus*

exteriore duplo majore. Plantis unguibus quatuor aequalibus, digitis coadunatis. Cauda longitudine fere corporis, pilis brevibus, ut corpus, vestita, non vero vulpina aut pilosa}.

The type locality assigned by Linnaeus was *America australi* (South America), but Thomas (1911) restricted it to Suriname, based on the description of Seba's plate, and since he usually received his material from Suriname, it is considered a plausible origin for the specimen that is illustrated in the Thesaurus. Oldfield Thomas also pointed out that Linnaeus' description was based on the specimen at the Adolphi Frederici Museum, referring to the previously mentioned catalogue.

Figure 12. Plate XXXVII from Albertus Seba (1734–1765), including illustration of *Myrmecophaga palmis didactylus*.

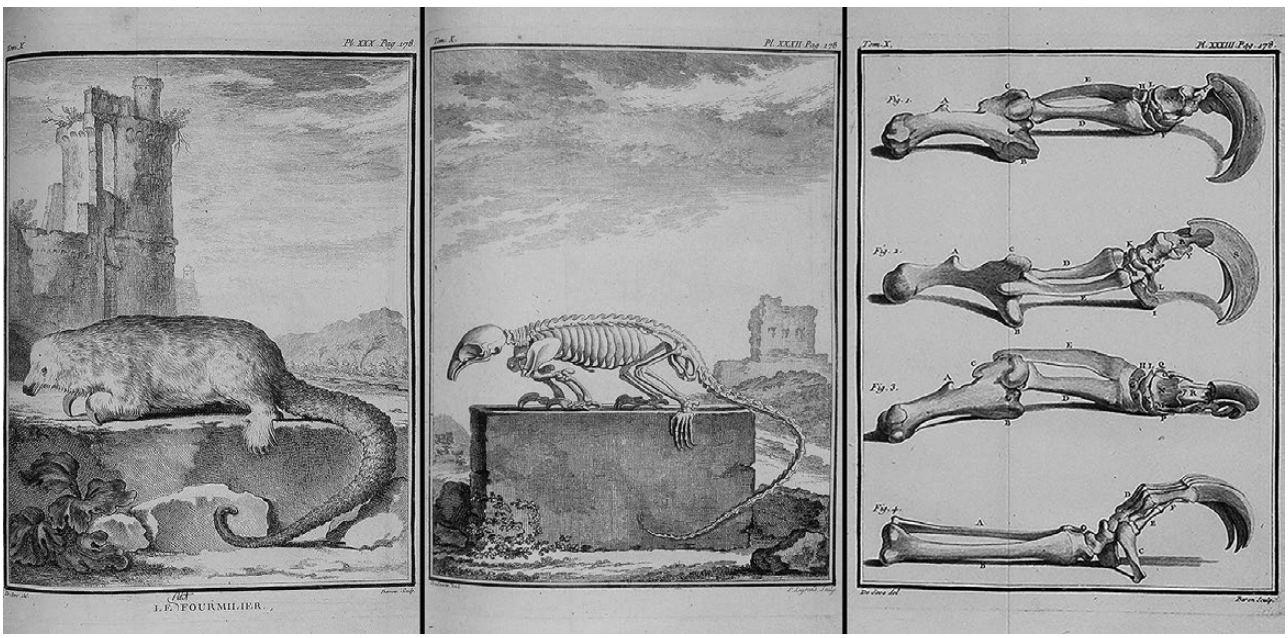

Figure 13. Plates XXX, XXXII and XXXIII from Buffon (1763), with illustrations of *Myrmecophaga didactyla*, evidencing the manus with two digits.

Following Linnaeus tenth edition of *Systema Naturae* (1758), the name *Myrmecophaga didactyla* is recognized as the first valid species name for *C. didactylus*. Brongniart (1792) misspelled it as *Myrmecophaga dydactyla*. In the same year, Kerr (1792) discussed differences between the drawings of Buffon (1763: pl.XXX) and Thomas Pennant (1793: pl.XCV) in respect of the number of toes on the manus of *Myrmecophaga didactyla*: the former depicted the animal with a single claw and the latter with two. Although Kerr (1792) states that he could not elucidate the reason for this difference and that the drawing of Buffon could represent a mutilated dry skin, he suggests the possibility of the existence of a second species and that it would deserve the name *Myrmecophaga monodactyla*. However, Buffon's illustrations clearly refer to a two-clawed specimen, as depicted in plate XXXII and, specially, in plate XXXIII (Buffon, 1763), where the limb skeletons of *Myrmecophaga didactyla* are depicted, clearly showing two digits (Fig. 13A–C).

Desmarest (1822), in a footnote, attributes to É. Geoffroy Saint-Hilaire the name *Myrmecophaga unicolor*, while specifically mentioning the presence of a dorsal stripe in *Myrmecophaga didactyla*. According to Desmarest, É. Geoffroy Saint-Hilaire considered specimens that lack the dorsal band to be a different species. No specific citation was provided to confirm this assertion. *Myrmecophaga unicolor* is mentioned in some later works, such as in Lesson (1827), where it is postulated that in Cayenne (French Guiana) the stripeless variety is considered the female of *Myrmecophaga didactyla*, and in Smith (1827), where the name is attributed to a manuscript (possibly meaning unpublished) by É. Geoffroy.

Different name combinations, such as *Myrmecolichnus didactylus* (Reichenbach, 1836), *Eurypterna didactyla* (Gloger, 1841) and *Cyclothurus didactyla* (Lesson, 1842), were proposed, but always referred to the type originally described by Linnaeus (1758). Oldfield Thomas (1900) was the first to use the current name combination, *Cyclopes didactylus*, while describing a new subspecies. Macalister (1875) mentions the dissection of a *Cyclothurus fulvus*, which he compares with *Cyclothurus didactylus*, but without further elaboration. The name itself does not appear anywhere else in the literature and is thus considered a *nomen nudum*. Cameron (1939), in a study about parasites from Trinidad, mentions the name of the species *Cyclopes pygmaeus*, even stating that *C. didactylus* would be synonymous, but no further comments are made. It is also considered here a *nomen nudum*.

In 1928, Lönnberg described the subspecies *C. didactylus melini*, with the holotype from São Gabriel da Cachoeira, Rio Negro, Brazilian Amazon. The description provided and the holotype conforms well with *C. didactylus*, with the yellowish body, grey limbs and dorsal stripe. However, the specimen lacks a ventral stripe. Given that other characters, including characters from the skull, agree more with a *C. didactylus* identity, we consider *C. didactylus melini* as synonymous with *C. didactylus*. Other specimens here attributed to *C. didactylus* also have an indistinct or absent ventral stripe (Supporting Information, File 33); therefore, its absence is attributed to a variation within the species, pending further data.

Cyclopes ida Thomas, 1900

(Fig. 14)

Cyclopes didactylus ida Thomas 1900: 302. Type locality 'Sarayacu, Upper Pastaza River', Ecuador.
Cyclopes didactylus codajazensis Lönnberg, 1942: 46. Type locality 'Rio Solimoes, Codajaz', Amazonas, Brazil.
Cyclopes juruanus Lönnberg 1942: 47. Type localities 'Rio Juruá, João Pessoa. Rio Juruá, Rio Eirú, Santo Antonio', Amazonas State, Brazil; restricted to the Rio Juruá by Cabrera (1958) and to João Pessoa, Rio Juruá by Gardner (2007).
Cyclopes didactylus jurnanus Cabrera 1958: 207. Incorrect subsequent spelling of *juruanus* Lönnberg 1942.

Holotype: Female, BMNH (80.5.6.67), collected by Mr Clarence Bukley (Fig. 15).

Type locality: 'Sarayacu, Upper Pastaza River', Pastaza, Ecuador.

Referred specimens: **Holotype:** BMNH (80.5.6.67), Sarayacu, Ecuador; **Brazil:** FMNH (20033), Plácido de Castro, Acre; MZUSP (19943), Cantagalo, Amazonas; NRM (1089, *C. d. codajazensis* Holotype), Codajás, Amazonas; MPEG (1905), Iauaretê, Amazonas; NRM (2389, *C. d. juruanus* Holotype), João Pessoa, Amazonas; INPA (189, 202), Lago Amanã, Amazonas; MNRJ (5965), Lago do Batista, Amazonas; MZUSP (4256, 4258), Manacapuru, Amazonas; AMNH (78636), São Gabriel da Cachoeira (right margin of Rio Negro), Amazonas; **Colombia:** AMNH (33918), Morelia, Caqueta; AMNH (207930), Leticia; AMNH (133484), Restrepo, Meta; AMNH (139228), Meta; **Peru:** AMNH (98523, 167845, 204662), Iquitos, Loreto; FMNH (89172), Iquitos, Loreto; AMNH (30107, 75281, 98519, 98521, 98524, 98525, 98526), Loreto; MVZ (157801), Río Santiago, AMNH (98518, 98520), Ucayali.

Distribution: The majority of the known distribution of *C. ida* covers areas south of the Negro and Uaupés Rivers (right bank), but a sample from Restrepo, Colombia indicates a northern reach for the species, although the precise limit is unknown. The southern limit is at Juruá River at the western portion of the distribution, and possibly at the Amazon River in the

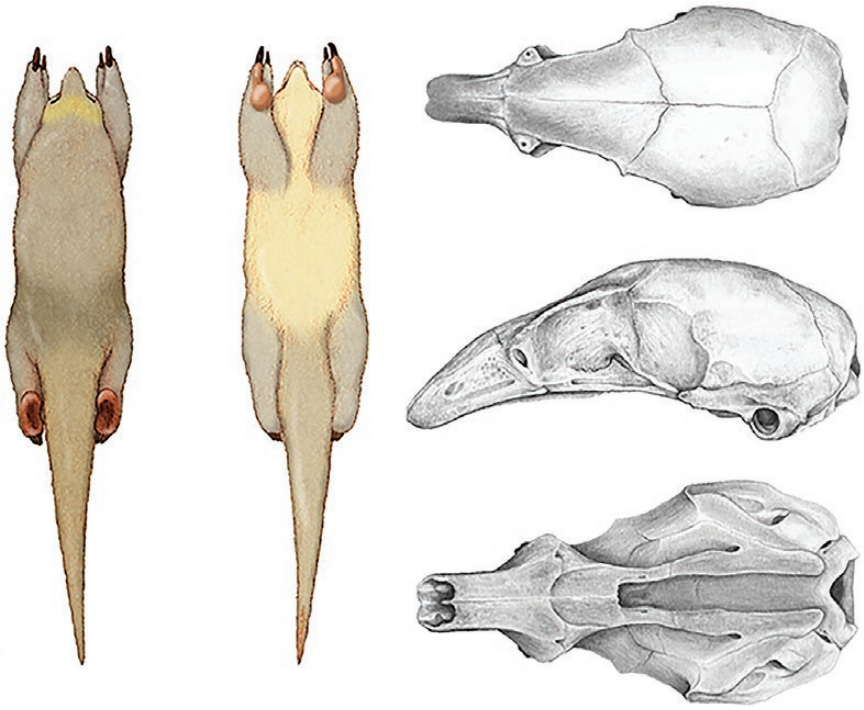

Figure 14. Illustration of *Cyclopes ida* Thomas, 1900, pelage and skull.

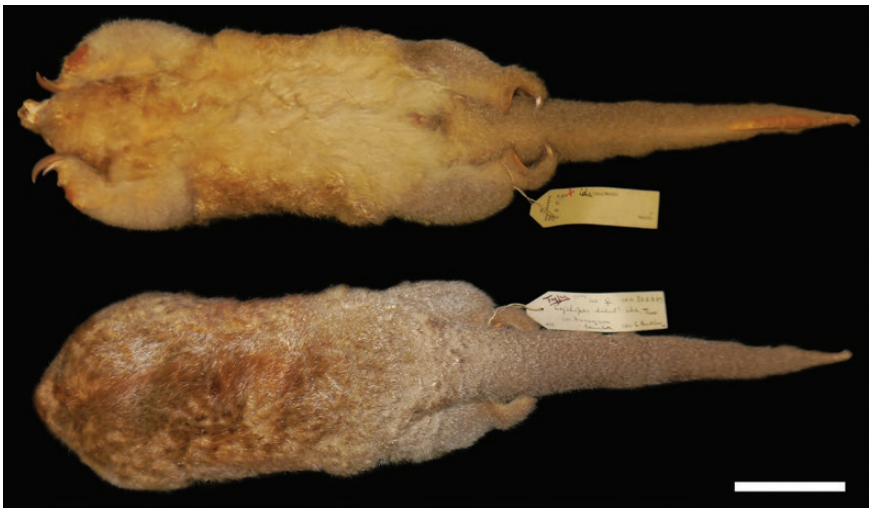

Figure 15. Holotype of *Cyclopes ida* – female, BMNH (80.5.6.67). Ventral view (above) and dorsal view (below). Photograph: Roberto Portela Miguez. Scale bar = 5 cm.

eastern portion. In addition, there is a record in the forests of eastern Andes, which is the western limit of the distribution for this species (Fig. 27).

Diagnosis: Dorsal pelage, legs and tail usually grey. Underparts light yellow, without a ventral stripe. Dorsal stripe, when present, indistinct and subsided into the dorsal fur. Fronto-nasal region of the skull depressed, with a concave profile. External aperture of the ear directed laterally. Naso-maxillary sutures approximately parallel, forming a wide fronto-maxillary suture. Fronto-parietal suture with horseshoe shape, and pterygoid bone partially overlaps tympanic bulla.

Comparisons: Cyclopes ida usually lacks both dorsal and ventral stripes. However, unlike the bright reddish yellow coloration of *Cyclopes rufus* sp. nov., and

the yellowish tone, with grey legs and tail, seen in *Cyclopes thomasi* sp. nov., the coloration of *C. ida* is mostly greyish yellow, with a yellow venter.

Remarks: Based on four specimens, Thomas (1900) described the subspecies *Cyclopes didactylus ida* from Ecuador with general colour more similar to *C. d. didactylus* than *C. d. dorsalis. Cyclopes didactylus codajazensis* was described in 1942 by Lönnberg. The description closely matches *C. ida*, with a uniformly grey body, limbs and tail and absence of ventral stripe. Despite Lönnberg (1942) stating the presence of a clearly marked dorsal stripe, examination of the holotype specimen (NRM 1089) reveals it to be much more indistinct, in conformation with the condition usually found in *C. ida*. The similarities were recognized by Cabrera (1958), who synonymized *C. d. codajazensis* with *C. ida*. Gardner (2007), however, suggested that *C. d. codajazensis* was synonymous with *C. d catellus*. Given the many differences between *C. catellus* and the holotype of *C. d. codajazensis* (see below), and the similarities of the latter with *C. ida*, including cranial characters, we tend to agree with Cabrera (1958) and consider *C. d. codajazensis* synonymous with *C. ida*. In the same article, in which he described *Cyclopes didactylus codajazensis*, Lönnberg (1942) also described a new species, *Cyclopes juruanus*, based on three specimens collected along the Juruá River, in Brazil. Lönnberg (1942) emphasised the many subtle variations in the pelage of the specimens, particularly on the brownish hue of the dorsal fur. However, an examination of the type specimens revealed a more brownish-grey tone, not unlike that found in other specimens of *C. ida*. The ventral stripe, also highlighted by Lönnberg (1942), is, however, indistinct and poorly defined and may be absent altogether. Cranial characters tend to agree with a *C. ida* identification. Gardner (2007) also considered *C. juruanus* a synonym of *C. didactylus ida*, and we tend to agree.

CYCLOPES DORSALIS (GRAY, 1865)

(FIG. 16)

Cyclothurus dorsalis Gray, 1865: 385. Type locality 'Costa Rica'.
C[*yclopes*]. *d*[*idactylus*]. *dorsalis*: Thomas, 1900: 302. Name combination.
Cyclopes dorsalis: Bangs, 1902: 20. First use of current name combination.
Cyclopes didactylus eva Thomas, 1902: 250. Type locality 'Rio Tapayo, N. W. Ecuador'.
[*Cyclopes didactylus*] *dorsalis*: Trouessart, 1905: 803. Name combination.
Cyclopes mexicanus Hollister, 1914: 210. Type locality 'Tehuantepee, Oaxaca, Mexico'.
Cyclopes didactylus mexicanus: Krumbiegel, 1940: 181. Name combination.

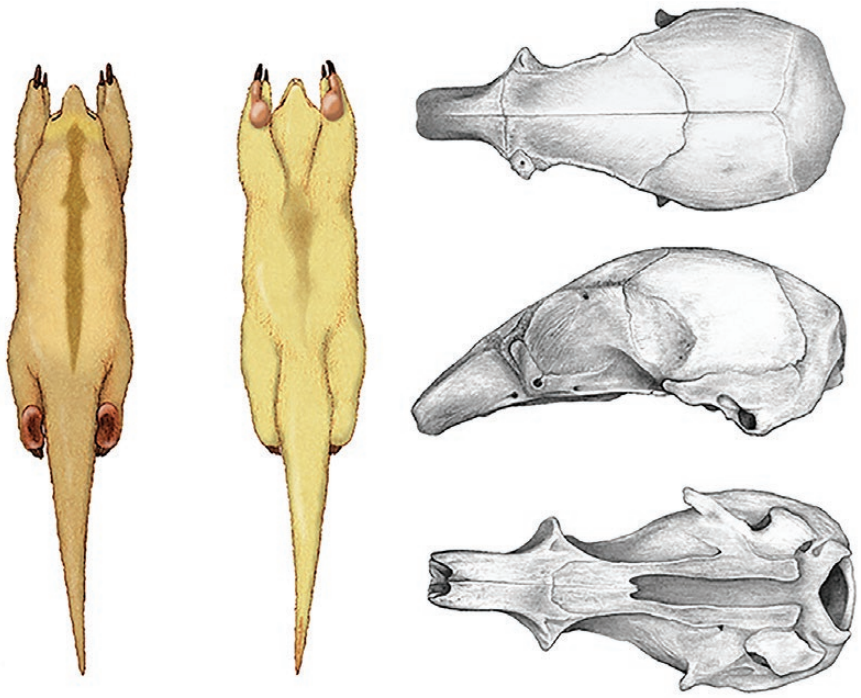

Figure 16. Illustration of *Cyclopes dorsalis* (Gray, 1865), pelage and skull.

Holotype: Female, BMNH (65.5.18.14), collected by Goodwin in 1946 (Fig. 17).
Type locality: 'Costa Rica'.

Referred specimens: **Holotype:** BMNH (65.5.18.14), Costa Rica; **Belize:** USNM (583067), Toledo; **Colombia:** FMNH (69971, 71002), Antioquia; LACM (27345, 56112), Magdalena; USNM (554227), Narino; FMNH (69969), Unguia; AMNH (37786), Valdivia; **Costa Rica:** AMNH (139460); BMNH (2.7.26.3, *C. d. eva* Holotype); **Ecuador:** AMNH (34298); FMNH (44056, 44055); USNM (121097, 11377); **Guatemala:** USNM (19456, 244949); **Honduras:** USNM (19472, 148761), Cortes; **Mexico:** MVZ (171801), La Poza, AMNH (214155); FMNH (64187, 64188); USNM [38534 (*C. d. mexicanus* Holotype), 77089, 78111, 100040, 100172, 100173, 100174, 111377]. **Nicaragua:** AMNH (28480, 30755); USNM (337712, 338772); **Panama:** MNZ (116810, 116811), Canal Zone; AMNH (18887, 69581); FMNH (122699); USNM (200288, 248343, 283876, 292250, 292251, 292252, 294075, 297891, 297892, 304941, 305592, 310356, 310357, 314573, 314574, 314575, 314576, 396434, 460157, 460158, 516629, 575607).

Distribution: This species, although mainly Central American in distribution, also occurs along the Pacific coast of Ecuador and Colombia, and in the Inter-Andean valleys of Colombia, extending northwards to southern Mexico (Fig. 27).

Diagnosis: Fur of the body, limbs and tail is very deeply yellow, dorsal stripe irregular but distinctive and ventral stripe weakly marked or absent. Fronto-nasal region of the skull not depressed, with a straight profile. External aperture of the ear directed anteriorly. Naso-maxillary sutures divergent proximally, with very short fronto-maxillary suture. Fronto-parietal suture with triangular or trapezoidal shape, pterygoid bone does not overlap tympanic bulla.

Comparisons: Cyclopes dorsalis has a very distinctive yellowish tone throughout the whole body with no greyish parts, which, in combination with the presence of a dorsal stripe and absence or weak ventral stripe, characterize this species. *Cyclopes xinguensis* sp. nov. also has only a dorsal stripe, but its coloration is mostly grey.

Remarks: Gray (1865) described *Cyclothurus dorsalis* as a new species from Central America based on the golden yellow back and always present, broad, dorsal black stripe and the yellow feet and tail, differing from *Cyclothurus didactylus*, which possessed fulvous back and grey feet and tail. Trouessart (1899) lowered it to a subspecies (Var. *dorsalis*) of *Cycloturus* [sic]. Bangs (1902) was the first to use the name combination *C. dorsalis*, the same used here, keeping it as a separate species. Trouessart (1905) considered *C. dorsalis* to be a subspecies of *C. didactylus*, using the name *Cyclopes didactylus dorsalis*.

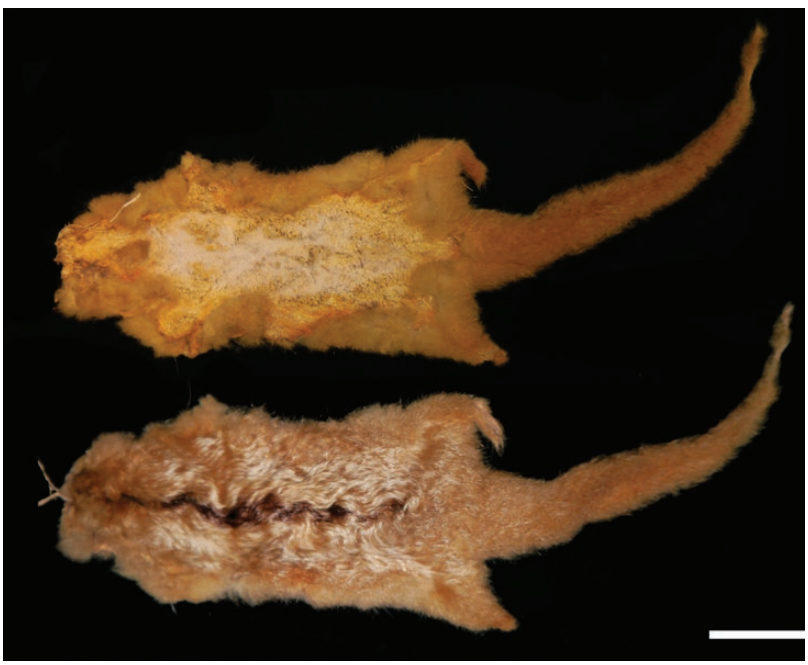

Figure 17. Holotype of *Cyclopes dorsalis* – Female, BMNH (65.5.18.14). Ventral view (above) and dorsal view (below). Photograph: Roberto Portela Miguez. Scale bar = 5 cm.

Oldfield Thomas (1902) described *Cyclopes didactylus eva* as a new subspecies from the west of the Andes, in northwest Ecuador, and considered it an intermediate between *C. d. dorsalis* and *C. d. didactylus* and *C. d. ida*. Given its distribution, continuous with the Central American populations and disjunct in relationship to the other South American populations of *Cyclopes*, and characteristics (see description), which conform well to *C. dorsalis*, it is here considered a synonym. Hollister (1914) described another species, *Cyclopes mexicanus*, from southern Mexico, based on some coloration differences. *Cyclopes mexicanus* was later considered a subspecies of *C. didactylus* by Krumbiegel (1940). Both the skull and pelage coloration of *C. mexicanus* also conform well to the characters of *C. dorsalis* and is also here considered a synonymous of this species. However, since our molecular sample of *C. dorsalis* consists of a single individual from 'Esmeraldas', in the forests of the Pacific coast of Ecuador, the present arrangement must be considered provisory, until further data permit a more complete analysis. We believe that the populations of *Cyclopes* from the west of the Andes deserve further scrutiny to clarify their taxonomic status.

CYCLOPES CATELLUS THOMAS, 1928

(FIG. 18)

Cyclopes didactylus catellus Thomas, 1928a: 293.

Holotype: Female, BMNH (26.1.12.17), collected by J. Steimback (Fig. 19).

Type locality: 'Buenavista, Santa Cruz, Bolivia'.

Referred specimens: **Holotype:** BMNH (26.12.17), Santa Cruz, Bolivia; **Bolivia:** AMHN (262656), Beni; FMNH (51889, 51890), Santa Cruz; MNK (637, 4075), Santa Cruz; USNM (262493), Santa Cruz.

Distribution: This species occurs in central Bolivia, probably inhabiting Andean slopes forests (Fig. 27).

Diagnosis: General colour brown-yellowish, tail and limbs more yellowish. Dorsal dark stripe absent, strongly developed and extensive sternal stripe present. Fronto-nasal region of the skull not depressed, with a straight profile. External aperture of the ear directed anteriorly. Naso-maxillary sutures divergent proximally, with a very short fronto-maxillary suture. Fronto-parietal suture with horseshoe shape, pterygoid bone overlaps tympanic bulla.

Comparisons: The absence of a dorsal stripe and the presence of a well-developed ventral stripe, as well the brownish tone, make this species readily recognizable. The only other species of *Cyclopes* with a ventral stripe and no dorsal stripe is *Cyclopes thomasi* sp. nov., but in the latter, the ventral stripe is faint and poorly developed, and the legs and tail are grey.

Remarks: Cyclopes didactylus catellus was described from the Santa Cruz region of Bolivia by Oldfield Thomas (1928), based on differences in pelage, shorter tail and absence of dorsal stripe, but with a clearly visible ventral (sternal) stripe, considered broader than in other taxa. Oldfield Thomas (1928) states that the

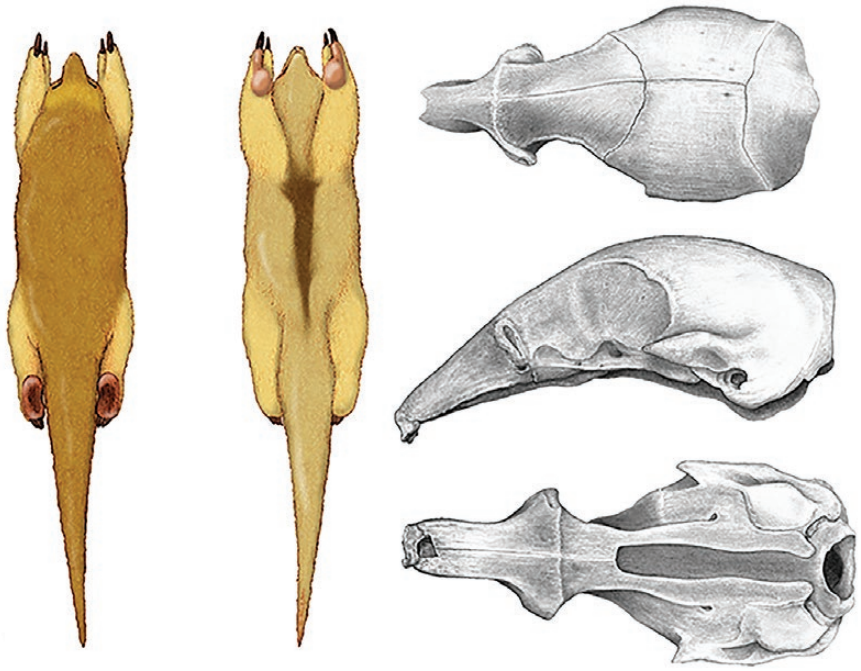

Figure 18. Illustration of *Cyclopes catellus* Thomas, 1928, pelage and skull.

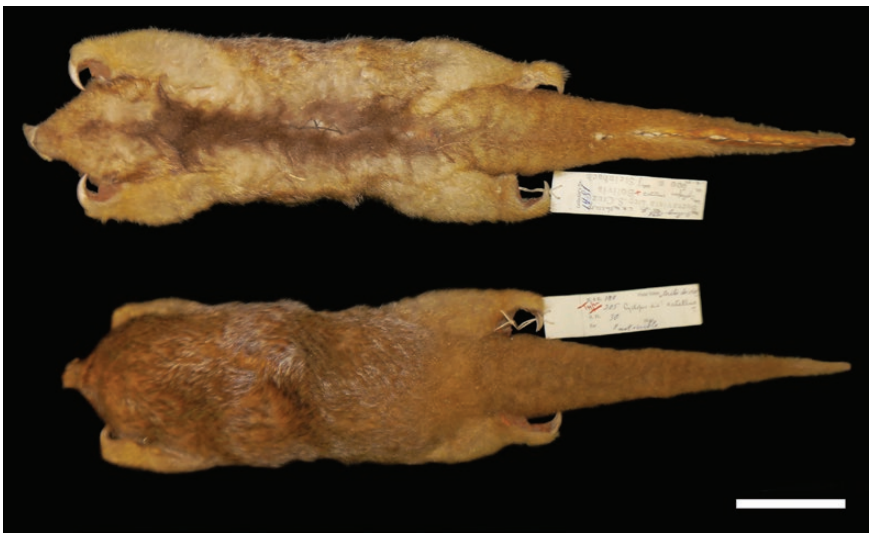

Figure 19. Holotype of *Cyclopes catellus* – female, BMNH (26.12.17). Ventral view (above) and dorsal view (below). Photograph: Roberto Portela Miguez. Scale bar = 5 cm.

observations were based on a uniform series of specimens and that even the young presented this colour pattern. Unfortunately, DNA samples of *C. catellus* were not available for this study, so its phylogenetic relationships and divergence in relation to other taxa of *Cyclopes* remain uncertain. It represents the southernmost occurrence of *Cyclopes*, being markedly different from its neighbours in qualitative characters, and its distribution may suggest an isolated occurrence, not in contact with other *Cyclopes* species. Based on the distinctive and very consistent colour pattern (the only taxon with a clearly marked ventral and no dorsal stripe), unique combination of cranial characters (see description) and geographic distribution, we recognize it as a different species, *Cyclopes catellus*, pending further genetic studies. Gardner (2007) considered *C. didactylus codajazensis* Lönnberg (1942) as a synonym of *C. d. catellus*, despite the description of *C. d. codajazensis* and the specimens being clear about the presence of a dorsal and no ventral stripe, while *C. catellus* has only a ventral stripe. In this study, *C. d. codajazensis* is considered a synonymous of *C. ida*.

CYCLOPES THOMASI SP. NOV.

(FIG. 20)

Holotype: Female, MZUSP (19944). Collected by Dr Paulo Emílio Vanzolini in 1985 (Figs 21, 26).

Type locality: Porto Walter, Acre, Brazil.

Referred specimens: **Holotype:** MZUSP (19944) Porto Walter, Acre, Brazil; **Brazil:** INPA (2876), Igarapé Porongaba, Acre; INPA (2877), Seringal Petropolis, Acre; MVZ (190355), Rio Juruá, Amazonas; **Peru:** USNM (364503), Pasco.

Etymology: The specific name honours Michael Rogers Oldfield Thomas, in recognition of his extensive contribution to mammalogy, and specifically to the taxonomy of *Cyclopes*.

Distribution: Cyclopes thomasi occurs in western Amazon, from the north limit on the Juruá River to the southwest, in the Ucayali River region, in the provinces of Pasco and Ucayali (Peru). The western limits are unknown, but may not extend beyond the Madera River (Fig. 27).

Diagnosis: Body colour strikingly orange to reddish-brown, legs and tail grey. Dorsal stripe absent. Ventral stripe little developed and faint. Fronto-nasal region of the skull not depressed, with a straight profile. External aperture of the ear directed anteriorly. Naso-maxillary sutures divergent proximally, with a very short fronto-maxillary suture. Fronto-parietal suture with triangular shape, pterygoid bone does not overlap tympanic bulla.

Comparisons: The only other species of *Cyclopes* with a ventral stripe and no dorsal stripe is *C. catellus*, which, however, has a very marked and distinct ventral stripe and no greyish tone on the limbs and tail.

CYCLOPES RUFUS SP. NOV.

(FIG. 22)

Holotype: Female, UFMG (6015). Collected by Eduardo Sábato (Figs 23, 26).

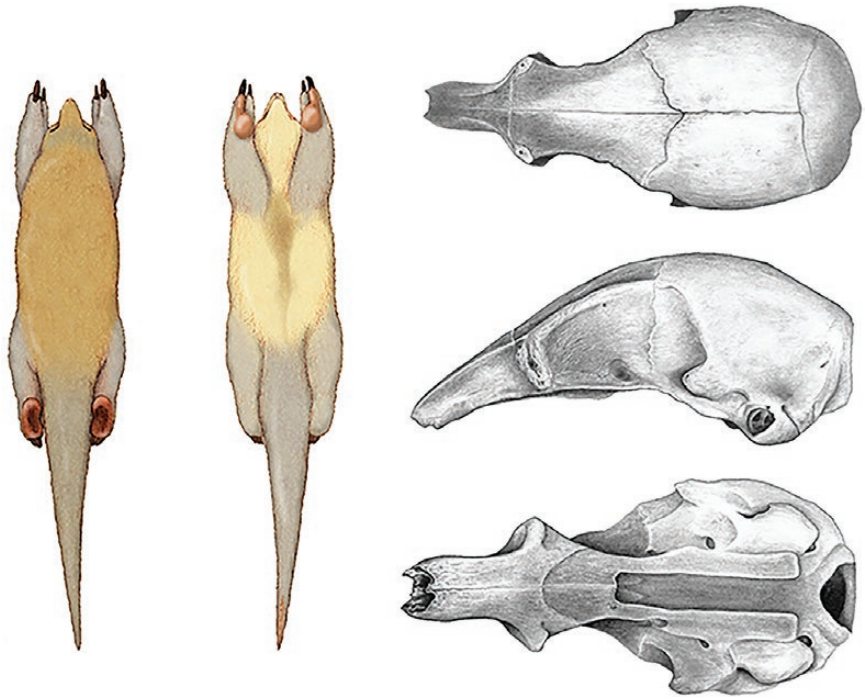

Figure 20. Illustration of ***Cyclopes thomasi* sp. nov.**, pelage and skull.

Figure 21. Holotype of *Cyclopes thomasi* – female, MZUSP (19944). Ventral view (above) and dorsal view (below). Photograph: Fabio Nascimento. Scale bar = 5 cm.

Type locality: Porto Velho, Rondônia, Brazil (08°51′16″S; 064°00′53″W).

Referred specimens: **Holotype:** UFMG (6015), Porto Velho, Rondônia, Brazil; **Brazil:** UFRO (518), Espigão do Oeste, Rondônia; UFRO (17, 184, 326), Porto Velho, Rondônia.

Etymology: The specific name *rufus* (meaning 'red' in Latin) refers to the reddish tone of the dorsal coloration of this species.

Distribution: Occurs in the interfluve between the Madeira and Aripuanã Rivers. The northern limit is

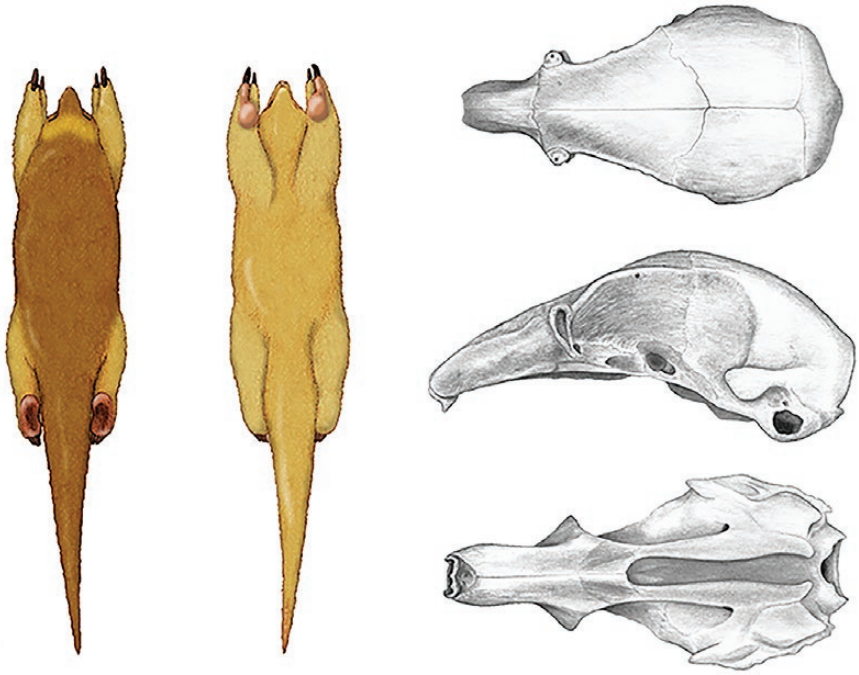

Figure 22. Illustration of ***Cyclopes rufus* sp. nov.**, pelage and skull.

Figure 23. Holotype of *Cyclopes rufus* – female, UFMG (6015). Ventral view (above) and dorsal view (below). Photograph: Daniel Casali. Scale bar = 5 cm.

possibly the Amazon River, and the southern limit is the Guaporé River (Fig. 27).

Diagnosis: Dorsal colour of a distinct reddish tone, tail and limbs more yellowish red. Ventral and dorsal stripes absent. Fronto-nasal region of the skull not depressed, with a straight profile. External aperture of the ear directed laterally. Naso-maxillary sutures approximately parallel, with a wide fronto-maxillary suture. Fronto-parietal suture with trapezoidal shape, pterygoid bone does not overlap tympanic bulla.

Comparisons: The absence of dorsal and ventral stripes and the striking reddish coloration of *Cyclopes rufus* allow easy differentiation from other species of *Cyclopes*. *Cyclopes ida* also does not usually have dorsal and ventral stripes, but it has a more subdued coloration, being mainly grey with yellowish underparts.

The body of *C. thomasi* also has a reddish-brown tone, but the limbs and tail are grey and a faint ventral stripe is present.

CYCLOPES XINGUENSIS SP. NOV.

(FIG. 24)

Holotype: Female, UFMG (4163). Collected by Dr Victor Yunes (Figs 25, 26).

Type locality: Vitória do Xingu, Pará, Brazil (Usina Belo Monte) (03°17′12″S; 051°53′48″W).

Referred specimens: **Holotype:** UFMG (4163), Vitória do Xingu, Pará, Brazil; **Brazil:** AMNH (92885), Parintins, Amazonas; MZUSP (4700), Caxiricatuba, Pará; MZUSP (19934, 19935, 19936, 19937, 19938, 19939), Fordlândia, Pará; MPEG (38512), Juriti, Pará; UFMG (4164), Porto de Moz, Pará; MNJR (11587), Santarém, Pará; MUZSP (3691), Santarém, Pará; MPEG (42641), Vitória do Xingu, Pará.

Etymology: The specific epithet *xinguensis* refers to the type locality of this species in Vitória do Xingu, Pará, Brazil. Xingu is an indigenous word meaning good and clean water.

Distribution: This species is limited in the north by the Amazonas River, in the east by the Xingu River and in the west by the Madeira River. The southern limit is unknown (Fig. 27).

Diagnosis: Dorsal coloration grey, yellow on the rump and venter pale yellowish. Legs and tail are grey. Dorsal stripe clearly marked and evident, ventral stripe indistinct and irregular. Fronto-nasal region of the skull not depressed, with a straight profile. External aperture of the ear directed laterally. Naso-maxillary sutures approximately parallel, with a wide fronto-maxillary suture. Fronto-parietal with a triangular shape, pterygoid bone overlaps tympanic bulla.

Comparisons: Cyclopes xinguensis is mostly grey, unlike most of the other species of *Cyclopes*. Its colour is somewhat similar to *C. ida*, but the rump is yellowish in *C. xinguensis* and completely grey in *C. ida*. Also, *C. ida* lacks a dorsal stripe, which is very evident in *C. xinguensis*.

DISCUSSION

The number of species recognized here may seem excessive when considering what was previously considered a single species, but we argue that the current classification of *Cyclopes* is too conservative, and much of the morphological and genetic diversity within the genus was unassessed or obscured by previous taxonomic treatments (Wetzel, 1982; Gardner, 2005, 2007; Hayssen *et al.*, 2012). Molecular data clearly support the identification of at least six species, maybe more. Take, for instance, the populations of *Cyclopes* that occur in northern South America, from the Guianas

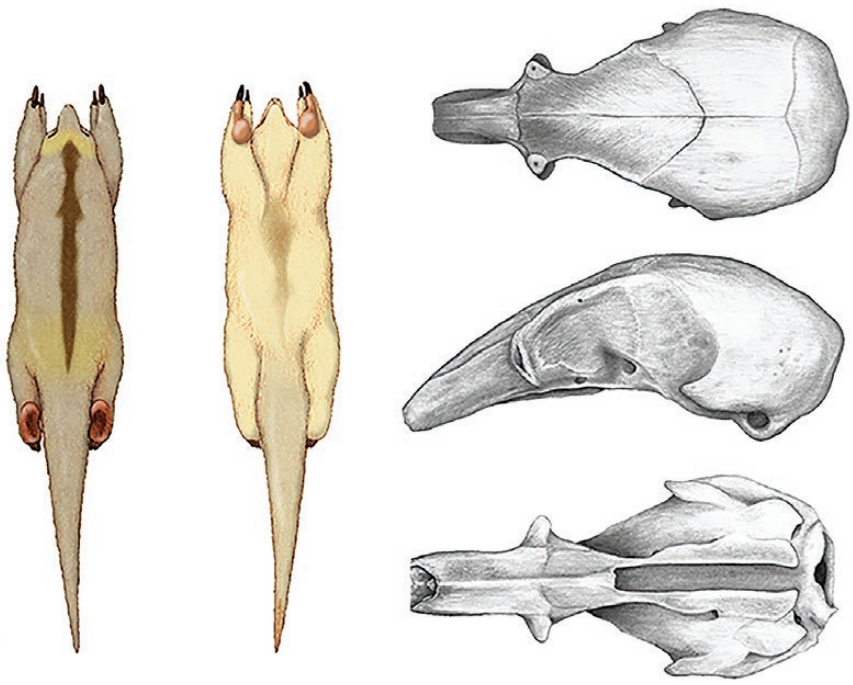

Figure 24. Illustration of ***Cyclopes xinguensis* sp. nov.**, pelage and skull.

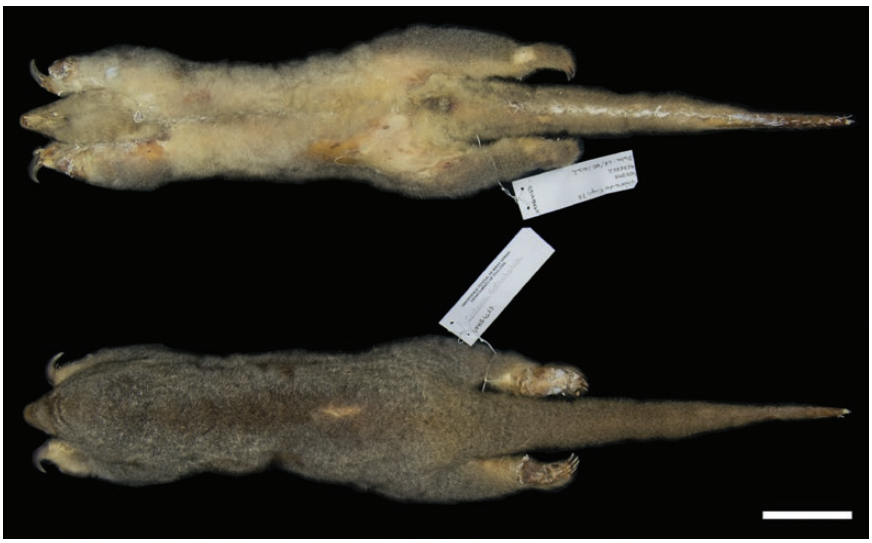

Figure 25. Holotype of ***Cyclopes xinguensis* sp. nov.** – female, UFMG (4163). Ventral view (above) and dorsal view (below). Photograph: Daniel Casali. Scale bar = 5 cm.

eastwards to the disjunct population in coastal northeastern Brazil, the nominal *C. didactylus*. Molecular results indicate that they constitute two well-defined, structured populations, diverging at *c*. 2.3 Myr and geographically isolated. However, since they constitute a monophyletic group and no major morphological differences were found between them, we prefer to be cautious and maintain both populations as part of a single species, despite strong support from some species delimitation analyses (GMYC and BPP) for the separation. The results of bPTP, however, do not support the separation of these populations into distinct species and, in addition, the total absence of phenotypic support leads us to be more conservative in our final taxonomic decision, maintaining Nordeste and Guiana populations as a single species. All other species recognized here are clearly and strongly supported by our data, both by the fact that they form well-supported clades and by the presence of unique morphological character combinations.

The genus *Cyclopes* is a morphologically conservative mammal genus, at least in terms of cranial morphology, reflected by the relatively low level of differentiation. Part of this lack of distinctive characters may be attributable to the cranial simplification common to all Vermilingua, a reflection of the extreme adaptations of the group to a diet of social insects, which usually implies a long and tubular skull and reduction of the dentition (McDonald *et al.*, 2008). This may be complicated by the fact that, as far as we know, all *Cyclopes* populations seem to have very similar ecologies, inhabiting the same kind of arboreal environment and eating the same prey items, which may imply a lack of ecomorphological differentiation. However, little is known about possible ecological differences among the species recognized here. Despite the uniformity in osteological anatomy, we could identify at least some few characters that separate different groups within the genus that can be used to discriminate the seven taxa, although at least some of these characters show some variation in some populations. Further and more detailed analyses, perhaps using new technologies to access morphological variation, such as CT scan-based analyses, may uncover more distinctive characters and complement those described here.

Coloration, on the other hand, is extremely variable within the genus, which is reflected by the great number of species and subspecies described in the past, based mainly on the different colour patterns and presence and absence of body stripes (Gray, 1865; Thomas, 1900, 1902, 1911, 1928; Lönnberg, 1928, 1942). However, since the mid-20th century, there has been a great tendency of considering *Cyclopes* as composed of a single species (Wetzel, 1982; Gardner, 2005, 2007; Hayssen *et al.*, 2012), which implies a huge variation in fur colour, although many of the subspecies were still considered valid, based mostly, again, on fur coloration. However, our data suggest that the observed molecular and morphological variation is consistent with many different species, despite the most widely distributed species, *C. didactylus* and *C. ida*, showing some variation throughout their ranges. Most likely, advances in *Cyclopes* systematics have been restricted due to the paucity and difficulty of accessing specimens, which has led to a more conservative approach in the taxonomy of the genus.

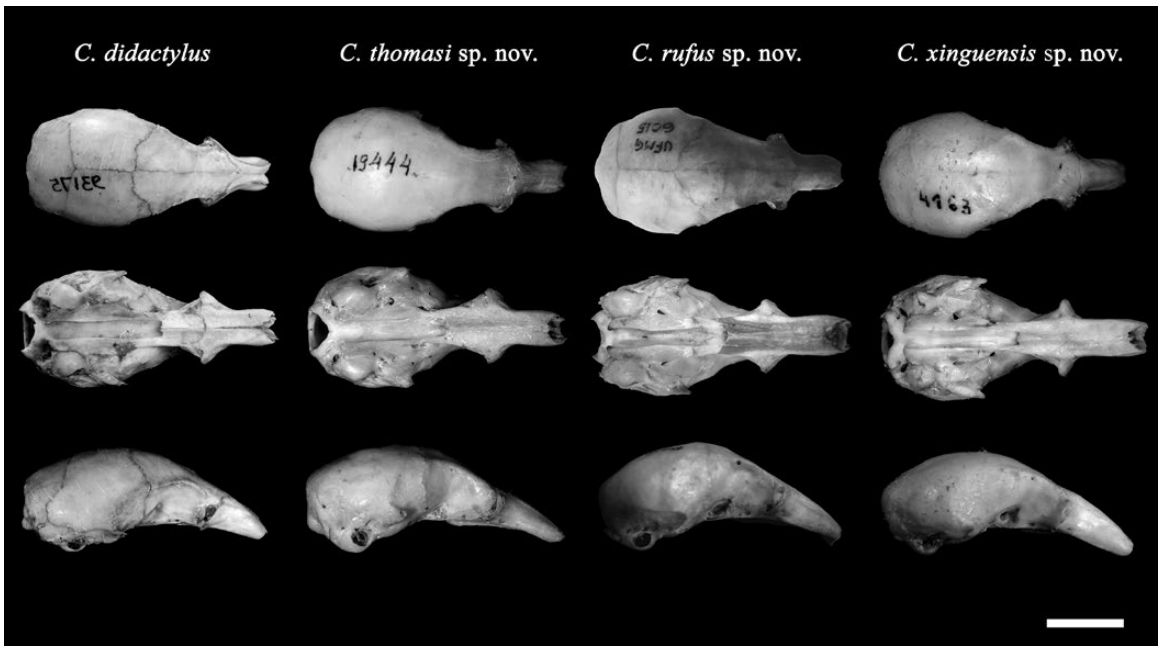

Figure 26. Skulls of type specimens assigned in this study in dorsal (up), ventral (middle) and lateral (down) views. Scale bar = 1 cm.

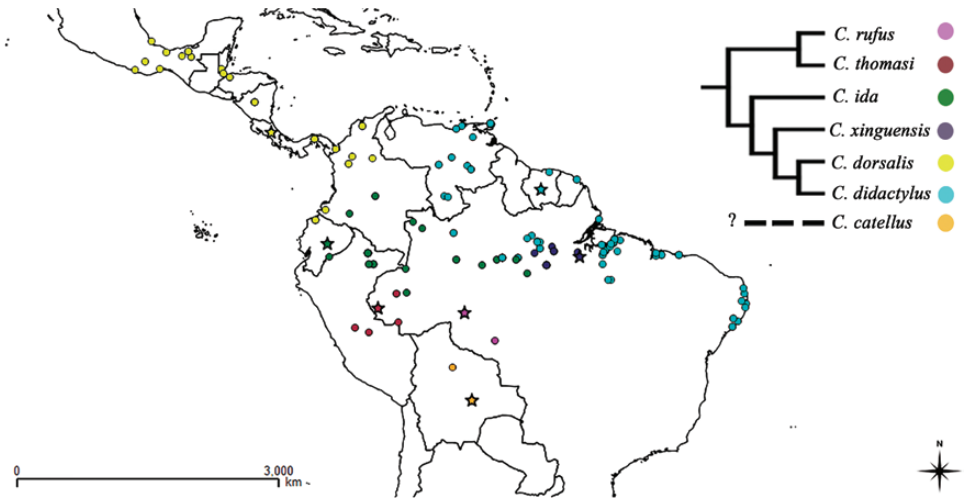

Figure 27. Suggested geographic distribution for the seven recognized species in this study, based on available data, indicated by coloured dots: *Cyclopes didactylus* (blue), *Cyclopes ida* (green), *Cyclopes dorsalis* (yellow), *Cyclopes catellus* (orange), *Cyclopes thomasi* (brown), *Cyclopes rufus* (lilac) and *Cyclopes xinguensis* (purple). Locality of type specimens for each species is indicated by stars. At the upper right corner, a cladogram depicts the phylogenetic relationships among species (unknown for *C. catellus*). Colour circles indicating the correspondence between taxa and geographic distribution.

Despite the uniform skulls and variable pelages, different combinations of qualitative characters support the uniqueness of the seven species recognized here, and it is significant that the morphological variation encountered corresponds mostly to the genealogical units recovered using molecular data.

Our geometric morphometric results are consistent with the idea that *Cyclopes* is remarkably conserved in terms of skull shape morphology. Even though all (M)ANOVAs were significant for divergence in size, shape and form, cross-validation reclassification rates of the discriminant analysis were low, showing the

morphological overlap between groups. This pattern of stability in morphometric variation within a single genus has also been observed for olingos (*Bassaricyon*), where *B. neblina*, the sister taxon to all other olingos, has a heterochronic-looking morphology compared to other species (Helgen *et al.*, 2013). In fact, stasis of shape characters is not uncommon in arboreal mammals (see Albrecht & Miller, 1993 for examples on primates) suggesting that this habit could be extremely demanding in terms of morphology and that changes, when present, are rare or small. This could also help explain the taxonomic conservatism that has been traditionally applied to *Cyclopes*.

The only exception to this pattern was *C. dorsalis* (Mesoamerican/Pacific coast taxon), which showed remarkably high reclassification rate (0.94). *Cyclopes dorsalis* differentiation is similar to the common axis of allometry for all *Cyclopes*, with this taxon having larger braincases and shorter snouts than its congeners. Even though *C. dorsalis* also has a smaller skull size on average, the shape divergence is not purely associated with allometric scaling, leading to the conclusion that, while *C. dorsalis* overlaps in size with other species, it has a morphology that is consistent with that of smaller individuals. This pattern could potentially be achieved by mosaic heterochrony (David, 1990), where developmentally decoupled regions (such as the neurocranium and the face) vary semi-independently, producing heterochronic differences that are not completely explained by size scaling alone (Sydney, Machado & Hingst-Zaher, 2012). This could potentially lead to the decoupling of allometric shape change and size, a pattern sometimes assumed to be evidence of species differentiation (Monteiro-Filho *et al.*, 2002; Prevosti *et al.*, 2013). The fact that *C. dorsalis* is nested within *Cyclopes*, not being one of the first lineages to separate from the remainder, suggests that the morphological divergence of this species from the others is not only due to phylogenetic distance, but it is probably related to other factors particular to this lineage, probably associated with its unique geographical distribution. More investigation about possible ecological differences between species could help to identify potential factors that might explain the observed differences.

In addition to geometric morphometric analysis, the distinction of *C. dorsalis* is also supported by the unique structure of its fur, with the presence of a medulla, differing from every other Pilosa (Miranda *et al.*, 2013), and only observed in *Tolypeutes* among xenarthrans (Santos, 2016). However, since we only analysed a single specimen of *C. dorsalis*, and our sampling of other populations of *Cyclopes* was also limited, further and more detailed studies of the fur structure in *Cyclopes* must be performed. Our molecular analysis is also limited in that respect, particularly considering the populations of *C. dorsalis* in Central America, although phenotypically the species is very consistent. Future studies should also expand sampling to the west of the Andes, from Colombia and Ecuador to southern Mexico, to clarify taxonomic status there. However, the greatest limitation of our study is probably the taxonomic status of *Cyclopes catellus*. We were not able to secure a DNA sample from populations of southeastern Peru and northeastern Bolivia. However, based on the relatively sharp and consistent phenotypic divergence when compared to other species of *Cyclopes* and its potentially isolated occurrence in the southwestern Amazon, we recognize it as a different species, pending further molecular studies.

The fact that most of the individuals used in the molecular analyses are not the same as those used in the morphological and morphometric evaluation also represents an obstacle to the full comprehension of the extension of the phenotypic variation within the genus, as well as the real limits of the distribution of the different species. However, the rarity of individuals in collections and the difficulty in obtaining them in the wild may be problems that will not have an immediate solution. This is especially complicated in the case of the clades for which we have few or no samples. Future studies using techniques for recovering ancient DNA from historical collections with verified location may ease this issue and represent a promising line of research to further support and clarify the conclusions presented here.

We found a strong association between the taxonomic boundaries recognized here and the geographical distribution of these species, suggesting that the speciation events that led to the current intrageneric diversity may have been influenced by historical events that shaped the distribution of these animals. For example, the first population split separates *Cyclopes* lineages from Rondonia and Inambari from all others, at *c.* 10.3 Myr. Despite constituting a monophyletic group, both lineages (Rondonia and Inambari) are considered here as two previously unrecognized species, respectively *C. rufus* and *C. thomasi*, having diverged at *c.* 3.4 Myr and differentiated by clear phenotypic characters in neighbouring areas of the western Amazon Basin. The time of differentiation of *C. rufus* and *C. thomasi* from the remainder of the genus *Cyclopes* is coincident with raised sedimentation rates in the Andean foreland basins that eventually became overfilled. At ~10 Myr, coinciding with global sea level drop and climate cooling, Andean sediments reached the Atlantic coast through the Amazon drainage system, with the initial stages of the 'Pebas' system change into a fluvial 'Acre' system (Hoorn *et al.*, 2010). With the end the Western Amazonian wetlands at ~7 Myr, there was the

return of forested habitats and terrestrial conditions, marked by an increase of plant diversity from 7 to 5 Myr (Hoorn *et al.*, 2010). Around this time (5.8 Myr), we recovered the divergence of the lineage of *Cyclopes ida* from the remainder of the *Cyclopes* species. The subsequent divergence occurs around 4.6 Myr and separates the lineage leading to *Cyclopes xinguensis*, which became restricted to the Xingu area. The isolation of *C. xinguensis* may have been influenced by neotectonic activity and modification of fluvial systems from 7 to 2.5 Myr (Hoorn *et al.*, 2010; Coimbra *et al.*, 2017). These events may also have been important for the speciation between *C. rufus* and *C. thomasi*, which could have happened with the Purus or Madeira River functioning as a vicariant barrier. *Cyclopes dorsalis* was probably separated from other South American lineages by the Northern Andes, with this divergence estimated at *c*. 3.0 Myr, a period that is chronologically coincident with the final stage of Andes' formation (Hoorn *et al.*, 2010). Although not recognized here as distinct taxonomic entities, the two clades that compose *C. didactylus* diverged at *c*. 2.3 Myr. From this period onwards, the Quaternary ice ages (Hoorn *et al.*, 2010) could have influenced the separation of these two populations.

The results presented here have clear implications for the conservation status and management practices of the genus *Cyclopes*. Although general deforestation is taking place over many parts of its range, *Cyclopes* remains widespread in the Amazon Basin. Some particular areas, such as the Madeira and Xingu regions of Brazilian Amazon, are subject to a more intensive exploration. These areas have faced an increasing pressure from large monocultures (particularly soybean and sugarcane) and livestock, especially in its southeastern range, resulting in locally high deforestation rates (Canale *et al.*, 2012). In addition, wildfires, illegal roads, logging activities, mineral prospecting, subsistence hunting and the lack of proper sanitation and health care further increase the pressure on natural habitats, consequently increasing the risk of decline of the populations of *C. rufus* and *C. xinguensis*.

The *C. didactylus* population inhabiting the Atlantic Forest in northeastern Brazil is currently considered data deficient (Miranda & Superina, 2010). The Atlantic Forest of northeastern Brazil currently represents one of the most degraded areas of the biome. The resulting landscape is a complex mosaic of small and largely disconnected forest fragments, near large urban centres and intensive farming activities, under intense economical and real estate pressure. Genetic analyses are in progress to evaluate whether the population can be considered an ESU (Flavia R. Miranda, Sofia S. Marques & Fabrício R. Santos, Unpublished data) or even if it deserves species status. In that case, if the degradation of the natural habitat is not halted and habitat restoration does not start, it is likely that this population will require special protection to ensure its long-term survival (Miranda & Superina, 2010).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Supplementary File 1: Values of cycling reactions for each marker.
Supplementary File 2: Complete sequence alignment, with the five molecular markers concatenated, as applied in our complete analyses.
Supplementary File 3: Molecular models applied in the analyses and outgroup accesion numbers in GenBank.
Supplementary File 4: Complete MR BAYES analysis Majority Rule tree file.
Supplementary File 5: Complete MR BAYES analysis RUN1 tree file.
Supplementary File 6: Complete MR BAYES analysis RUN2 tree file.
Supplementary File 7: Complete BEAST analysis Major clade credibilty tree file.
Supplementary File 8: Complete BEAST analysis RUN1 tree file.
Supplementary File 9: Complete BEAST analysis RUN2 tree file.
Supplementary File 10: *COI* BEAST analysis Major clade credibilty tree file.
Supplementary File 11: *COI* BEAST analysis RUN1 tree file.
Supplementary File 12: *COI* BEAST analysis RUN2 tree file.
Supplementary File 13: *COI* MR BAYES analysis Majority Rule tree file.

Supplementary File 14: *COI* MR BAYES analysis RUN1 tree file.
Supplementary File 15: *COI* MR BAYES analysis RUN2 tree file.
Supplementary File 16: GMYC single threshold plot file.
Supplementary File 17: GMYC single threshold output file.
Supplementary File 18: GMYC multiple threshold output file.
Supplementary File 19: GMYC multiple threshold plot file.
Supplementary File 20: bPTP Bayesian solution plot file.
Supplementary File 21: bPTP Bayesian solution results delimitation file.
Supplementary File 22: bPTP Maximum likelihood plot file.
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Supplementary File 24: bPTP trace output file.
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Supplementary File 27: BPP run 2a output file.
Supplementary File 28: BPP run 2b output file.
Supplementary File 29: BPP run 3a output file.
Supplementary File 30: BPP run 3b output file.
Supplementary File 31: BPP run 4a output file.
Supplementary File 32: BPP run 4b output file.
Supplementary File 33: List of specimens evaluated and discrete character interpretation for each specimen.
Supplementary File 34: Results of analyses of variance and covariance for morphometric data.
Supplementary File 35: Cross-validation output for morphometric data.