

This is a repository copy of *Convergent evolution in the Euarchontoglires*.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/id/eprint/133262/>

Version: Accepted Version

---

**Article:**

Morris, Philip James Rencher, Cobb, Samuel Nicholas Frederick [orcid.org/0000-0002-8360-8024](https://orcid.org/0000-0002-8360-8024) and Cox, Philip Graham [orcid.org/0000-0001-9782-2358](https://orcid.org/0000-0001-9782-2358) (2018) Convergent evolution in the Euarchontoglires. *Biology letters*. 2018036. ISSN: 1744-957X

<https://doi.org/10.1098/rsbl.2018.0366>

---

**Reuse**

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing [eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk) including the URL of the record and the reason for the withdrawal request.

**TITLE: Convergent evolution in the Euarchontoglires**

**AUTHORS:** Philip J.R. Morris<sup>1</sup>, Samuel N.F. Cobb<sup>2</sup>, Philip G. Cox<sup>2</sup>

**AFFILIATIONS:**

<sup>1</sup>Hull York Medical School

University of Hull

Hull

HU6 7RX

<sup>2</sup>Department of Archaeology and Hull York Medical School

University of York

York

YO10 5DD

## ABSTRACT

Convergence – the independent evolution of similar phenotypes in distantly related clades – is a widespread and much-studied phenomenon. An often-cited, but hitherto untested, case of morphological convergence is that between the aye-aye and squirrels. The aye-aye (*Daubentonia madagascariensis*) is a highly unusual lemuriform primate that has evolved a dentition similar to that of rodents: it possesses large, ever-growing incisors which it uses to strip the bark from tree in order to feed on wood-boring beetle larvae. Indeed, such is the similarity that some of the earliest classifications of the aye-aye placed it in the genus *Sciurus*. Here, we aimed to test the degree of convergence between the skulls and lower jaws of squirrels and the aye-aye. 3D landmarks were recorded from the crania and mandibles of 46 taxa representing the majority of families in the Euarchontoglires. Results were plotted as phylomorphospaces and convergence measures were calculated. The convergence between squirrels and the aye-aye was shown to be statistically significant for both the cranium and mandible, although the mandibles seem to converge more closely in shape. The convergence may indicate strong functional drivers of morphology in these taxa i.e. the use of the incisors to produce high bite forces during feeding. Overall, we have shown that this classic case of convergence stands up to quantitative analysis.

## KEYWORDS

Convergent evolution; cranium; mandible; morphology; aye-aye; rodents

## INTRODUCTION

Convergence, the independent evolution of similar phenotypes in phylogenetically distinct lineages, is an important and widespread evolutionary process [1,2], and one that has been recognised since the beginnings of evolutionary biology as a field [3]. Convergent evolution is often thought to represent adaptation of distantly related organisms to a similar environment, but may also indicate the presence of a biological constraint limiting the available range of phenotypes [4]. Recent developments in the quantification of convergence [2,5] have enabled researchers not just to identify instances of convergent evolution, but also to test its statistical significance (e.g. [6-9]). Therefore, iconic examples of convergence, hitherto classified as such qualitatively, can now be tested quantitatively.

One such classic example of convergence is that of the aye-aye and rodents. The aye-aye (*Daubentonia madagascariensis*) is a lemuriform primate, native to Madagascar. Its unusual diet, which includes wood-boring beetle larvae [10], has driven a number of morphological adaptations, such as acute hearing and an elongate middle digit for percussive foraging, and enlarged, ever-growing incisors for stripping the bark from trees to reveal larval burrows [11]. In fact, the entire dentition, not just the incisors, is strikingly rodent-like, with the dental formula being 1.0.1.3 in the upper jaw and 1.0.0.3 in the lower [12]. Indeed, so close is the resemblance to rodents, that in some of the earliest taxonomies of mammals, the aye-aye was classified as a squirrel, and placed in the genus *Sciurus* (e.g. [13-14]).

Although the morphological similarities between the aye-aye and sciurid rodents have been noted by many authors [15,16], the degree of convergence between them has never been formally tested. In this study, we used geometric morphometric methods (GMM) to test the *a priori* hypothesis that both the cranium and the mandible of the aye-aye are convergent with

those of squirrels. Although it is possible to identify convergence without an *a priori* hypothesis using multivariate data, such methods are not suitable for the high-dimensional shape data gathered here [9]. Morphological similarity between squirrels and the aye-aye, despite their phylogenetic separation, is predicted based on the previous misclassification of the aye-aye as a squirrel, and also because both groups engage in mechanically-demanding feeding activities with their teeth [17]. We predicted that the bony elements of the skull, not just the teeth, would show morphological convergence owing to the structural constraints of housing enormously enlarged incisors and the functional constraints of using the incisors to generate high bite forces.

## **MATERIALS AND METHODS**

MicroCT scans of the crania and mandibles of 46 species of Euarchontoglires were obtained, either from the online repository Morphosource ([www.morphosource.org](http://www.morphosource.org)), or by imaging osteological specimens from museum collections. Virtually reconstructed surfaces of each specimen were created with the segmentation editor of Avizo 8.0 (FEI, Hillsboro, OR, USA), and 22 cranial and 16 mandibular three-dimensional landmarks were collected from the left side of each surface. GMM analyses were implemented in MorphoJ [18]. Further details of sample choice, landmarking methods and GMM are given in electronic supplementary material, methods. Specimens, landmark co-ordinates and PC scores are listed in electronic supplementary material, datafile S1.

A phylogeny of the sample species (figure 1) was constructed from previously published data [19-21], and was combined with the morphometric data to construct a phylomorphospace, using the *phytools* package (version 0.6-44) in R (version 3.4.2) [22,23]. The degree of convergence between the crania and the mandibles of the aye-aye and the two squirrels in the

sample was determined using Stayton's convergence measure  $C_1$  [2]. The significance of the convergence was assessed by comparing the metrics to values obtained from 1000 simulations of evolution under a Brownian motion model. Convergence tests were conducted using the *convevol* R package (version 1.1) [2].

## RESULTS

The first principal component in the cranial analysis (figure 2a) shows a clear split between Glires and primates, with the treeshrew and colugo positioned between them. This axis represents a shift from a skull with an elongated rostrum and a flattened cranial vault (positive values, rodents) to a more rounded and taller skull with a flatter face (negative values, primates). Along the second principal component, taxa at the negative extreme of the axis (lagomorphs, prosimians) tend to have flexed cranial bases and relatively large eyes, whilst taxa at the positive extreme (anthropoid primates, hard-object feeding rodents) have flatter skulls with comparatively smaller eyes. The aye-aye is notably separated from its closest relatives, the strepsirrhines, and is found almost midway between the primates and rodents on PC1, and towards the positive end of PC2. Significant convergence was calculated between the aye-aye and the two sciurid taxa, with a  $C_1$  value of 0.394 ( $P < 0.001$ ), indicating that evolution has closed the distance between the aye-aye and squirrel lineages by almost 40%.

The first principal component of the mandibular analysis (figure 2b) again shows a clear distinction between Euarchonta and Glires. The primates, treeshrew and colugo are found towards the positive end of PC1 and are distinguished by a tall coronoid process but only a small angular process, whereas the rodents and lagomorphs at the other end of the axis have a much more prominent angle but a lower coronoid process. The aye-aye is located amongst the rodents rather than the primates, and is particularly close to the squirrel-related rodents on both

PC1 and PC2. Significant convergence between the mandibles of the aye-aye and the squirrels was found ( $C_1 = 0.223$ ;  $P < 0.01$ ), with an average of 22% convergence between their respective lineages. Shape changes along PC axes are shown in electronic supplementary material, figure S2.

## DISCUSSION

The results of this study show that both the cranium and the mandibles of the aye-aye are morphologically convergent with those of sciurid rodents, supporting the *a priori* hypothesis of this study (see electronic supplementary material, figure S3 for a comparison of aye-aye and squirrel skulls). The  $C_1$  values [2] calculated for the crania and mandibles are statistically significant, indicating that the aye-aye and squirrels are positioned more closely in morphospace than would be expected under a Brownian motion model of evolution. Morphological similarities are not restricted to the possession of large, ever-growing incisors, but also extend to the bony anatomy of the skull (e.g. rostral length and braincase morphology) and lower jaw (e.g. relative positions of the coronoid and condylar processes). Potentially, such convergence may have been driven by the biomechanical demands of incisor gnawing, which squirrels and the aye-aye both use extensively when feeding. The incisors are used by squirrels to penetrate hard nuts [24], and by the aye-aye for stripping tree bark [11]. Thus the aye-aye and squirrels may have converged on a similar morphology to enable efficient operation of the jaws by the masticatory muscles.

The  $C_1$  values suggest that the crania of the aye-aye and squirrels are more convergent than are the mandibles. However, these values refer to the degree of convergence, not the absolute amount of phenotypic evolution that has occurred [2], nor the level of morphological similarity. From inspection of the morphospaces in figure 2, it appears that the aye-aye mandible more

151 closely resembles that of squirrels, than does the cranium. This was expected as the function  
152 of the mandible is almost exclusively related to feeding, whereas the skull must perform other  
153 functions such as housing the brain and sensory organs. Furthermore, the shape of the mandible  
154 has been shown to correlate closely with diet in squirrels [25], especially amongst hard nut  
155 specialists [9]. Overall, we have shown that the classic example of convergence between the  
156 aye-aye and squirrels stands up to quantitative analysis, at least with regard to the skull and  
157 lower jaw. This may go some way to explaining the erroneous classification of the aye-aye in  
158 the genus *Sciurus* in some of the first descriptions of this unusual primate [13,14].

160 The structure of a morphospace is driven by the taxa included within it. Primates and rodents  
161 are both highly speciose orders [26] and it was not possible to include all species, or even all  
162 genera, in this analysis. Nevertheless, the specimens chosen represent almost all families of  
163 Euarchontoglires and, we feel, reflect the predominant cranial and mandibular morphology  
164 seen in each family. As such the sample covers the majority of morphological variation found  
165 in Euarchontoglires. Given the distinct split between primates and rodents in both the cranial  
166 and mandibular analyses, and the clear deviation of the aye-aye from this pattern, we feel that  
167 addition of further specimens would only strengthen our conclusions.

169 **DATA ACCESSIBILITY** All morphometric data is available in the electronic supplementary  
170 material, datafile S1. Surface reconstructions or original microCT scans of all specimens are  
171 available from [www.morphosource.org](http://www.morphosource.org) (doi numbers given in datafile S1).

172 **AUTHORS' CONTRIBUTIONS** P.G.C. and S.N.F.C. conceived the study. P.G.C. collected  
173 image data. P.J.R.M. and P.G.C. collected and analysed landmark data. All authors interpreted  
174 the data, drafted and revised the manuscript. All authors approved the final version of the  
175 manuscript and agree to be held accountable for the content of this manuscript.



**COMPETING INTERESTS** We have no competing interests.

**FUNDING** P.J.R.M. was funded by a University of Hull PhD studentship. This work was supported by the Natural Environment Research Council (grant number NE/G001952/1). Datasets downloaded from [www.morphosource.org](http://www.morphosource.org) were originally funded by NSF (DDIG 0925793; BCS 1317525; BCS 1552848), The Leakey Foundation and the Wenner-Gren Foundation.

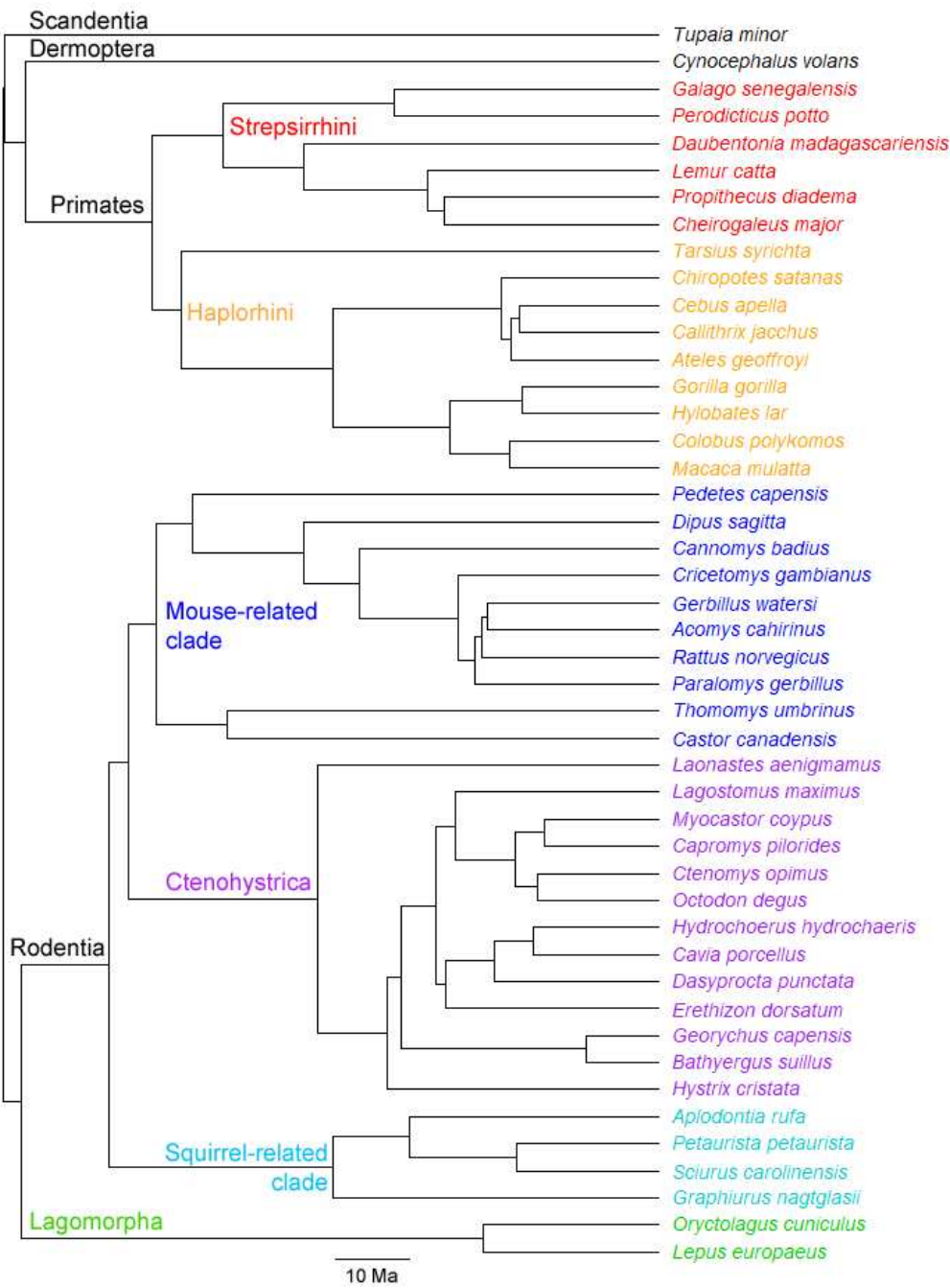
**ACKNOWLEDGEMENTS** We thank the many institutions and colleagues that provided access to specimens and/or assisted with imaging: Rob Asher and Matt Lowe (University Museum of Zoology, Cambridge); Anthony Herrel, Christiane Denys and Violaine Nicolas (Muséum National d'Histoire Naturelle, Paris); Tony Parker (National Museums Liverpool); Clare Brown (Leeds Museums and Galleries); David Orton (York Zooarchaeology Laboratory, University of York), Doug Boyer (Duke University and Morphosource); Michael Fagan and Sue Taft (University of Hull); Nathan Jeffery (University of Liverpool); and Gwen Haley (The York Hospital). We thank Pierre-Henri Fabre (University of Montpellier) for providing and editing the rodent phylogeny, and Tristan Stayton (Bucknell University) for advice on the use of *convevol*.

## REFERENCES

1. Conway Morris S. 2003 *Life's solution: inevitable humans in a lonely universe*. Cambridge, UK: Cambridge University Press.
2. Stayton CT. 2015 The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. *Evolution* **69**, 2140-2153.
3. Darwin C. 1859 *On the origin of species*, 1st edition. London, UK: John Murray.
4. Losos JB. 2011 Convergence, adaptation, and constraint. *Evolution* **65**, 1827-1840.

- 201 5. Arbuckle K, Bennett CM, Speed MP. 2014 A simple measure of the strength of  
202 convergent evolution. *Methods Ecol. Evol.* **5**, 685-693.
- 203 6. Friedman ST, Price SA, Hoey AS, Wainwright PC. 2016 Ecomorphological  
204 convergence in planktivorous surgeonfishes. *J. Evol. Biol.* **29**, 965-978.
- 205 7. Rowe KC, Achmadi AS, Esselstyn JA. 2016 Repeated evolution of carnivory among  
206 Indo-Australian rodents. *Evolution* **70**, 653-665.
- 207 8. Page CE, Cooper N. 2017 Morphological convergence in ‘river dolphin’ skulls. *PeerJ*  
208 **5**, e4090.
- 209 9. Zelditch ML, Ye J, Mitchell JS, Swiderski DL. 2017 Rare ecomorphological  
210 convergence on a complex adaptive landscape: body size and diet mediate evolution  
211 of jaw shape in squirrels (Sciuridae). *Evolution* **71**, 633-649.
- 212 10. Sterling EJ. 1994 Aye-ayes: specialists on structurally defended resources. *Folia*  
213 *Primatol.* **62**, 142-154.
- 214 11. Erickson CJ. 1991 Percussive foraging in the aye-aye, *Daubentonia*  
215 *madagascariensis*. *Anim. Behav.* **41**, 793-801.
- 216 12. Quinn A, Wilson DE. 2004 *Daubentonia madagascariensis*. *Mammal. Rev.* **740**, 1-6.
- 217 13. Gmelin JF. 1788 *Caroli a Linné, systema naturae. 13<sup>th</sup> ed., vol. 1*. Lipsiae: G.E. Beer.
- 218 14. Cuvier G. 1797 *Tableau élémentaire de l’histoire naturelle des animaux*. Paris,  
219 France: Baudouin.
- 220 15. Oxnard CE. 1981 The uniqueness of *Daubentonia*. *Am. J. Phys. Anthropol.* **54**, 1-21.
- 221 16. Iwanu T, Iwakawa C. 1988 Feeding behaviour of the aye-aye (*Daubentonia*  
222 *madagascariensis*) on nuts of rami (*Canarium madagascariensis*). *Folia Primatol.*  
223 **50**, 136-142.
- 224 17. Nowak R. 1999 *Walker’s mammals of the world*. Baltimore, MA: Johns Hopkins  
225 University Press.

18. Klingenberg CP. 2011 MorphoJ: An integrated software package for geometric morphometrics. *Mol. Ecol. Res.* **11**, 353-357.
19. Bininda-Emonds ORP, Cardillo M, Jones KE, MacPhee RDE, Beck RMD, Grenyer R, Price SA, Vos RA, Gittleman JL, Purvis A. 2007 The delayed rise of present-day mammals. *Nature* **446**, 507-512.
20. Arnold C, Matthews LJ, Nunn CL. 2010 The 10kTrees Website: a new online resource for primate phylogeny. *Evol. Anthropol.* **19**, 114-118.
21. Fabre P-H, Hautier L, Dimitrov D, Douzery E. 2012 A glimpse on the pattern of rodent diversification: a phylogenetic approach. *BMC Evol. Biol.* **12**, 88.
22. Revell LJ. 2012 phytools: an R package for phylogenetic comparative biology (and other things). *Methods. Ecol. Evol.* **3**, 217-223.
23. R Core Team. 2016 A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
24. Smith CC, Follmer D. 1972 Food preferences of squirrels *Ecology* **53**, 82-91.
25. Casanovas-Vilar I, van Dam J. 2013 Conservatism and adaptability during squirrel radiation: what is mandible shape telling us? *PLoS ONE* **8**, e61298.
26. Burgin CJ, Colella JP, Kahn PL, Upham NS. 2018 How many species of mammals are there? *J. Mammal.* **99**, 1-14.



252

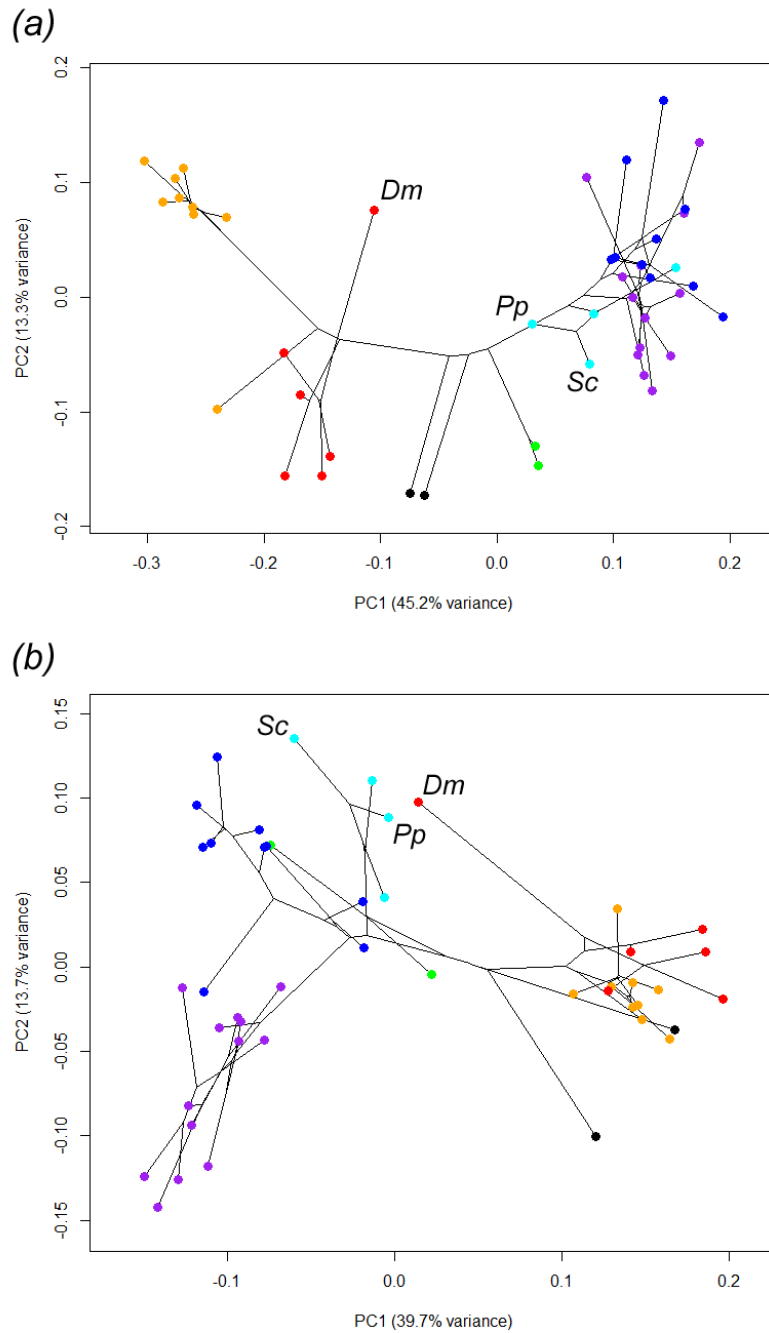
253 **Figure 1.** Phylogeny of Euarchontoglires taxa used in this analysis. Topology and dating

254 compiled from Bininda-Emonds et al (2007), Arnold et al (2010) and Fabre et al (2012).

255 Scale bar = 10 million years. Colour coding of taxa matches figure 2.

256

257



**Figure 2.** Phylomorphospace showing first two principal components of variation of (a) cranial and (b) mandibular morphology in Euarchontoglires. Key: red, strepsirrhine primates; orange, haplorhine primates; black, treeshrew and colugo; green, lagomorphs; cyan, squirrel-related rodents; blue, mouse-related rodents; purple, ctenohystrican rodents. *Dm*, *Daubentonia madagascariensis*; *Pp*, *Petaurista petaurista*; *Sc*, *Sciurus carolinensis*.