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Morris, Philip James Rencher, Cobb, Samuel Nicholas Frederick orcid.org/0000-0002-8360-8024 and Cox, Philip Graham 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>

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1 **TITLE: Convergent evolution in the Euarchontoglires**

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26 **ABSTRACT**

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

43

44 **KEYWORDS**

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

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51 **INTRODUCTION**

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

61

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

71

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

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

85

86 **MATERIALS AND METHODS**

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

96

97 A phylogeny of the sample species (figure 1) was constructed from previously published data
98 [19-21], and was combined with the morphometric data to construct a phylomorphospace,
99 using the *phytools* package (version 0.6-44) in R (version 3.4.2) [22,23]. The degree of
100 convergence between the crania and the mandibles of the aye-aye and the two squirrels in the

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

105

106 **RESULTS**

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

119

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

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

130

131 **DISCUSSION**

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

146

147 The C_1 values suggest that the crania of the aye-aye and squirrels are more convergent than are
148 the mandibles. However, these values refer to the degree of convergence, not the absolute
149 amount of phenotypic evolution that has occurred [2], nor the level of morphological similarity.
150 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].

159

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.

168

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 (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.

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

177 **FUNDING** P.J.R.M. was funded by a University of Hull PhD studentship. This work was
178 supported by the Natural Environment Research Council (grant number NE/G001952/1).
179 Datasets downloaded from www.morphosource.org were originally funded by NSF (DDIG
180 0925793; BCS 1317525; BCS 1552848), The Leakey Foundation and the Wenner-Gren
181 Foundation.

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

192

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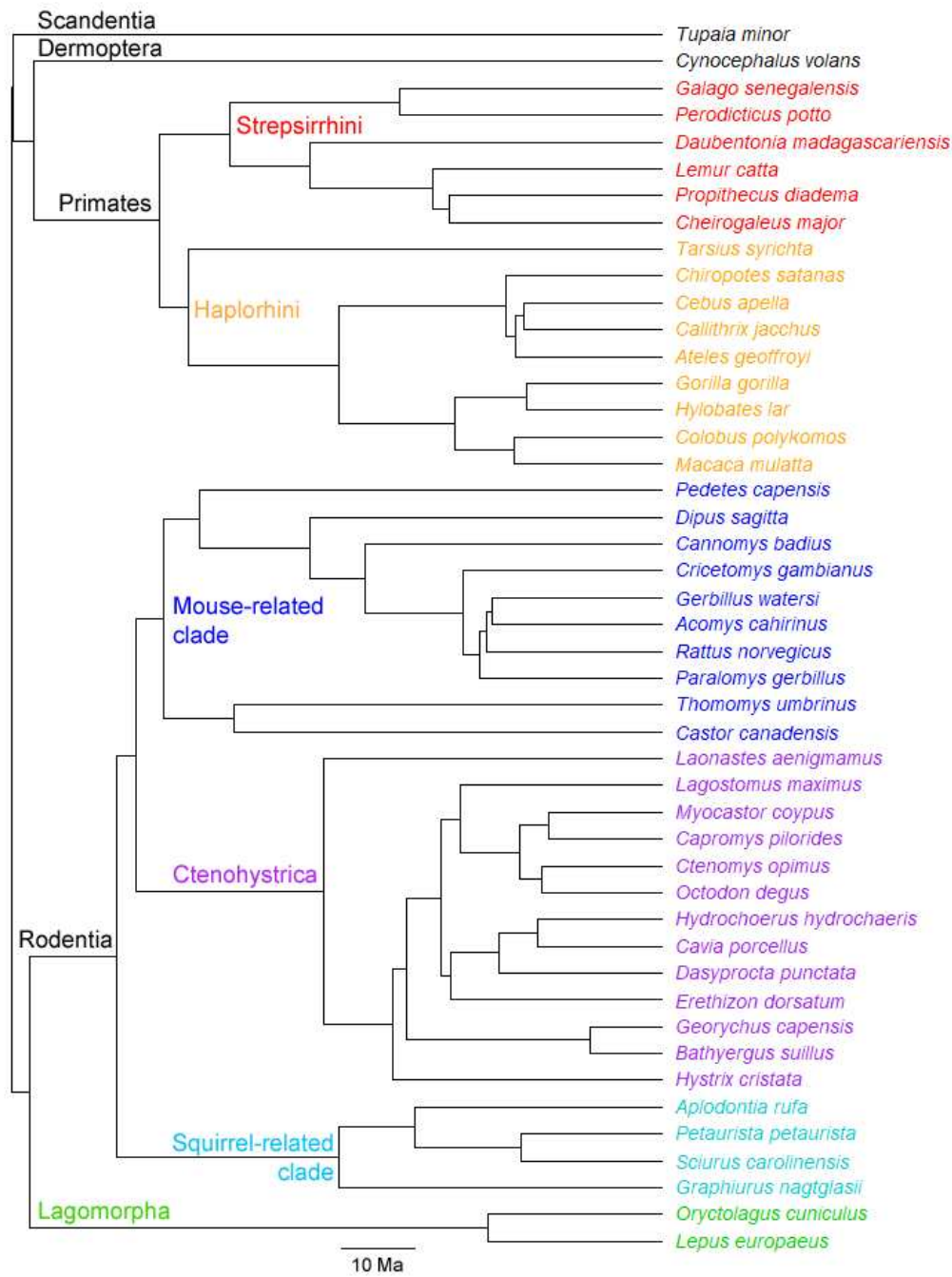
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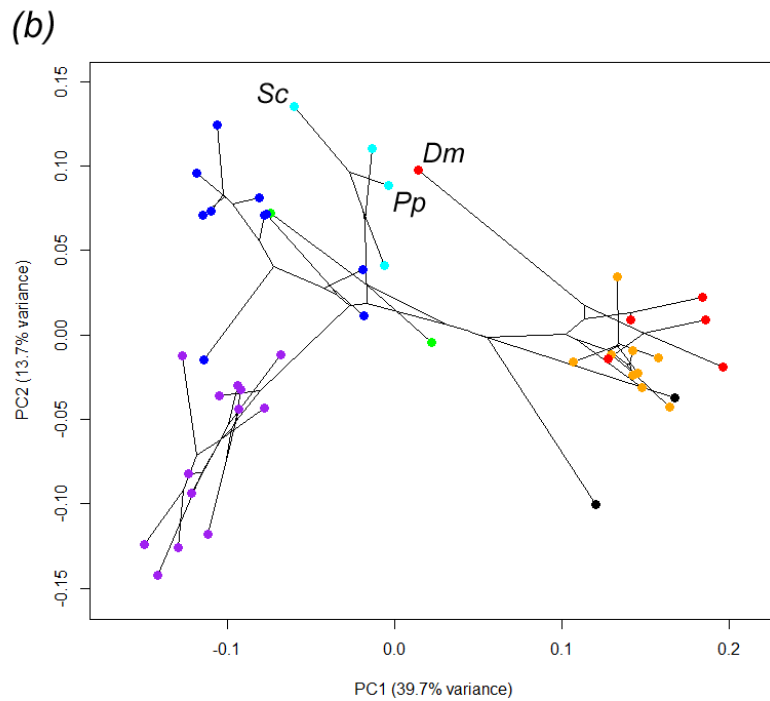
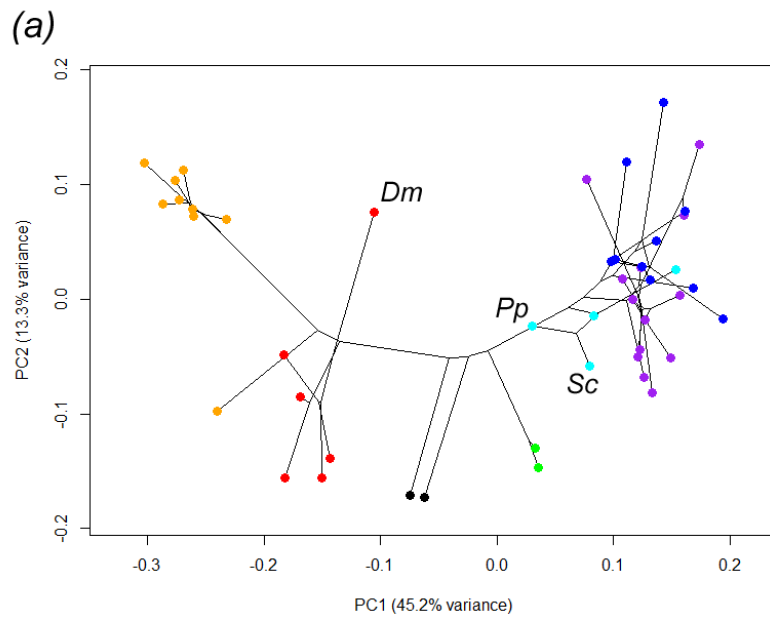
253 **Figure 1.** Phylogeny of Euarchontoglires taxa used in this analysis. Topology and dating

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



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259

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