

1 **Tent-roosting may have driven the evolution of yellow skin**
2 **coloration in Stenodermatinae bats**

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4 Running title: Tent-roosting and bat color evolution

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26 **Abstract**

27 The recent discovery of the first mammal that deposits significant amounts of carotenoid
28 pigments in the skin (the Honduran white bat *Ectophylla alba*) has highlighted the
29 presence of conspicuous yellow coloration in the bare skin of some bats. This is patent in
30 the subfamily Stenodermatinae, where many species build tents with plant leaves for
31 communal roosting at daytime. On the basis that tents offer rich light conditions by partly
32 allowing sunlight to pass through the leaves and this makes that yellow coloration probably
33 provides camouflage benefits to tent-roosting bats, that gregariousness facilitates visual
34 communication, and that all Stenodermatinae bats possess retinal L-cones that allow the
35 perception of long-wavelength light and have a frugivorous diet from which carotenoids are
36 obtained, we hypothesized that tent-roosting may have driven the evolution of yellow skin
37 coloration in this group of bats. We tested this prediction in 71 species within
38 Stenodermatinae. Reconstructions of ancestral states showed that the common ancestor
39 was most likely not colorful and did not roost in tents, but both traits early appeared in the
40 first phylogenetic ramification. Phylogenetically-controlled analyses showed that, as
41 predicted, yellow skin coloration and tent-roosting coevolved after their appearance. This
42 is the first explanation for the evolution of body coloration in nocturnal mammals. As the
43 light environment of nocturnal forests is dominated by yellow-green wavelengths that
44 coincides with the spectral sensitivity of some bats, nocturnal light conditions may have
45 acted jointly with diurnal light conditions in tents to favor the evolution of yellow skin
46 coloration in these animals.

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52 **Introduction**

53 Darkness can be considered a resource for animals able to exploit it (Gerrish *et al.*, 2009).
54 The ability to exploit nocturnal niches is provided by very specific sensory capacities
55 (Martin, 1986), which allow to escape from competitors or predators (Rydell & Speakman,
56 1995). Nocturnality is thus a successful strategy that has led to the evolution of particular
57 physiological and morphological traits in many groups of animals, such as those involved
58 in echolocation in bats (Jones & Teeling, 2006). Due to limited light conditions, vision is not
59 the most developed sense in nocturnal animals, thus it has long been assumed that these
60 species are blind or have simple visual systems. This is the case of bats that use
61 echolocation, in which the high level of specialization and effectiveness of echolocation
62 leads to conclude that the role of vision in shaping life-histories is considerably less
63 significant than that of acoustic sense (Boonman *et al.*, 2013).

64 However, nocturnal animals have the need of communicating with conspecifics, like
65 diurnal animals do, despite their nocturnal habits. These needs are partially fulfilled by
66 acoustic cues (e.g., Gamble *et al.*, 2015), but a detailed assessment of potential mates or
67 rivals can only be conducted using visual traits. A number of traits have evolved because
68 of their capacity to overcome these problems under limited light conditions. Some birds, for
69 example, have evolved high contrasting white plumage patches that maximize reflectance
70 of light (Aragonés *et al.*, 1999; Penteriani & Delgado, 2009). These traits mostly function
71 as signals of presence that attract receivers. However, a detailed assessment of visual
72 traits require, by definition, the capacity to perceive color under limited ambient light. This
73 capacity has been probed in the European tree frog *Hyla arborea* (Linnaeus, 1758), in
74 which females are able to assess the color properties of a vocal sac in males to choose
75 mates at night (Gomez *et al.*, 2009, 2010). Nocturnal color vision is probably also present
76 in higher vertebrates, as a comparative analysis showed a match between peak irradiance
77 flux in nocturnal forests and long-wavelength-sensitive cone spectral sensitivity in several

78 mammals, including primates, rodents, marsupials, carnivorans and bats (Veilleux &
79 Cummings, 2012).

80 Bats are among those groups of animals in which the importance of visual
81 communication has been neglected due to the nocturnal habits of most of them. Few
82 works have tried to explain the between-species variability in achromatic (dark/light)
83 pelage markings in bats, finding an association with the type of communal roosting that
84 may suggest a role in camouflage by providing disruptive coloration (Santana *et al.*, 2011;
85 Garbino & Tavares, 2018). The function of these achromatic pelage markings has not
86 been investigated in the context of intraspecific communication, as it is the case for colorful
87 traits in bats. However, different findings made in the last decade indicate that even bats
88 with a long evolutionary history of nocturnality can perceive color, as inferred from a
89 functional *M/LWS* opsin gene tuned to light wavelengths corresponding to yellow and red
90 (Zhao *et al.*, 2009). In this regard, the conspicuous bare skin yellow coloration of a fruit-
91 eating bat, the Honduran white bat *Ectophylla alba* (Allen, 1892), has recently been
92 described (Galván *et al.*, 2016; Fig. 1). This yellow coloration is generated by the
93 esterification and accumulation in the skin of a carotenoid pigment (lutein) that Honduran
94 white bats obtain by ingesting fruits of the fig tree *Ficus colubrinae* (Galván *et al.*, 2016;
95 Fig. 1). Carotenoids are indeed the only pigments known to produce bright yellow
96 coloration in animals, with the exception of particular groups of birds that have evolved
97 specific bright yellow pigments (Thomas *et al.*, 2013; Cooke *et al.*, 2017; Galván *et al.*,
98 2019). The Honduran white bat is the first mammal so far reported to accumulate
99 significant amounts of carotenoids in the skin, but conspicuous yellow coloration in bare
100 skin is also observed in many other species in the same subfamily of Neotropical bats,
101 Stenodermatinae (Rodríguez-Herrera *et al.*, 2007; Fig. 2). These bats thus represent an
102 opportunity to get insight into the evolution of conspicuous body coloration in a group of
103 nocturnal vertebrates, which remains unexplored to date.

104 Like other groups of bats, most Stenodermatinae bats are gregarious and roost in
105 colonies at daytime. At least in insects, gregariousness is known to promote the evolution
106 of conspicuous coloration because this facilitates visual communication (Leo Lester *et al.*,
107 2005). Although all Stenodermatinae bats have nocturnal activity, diurnal roosts
108 necessarily increase the number of interactions with conspecifics. Apart from the
109 nocturnal color vision that at least some bats seem to possess (Veilleux & Cummings,
110 2012), communal roosting may thus promote the evolution of yellow skin coloration in bats.
111 However, not all Stenodermatinae bats exhibit yellow skin coloration (Fig. 1b), suggesting
112 that communal roosting alone cannot explain skin color evolution in this group.

113 Some species of Stenodermatinae bats, though, roost in tents that they construct
114 using large plant leaves, where several individuals congregate, while other species do not
115 roost in tents (Rodríguez-Herrera *et al.*, 2007). Roosts in tents probably have richer light
116 conditions than roosts in other structures such as caves or hollow trees because solar
117 radiation partly passes through the leaves that form the tents (Fig. 2a). This may affect
118 color evolution, like canopy-related variability of light conditions influences the evolution of
119 plumage coloration in neotropical birds (Gomez & Théry, 2004). Tent-roosting may
120 therefore have promoted the evolution of carotenoid-based yellow skin coloration in
121 Stenodermatinae bats. Evidence of this has already been provided for one
122 Stenodermatinae species that roosts in tents (the Honduran white bat), where the
123 resemblance of the yellow skin color with the color of tent leaves suggests that camouflage
124 benefits have favored the evolution of this trait, and gregariousness in roosts then led it to
125 secondarily evolve a signalling function (Rodríguez-Herrera *et al.*, 2019). However,
126 conclusive evidence of a role of tent-roosting in the evolution of yellow skin coloration can
127 only be obtained by comparing different species, but comparative studies are lacking. Here
128 we explore this hypothesis by reconstructing ancestral states of skin coloration and tent-

129 roosting behavior, and testing for an association between both traits along the phylogeny
130 of Stenodermatinae.

131

132 **Materials and methods**

133 **Data collection**

134 We made an exhaustive bibliographic review of species description and natural history
135 data of Stenodermatinae bats. For each bat species, we collected data of
136 presence/absence of yellow coloration in the skin of the nose-leaf and/or ears, considering
137 existing information on intraspecific variation. We also searched for information on the
138 presence/absence of tent-roosting behavior. Data was collected using a combination of
139 field guides (LaVal & Rodríguez-Herrera, 2002; Gardner, 2007; Reis *et al.*, 2007, 2013;
140 Reid, 2009; Brito *et al.*, 2018) and ca. 30 peer-reviewed articles describing the
141 characteristics of particular species. Additionally, we surveyed photographs of
142 Stenodermatinae bats collected during our own field work with the species and
143 photographs in the Internet (confirming the taxonomic identity) to corroborate the presence
144 or absence of yellow skin coloration as described in the literature. We excluded recently
145 described species whose phylogenetic relationships with other species are still not solved
146 (Rojas *et al.*, 2016). In total, we obtained information on skin coloration and tent-roosting
147 behavior for 71 species (Table 1), representing the large majority of Stenodermatinae
148 species (Rojas *et al.*, 2016). Among the species with yellow skin coloration, only three [the
149 Bogota fruit-eating bat *Artibeus bogotensis* (Andersen, 1906), the Honduran fruit-eating
150 bat *Artibeus inopinatus* (Davis & Carter, 1964) and the great fruit-eating bat *Artibeus*
151 *lituratus* (Olfers, 1818)] are known to occasionally roost in caves or hollow trees.

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153 **Reconstruction of ancestral states**

154 The phylogenetic relationships between the 71 species of Stenodermatinae bats
155 considered in the study were obtained from the maximum likelihood phylogeny of New
156 World Noctilionoidea made by Rojas *et al.* (2016) with seven nuclear loci, two
157 mitochondrial loci and three ribosomal RNAs sequences. We included the recently
158 described species *Chiroderma vizzotoi* as the sister species of the Brazilian big-eyed bat
159 *Chiroderma doriae* (Thomas, 1891), according to Taddei & Lim (2010).

160 We made separate reconstructions of ancestral states for presence/absence of
161 yellow coloration in the skin of nose-leaf and/or ears, and for presence/absence of tent-
162 roosting. This was made by stochastic character mapping, using an empirical Bayesian
163 Monte Carlo Markov Chains (MCMC) approach (Huelsenbeck *et al.*, 2003) as
164 implemented in the R package *phytools* (Revell, 2012). This procedure therefore consists
165 in randomly sampling possible character histories for presence/absence of yellow
166 coloration and for presence/absence of tent-roosting, such that the probability of sampling
167 any specific history varies in direct relation to its posterior probability under a continuous-
168 time discrete-state Markov chain model of evolution (Revell, 2014).

169

170 **Relationship between variables and phylogenetic signal**

171 We tested for a possible dependency of bare skin yellow coloration on tent-roosting in
172 Stenodermatinae bats using a phylogenetic logistic regression model (Ives & Garland,
173 2010), considering the presence/absence of tent-roosting as a fixed factor. We employed
174 the simulation algorithm implemented by Ho & Ané (2014) in the R package *phylolm*, using
175 1000 permutations.

176 Lastly, we estimated the phylogenetic signal in skin yellow coloration and tent-
177 roosting using the parameter D developed by Fritz & Purvis (2010) for binary traits. We
178 calculated the estimated value of D and associated P -values for $H_0: D = 1$ with the R
179 package *caper* (Orme *et al.*, 2013). When $D = 1$, a random phylogenetic structure (i.e.,

180 absence of phylogenetic signal) exists, whereas a D value of 0 is indicative of a Brownian
181 motion mode of evolution (i.e., changes in the trait along the phylogeny are proportional to
182 the degree of relatedness among species). Negative D values are indicative of highly
183 clustered traits (Fritz & Purvis, 2010).

184

185 **Results**

186 The reconstruction of ancestral states for skin coloration shows that the common ancestor
187 of Stenodermatinae bats was most likely not colorful, but yellow skin coloration early
188 appeared in the first ramification of the phylogeny, being *Sturnira* the only lineage in which
189 yellow skin has not evolved (Fig. 3). In the lineage that evolved yellow skin coloration
190 (Stenodermatini), this trait then experienced seven independent losses in six species of
191 *Platyrrhinus*, *Artibeus* and *Enchisthenes*, and in a common ancestor of seven *Artibeus*
192 species (Fig. 3). This results in a strong phylogenetic signal, as indicated by a D value of -
193 15.61 significantly different from a random phylogenetic structure ($P < 0.0001$). The large
194 negative D value thus indicates that yellow skin coloration is a highly conserved and
195 clustered trait in Stenodermatinae.

196 The ancestral states of tent-roosting show a more complex evolutionary scenario,
197 with several gains and losses since the first ramifications of the phylogeny, although the
198 common ancestor most likely did not use tents for roosting (Fig. 4). This results in a D
199 value of -12.23 indicative of a less clustered trait than skin coloration, but still showing a
200 very strong phylogenetic signal representative of a highly conserved trait ($P < 0.0001$).

201 From the distribution of traits along the tips of the phylogeny of Stenodermatinae, a
202 tendency of yellow skin coloration to be associated with tent-roosting can be envisaged
203 (Figs. 3-4). This association was confirmed by the phylogenetic logistic regression model,
204 which resulted in a significant positive effect of tent-roosting on the presence of skin yellow
205 coloration (regression coefficient = 1.84, $z = 2.90$, $P = 0.004$).

206

207 **Discussion**

208 Our study shows that the common ancestor of Stenodermatinae was not colorful and did
209 not roost in tents, but yellow skin coloration and tent-roosting early appeared in this
210 lineage of bats and a coevolution of both traits may have then occurred. This contrasts
211 with the recent review of Garbino and Tabares (2018), who concluded that the common
212 ancestor of Stenodermatinae bats most probably roosted in tents. This discordance may
213 be due to the difference in sample size, as Garbino & Tabares' (2018) study included 43
214 species of Stenodermatinae bats, about 40% less than ours, but also to the absence of
215 species out of Stenodermatinae in our study. As we do not have any hypothesis that could
216 predict an effect of yellow skin coloration on the occurrence of tent-roosting, a role of tent-
217 roosting as a driver of skin coloration should be considered as the most likely explanation.
218 We predicted such effect on the basis of the known influence of gregariousness on the
219 evolution of conspicuous coloration (Leo Lester *et al.*, 2005) and the structure of tents built
220 with plant leaves, which allows sunlight to partly reaches the bats and thus potentially
221 affects their body coloration like ambient light affects the plumage color of birds (Gomez &
222 Théry, 2004). This association is not cofounded by the presence of roosting behaviors
223 different from tent-roosting, as among those species with yellow skin coloration, only three
224 are known to form roosts in caves or hollow trees.

225 The combined effect of gregariousness in tents, which obviously increases social
226 interactions as compared to solitary bats (e.g., Kerth *et al.*, 2003), and prevalent light
227 conditions in tents (Fig. 2a), which create opportunities to use visual signals that facilitates
228 communication during social interactions, is a likely explanation for the evolution of yellow
229 skin coloration in Stenodermatinae bats. In this regard, it is worth mentioning that, in the
230 case of the Honduran white bat, the back side of *Heliconia* leaves that this species uses to
231 build tents exhibits a reflectance peak that coincides with a peak in the yellow skin of bats,

232 suggesting that camouflage may also have a role in the evolution of skin coloration
233 (Rodríguez-Herrera *et al.*, 2019). The yellow skin coloration of the Honduran white bat is
234 also a sexually dichromatic trait, which suggests that gregariousness in roosts may have
235 favored a secondary evolution as a sexually selected trait (Rodríguez-Herrera *et al.*, 2019).
236 Therefore, the coevolution pattern between yellow skin coloration and tent-roosting that we
237 have found here in all Stenodermatinae bats may respond to the same scenario proposed
238 for the Honduran white bat: camouflage benefits derived from color resemblance with
239 leaves used as tents could have driven the evolution of yellow skin coloration in these
240 bats, while the signalling potential of gregariousness in tent-roosts could have then
241 favored the evolution of a secondary role of skin coloration in visual communication. Both
242 evolutionary pressures may have maintained the association between yellow skin
243 coloration and tent-roosting in Stenodermatinae bats.

244 In any case, the yellow skin coloration of the Honduran white bat is produced by a
245 carotenoid pigment (lutein) that animals obtain from its main dietary source, a fig fruit
246 (Galván *et al.*, 2016), thus it is most likely that the yellow skin coloration of other
247 Stenodermatinae bats is also produced by the same mechanism. With the exception of
248 two species [the Jamaican fig-eating bat *Ariteus flavescens* (Gray, 1831) and the
249 Northern-yellow shouldered bat *Sturnira parvidens* (Geoffroy, 1810)] that have an
250 omnivorous diet and do not show yellow skin coloration, the diet of most Stenodermatinae
251 bats is mostly frugivorous, though some may supplement their diets with nectar and
252 insects (Gardner, 1977). In fact, it has recently been found that frugivory has favored the
253 evolutionary maintenance of retinal S-cones with opsin pigments that allow perceiving
254 short-wavelength light (UV-blue) in bats, making that all Stenodermatinae bats possess
255 them in addition to L-cones (Sadier *et al.*, 2018). The same has been found in other
256 nocturnal mammals (Veilleux & Cummings, 2012). Although the presence of L-cones
257 alone may suffice to perceive long-wavelength colors such as yellow, the possession of

258 both S- and L-cones may allow a better discrimination of colors, as bats are expected to
259 be monochromatic or dichromatic at daylight and conditionally dichromatic or trichromatic
260 under crepuscular light (Zelev & Cao, 2015; Sadier *et al.*, 2018). Therefore, frugivory diet
261 provided the resources for skin coloration (carotenoids), and social (gregariousness in
262 roosts) and light (solar radiation in plant tents) conditions created opportunities to use
263 visual signals that facilitate communication. These factors may have acted together,
264 favored by the presence of retinal cones and pigments allowing color perception, to drive
265 the evolution of yellow skin coloration in Stenodermatinae bats.

266 Although the abovementioned refers to daytime conditions at tent-roosts, where
267 several bat individuals congregate and the number of social interactions is probably high, it
268 must be considered that all Stenodermatinae bats echolocate and are mainly active by
269 night (Rodríguez-Herrera *et al.*, 2007). In this regard, our study is first in providing insight
270 into the evolution of body coloration in nocturnal animals. The fact that Stenodermatinae
271 bats are mainly active by night actually suggests that a number of social interactions might
272 also occur at this time (Ortega, 2016). Interestingly, the light environment of nocturnal
273 forests and woodlands is dominated by yellow-green wavelengths, with a peak flux that
274 coincides with the spectral sensitivity of L-cones in bats (Veilleux & Cummings, 2012).
275 Therefore, nocturnal light conditions may have contributed, together with light conditions in
276 tent-roosts at daytime, to the evolution of yellow skin coloration in Stenodermatinae bats.

277 In conclusion, the construction of tents with plant leaves for roosting seems to have
278 favored the evolution of conspicuous yellow skin coloration in Stenodermatinae bats,
279 suggesting that visual communication may have a more relevant role in the life histories of
280 nocturnal bats than previously assumed. The seven evolutionary losses of yellow skin
281 coloration that occurred in Stenodermatinae after the appearance of the trait do not seem
282 to respond to some groups of species obtaining adaptation, given the strong phylogenetic
283 signal that we found in yellow skin coloration (Blomberg *et al.*, 2003), thus it will be

284 interesting to investigate the causes that have led to the loss of coloration in these
285 species. It will also be worth investigating the factors affecting the evolution of yellow
286 coloration in non-Stenodermatinae bats. Although we could not extend our investigation to
287 other groups of bats, a non-exhaustive examination indicates that yellow coloration in bare
288 skin is also observed in at least 14 nocturnal species of other families in the Afrotropical,
289 Oriental and Australasian regions, including Nycteridae [*Nycteris hispida* (Schreber,
290 1775)], Pteropodidae [*Nyctimene aello* (Thomas, 1900), *Nyctimene albiventer* (Gray,
291 1863), *Nyctimene cephalotes* (Pallas, 1767), *Nyctimene draconilla* (Thomas, 1922),
292 *Nyctimene rabori* (Heaney & Peterson, 1984), *Nyctimene robinsoni* (Thomas, 1904),
293 *Nyctimene papuanus* (Andersen, 1910), *Epomophorus gambianus* (Ogilby, 1835) and
294 *Myonycteris leptodon*] and Megadermatidae [*Lavia frons* (Geoffroy, 1810), *Macroderma*
295 *gigas* (Dobson, 1880), *Megaderma spasma* (Linnaeus, 1758) and *Megaderma lyra*
296 (Geoffroy, 1810)]. These species do not construct tents for roosting, and some of them are
297 carnivorous, indicating that factors different from tent-roosting are responsible for the
298 evolution of yellow skin coloration in bats out of the Neotropics. Future studies should
299 clarify these questions.

300

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437 **Legends to figures:**

438

439 **Figure 1.** Image a of an Honduran white bat *Ectophylla alba* eating a fig tree *Ficus*
440 *colubrinae* fruit in Costa Rica. The yellow color of the skin of ears and nose-leaf is
441 produced by lutein provided by the fig fruit. Credit: Bernal Rodríguez-Herrera.

442

443 **Figure 2.** Images of Stenodermatinae bats. a: Thomas's fruit-eating bats *Artibeus watsoni*
444 roosting in a tent made of palm leaves in Costa Rica, showing yellow coloration in the skin
445 of ears and nose-leaf (credit: Ismael Galván). b: Flat-faced fruit-eating bats *Artibeus*
446 *planirostris* roosting in a cave in Brazil, showing absence of yellow skin coloration (credit:
447 Juan Carlos Vargas-Mena).

448

449 **Figure 3.** Stochastic character map of yellow skin coloration along the phylogeny of 71
450 species of Stenodermatinae bats considered in the study. Yellow branches represent
451 presence of yellow skin coloration, while black branches represent absence of skin
452 coloration. Tip symbols represent the character state of extant species.

453

454 **Figure 4.** Stochastic character map of tent-roosting along the phylogeny of 71 species of
455 Stenodermatinae bats considered in the study. Red branches represent occurrence of
456 tent-roosting, while black branches represent absence of tent-roosting. Tip symbols
457 represent the character state of extant species.

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Figure 1





Figure 3

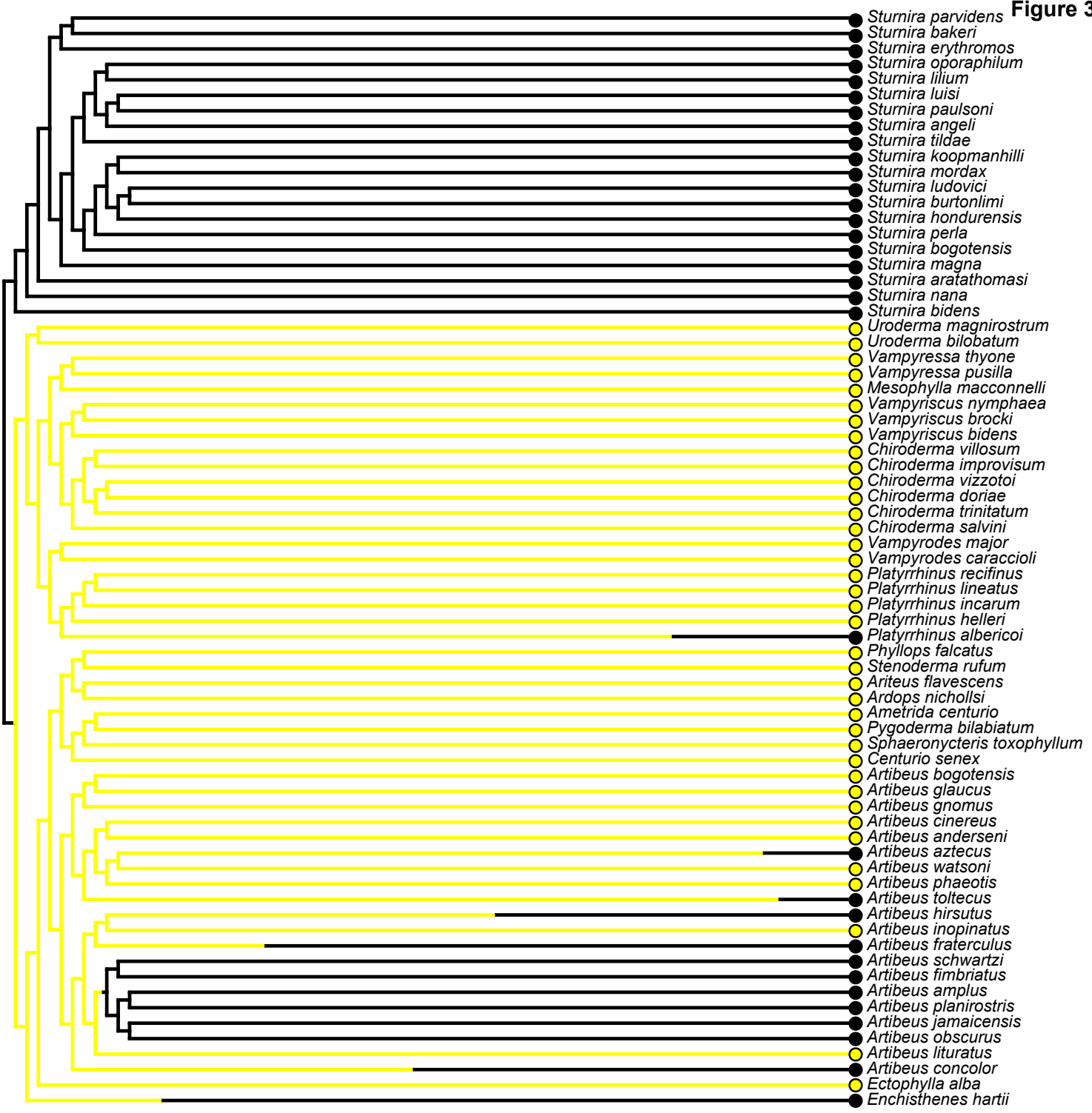
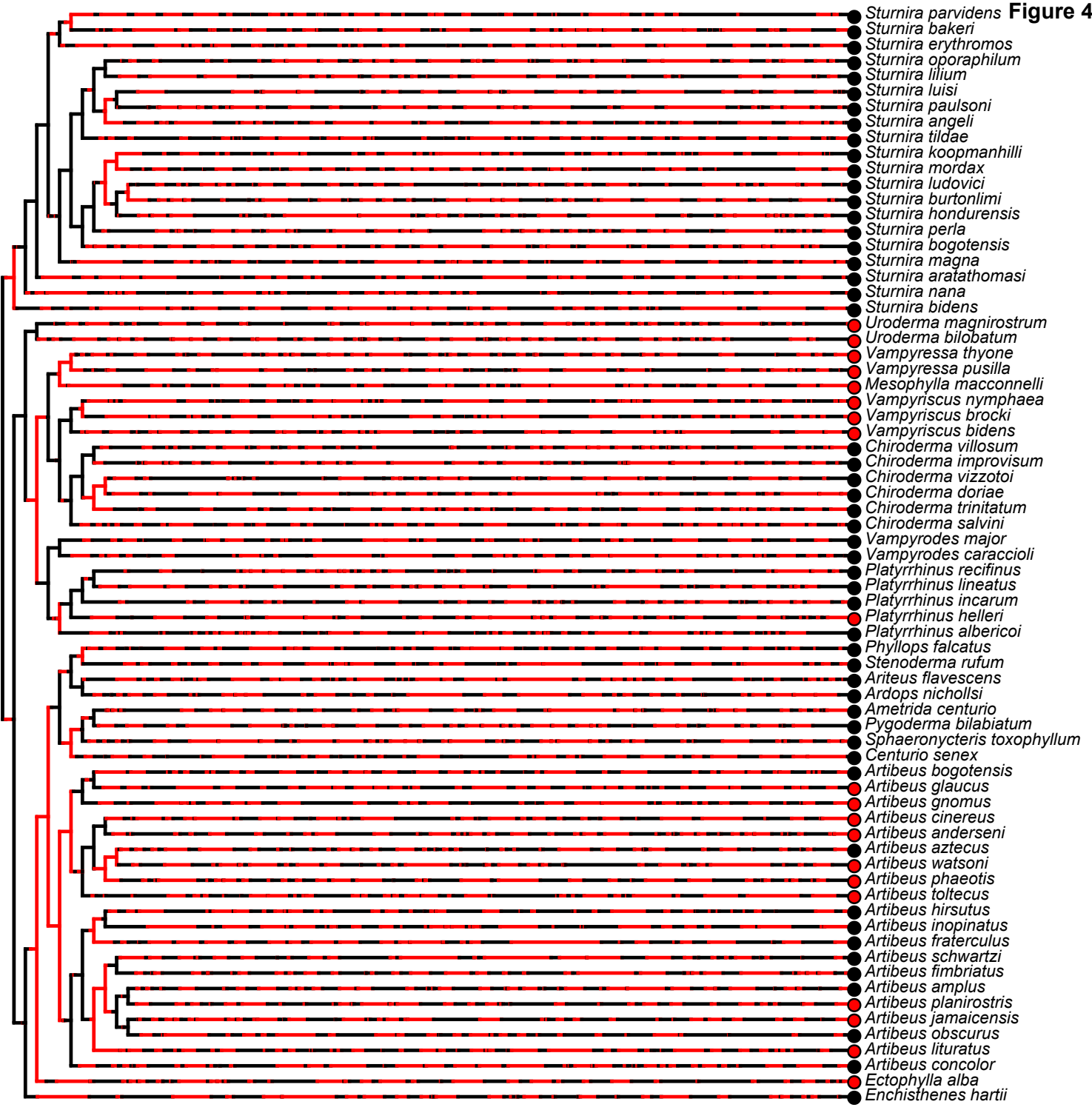


Figure 4



463 **Table 1.** Species used in the study. The presence (1) or absence (0) of yellow skin
 464 coloration and tent-roosting is indicated.

Species	Yellow skin	Tent-roosting
<i>Ametrida centurio</i> (Gray, 1847)	1	0
<i>Ardops nichollsi</i> (Thomas, 1891)	1	0
<i>Ariteus flavescens</i> (Gray, 1831)	1	0
<i>Artibeus amplus</i> (Handley, 1987)	0	0
<i>Artibeus concolor</i> (Peters, 1865)	0	0
<i>Artibeus fimbriatus</i> (Gray, 1838)	0	0
<i>Artibeus fraterculus</i> (Anthony, 1924)	0	0
<i>Artibeus hirsutus</i> (Andersen, 1906)	0	0
<i>Artibeus inopinatus</i> (Davis & Carter, 1964)	1	0
<i>Artibeus jamaicensis</i> (Leach, 1821)	0	1
<i>Artibeus lituratus</i> (Olfers, 1818)	1	1
<i>Artibeus obscurus</i> (Schinz, 1821)	0	0
<i>Artibeus planirostris</i> (Spix, 1823)	0	1
<i>Artibeus schwartzi</i> (Jones, 1978)	0	0
<i>Centurio senex</i> (Gray, 1842)	1	0
<i>Chiroderma doriae</i> (Thomas, 1891)	1	0
<i>Chiroderma improvisum</i> (Baker & Genoways, 1976)	1	0
<i>Chiroderma salvini</i> (Dobson, 1878)	1	0
<i>Chiroderma trinitatum</i> (Goodwin, 1958)	1	0
<i>Chiroderma villosum</i> (Peters, 1860)	1	0
<i>Chiroderma vizzotoi</i> (Taddei & Lim, 2010)	1	0
<i>Artibeus anderseni</i> (Osgood, 1916)	1	1
<i>Artibeus aztecus</i> (Andersen, 1906)	0	0
<i>Artibeus bogotensis</i> (Andersen, 1906)	1	0
<i>Artibeus cinereus</i> (Gervais, 1856)	1	1
<i>Artibeus glaucus</i> (Thomas, 1893)	1	1
<i>Artibeus gnomus</i> (Handley, 1987)	1	1
<i>Artibeus phaeotis</i> (Miller, 1902)	1	1
<i>Artibeus toltecus</i> (Saussure, 1860)	0	1
<i>Artibeus watsoni</i> (Thomas, 1901)	1	1
<i>Ectophylla alba</i> (Allen, 1892)	1	1

<i>Enchisthenes hartii</i> (Thomas, 1892)	0	0
<i>Mesophylla macconnelli</i> (Thomas, 1901)	1	1
<i>Phyllops falcatus</i> (Peters, 1865)	1	0
<i>Platyrrhinus albericoi</i> (Velazco, 2005)	0	0
<i>Platyrrhinus incarum</i> (Thomas, 1912)	1	0
<i>Platyrrhinus helleri</i> (W. Peters, 1866)	1	1
<i>Platyrrhinus lineatus</i> (Geoffroy, 1810)	1	0
<i>Platyrrhinus recifinus</i> (Thomas, 1901)	1	0
<i>Pygoderma bilabiatum</i> (Wagner, 1843)	1	0
<i>Sphaeronycteris toxophyllum</i> (Peters, 1882)	1	0
<i>Stenoderma rufum</i> (Desmarest, 1820)	1	0
<i>Uroderma bilobatum</i> (Peters, 1866)	1	1
<i>Uroderma magnirostrum</i> (Davis, 1968)	1	1
<i>Vampyressa pusilla</i> (Wagner, 1843)	1	1
<i>Vampyressa thyone</i> (Thomas, 1909)	1	1
<i>Vampyriscus bidens</i> (Dobson, 1878)	1	1
<i>Vampyriscus brocki</i> (Peterson, 1968)	1	1
<i>Vampyriscus nymphaea</i> (Thomas, 1909)	1	1
<i>Vampyrodes caraccioli</i> (Thomas, 1889)	1	0
<i>Vampyrodes major</i> (Allen, 1908)	1	0
<i>Sturnira angeli</i> (de la Torre, 1961)	0	0
<i>Sturnira aratathomasi</i> (Peterson & Tamsitt, 1968)	0	0
<i>Sturnira bakeri</i> (Velazco & Patterson, 2014)	0	0
<i>Sturnira bidens</i> (Thomas, 1915)	0	0
<i>Sturnira bogotensis</i> (Shamel, 1927)	0	0
<i>Sturnira burtonlimi</i> (Velazco & Patterson, 2014)	0	0
<i>Sturnira erythromos</i> (Tschudi, 1844)	0	0
<i>Sturnira hondurensis</i> (Goodwin, 1940)	0	0
<i>Sturnira koopmanhilli</i> (McCarthy, Albuja, & Alberico, 2006)	0	0
<i>Sturnira liliium</i> (Geoffroy, 1810)	0	0
<i>Sturnira ludovici</i> (Anthony, 1924)	0	0
<i>Sturnira luisi</i> (Davis, 1980)	0	0
<i>Sturnira magna</i> (de la Torre, 1966)	0	0
<i>Sturnira mordax</i> (Goodwin, 1938)	0	0
<i>Sturnira nana</i> (Gardner & O'Neill, 1971)	0	0

<i>Sturnira oporaphilum</i> (Tschudi, 1844)	0	0
<i>Sturnira parvidens</i> (Goldman, 1917)	0	0
<i>Sturnira paulsoni</i> (de la Torre & Schwartz, 1966)	0	0
<i>Sturnira perla</i> (Jarrín & Kunz, 2011)	0	0
<i>Sturnira tildae</i> (de la Torre, 1959)	0	0
