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1 **Revisiting the components of Macroscelidea social systems: Evidence for variable social**
2 **organization, including pair-living, but not for a monogamous mating system**

3
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31

32 **Conflict of interest statement and ethical considerations**

33 The authors and co-authors have no conflict of interest to declare. Ethics approval was not
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35 **Abstract**

36 Elephant-shrews (Macroscelidea) have long been considered the only mammalian order to be
37 completely monogamous, based on observations of their pair-living social organization. We
38 reviewed primary studies on the four components of social systems (social organization, mating
39 system, social structure and care system) in elephant-shrews to evaluate whether they truly are
40 monogamous. To identify gaps in our knowledge of their social system, we reviewed evidence
41 for a pair-living social organization, mate fidelity (mating system), pair bonds (social structure),
42 and biparental care (care system). Field data were available for eight species, and seven were
43 often pair-living. However, these seven species exhibited intra-specific variation in social
44 organization; two of these species were also solitary living, two species were also group-living,
45 and the remaining three species were both solitary and group-living. The eighth species was
46 exclusively solitary. We reconstructed the ancestral social organization of Macroscelidea using
47 Bayesian phylogenetic mixed-effects models and found that variable social organization, rather
48 than exclusive pair-living, was the most likely ancestral state, though there was high
49 uncertainty. No socio-ecological factors (body size, population density and habitat) predicted a
50 specific social organization. Observations of mating have been rare, such that no firm
51 statements can be made. However, one unpublished study indicated high levels of extra-pair
52 paternity. Regarding social structure, there was no evidence of pair-bonding, but there was
53 evidence of mate guarding. Only maternal care has been observed, with females having very
54 short nursing bouts. Evidence suggests that despite having often a pair-living form of social
55 organization, Macroscelidea should not be described as a monogamous order, as little or no

56 evidence supports that designation, nor are they exclusively pair-living (social organization)
57 and we urge further field studies on Macroscelidea social systems.

58

59 **Key words:** sengi, intra-specific variation, social flexibility, *Elephantulus*, *Macroscelides*,
60 *Rhynchocyon*, *Petrodromus*

61

62 **Introduction**

63 Kappeler (2019) suggested that animal social systems are composed of four inter-related
64 components: social organization, social structure, mating system, and care system. The social
65 organization describes the size, sexual composition and spatiotemporal cohesion of a group
66 (Kappeler & van Schaik, 2002). Three major categories of social organization occur: solitary
67 living, pair-living, or group living. The social structure describes the different interactions
68 between members of the same group and the resulting relationships. The mating system
69 describes who mates with whom and the reproductive consequences (e.g. paternity). There are
70 four types of mating system, depending on the number of mating partners for males and females
71 (Clutton-Brock, 1989; Loue, 2007): monogamy, polygyny, polyandry or polygynandry.
72 Finally, the care system is about who cares for the dependent offspring (Kappeler, 2019).

73 Over the last decades, the study of animal social systems has undergone significant
74 progress due to long-term studies and advances in technology (e.g genotyping ; Clutton-Brock
75 2021). Often the focus has been on specific social systems such as monogamy (Kleiman 1977;
76 Mock & Fujioka, 1990; Lukas & Clutton-Brock 2013). Initially, pair-living (a form of social
77 organization) was often regarded to be indicative of a monogamous social system in mammals
78 (Kleiman 1977, 1981). However, genetic fingerprinting revealed that extra-pair paternity is
79 common in many pair-living species (Cohas & Allainé, 2009), leading to the realization that
80 seemingly monogamous relationships do not necessary predict genetic outcomes (i.e., genetic

81 monogamy). As a result, some researchers introduced the term “social monogamy” (Dobson,
82 Way & Baudoin 2010; Gowaty & Buschhaust 1998) to distinguish social behaviour within pairs
83 from genetic monogamy. Recent reviews from multiple research groups advocate abandoning
84 the term “social monogamy”, and using the term “monogamy” only in the context of mating
85 systems (Fernandez-Duque et al. 2020; Garber et al. 2016; Huck, Di Fiore & Fernandez-Duque
86 2020; Kappeler & Pozzi 2019; Kvarnemo 2018; Tecot, Singletary & Eadie 2016). Arguments
87 against the use of the term “social monogamy” are centered on the importance of distinguishing
88 between the different components of social systems for understanding their evolution. For
89 example, if one wants to understand why animals live in pairs, it is not necessary to assume that
90 they mate monogamously, only, that pair-living adds to a higher fitness than alternative forms
91 of social organization. It is therefore necessary when describing the social system of a species,
92 that social organization, mating system, social structure and care system are considered
93 (Kappeler 2019).

94 Describing all four components of a social systems is a challenge, for a number of
95 reasons. For example, it was previously assumed that “socially monogamous” species are pair-
96 living (social organization), have pair bonds (social structure), and engage in biparental care
97 (Kleiman, 1977; Mock & Fujioka, 1990). However, it is well known that several pair-living
98 taxa do not fit this syndrome (Kleiman, 1977), such as dwarf antelopes (Bovidae) that do not
99 exhibit biparental care (Komers, 1996), elephant-shrews (Macroscelididae) that do not have
100 pair bonds (i.e. individuals showing a preference for a specific opposite sex-individual, which
101 can be tested experimentally: Carter et al., 1995; Garnier and Schradin 2019) or exhibit
102 biparental care (Rathbun & Rathbun, 2006). Most confusion, however, arises from the
103 inconsistent use of the term “monogamy” (see above and Kappeler, 2019; Solomon & Ophir,
104 2020), which should be restricted to describe the mating system where reproduction occurs
105 mainly within pairs (Kappeler, 2019; Kappeler & van Schaik, 2002; Mock & Fujioka, 1990)

106 pFor understanding the evolution of pair living, the different components of social systems
107 should be studied separately from each other (Fernandez-Duque et al., 2020; Huck et al., 2020;
108 Kappeler, 2019).

109 A species' social organization is typically characterized by the most frequent form, an
110 approach that ignores intra-specific variation (Schradin et al., 2018). For example, the greater
111 white-toothed shrew (*Crocidura russula*) has a variable social organization including solitary,
112 pair and group-living (Cantoni & Vogel, 1989; Ricci & Vogel, 1984). Intra-specific variation
113 in social organization (IVSO) has now been reported in many mammalian taxa, including
114 Artiodactyla (Jaeggi et al., 2020), Carnivora (Dalerum, 2007), Eulipotyphla (Valomy et al.,
115 2015), and Strepsirrhini (Agnani et al., 2018). IVSO may be more common in other mammalian
116 taxa as well, where variation has been possibly ignored to emphasize the most frequent or the
117 most interesting form of social organization (Schradin et al., 2018). A consideration of IVSO,
118 and variation within the three other components of social systems can transform our
119 understanding of social evolution (Jaeggi et al., 2020; Schradin et al., 2018).

120 The mammalian order Macroscelidea (elephant-shrews or sengis) includes 19 extant
121 species in four genera, all occurring in Africa, ranging in body mass from 27g to 700g (Rathbun
122 & Dumbacher, 2015; Rovero et al., 2008) and occupying a diversity of habitats including
123 deserts, semi-deserts, savannahs, rocky mountains, lowland forests and tropical rain forests
124 (Kingdon et al., 2013 ; Rathbun, 1979). Macroscelidea is the only mammalian order for which
125 all extant species are believed to be monogamous (Lukas & Clutton-Brock, 2013; Rathbun &
126 Rathbun, 2006; Ribble & Perrin, 2005), though this typically refers to a pair-living social
127 organization (Schubert et al., 2009). Theory predicts that the ability of males to monopolize
128 access to females, which depends on ecological factors and population density, will greatly
129 influence mating systems (Emlen & Oring, 1977). The main hypothesis for monogamy in
130 Macroscelidea is that low population density, possibly due to their insectivorous diet, makes it

131 unfeasible for males to defend more than one female (Ribble & Perrin, 2005; Schubert et al.,
132 2009). Males generally mate-guard a single female, leading to pair-living and potentially
133 monogamous mating (Fitzgibbon, 1997; Ribble & Perrin, 2005; Schubert et al., 2009). Thus,
134 their small body size combined with low population density is believed to have favored the
135 evolution of monogamy.

136 The long-held assumption that all elephant-shrews are monogamous might have led to
137 an underappreciation of variation in their social systems. The last detailed review on monogamy
138 in elephant-shrews was published more than 40 years ago (Rathbun, 1979), and was updated
139 within the discussion of a more recent case study (Rathbun & Rathbun, 2006). Therein, the
140 importance of considering intra-specific variation for understanding the social systems of
141 elephant-shrews, which were still considered to be all monogamous, was emphasized (Rathbun
142 & Rathbun, 2006). To date, no review has differentiated between the four different components
143 of social systems in elephant-shrews or summarized the observed intra-specific variation.

144 The overall aim was to describe all four components of the social system of elephant-
145 shrews, taking intra-specific variation into account. First, we conducted a systematic review of
146 the primary literature on elephant-shrew social organization, mating systems, social structure
147 and parental care. This approach allowed us to evaluate the empirical evidence suggesting that
148 elephant-shrews are pair-living and monogamous. Second, we compared our dataset on
149 elephant-shrew social organization – the component of the social system with the most data –
150 with other available datasets that also used secondary sources to summarize their social systems
151 (Heritage, 2018; Lukas and Clutton-Brock, 2013; Nowak & Wilson, 1999). Third, we report
152 the results of phylogenetic comparative analyses to estimate the ancestral state of all elephant-
153 shrews. Social organization was the only component for which sufficient data were available
154 to conduct such an analysis. Based on previous reports, we expected the ancestral social
155 organization to be pair-living. Body mass and habitat diversity differ widely between species

156 and could influence their social organization. For example, living in variable habitats can affect
157 density or grouping pattern of a population, through food availability or predation pressure
158 (Geist 1974). We therefore expected that variability in social organization will increase with
159 variability in habitats (Schradin et al., 2018). Population density is the factor most emphasized
160 to have influenced the evolution of pair-living in elephant-shrews (Rathbun & Rathbun, 2006)
161 and mammals more broadly (Lukas & Clutton-Brock, 2013 but see Dobson et al. 2010), such
162 that we predicted pair-living to be associated with low population density, making it difficult
163 for a male to associate with more than one female.

164

165 **Materials and Methods**

166 *Literature searches*

167 The 19 species of elephant-shrews were identified using the IUCN (International Union for
168 Conservation of Nature) database (2019). Literature searches on the four social system
169 components were conducted in Web of Science (Thomson Reuters) and in Google Scholar
170 between November 2019 and March 2020 using specific key words (see the different sections
171 below). This search yielded 166 articles that were scanned for information on social systems.
172 Additional papers cited in those 166 articles were also studied. Data were recorded at the
173 population-level.

174

175 *Social organization*

176 For each species, the current and previously used Latin name of the species and the term
177 “social” was searched. If no literature on social organization was found, the search was repeated
178 in Web of Science and Google Scholar, only with the Latin name (for 10 species). To obtain
179 information on social organization, only peer-reviewed literature from studies conducted in the
180 field about elephant-shrews were taken into account, and reviews and studies in captivity were

181 ignored. For each study, the following keywords were searched throughout the PDF's: "social",
182 "solitary", "group", "pair". All figures and tables were examined. Data on social organization
183 were found in 11 papers on 8 species.

184 Seven categories of social organization including solitary living, pair-living, and
185 different forms of group-living (one male with multiple females, multiple males with multiple
186 females, one female with multiple males, multiple females and multiple males) were defined,
187 of which only three were reported in the elephant-shrew studies (Table 1). For our study, we
188 only considered adult and mature individuals. For each paper, we recorded the number of social
189 units reported as solitary, pair-living, or group-living. Individuals of a species were considered
190 as solitary only if both sexes have been observed to be solitary, as single individuals of one sex
191 could represent dispersers. Identified dispersers were always ignored. For solitary living, we
192 used the smaller number of the two sexes to have a number comparable to pairs (e.g. when four
193 solitary males and three solitary females were observed, we recorded "3" solitary social units).
194 Individuals of a species were considered as being pair-living when a male and a female have a
195 significant overlap of their home ranges with each other but not with other individuals.
196 Populations in which two or more forms of social organization were recorded were categorized
197 as variable resulting in four possible social organizations within populations: solitary, pair-
198 living, group-living, and "variable" (solitary/pair; pair/group; solitary/pair/group). In addition,
199 we recorded whether the study took place during the breeding season, during the non-breeding
200 season or throughout the year.

201

202 *Mating system*

203 For the mating system, peer-reviewed literature from studies conducted in the field and in
204 captivity were taken into account. Searches included the following key words: "monogamy",

205 “polygamy”, “polyandry”, “polygyandry” and “promiscuity”. In addition, we report data
206 presented on a poster available on researchgate (Peffley et al. 2009).

207

208 *Social structure*

209 For the social structure, peer-reviewed literature from studies conducted in the field and in
210 captivity were taken into account. Searches were made using the following key words: “solitary
211 foragers”, “pair bond”, “aggression”, “mate guarding”. This resulted in five suitable studies on
212 social structure. Information on pair-bonds, aggression toward offspring, foraging, time spent
213 between individuals, chasing, mate guarding and aggression between females or between males
214 was recorded as present or absent.

215

216 *Care system*

217 For the care system, peer-reviewed literature from studies conducted in the field and in captivity
218 were used. Searches were made using the following key words: “maternal care”, “paternal
219 care”, “offspring”, “direct paternal care”, “indirect paternal care” and “absentee strategy” which
220 are common terms for Macroscelidea (Rathbun, 1979). Indirect paternal care represents
221 behaviors shown by the fathers independent of the presence of offspring which are beneficial
222 for the offspring (while direct paternal care is a direct response to the presence of offspring)
223 (Kleiman, 1977). This resulted in six suitable studies of care systems. We reported whether
224 maternal and paternal care was observed.

225

226 *Dataset comparison*

227 We compared our data with the database from Lukas and Clutton-Brock (Lukas & Clutton-
228 Brock, 2013). Additionally, we compared our database with information in secondary literature,
229 specifically in Walker’s Mammals of the World Volume II (Nowak & Wilson, 1999) and the

230 Handbook Mammals of the World (Heritage, 2018), compiled by taxon-specific experts. This
231 comparison was only made for social organization, the only category for which sufficient data
232 from peer-reviewed literature were available.

233

234 *Predictors for social organization*

235 We included the following predictors in our Bayesian model described below: body mass,
236 population density, number of studies per population and habitat heterogeneity (see Supporting
237 Information 1, 2 and 3). Habitat heterogeneity represents the maximum number of habitats per
238 population. Habitat type was reported from the primary literature and categorized on IUCN
239 classification as shrubland, rocky areas, bushlands, desert or forest. Habitat heterogeneity and
240 whenever possible, body mass and population density, were extracted from the same study in
241 which data on social organization had been reported. If no information was available in that
242 same study, we searched for other studies of the same population (two species). Finally, if no
243 information was available, we searched the primary literature for data on the same species in
244 other populations (one species).

245

246 *Phylogenetic comparative analysis*

247 All statistical analyses were conducted in R v.3.6.1 (The R foundation for statistical
248 computing). To analyze social organization, Bayesian phylogenetic mixed-effects models were
249 used in order to account for the multilevel structure of the dataset (populations nested within
250 species) and the phylogenetic relationships among species (de Villemereuil, 2014). To represent
251 the phylogenetic relationships and their uncertainty a sample of 100 phylogenetic trees was
252 downloaded from the online database VertLife (<http://vertlife.org/data/>). The parameter used to
253 create the tree was “Mammals birth death node dated completed tree”. We used the R package
254 *brms* (Bürkner) to fit multinomial models to the response variable social organization, wherein

255 each population could occupy one of several mutually exclusive states. We created three
256 models. In model 1, the social organization (solitary, pair-living, group-living and variable) was
257 the response variable. In model 2, the response variable was separated into all possible
258 combinations (solitary+pair-living, pair+group-living and solitary+pair-living+group-living) to
259 estimate the most likely ancestral social organization. In model 3, we used the main (i.e. the
260 modal or most common) form of social organization, defined as the social organization for
261 which the most social units were observed (solitary, pair-living and group-living) as the
262 response variable. In this model, variability was not included except for one species,
263 *Macroselides flavicaudatus*, where an equal number of social units were solitary and pair-
264 living.

265 For each model, we also calculated the percentage of the difference between the
266 probability of two different social organization using the posterior samples (e.g. all samples for
267 the probability of variable social organization minus all samples for the probability of pair-
268 living) and whether the probability of that difference was greater than zero (i.e. the proportion
269 of the resulting samples >0); the ability to compute such contrasts between model parameters
270 is a notable strength of Bayesian inference (McElreath 2019), whereas frequentist models are
271 limited to comparing estimated parameters to 0. Hence we can directly express the model's
272 greater confidence that a given social organization had a higher probability than others, which
273 cannot be learned by merely comparing each social organization's mean probability and
274 confident intervals. Thus, even if the exact probability of each social organization is estimated
275 with high uncertainty (large 95% CIs), we can have more confidence in the probability of
276 differences between the probabilities of two social organizations.

277 We included the following predictors in our models: body mass, population density,
278 number of studies per population and habitat heterogeneity (number of habitat per population)
279 (see Supporting Information 1, 2 and 3). The number of studies per population (one or two) was

280 added to control for research effort. The number of studies per population and habitat
281 heterogeneity were centered on one. Body mass and population density were centered on their
282 mean.

283 Our model converged well with Rhat values (potential scale reduction factor) ≤ 1.01 .
284 The likelihood of each social organization being the ancestral state was inferred from the
285 intercepts of the model, i.e. the probability of each social organization when predictors were at
286 their means. Pair-living was the reference category in our two models.

287 The phylogenetic signal (λ) was calculated as the proportion of variance captured by the
288 phylogenetic random effects (Nakagawa & Schielzeth, 2013):

289
$$\lambda = \frac{\sigma_p^2}{\sigma_p^2 + \sigma_r^2 + \sigma_d^2}$$

290 σ_p^2 represents the variance of the phylogeny random effect, σ_r^2 is the variance of the species-
291 level random effect and σ_d^2 is the distribution-specific variance equal to $\pi^2/3$ (Nakagawa and
292 Schielzeth, 2013).

293

294 **Results**

295 *Social organization*

296 Data on social organization were reported for twelve populations of eight species (Table 2).
297 One species (*Macroscelides micus*) was only reported to be solitary living whereas the other
298 seven species had variable social organizations. Two species were solitary and pair-living, three
299 species were solitary, pair- and group-living and two species pair- and group-living (Table 2).
300 Of the twelve studied populations, one population was solitary (*Macroscelides micus*) and two
301 populations of *Petrodromus tetradactylus* were pair-living. The other 10 populations (75%) had
302 a variable social organization (Table 2).

303

304 *Mating system*

305 Our search generated only one paper that reported observations of mating in the field (Rathbun,
306 1979). A male *Rhynchocyon chrysopygus* chased the female and then copulated with her during
307 two seconds with five rapid copulations. Schubert et al. (2012) found in captive experiments
308 that female *Macroscelides proboscideus* showed as many sexual interactions with a
309 neighboring male as with her pair partner, and that males actively aimed to mate with non-pair
310 neighboring females. In an unpublished poster on a study using micro-satellites to determine
311 paternity in *Macroscelides proboscideus*, Peffley et al. (2009) found for the population studied
312 by Schubert et al. (2009) that only two out of six mother-offspring families resulted from
313 serially monogamous mating. From a sample of 19 offspring, the male of the pair was the sire
314 of only seven. At least six offspring were sired by another male than the female's social mating
315 partner.

316
317 *Social structure*

318 Our search generated six studies reporting information about social interactions (Table 3).
319 Individuals living together had little social interaction, there were no pair-bonds, and they were
320 solitary foragers (Rathbun, 1979). Mate guarding was said to occur in five species (Table 3). In
321 *Elephantulus myurus* (Ribble & Perrin, 2005) and in *Rhynchocyon chrysopygus* (Fitzgibbon,
322 1997), males defended territories containing females, and these territories were quickly taken
323 over by other males after the pair male disappeared (resulting in a change of the adult sex ratio.
324 This was regarded as evidence of male mate guarding. The same association pattern has been
325 interpreted as mate guarding in several other species, where males followed their females when
326 in estrus, though mate guarding was not measured directly (Rathbun, 1979). The only study
327 that directly measured mate guarding was in *Macroscelides proboscideus*, where males reduced
328 the distance to their female in the periods they were receptive (Schubert et al., 2009). Similarly,
329 in the solitary species *Macroscelides flavicaudatus*, males associated with females when these
330 were receptive, but then male left, searching for other females (Sauer, 1973). Moreover, both

331 sexes defend a territory and are very aggressive towards conspecifics of the same sex
332 (FitzGibbon, 1997; Rathbun, 1979). Schubert et al. (2012) found in captive experiments no
333 evidence for pair-bonding, but individuals of both sexes readily interacted with opposite sex
334 conspecifics with which they were not paired.

335 In several species, aggression towards young was observed around weaning. Some
336 species tolerated their weaned offspring for periods ranging from 21 to 40 days old (Rathbun,
337 1979; Schubert et al., 2012) while in *Elephantulus rufescens*, parents tolerated one of their
338 young for the entire period of 193 days. In *Elephantulus rufescens*, some offspring can remain
339 in their parents' territory long after reaching adulthood (Rathbun, 1979).

340

341 *Care system*

342 We found information on the care system for six of the 19 species (Table 4). The precocial
343 young were visited and nursed by the mother for very short periods of 10-60 seconds, which
344 has been called an absentee strategy (Rathbun, 1979). During this period, the female was not
345 engaged in other care activities, such as cleaning or huddling the offspring. Maintenance of
346 pathways by males to allow offspring to move quickly and escape from a predator was reported
347 for five species (Table 4) and interpreted as indirect paternal care while no direct paternal care
348 was observed.

349

350 *Dataset comparison*

351 In our database, the most frequent form of social organization observed of six of the eight
352 species of Macroscelidea was pair-living (Table 5), while one species had a solitary main social
353 organization (*M. micus*) and another had an equal number of solitary and pair-living social
354 units, hence a variable main social organization (*M. flavicaudatus*). Thus, our results of main
355 social organization were similar to what was reported by Lukas and Clutton-Brock (2013).

356 Seven (87.5%) of the species with information available showed IVSO and the only species
357 (12.5%) with a single form of social organization was solitary. This high prevalence of IVSO
358 was not represented in the database of Lukas and Clutton-Brock (2013), in which 15 (93.3%)
359 of the elephant-shrew species were reported to be pair-living and one (6.7%) to be solitary
360 (Table 5 and Supporting Information 4). They reported *Petrodromus tetradactylus* to be
361 solitary, which we found to be variable with pair and group-living, while the species we
362 reported to be solitary, *Macroscelides micus*, was studied after the paper from Lukas & Clutton-
363 Brock (2013) by Rathbun & Dumbacher (2015) (see Supporting Information 4).

364 The Handbook Mammals of the World (Heritage, 2018) reported all elephant-shrew
365 species to be pair-living. Walker's Mammals of the World (Nowak & Wilson, 1999) reports
366 data on eight species, with five (62.5%) of them showing IVSO, two (25%) being pair-living
367 and one (12.5%) being solitary living (Table 5).

368

369 *Phylogenetic comparative analysis*

370 The phylogenetic mixed effects models showed no significant effects of habitat heterogeneity,
371 population density, body mass and number of studies on social organization (see Supporting
372 Information 5, 6 and 7). The phylogenetic signal for model 1 was moderate ($mean=0.35$, 95%
373 $CI= 0.008- 0.75$). Variable social organization had the highest probability as ancestral state
374 ($mean\ probability = 0.67$, 95% $CI = 0-1$) compared to solitary living ($mean = 0.15$, 95% $CI =$
375 $0 - 1.0$), group-living ($mean = 0.09$, 95% $CI = 0 - 0.85$), and pair-living ($mean = 0.08$, 95%
376 $CI = 0 - 0.69$). Despite the large confident intervals surrounding the exact probability of each
377 social organization, we can express greater confidence about the differences between these
378 probabilities; namely, we are 82% confident that variable was more likely than pair-living, 32%
379 confident that group-living was more likely than pair-living and 38% confident that solitary
380 was more likely than pair-living (Fig. 1; Supporting Information 8).

381 In order to understand which kind of variable social organization was the most likely ancestral
382 state, a second analysis was conducted using all different categories of variable social
383 organization (model 2; Fig. 2; Supporting Information 9). The phylogenetic signal of this
384 analysis was moderate (*mean* = 0.32, 95% *CI* = 0.0027 – 0.74). Solitary+pair-living+group-
385 living was the most likely ancestral state (*mean* = 0.29, 95% *CI* = 0 – 1), followed by
386 pair+group-living (*mean* = 0.28, 95% *CI* = 0 – 1) and solitary+pair-living (*mean* = 0.19, 95%
387 *CI* = 0 – 1). Those three social organizations were part of the category “variable” in our first
388 analysis (Fig. 1) and were respectively 60%, 67% and 45% more likely than pair-living (Fig. 2;
389 Supporting Information 9). The probability that the ancestral social organization was solitary
390 was relatively low (*mean* = 0.12, 95% *CI* = 0 – 0.99). Group-living (*mean* = 0.06, 95% *CI* = 0
391 – 0.52) and pair-living (*mean* = 0.05, 95% *CI* = 0 – 0.32) were the least likely ancestral social
392 organization.

393 In model 3, we calculated what the ancestral state would be if we only took the main social
394 organization into account, neglecting variability (Fig. 3). The phylogenetic signal was again
395 moderate (*mean* = 0.36, 95% *CI* = 0.00008 – 0.8). Pair-living was the most likely ancestral state
396 (*mean probability* = 0.58, 95% *CI* = 0 – 1), but again with large uncertainty. Group-living (*mean*
397 = 0.08, 95% *CI* = 0 – 0.74), solitary (*mean* = 0.20, 95% *CI* = 0 – 1) and solitary/pair-living
398 (*mean* = 0.14, 95% *CI* = 0 – 1) had lower mean probabilities and similar uncertainties (Fig. 3 ;
399 Supporting Information 10).

400

401 **Discussion**

402 Our comprehensive review of the literature on Macroscelidea indicated that their best studied
403 social system component is social organization. The most frequent form of social organization
404 was pair-living, though all pair-living species exhibited a variable social organization, including
405 either solitary and/or group-living. Our approach revealed that (1) elephant-shrew social

406 organization is best characterized as variable, (2) the ancestral form of social organization could
407 not be reliably determined, but pair-living had the lowest probabilities when IVSO was taken
408 into account, and (3) there is no empirical evidence that any of the species typically exhibit a
409 monogamous mating system.

410

411 *Social system*

412 Consistent with a previous report (Rathbun & Rathbun, 2006), our literature review indicates
413 Macroscelidea have a variable form of social organization, with pair-living occurring in 87.5%
414 of the species, solitary living occurring in 75% of the species and group-living occurring in
415 62.5% of the species. While pair-living is common in many species of Macroscelidea, it is
416 neither the only form of social organization nor the main form of social organization in all
417 species. Solitary living occurred in most species and was as common as pair-living in one
418 species and the only form of social organization for another species. Importantly, pair-living
419 was mainly derived from the extensive home range overlap of one male and one female with
420 each other but not with other individuals. Thus, even though spatial organization indicated pair-
421 living, individuals spent most of their time alone, and other researchers might categorize these
422 individuals as solitary rather than pair-living. In some cases, the home ranges of two females
423 and one male overlapped heavily such that the social units were categorized as single male /
424 multi-female groups. These associations lasted for a few weeks up to several months
425 (Fitzgibbon, 1997; Rathbun, 1979; Schubert et al., 2009), which is long for species that lives
426 between two and four years (Rathbun, 1979). Typically, such groups occurred because of the
427 death / disappearance of the male of a neighboring pair (Rathbun, 1979; Schubert et al., 2009).
428 However, pairs were more stable than groups in *Elephantulus rufescens* (pairs=one year,
429 groups=2 months; Rathbun, 1979), *Rhynchocyon chrysopygus* (pairs=up to 16 months,

430 groups=up to 3 months; Fitzgibbon, 1997), and *Macroscelides proboscideus* (pair=2 years,
431 groups=5-6 weeks; Schubert et al., 2009).

432 Our study suggests that the long-held assertion that Macroscelidea is the only
433 monogamous mammalian order (Lukas & Clutton-Brock, 2013; Rathbun, 1979; Rathbun &
434 Rathbun, 2006; Ribble & Perrin, 2005; Handbook Mammals of the World 2018) is an over-
435 simplification of elephant-shrew mating systems. The only available information regarding the
436 mating system is from an unpublished study that was presented as a poster, representing data
437 from the study population of Schubert et al. 2009 (samples had been collected by Schradin &
438 Schubert). These non-peer-reviewed data indicate that *M. proboscideus* are not genetically
439 monogamous and that females tend to reproduce with more than one male (Peffley et al., 2009).
440 Many pair-living mammal species do not have a monogamous mating system but show extra-
441 pair paternity, varying between 0 and 92% (Cohas & Allainé, 2009). Future studies will have
442 to investigate how common extra-pair paternity is in the different Macroscelidea species.

443

444 *Dataset comparison*

445 We found that 75% of the species had pair-living as their most frequent form of social
446 organization. In comparison, the Handbook Mammals of the World (Heritage, 2018) considers
447 all species of elephant-shrews to be pair-living and Lukas & Clutton-Brock (2013) reported
448 93% of species as pair-living. There are several explanations for these differences. We relied
449 only on information from field studies, whereas Lukas & Clutton-Brock (2013) also included
450 data from captivity and assumed that species without data have the same form of social
451 organization as closely related species. Thus, their database comprised of 15 species while we
452 only found field data for eight species. The references in their database include one paper
453 making the general statement that Macroscelidea are monogamous (Rathbun & Rathbun, 2006),
454 one paper reporting data from captivity (Lawes & Perrin, 1995), one paper that cannot resolve
455 the social organization of the studied species (*Petrodromus tetradactylus*; Jennings & Rathbun,

456 2001), as well as one paper that does not provide data on social organization (Koontz & Roeper,
457 1983). Interestingly, the only species which they do not regard to be monogamous but solitary,
458 *Petrodromus tetradactylus*, was reported by us to be group or pair-living. Our results compare
459 well with the expert opinions published in the book Walker's Mammals of the World (Nowak
460 & Wilson, 1999). Like us, they report data for only eight species, 12.5% of which were believed
461 to be solitary, 25% to be pair-living and 62.5% to be variable. Based on these differences, we
462 argue that our database based on primary field studies is the most robust of these datasets.

463

464 *Phylogenetic comparative analysis*

465 We could not reliably identify the ancestral form of social organization, but found in all analyses
466 a moderate phylogenetic signal indicating that social organization is influenced by phylogenetic
467 history. Considering a posteriori the small sample size and the high variation between species
468 and populations, this is not surprising. Nevertheless, the phylogenetic analyses revealed that
469 variable social organization was 82% more likely to be the ancestral state than pair-living.

470 Most Macroscelidea had a variable type of social organization which was also the most
471 likely ancestral form of social organization. More precisely, it was solitary+pair-living+group-
472 living followed by pair+group-living that were the most likely ancestral forms of social
473 organization. The uncertainty surrounding these inferences was large. Of note is that the
474 previous assumption, of a pair-living ancestral social organization was the least supported.
475 Importantly, when considering the variation reported from the field, pair-living always received
476 very little support as the ancestral form. In contrast, when we considered only the main social
477 organization (and ignored variation), pair-living became the most likely ancestral form of social
478 organization, but with a lower mean probability than the variable ancestral state in the first
479 analysis. What we can hypothesize is that the ancestor of all Macroscelidea was able to be pair-
480 living, but with significant variation in its social organization that also allowed for solitary and
481 group-living.

482 Low population density has been considered as the main factor leading to pair-living in
483 animals (Emlen & Oring, 1977) and specifically in Macroscelidea, since it makes it difficult for
484 males to defend more than one female (Rathbun & Dumbacher, 2015; Rathbun & Rathbun,
485 2006). However, we found no indication that social organization was related to population
486 density. This might be because the lowest population densities (reported for two species of the
487 genus *Macroscelides*) were associated with solitary living, which is in contrast to Rathbun &
488 Rathbun's (2006) prediction of an increased incidence of pair-living with decreasing population
489 density. Body mass and habitat type, two factors varying widely between populations and
490 species, also had no influence on social organizations. Thus, even though we found important
491 variation in social organization within and between populations, we could not explain this
492 variation by the ecological and life history factors included in our analysis. To gain a better
493 understanding of the evolution and diversity of Macroscelidea social organization, more field
494 studies would be needed, especially on the 11 species for which we could not find any data.

495

496 *Social monogamy vs. sengi syndrome*

497 Aspects of the care system and of the social structure have been discussed in the literature to be
498 associated with monogamy. Social monogamy has been characterised by pair-living,
499 monogamous mating, biparental care, pair bonding and mate guarding (Lukas & Clutton-Brock,
500 2013; Mock & Fujioka, 1990). Direct paternal care is absent in Macroscelidea, though indirect
501 paternal care, i.e. behaviours of the male which benefit the offspring but which are shown to be
502 independent to the presence of offspring, has been reported for several species (Rathbun, 1979).
503 However, indirect paternal care did not evolve because of its benefits for the offspring, but
504 because it has direct survival benefits for the males, such as improved ability to escape predators
505 (Rathbun, 1979; Ribble & Perrin, 2005). Macroscelidea is the only taxon where indirect
506 paternal care has been discussed in detail, possibly to fit the proposed social monogamy. There

507 is also general consensus that pair-bonding (i.e. individuals showing an attachment to a specific
508 opposite-sex individual, Carter et al.,1995) does not exist in Macroscelidea (Rathbun &
509 Rathbun, 2006).

510 In Macroscelidea, individuals of a pair spend little time together (Fitzgibbon, 1997;
511 Koontz & Roeper, 1983; Rathbun, 1979) apart from the period when the female is receptive
512 (Fitzgibbon, 1997; Schubert et al., 2012). This represents the behavioural pattern of many
513 solitary living species (Schülke & Kappeler, 2003). Females defend territories against other
514 females and males against other males (Rathbun, 1979). Mate guarding has been observed in
515 several elephant-shrew species (FitzGibbon, 1997; Rathbun, 1979; Sauer, 1973; Schubert et al.,
516 2012). This tactic consists of a male keeping within a short distance to a female as long as she
517 is receptive, possibly to prevent male competitors to have access to that female (Huck et al.,
518 2004). For example, in *M. proboscideus*, a male and female sharing a home range were much
519 closer to each other in the period during which the female was sexually receptive than when
520 she was not (Schubert et al., 2009). Our evaluation of the four components of social systems
521 independently in Macroscelidea shows that this taxon is in general neither pair-living nor
522 monogamous, and thus not “socially monogamous”.

523 It was recognized early on that Macroscelidea did not fit the typical description of social
524 monogamy (Kleiman, 1977; Rathbun & Rathbun, 2006). Instead, Rathbun & Rathbun 2006
525 discussed a “sengi syndrome” for small mammals with the sengi typic morphology: compact
526 body, large head and long and narrow snout. Species falling under this syndrome have a
527 relatively long life expectancy, produce few precocial young and have an insectivorous diet,
528 which can explain a conserved social organization of pair-living even though the different
529 species inhabit diverse habitats. The sengi syndrome has been discussed in relation to their
530 phylogenetic ancestry (Rathbun & Rathbun, 2006). We found that phylogeny has a moderate
531 effect on social organization, suggesting that social organization is somewhat constrained by

532 phylogenetic history, but can also adapt to local ecology. Indeed, the phylogenetic signal in all
533 of our three models had a much higher mean probability compared to other studies (e.g. 0.05 in
534 Jaeggi et al., 2020 on Artiodactyla social organization). Thus, our study is not in contrast to the
535 suggested sengi syndrome but indicates that instead of fixed pair-living, a flexible social
536 organization including solitary and pair-living is likely part of this syndrome.

537

538 *Conclusions*

539 The Macroscelidea (elephant-shrews or sengis) have been regarded for decades as the only
540 mammalian order in which all extant species are monogamous. Reviewing field studies of the
541 last 5 decades we found that the social organization of elephant-shrews is much more flexible
542 than previously recognized and not all species are pair-living. More species must be studied in
543 the field to reliably infer the ancestral form of social organization and the ecological and life
544 history factors related to Macroscelidea social evolution. Our analysis predicts a socially
545 variable ancestor that had pair-living as one of several possible forms of social organization.
546 Paternity studies are needed to determine the genetic mating system, but the flexible social
547 organization predict that extra-pair paternity is common and that Macroscelidea are not a
548 monogamous order. In sum, elephant-shrews are not exclusively pair-living, do not fit the
549 definition of socially monogamous (Kleiman 1977; Rathbun 2006), and there is no evidence
550 for a genetically monogamous mating system.

551

552

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719 primates, monogamy: mating strategies and partnerships in birds, humans and
720 other mammals. Cambridge University Press(pg. 59-80).

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729 **Table 1.** Types of social organization reported in field studies on elephant-shrews.

Social organization	Definition
Solitary living	Both resident adult solitary males and solitary females occur in the population (excluding dispersing individuals)
Pair	One adult female and one adult male share a home range, with or without dependant offspring
One male multi female groups	Multiple breeding females and one breeding male share a home range

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732 **Table 2.** The different forms of social organization reported in the primary literature. Numbers
733 refer to the numbers of social units observed. BS: breeding season; NBS: non-breeding season;
734 BOTH: breeding and non-breeding season; ALL: non-seasonal breeding throughout the year.
735 No data could be found on social organization of the remaining species (*Elephantulus*
736 *brachyrhynchus*, *Elephantulus edwardii*, *Elephantulus fuscipes*, *Elephantulus fuscus*,
737 *Elephantulus pilicaudus*, *Elephantulus rozeti*, *Elephantulus rupestris*, *Rhynchocyon cirnei*,
738 *Rhynchocyon petersi* and *Rhynchocyon udzungwensis*).

Species	Population	Solitary	Pair-living	One male several females	References
<i>Elephantulus intufi</i>	Erongo Wilderness Lodge Okapekaha Farm, Namibia	-	6 (BOTH)	1 [‡] (BOTH)	Rathbun & Rathbun, 2006
<i>Elephantulus myurus</i>	Weenen Nature Reserve, South Africa	5 (BOTH)	18 (BOTH)	-	-
	Goro Game Reserve, South Africa	1 (BS)	12 (BS)	-	Ribble & Perrin, 2005
		2 (BS)	4 (BS)	-	Hoffmann et al., 2019
		2 (NBS)	2 (NBS)	-	
<i>Elephantulus rufescens</i>	Bushwacker, Kenya	2 (ALL)	7 (ALL)	1 [‡] (ALL)	Rathbun, 1979
<i>Macroselides flavicaudatus</i>	Namib Desert, Namibia	2 (BS)	2 (BS)	-	Sauer, 1973
<i>Macroselides micus</i>	Eastern Goboboseb Mountains, Namibia	2 (BS)	-	-	Rathbun & Dumbacher, 2015
<i>Macroselides proboscideus</i>	Goegap Nature Reserve, South Africa	1 (BOTH)	32 (BOTH)	1 [‡] (BOTH)	Schubert et al., 2009
<i>Petrodromus tetradactylus</i>		-	5 (BOTH)	1 (BS)	-
	Tembe Elephant Park, South Africa	-	4 (NBS)	-	Oxenham & Perrin, 2009
	Arabuko Sokoke Forest, Kenya	-	1 (BOTH)	-	Fitzgibbon, 1995
	Sodwana Bay National Park, South Africa	-	-	1 (BS)	Linn et al., 2007

<i>Rhynchocyon</i>		1	12	3	-
<i>chrysopygus</i>		(ALL)	(ALL)	(ALL)	
	Arabuko				
	Sokoke Forest,	-	5	2‡	Fitzgibbon, 1997
	Kenya		(ALL)	(ALL)	
	Gedi Forest	1	7	1‡	Rathbun, 1979
		(ALL)	(ALL)	(ALL)	

739 ‡ One male and several female association (group-living) lasted two weeks for *Elephantulus intufi*, 42 days for *Elephantulus*
740 *rufescens*, five to six weeks for *Macroscelides proboscideus*, six weeks, two and three months for *Rhynchocyon chrysopygus*.
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743 **Table 3.** The different components of social structure identified in our primary literature
744 research. Pair-bond (PB); aggression toward their offspring (ATO); solitary foragers (SF) ;
745 Male and female spend considerable time together (Time MF); chase conspecific that entered
746 their territory (Chase); mate guarding (MG); aggression between neighboring females (Ag FF);
747 aggression between neighboring males (Ag MM).

Species	PB	ATO	SF	Time MF	Chase	MG	Ag FF	Ag MM	References
<i>Elephantulus myurus</i>	-	-	-	-	-	yes	-	-	Ribble & Perrin, 2005
<i>Elephantulus rufescens</i>	no	yes (40 days old)	yes	-	-	yes	yes	yes	Rathbun, 1979
<i>Macroscelides flavicaudatus</i>	no	-	yes	no	-	yes	-	-	Sauer, 1973
<i>Macroscelides proboscideus</i>	no	yes (21 days old)	-	-	yes	yes	-	yes	Schubert et al., 2012; Schubert et al., 2009
<i>Petrodromus tetradactylus</i>	no	-	yes	-	-	-	yes	yes	Rathbun, 1979
<i>Rhynchocyon chrysopygus</i>	-	no (193 days old)	yes	no	yes	yes	yes	yes	Rathbun, 1979, 1978; FitzGibbon, 1997

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750 **Table 4.** Care system identified in literature for Macroscelidea.
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Species	Direct maternal care	Direct paternal care	Indirect paternal care	References
<i>Elephantulus intufi</i>	yes	no	yes	Rathbun & Rathbun, 2006
<i>Elephantulus myurus</i>	-	no	yes	Perrin & Ribble, 2005 Rathbun, 1979
<i>Elephantulus rufescens</i>	yes	no	yes	
<i>Macroscelides flavicaudatus</i>	yes	-	-	Sauer, 1973
<i>Rhynchocyon chrysopygus</i>	yes	no	yes	Rathbun, 1979 ; FitzGibbon, 1997
<i>Rhynchocyon petersi</i>	-	no	yes	Baker et al., 2005

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754 **Table 5.** Social organization of Macroscelidea reported in primary literature and compared to
 755 three published databases (Lukas and Clutton-Brock 2013, the book Mammals of the World by
 756 Nowak and Wilson, 1999, and the Handbook Mammals of the World by Heritage 2018). Note
 757 that Lukas and Clutton-Brock as well as Handbook Mammals of the World only report the most
 758 frequently observed form of social organization and did not consider IVSO. WMW=Walker's
 759 Mammals of the World; HMW=Handbook of the Mammals of the World.

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	Our study	Our study (main social organization)	Lukas and Clutton-Brock 2013	WMW 1999	HMW 2018
Number of species with information on social organization	8	8	15	8	10
Number of species showing IVSO	7 (87.5%)	1 (12.5%)	0	5 (62.5%)	0
Number of exclusively solitary species	1 (12.5%)	1 (12.5%)	1 (6.66%)	1 (12.5%)	0
Number of exclusively pair-living species	0	6 (75%)	14 (93.33%)	2 (25%)	10 (100%)
Number of exclusively group-living species	0	0	0	0	0

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771 **Supporting Information**

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773 **Supporting Information 1.** Table of social organization of Macroscelidea used for the
774 Bayesian analysis.

775 **Supporting Information 2.** Population density for Macroscelidea species.

776 **Supporting Information 3.** Body mass for Macroscelidea species.

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778 **Supporting Information 4.** The different forms of social organization identified in our primary
779 literature research, compared to the social organization provided by Lukas and Clutton-Brock
780 (2013), Mammals of the world and the Handbook Mammals of the World.

781 **Supporting Information 5.** Outputs of the phylogenetic mixed effects model when including
782 variable social organization as an outcome category.

783 **Supporting Information 6.** Outputs of the phylogenetic mixed effects model when including
784 each social organization as an outcome category.

785 **Supporting Information 7.** Outputs of the phylogenetic mixed effects model when using only
786 the main social organization as outcome categories.

787 **Supporting Information 8.** Table of the percentages representing the probability that the
788 difference between the estimated probabilities of different social organizations compared to
789 pair-living was greater than 0 in model 1.

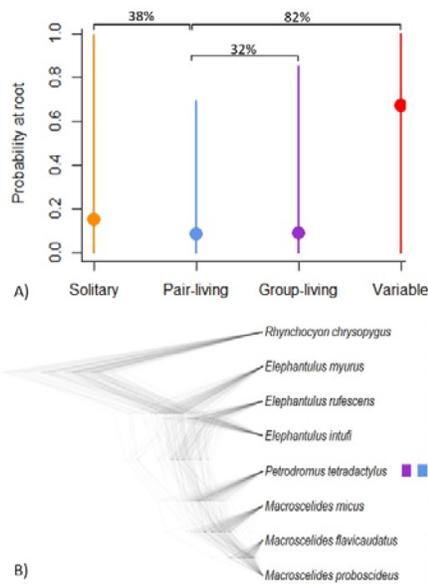
790 **Supporting Information 9.** Table of the percentages representing the probability that the
791 difference between the estimated probabilities of different social organizations compared to
792 pair-living was greater than 0 in model 2.

793 **Supporting Information 10.** Table of the percentages representing the probability that the
794 difference between the estimated probabilities of different social organizations compared to
795 pair-living was greater than 0 in model 3.

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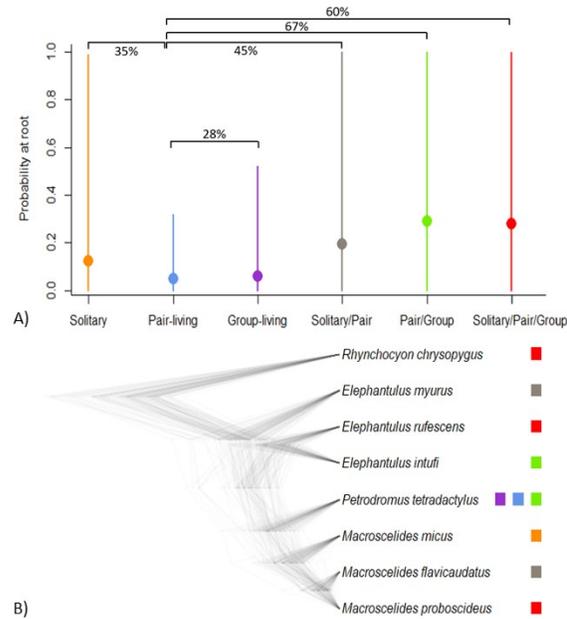
798 **Figure Legends**



799

800 **Fig. 1.** (A) The likelihood of each social organization (solitary, pair-living, group-living and
 801 variable) being the ancestral state (“probability at root”). Percentages represent the probability
 802 that the difference between the estimated probabilities of different social organizations
 803 compared to pair-living was greater than 0 (e.g. variable is 82% more likely than pair-living).
 804 (B) Phylogeny of the eight Macroscelidea species with data on social organization from 12
 805 populations. Colored boxes at the tip of phylogenetic tree correspond to social organization(s)
 806 observed within species (orange = solitary; blue = pair-living; violet = group-living and red =
 807 variable), and if two populations of the same species had different social organization, then two
 808 boxes are shown.

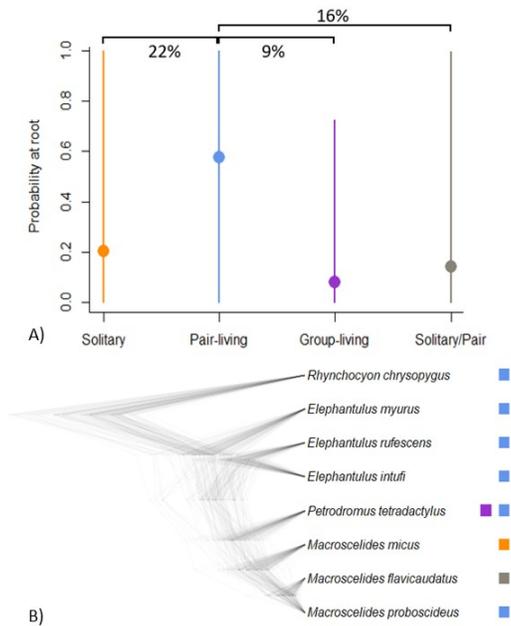
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811 **Fig. 2.** (A) The likelihood of each social organization (solitary, pair-living, group-living,
 812 solitary+pair-living, pair+group-living and solitary+pair-living+group-living) being the
 813 ancestral state (“probability at root”). Percentages represent the probability that the difference
 814 between the estimated probabilities of different social organizations compared to pair-living
 815 was greater than 0. (B) Phylogeny of the eight Macroscelidea species with data on social
 816 organization from 12 populations. Colored boxes at the tip of phylogenetic tree correspond to
 817 social organization(s) observed within species (orange = solitary; blue = pair-living; violet =
 818 group-living; grey = solitary+pair-living; green = pair+group-living; red = solitary+pair-
 819 living+group-living), and if two populations of the same species had different social
 820 organization, then two boxes are shown.

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823 **Fig. 3.** (A) The likelihood of each main form of social organization (solitary, pair-living, group-
 824 living, and solitary with pair-living) being the ancestral state (“probability at root”), ignoring
 825 the observed variation. Percentages represent the probability that the difference between the
 826 estimated probabilities of different social organizations compared to pair-living was greater
 827 than 0. (B) Phylogeny of the eight Macroscelidea species with data on social organization for
 828 12 populations. Colored boxes at the tip of phylogenetic tree correspond to social
 829 organization(s) observed within species (orange = solitary; blue = pair-living; violet = group-
 830 living; grey = solitary and pair-living), and if two populations of the same species had different
 831 social organization, then two boxes are shown.