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# The evolution of sociality in termites from cockroaches: A taxonomic and phylogenetic perspective

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1 ***Running title***

2 SYSTEMATICS AND SOCIALITY EVOLUTION

3

4 ***Title***

5 **The evolution of sociality in termites from cockroaches: a taxonomic and phylogenetic**  
6 **perspective**

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## **ABSTRACT**

Despite multiple studies and advances, sociality still puzzles evolutionary biologists in numerous ways, which might be partly addressed with the advent of sociogenomics. In insects, the majority of sociogenomic studies deal with Hymenoptera, one of the two groups that evolved eusociality with termites. But, to fully grasp the evolution of sociality, studies must obviously not restrict to eusocial lineages. Multiple kinds of social system transitions have been recorded and they all bring complementary insights. For instance, cockroaches, the closest relatives to termites, display a wide range of social interactions and evolved convergently subsocial behaviours (i.e. brood care). In this context, we emphasize the need for natural history, taxonomic and phylogenetic studies. Natural history studies provide the foundations on which building hypotheses, whereas taxonomy provides the taxa to sample to test these hypotheses, and phylogenetics brings the historical framework necessary to test evolutionary scenarios of sociality evolution.

**Keywords:** fieldwork, life history traits, natural history, phylogeny, social categories, sociality evolution, systematics, taxonomy

## **RESEARCH HIGHLIGHTS**

Sociogenomics must diversify its targeted taxa and extends to non-eusocial organisms. Taxa can only be targeted when known, but many lineages lack natural history data or are just unknown, especially in non-charismatic organisms like cockroaches.

## **GRAPHICAL ABSTRACT**

Multiple subsocial and wood-eating cockroach lineages placed in a phylogenetic context

50

## 51 INTRODUCTION

52

53 Sociality and social groups are common terms, broadly understood, but not so easily defined  
54 (Wilson and Wilson, 2007; Bourke, 2011). One of the earliest explicit definition emphasized  
55 reciprocal stimulation among individuals of a social group (Grassé, 1952). These reciprocal  
56 stimulations encompass a wide array of behaviours, and the most integrated level of  
57 organization, as observed in termites for instance, is called eusociality. Eusociality is defined  
58 by cooperative brood care, overlapping generations within a colony of adults, and division of  
59 labour (Wilson and Hölldobler, 2005). This social system, arguably the most spectacular, is  
60 widely investigated from its multiple origins within the tree of life (reviewed in Bourke,  
61 2011) and the mechanisms related to its evolution (e.g., Wilson and Hölldobler, 2005; Nowak  
62 et al., 2010; Nonacs, 2011; Rousset and Lion, 2011; Johnstone et al., 2012) to the factors  
63 behind the diversification of eusocial groups (e.g., Farrell et al., 2001; Moreau et al., 2006;  
64 Cardinal and Danforth, 2013) or the role of eusociality as a driver of diversification (Davis et  
65 al., 2009; Ware et al., 2010; Legendre and Condamine, 2018).

66

67 Despite multiple studies and advances, sociality still puzzles evolutionary biologists in  
68 numerous ways, which might be partly addressed with the advent of sociogenomics  
69 (Robinson, 1999). The term sociogenomics illustrate how genomics has entered the field of  
70 social behaviour evolution through recent advances in molecular biology. Studies focusing on  
71 the molecular basis of sociality flourish and aim at providing insights into its evolution  
72 (Robinson et al., 2005; Sumner, 2006). Important advances have been already made,  
73 especially in Hymenoptera (e.g., Weinstock et al., 2006; Bonasio et al., 2010; Toth et al.,  
74 2010), and these advances highlight the role of changes in gene family sizes (Woodard et al.,  
75 2011; Simola et al., 2013) as well as the importance of changes in gene regulation (Kapheim  
76 et al., 2015).

77

78 The evolution of eusociality in Isoptera (termites), which occurred convergently with and  
79 before eusociality in Hymenoptera (Moreau et al., 2006; Howard and Thorne, 2011; Legendre  
80 et al., 2015a), has started to be investigated as well with genomic tools (e.g., Terrapon et al.,  
81 2014; Korb et al., 2015; Harrison et al., 2018). Diversifying the taxonomic groups studied in  
82 sociogenomics provides decisive information on the evolution of eusociality and on  
83 convergence evolution, one of the rare potentially predictable patterns in nature over

84 macroevolutionary time because it involves repeatability (Mahler et al., 2013). It opens  
85 avenues for our understanding of the evolution of eusociality, including in diploid organisms,  
86 and has already revealed different specific solutions between Hymenoptera and termites  
87 (Harrison et al., 2018).

88

89 To fully grasp the evolution of sociality, studies must obviously not restrict to eusocial  
90 lineages. Multiple kinds of social system transitions have been recorded and they all bring  
91 complementary insights, necessary to get as comprehensive as possible a picture of the  
92 molecular basis of social behaviours (Rehan and Toth, 2015). In addition to taxonomic  
93 diversity, social group diversity must also be investigated. This necessity has been early  
94 recognized and partly explains why so many studies focused in Hymenoptera, a group  
95 wherein solitary, subsocial and eusocial lineages evolved multiple times (Wilson, 1971). It is  
96 pivotal to continue in this direction taking into account as much social diversity as possible.  
97 But, because of a lack of natural history studies, this social diversity is not so well-known in  
98 less charismatic organisms such as cockroaches.

99

100 In this context, we provide here a taxonomic and phylogenetic perspective on sociality  
101 evolution in termites and the closely related cockroaches. We aim at emphasizing the role of  
102 natural history and systematics in the quest to decipher the molecular basis of social  
103 behaviours. We first restate a few theories about sociality evolution because theories provide  
104 the background for hypotheses, which in turn point to the taxa to sample preferentially to  
105 robustly test these hypotheses. Then, we recall that social behaviour diversity extends way  
106 beyond a few social categories. This very diversity represents what really occur in nature and  
107 it can only be recorded through detailed natural history observations. In the last section, we  
108 put our remarks in a phylogenetic context and suggest a few taxa to consider in the future,  
109 which can be seen, hopefully, as so many guidelines for sociogenomics projects.

110

111 ***The theories behind the evolution of sociality and their links with what we observe in***  
112 ***nature***

113 Several theories have been postulated to explain the origin of sociality, and more specifically  
114 the origin of eusociality in Hymenoptera, from the inclusive-fitness to group-selection  
115 hypotheses (e.g., Hamilton, 1964; Trivers, 1971; Lin and Michener, 1972; Axelrod and  
116 Hamilton, 1981; Slobodchikoff, 1984; Myles, 1988; Wilson and Sober, 1989; Griffin and  
117 West, 2002; Okasha, 2003, 2006; Korb and Heinze, 2004; Lehmann and Keller, 2006; Garcia

118 and De Monte, 2013). In termites, diploid organisms for which the inclusive fitness  
119 hypothesis is not as convincing as for haplo-diploid Hymenoptera, additional theories have  
120 been proposed (Bartz, 1979; Lacy, 1980; Nalepa, 1984, 1994; Myles and Nutting, 1988;  
121 Roisin, 1994, 1999; Thorne and Traniello, 2003; Korb, 2009; Korb et al., 2012; Bourguignon  
122 et al., 2016). While most theories underline properties that all social organisms share (e.g., the  
123 need for communication among individuals), others stress their own lineage-specific  
124 peculiarities (e.g., wood-dependence in the symbiont transfer hypothesis or genomic events in  
125 the chromosome-linkage hypothesis for termites; Thorne, 1997).

126

127 These theories determine the hypotheses to test – and the species to use to conduct these tests,  
128 when looking for molecular signatures of sociality evolution. Genomic insights linked to  
129 properties shared between multiple hypotheses have been first targeted because they most  
130 likely have a general explanatory power. Accordingly, Harrison et al. (2018) focused on  
131 chemical communication and gene regulation along the evolution of castes, two features of  
132 eusocial evolution but neither theory- nor termites-specific. To fully grasp how sociality has  
133 evolved, these general insights must be complemented with knowledge that is more specific.  
134 To gain this knowledge, however, and assess the relative importance of various hypotheses,  
135 we first need to clearly define these hypotheses and specifically target species in consequence.

136

137 For some termite-specific hypotheses on the evolution of sociality, taxa can be quite  
138 straightforwardly identified. For instance, several theories (reviewed in Thorne, 1997) have  
139 pointed out that the evolution of eusociality in termites would be linked to the need for  
140 transmitting intestinal symbionts in relation to wood consumption, which would be better  
141 ensured with long brood care. Nevertheless, a short brood care might evolve in subsocial  
142 wood-eating species (Pellens et al., 2007a), suggesting that how life traits associated to wood  
143 consumption actually constrains social evolution remains to be better assessed. Still, wood-  
144 eating and wood-living species would be logical first picks. In another example, Roisin  
145 (1994) suggested a theory underlining the role of intragroup conflicts, so that species with  
146 different levels of aggressive behaviour could be targeted. But some theories might be more  
147 complicated to test because of a lack of species compatible with them. Thus, a hypothesis  
148 postulated that winged-wingless diphenism evolved before eusociality in termites  
149 (Bourguignon et al., 2016) but no such taxon exist in termites and cockroaches. One can still  
150 envision that species with a (sexual) dimorphism in winged length could bring important

151 insights in line with this theory. But, as stimulating as this theory is, there is no getting away  
152 from the facts, and these facts rely on what is observed in nature.

153

#### 154 **Beyond social (and other) categories**

155 There is no doubt that the evolution of eusociality in termites occurred through the subsocial  
156 route (Kennedy, 1966; Nalepa, 1994; Roisin, 1994; Pellens et al., 2007a) as opposed to the  
157 semisocial route (Thorne, 1997), though both routes can be reconciled in a general  
158 evolutionary perspective (Grandcolas, 1997a). The terms subsocial and semisocial refer to  
159 social categories, wherein brood care is carried out by the parents or a group of adults,  
160 respectively. These categories were delimited to clarify the situation among the wealth of  
161 social behaviours observed in nature. Several authors have contributed to this categorization  
162 process (e.g., Wheeler, 1923; Batra, 1966) and, today, the categories as defined by Michener  
163 (1969) and popularized by Wilson (1971) are widely used, even though new propositions  
164 have been formulated (e.g., Korb and Heinze, 2008).

165

166 Although necessary to ease communication, social categories as proposed by the authors  
167 suffer from two major limitations. First, these categories are either too broad or too  
168 constraining to accurately reflect the behavioural interactions observed in nature (Shellman-  
169 Reeve, 1997; Wcislo, 1997a,b; Lacey and Sherman, 2005; Doody et al., 2013; Legendre et al.,  
170 2014, 2015b). This drawback of the categorization process has also been underlined in other  
171 typologies (e.g., Bosch and De la Riva, 2004; Robillard et al., 2006; Grandcolas et al., 2011;  
172 Goutte et al., 2016, 2018). Second, social classification has been delimited following a “top-  
173 down development” (Costa and Fitzgerald, 1996), wherein the supposedly most complex  
174 category is defined first (i.e. eusociality with ‘cooperative brood care’, ‘reproductive castes’  
175 and ‘overlap between generations’). Other categories are subsequently defined after  
176 successive removal of distinctive features (e.g. semisociality with ‘cooperative brood care’  
177 and ‘reproductive castes’ but no ‘overlap between generations’). Beyond the conceptual issue  
178 it triggers – because categories should not be defined on the absence of a quality (Mahner and  
179 Bunge, 1997) – it also inherently imply an unnecessary gradistic view of social evolution,  
180 narrowing our understanding (Gadagkar, 1994; Kukuk, 1994; Crespi and Yanega, 1995;  
181 Sherman et al., 1995).

182

183 In the study of sociality evolution in termites, the categorization process and its drawbacks  
184 apply in diverse ways. To understand the first step of this evolution, cockroach relatives, be

185 they subsocial, gregarious or solitary, must be studied. However, these terms are too  
186 restrictive to accurately reflect the rich behavioural interactions and the variety in group  
187 composition observed in cockroach species (e.g., van Baaren et al., 2002, 2003; Legendre et  
188 al., 2008a, 2014). In the same line of reasoning, two different worker castes have been early  
189 distinguished in termites (i.e. pseudergates and ‘true’ workers – Noirot and Pasteels, 1987)  
190 and inconclusive or contradicting hypotheses have been formulated to suggest which caste  
191 evolved first (pseudergates: Noirot, 1985; Inward et al., 2007; vs ‘true’ workers: Watson and  
192 Sewell, 1985; Thompson et al., 2000, 2004 but see Grandcolas and D’Haese, 2002, 2004;  
193 Legendre et al., 2013; vs inconclusive: Legendre et al., 2008b). These two castes, however,  
194 are inadequate to describe the different phenotypes observed in nature, as some phenotypes do  
195 not fit with either definition (Bourguignon et al., 2009, 2012; Legendre et al., 2013). Finally,  
196 feeding habits have been investigated and categorized in termites. This has consequences on  
197 sociality evolution because of, for instance, the role of wood-eating in the symbiont transfer  
198 hypothesis (Lin and Michener, 1972; Nalepa, 1984, 1994). Thus, Mastotermitidae, the first  
199 diverging lineage within termites (Inward et al., 2007a; Legendre et al., 2008b, 2015a), has  
200 been grouped with other lower termites (group I dead wood and grass-feeders of Donovan et  
201 al., 2001). Yet, *Mastotermes darwiniensis* Froggatt, 1897 is not strictly speaking a wood-  
202 eating species such as dampwood or drywood termites as it may also feed on litter (Donovan  
203 et al., 2001). In other words, different regime diets and gut anatomy may hide behind this  
204 ‘group I’ category, preventing fine-scale analyses of the role of feeding habits in sociality  
205 evolution in termites.

206

207 ***Taxonomy and natural history data: so many unanswered questions and gaps to fill***

208 The limitations of broad categories, and the connected progresses it hampered, have been  
209 progressively revealed through the observation of large sample of organisms. Indeed, with  
210 observations encompassing a larger taxonomic coverage comes a higher chance to identify  
211 organisms that fall out of the previously defined categories, thus betraying classification  
212 defects. But, unfortunately, these observations, sometimes called ‘natural history’  
213 observations, remain scarce and our ignorance in the ecology or behaviour of numerous taxa  
214 is colossal (Greene, 2005). This unfortunate situation must be advertised to be comprehended  
215 and resolved (e.g., Greene, 2005; Page, 2005; Tewksbury et al., 2014; Able, 2016; King and  
216 Achiam, 2017), which would speed up progresses in all biological disciplines, including  
217 sociogenomics, as they all somehow rely on natural history and taxonomy (May, 1990;  
218 Grandcolas, 2017; Troudet et al., 2017).

219

220 This situation is even more worrying that we face a massive biodiversity loss affecting all  
221 organisms (Dirzo and Raven, 2003; Ceballos et al., 2015), some of them going extinct before  
222 any formal description. The species-rich and understudied Insecta class is most likely the  
223 most impacted but even for birds, arguably the best-known taxonomic class (Troutet et al.,  
224 2017), natural history data are missing for the majority of species (Xiao et al., 2017). The  
225 situation is undoubtedly worse for less emblematic organisms, such as cockroaches and  
226 termites whose majority of species are still unknown (Grandcolas, 1994a,b; Legendre and  
227 Grandcolas, in press). Yet, natural history observations provide both the facts upon which  
228 building hypotheses and the taxa upon which testing these hypotheses.

229

230 A few population or habitat studies on cockroaches have been conducted in the field (e.g.,  
231 Shelford, 1906; Roth and Willis, 1960; Gautier, 1974; Nalepa, 1984; Schal et al., 1984;  
232 Grandcolas, 1991, 1992, 1993a, 1994a, 1995a, 1997b,c, 1998; Park et al., 2002; Pellens and  
233 Grandcolas, 2003; Pellens et al., 2007b). These studies have brought important insights on our  
234 understanding of cockroach evolution, and more specifically social evolution. For instance,  
235 different subsocial lineages have been identified (Fig. 1), such as the Thoracini and  
236 Notolamprini tribes (Shelford, 1906), the genus *Cryptocercus* Scudder, 1862 (Cleveland,  
237 1934; Nalepa, 1984; Park et al., 2002) or the species *Parasphaeria boeiriana* Grandcolas and  
238 Pellens, 2002 (Pellens et al., 2002), lineages wherein at least one parent offers protection or  
239 food to its newborns. Other lineages have been first suspected from natural history collection  
240 such as in the genus *Perisphaerus* Serville, 1831, where young nymphs would obtain  
241 nourishment from their mother (Roth, 1981). In addition, numerous Blaberidae species have  
242 been observed in a close relationship between females and their newly hatched offspring  
243 (Roth, 1981; Grandcolas, 1993a; Pellens and Grandcolas, 2003; Perry and Nalepa, 2003).  
244 Hence, subsocial behaviour is not rare in cockroaches and all the aforementioned lineages  
245 might contain important species to target to better understand the molecular basis of eusocial  
246 evolution in termites through the subsocial route. Comparative analyses of genomic data of  
247 these different lineages would allow disentangling the genetic basis of various features related  
248 to subsociality in itself or largely shared among cockroaches (e.g. physical protection) from  
249 those putatively more specifically involved in the first steps of eusocial evolution in termites  
250 (e.g. nourishment).

251

252 Other studies have provided information on cockroach diets, and notably on wood-feeding.  
253 Apart from the genera *Parasphaeria* Brunner von Wattenwyl, 1865 and *Cryptocercus*  
254 Scudder, 1862 already mentioned (Grandcolas, 1995b), the genus *Lauraesilpha* Grandcolas,  
255 1997 has been shown to be closely associated to wood, as well as its sister genus *Tryonicus*  
256 Shaw, 1925 – although to a lesser extent (Grandcolas, 1997b). Interestingly, ciliates have  
257 been found in the digestive tracts of all specimens of *Lauraesilpha* spp. studied, which are  
258 solitary (Grandcolas et al., 2008). In Blaberidae, Panesthiinae cockroaches include numerous  
259 species living in and feeding on wood in Australasia (Roth, 1977), and the Perisphaerinae  
260 genera *Compsagis* Chopard, 1952 and *Cyrtotria* Stål, 1871 (Grandcolas, 1997d) comprise  
261 species living in wood. In addition, in Ectobiidae, the Nyctiborinae species *Paramuzoa alsopi*  
262 Grandcolas, 1993 feeds on wood (Grandcolas, 1993b). These studies show a combination of  
263 social behaviour, wood and symbiont associations. This suggest that wood-eating/wood-living  
264 is not necessarily associated to a subsocial behaviour (and vice versa) and that is has evolved  
265 convergently in cockroaches (at least in three families).

266

### 267 ***Phylogenetic perspective in cockroaches and termites***

268 These examples illustrate the need for natural history data and taxonomic works because they  
269 enable us to generate hypotheses and refine them (Greene, 2005; Willson and Armesto, 2006;  
270 Agrawal, 2017). To be optimally tested, these hypotheses must be then integrated in a clear  
271 phylogenetic context (Rehan and Toth, 2015). Phylogenetic trees allow taking into account  
272 the phylogenetic history of the species compared, their phylogenetic relatedness and  
273 distinguishing plesiomorphic, apomorphic and convergent conditions. They also bring the  
274 framework to compute statistically robust results (Felsenstein, 1985) and provide natural  
275 replicates (i.e. convergences), which is the only way to reach generalization about biological  
276 processes.

277

278 We provide here this phylogenetic context from the latest study with the largest taxonomic  
279 sampling in Dictyoptera (Fig. 2; Legendre et al., 2015a). We underline the different lineages  
280 discussed in this paper with regard to subsociality and wood-eating. This phylogenetic context  
281 allows identifying the species most closely related to termites and the number of convergent  
282 origins of subsociality and wood-eating. It must be recalled, however, that i) numerous taxa  
283 have not been included in this phylogenetic study, ii) numerous described species are devoid  
284 of any natural history data and iii) most species have not been described yet.

285

286 Because of both its phylogenetic position (Inward et al., 2007b; Legendre et al., 2015a) and  
287 its life history traits (Nalepa, 1984, 1988), the genus *Cryptocercus* Scudder, 1862 is a priority  
288 target. But other subsocial and wood-eating species must be studied to disentangle attributes  
289 shared among these species from those specific to *Cryptocercus*. The aforementioned  
290 taxonomic groups, viz. Notolamprini, Thoracini, *Perisphaerus* (subsocial), Panesthiinae,  
291 *Lauraesilpha* Grandcolas, 1997, *Cyrtotria* Stål, 1871, *Paramuzoa* Roth, 1973, *Compsagis*  
292 Chopard, 1952 (wood-eating) and *Parasphaeria* Brunner von Wattenwyl, 1865 (wood-eating  
293 and subsocial), would undoubtedly bring important insights in the molecular basis of sociality  
294 evolution when investigated in a sociogenomics context.

295

296 In addition to the lineages previously discussed, the Lamproblattinae subfamily deserves to be  
297 mentioned due to its alleged phylogenetic position as sister-group to (*Cryptocercus* +  
298 termites) (Legendre et al., 2015a). This phylogenetic position is controversial (Djernaes et al.,  
299 2012, 2015) and not strongly supported (Legendre et al., 2015a), even if McKittrick (1964)  
300 early suggested a close affinity between *Cryptocercus* Scudder, 1862 and *Lamproblatta*  
301 Hebard, 1919 from morphological observations, a view supported more recently after the  
302 description of the genus *Eurycanthablatta* Fritzsche and Zompro, 2008 (Fritzsche et al.,  
303 2008).

304

305 Unfortunately, natural history data on the three Lamproblattinae genera (i.e. *Lamproblatta*  
306 Hebard, 1919, *Eurycanthablatta* Fritzsche and Zompro, 2008 and *Lamproglanidifera* Roth,  
307 2003) are scarce (Gautier and Deleporte, 1986; Grandcolas, 1994a; Grandcolas and Pellens,  
308 2012). *Lamproblatta* Hebard, 1919 is a genus composed of eight solitary species that refuge  
309 in dead trunks or litter accumulations and forage in ground litter, whereas individuals of  
310 *Eurycanthablatta pugionata* Fritzsche and Zompro, 2008 seem to live in the ground  
311 (Fritzsche et al., 2008). We are unaware of behaviours or dietary regimes that would call for  
312 investigating this subfamily in priority to better understand the molecular basis of eusocial  
313 evolution in termites, but its alleged phylogenetic position shows it should not be neglected  
314 either.

315

316 Finally, lineages poorly known or rarely sampled should be specifically targeted in future  
317 works. One of them, the superfamily Corydioidea is often undersampled in phylogenetic  
318 analyses and its constituting species are very little known. Individuals of *Ergaula capensis*  
319 (Saussure, 1893), for instance, live in treeholes but their social interactions are not known

320 (Grandcolas, 1997c); are they gregarious like *Gyna* spp. that are found in similar habitats? It  
321 is impossible to say for now and it is yet one of the better-known Corydiidae. The superfamily  
322 comprises ca. 250 extant species (Beccaloni and Eggleton, 2013) with a worldwide  
323 distribution, which is not insignificant in cockroach history. Such gaps are troublesome and  
324 should be filled to get a comprehensive picture of cockroach evolution, which thus requires  
325 natural history and taxonomic studies (Greene, 2005).

326

327

327

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## FIGURE LEGENDS



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Fig. 1. Eight cockroach genera relevant for the investigation of the molecular basis of sociality in cockroaches and termites. A. *Lauraesilpha mearetoi* Grandcolas, 1997 excavated from its log in New Caledonia, B. Female of *Thanatophyllum akinetum* Grandcolas, 1991, solitary species, with its newborns, C. *Notolampra punctata* (Saussure, 1873) foraging on leaves at night in Mitaraka (French Guiana), D. *Cryptocercus punctulatus* Scudder, 1862 excavated from its log in Virginia (USA), E. *Perisphaerus* sp. observed on a trunk at night in Indonesia, F. *Parasphaeria boleiriana* Grandcolas and Pellens, 2002 excavated in Brazil, G. Gregarious nymphs of *Lanxoblatta emarginata* (Burmeister, 1838) found under bark, H. Xylophagous *Paramuzoa* sp. observed in Brazil (credits: A,F-H. Grandcolas P.; B-C. Hugel S.; D-E. Legendre F.)



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727 Fig. 2. Phylogenetic tree derived from the study in Legendre et al. (2015a) with subsocial and  
 728 wood-eating lineages cited in the text highlighted. Obviously, only lineages sampled in this  
 729 phylogeny are highlighted, meaning that other lineages have evolved wood-eating or  
 730 subsociality. Stripes for the Panesthiinae indicates that some lineages are not sufficiently  
 731 studied to ascertain they are subsocial (credits: F. Legendre).

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