



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

Frédéric Legendre, Philippe Grandcolas

► To cite this version:

Frédéric Legendre, Philippe Grandcolas. The evolution of sociality in termites from cockroaches: A taxonomic and phylogenetic perspective. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 2018, 330 (5), pp.279-287. 10.1002/jez.b.22812 . mnhn-02520946

HAL Id: mnhn-02520946

<https://mnhn.hal.science/mnhn-02520946>

Submitted on 1 Apr 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Running title

SYSTEMATICS AND SOCIALITY EVOLUTION

Title

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

Authors' names

FRÉDÉRIC LEGENDRE* AND PHILIPPE GRANDCOLAS

Authors' affiliations

Institut Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, 57 rue Cuvier, CP50, 75005 Paris, France

**Correspondence to: Institut Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, CP50, 57 rue Cuvier, 75231 Paris Cedex 05, France; Tel: +33 1 40 79 81 26 ; E-mail: frederic.legendre@mnhn.fr*

Figures: 2

Tables: 0

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

INTRODUCTION

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

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

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

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

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, necessary to get as comprehensive as possible a picture of the molecular basis of social behaviours (Rehan and Toth, 2015). In addition to taxonomic diversity, social group diversity must also be investigated. This necessity has been early recognized and partly explains why so many studies focused in Hymenoptera, a group wherein solitary, subsocial and eusocial lineages evolved multiple times (Wilson, 1971). It is pivotal to continue in this direction taking into account as much social diversity as possible. But, because of a lack of natural history studies, this social diversity is not so well-known in less charismatic organisms such as cockroaches.

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

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

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

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

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

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

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

Beyond social (and other) categories

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

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

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

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

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

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

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

Phylogenetic perspective in cockroaches and termites

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

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

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

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

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

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

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

327

328 **ACKNOWLEDGMENTS**

329 We are grateful to Erich Bornberg-Bauer for soliciting this contribution. We warmly thank all
330 the scientific programs and institutions that funded the different natural history observations
331 that we have been able to conduct. We thank Sylvain Hugel for sharing some of his photos.

332 The authors declare no conflict of interest.

333

334

LITERATURE CITED

- Able KW. 2016. Natural history: an approach whose time has come, passed, and needs to be resurrected. *ICES J Mar Sci* 73:2150–2155.
- Agrawal AA. 2017. Toward a Predictive Framework for Convergent Evolution: Integrating Natural History, Genetic Mechanisms, and Consequences for the Diversity of Life. *Am Nat* 190:S1–S12.
- Axelrod R, Hamilton WD. 1981. The evolution of cooperation. *Science* 211:1390–6.
- Bartz SH. 1979. Evolution of eusociality in termites. *Proc Natl Acad Sci* 76:5764–5768.
- Batra SWT. 1966. Nests and social behavior of halictine bees of India (Hymenoptera: Halictidae). *Indian J Entomol* 28:375–393.
- Beccaloni GW, Eggleton P. 2013. Order Blattodea. *Zootaxa* 3703:46–48.
- Bonasio R, Zhang G, Ye C, Mutti NS, Fang X, Qin N, Donahue G, Yang P, Li Q, Li C, Zhang P, Huang Z, Berger SL, Reinberg D, Wang J, Liebig J. 2010. Genomic Comparison of the Ants *Camponotus floridanus* and *Harpegnathos saltator*. *Science* 329:1068–1071.
- Bosch J, De la Riva I. 2004. Are frog calls modulated by the environment? An analysis with anuran species from Bolivia. *Can J Zool* 82:880–888.
- Bourguignon T, Sobotnik J, Hanus R, Roisin Y. 2009. Developmental pathways of *Glossotermes oculatus* (Isoptera, Serritermitidae): at the cross-roads of worker caste evolution in termites. *Evol Dev* 11:659–668.
- Bourguignon T, Šobotník J, Sillam-Dussès D, Jiroš P, Hanus R, Roisin Y, Miura T. 2012. Developmental pathways of *Psammotermes hybostoma* (Isoptera: Rhinotermitidae): old pseudergates make up a new sterile caste. *PLoS One* 7:e44527.
- Bourguignon T, Chisholm RA, Evans TA. 2016. The Termite Worker Phenotype Evolved as a Dispersal Strategy for Fertile Wingless Individuals before Eusociality. *Am Nat* 187:372–387.
- Bourke A. 2011. Principles of social evolution. Oxford University Press, Oxford.
- Cardinal S, Danforth B. 2013. Bees diversified in the age of eudicots. *Proc R Soc B* 280:20122686.
- Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015. Accelerated modern human – induced species losses: entering the sixth mass extinction. *Sci Adv* 1:1–5.

368 Cleveland LR. 1934. The wood-feeding roach *Cryptocercus*, its protozoa, and the symbiosis
 369 between protozoa and roach. Mem Amer Acad Arts Sci, Menasha 17:185–342.
 370 Costa JT, Fitzgerald TD. 1996. Developments in social terminology: semantic battles in a
 371 conceptual war. Trends Ecol Evol 11:285–289.
 372 Crespi BJ, Yanega D. 1995. The definition of eusociality. Behav Ecol 6:109–115.
 373 Davis RB, Baldauf SL, Mayhew PJ. 2009. Eusociality and the success of the termites: insights
 374 from a supertree of dictyopteran families. J Evol Biol 22:1750–1761.
 375 Dirzo R, Raven PH. 2003. Global state of biodiversity and loss. Annu Rev Environ Resour
 376 28:137–67.
 377 Djernæs M, Klass K-D, Picker MD, Damgaard J. 2012. Phylogeny of cockroaches (Insecta,
 378 Dictyoptera, Blattodea), with placement of aberrant taxa and exploration of out-group
 379 sampling. Syst Entomol 37:65–83.
 380 Djernæs M, Klass K-D, Eggleton P. 2015. Identifying possible sister groups of
 381 Cryptocercidae+Isoptera: A combined molecular and morphological phylogeny of
 382 Dictyoptera. Mol Phylogenet Evol 84:284–303.
 383 Donovan SE, Eggleton P, Bignell DE. 2001. Gut content analysis and a new feeding group
 384 classification of termites. Ecol Entomol 26:356–366.
 385 Doody JS, Burghardt GM, Dinets V. 2013. Breaking the Social-Non-social Dichotomy: A
 386 Role for Reptiles in Vertebrate Social Behavior Research? Ethology 119:95–103.
 387 Farrell BD, Sequeira AS, O’Meara BC, Normark BB, Chung JH, Jordal BH. 2001. The
 388 evolution of agriculture in beetles (Curculionidae: Scolytinae and Platypodinae).
 389 Evolution 55:2011–27.
 390 Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat 125:1–15.
 391 Fritzsche I, Zompro O, Adis J. 2008. A remarkable “ancient” cockroach from Brazil (Insecta:
 392 Oothecariformia: Blattodea: Blattidae: Cryptocercinae). Arthropoda 16:34–37.
 393 Gadagkar R. 1994. Why the definition of eusociality is not helpful to understand its evolution
 394 and what should we do about it. Oikos 70:485–488.
 395 Garcia T, De Monte S. 2013. Group formation and the evolution of sociality. Evolution
 396 67:131–141.
 397 Gautier JY, 1974. Etude comparée de la distribution spatiale et temporelle des adultes de
 398 *Blaberus atropos* et *B. colosseus* (Dictyoptères) dans cinq grottes de l’île de trinidad.
 399 Rev Comportement Animal 9:237-258.

400 Gautier JY, Deleporte P. 1986. Behavioural ecology of a forest living cockroach,
 401 *Lamproblatta albipalpus* in French Guyana. In: Drickamer LC, editor. Behavioral
 402 ecology and population ecology. Toulouse: Privat, I.E.C. p 17–22.

403 Goutte S, Dubois A, Howard SD, Marquez R, Rowley JJJ, Dehling JM, Grandcolas P, Xiong
 404 R, Legendre F. 2016. Environmental constraints and call evolution in torrent dwelling
 405 frogs. *Evolution* 70:811–826.

406 Goutte S, Dubois A, Howard SD, Márquez R, Rowley JJJ, Dehling JM, Grandcolas P, Xiong
 407 R, Legendre F. 2018. How the environment shapes animal signals: a test of the Acoustic
 408 Adaptation Hypothesis in frogs. *J Evol Biol* 31:148–158.

409 Grandcolas P. 1991. Descriptions de nouvelles Zetoborinae Guyanaïses avec quelques
 410 remarques sur la sous-famille. *Bull la Soc Entomol Fr* 95:241–246.

411 Grandcolas P. 1992. Evolution du mode de vie, répartition et nouveaux taxons dans le genre
 412 *Xestoblatta* Hebard, 1916 (Dictyoptera, Blattellidae, Blattellinae). *Rev Française*
 413 *d'Entomologie* 14:155–168.

414 Grandcolas P. 1993a. Habitats of solitary and gregarious species in the Neotropical
 415 Zetoborinae (Insecta, Blattaria). *Stud Neotrop Fauna Environ* 28:179–190.

416 Grandcolas P. 1993b. Le genre *Paramuzoa* Roth, 1973 : sa répartition et un cas de xylophagie
 417 chez les Nyctiborinae (Dictyoptera, Blattaria). *Bull la Soc Entomol Fr* 98:131–138.

418 Grandcolas P. 1994a. Les blattes de la forêt tropicale de Guyane française : structure du
 419 peuplement (Insecta, Dictyoptera, Blattaria). *Bull la Soc Zool Fr* 119:59–67.

420 Grandcolas P. 1994b. La richesse spécifique des communautés de blattes du sous-bois en
 421 forêt tropicale de Guyane française. *Rev d'Ecologie la Terre la Vie* 49:139–150.

422 Grandcolas P. 1995a. Bionomics of a desert cockroach, *Heterogamisca chopardi* Uvarov,
 423 1936 after the spring rainfalls in Saudi Arabia (Insecta, Blattaria, Polyphaginae). *J Arid*
 424 *Environ* 31:325–334.

425 Grandcolas P. 1995b. The Appearance of Xylophagy in Cockroaches : Two Case Studies with
 426 Reference to Phylogeny. *J Orthoptera Res* 4:177–184.

427 Grandcolas P. 1997a. What did the ancestors of the woodroach *Cryptocercus* look like? A
 428 phylogenetic study of the origin of subsociality in the subfamily Polyphaginae
 429 (Dictyoptera, Blattaria). In: Grandcolas P, editor. The origin of Biodiversity in Insects:
 430 phylogenetic tests of evolutionary scenarios. Paris: Mémoires du Muséum national
 431 d'Histoire naturelle 173. p 231–252.

432 Grandcolas P. 1997b. Systématique phylogénétique de la sous-famille des Tryonicinae
 433 (Dictyoptera, Blattaria, Blattidae). In: Najt J, Matile L, editors. *Zoologica*

Neocaledonica. Vol. 4. Paris: Mémoires du Muséum national d'Histoire naturelle. p 91–124.

Grandcolas P. 1997c. Habitat use and population structure of a polyphagine cockroach, *Ergaula capensis* (Saussure 1893) (Blattaria Polyphaginae) in Gabonese rainforest. *Trop Zool* 10:215–222.

Grandcolas P. 1997d. The monophyly of the subfamily Perisphaeriinae (Dictyoptera: Blattaria: Blaberidae). *Syst Entomol* 22:123–130.

Grandcolas P. 1998. The evolutionary interplay of social behavior, resource use and anti-predator behavior in Zetoborinae + Blaberinae + Gyninae + Diplopterinae cockroaches: a phylogenetic analysis. *Cladistics* 14:117–127.

Grandcolas P. 2017. Loosing the connection between the observation and the specimen: a by-product of the digital era or a trend inherited from general biology? *Bionomina* 12 :57-62.

Grandcolas, P., D’Haese, C. A. 2002. The origin of a ‘true’ worker caste in termites: phylogenetic evidence is not decisive. *Journal of Evolutionary Biology*, 15,885–888.

Grandcolas, P., D’Haese, C. A. 2004. The origin of a “true” worker caste in termites: mapping the real world on the phylogenetic tree. *Journal of Evolutionary Biology*, 17,461–463.

Grandcolas, P., Pellens, R. 2012. Capítulo 27. Blattaria. In: J. A. Rafael, G. A. Rodrigues de Melo, C. J. Barros de Carvalho, S. A. Casari, R. Constantino (Eds.), *Insetos do Brasil. Diversidade e Taxonomia* (pp. 333-346). Holos Editora, Ribeirão Preto.

Grandcolas, P., Murienné, J., Robillard, T., Desutter-Grandcolas, L., Jourdan, H., Guilbert, E., & Deharveng, L. 2008. New Caledonia: a very old Darwinian island? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 363,3309–17.

Grandcolas P, Nattier R, Legendre F, Pellens R. 2011. Mapping extrinsic traits such as extinction risks or modelled bioclimatic niches on phylogenies: does it make sense at all? *Cladistics* 27:181–185.

Grassé PP. 1952. Le fait social : ses critères biologiques, ses limites. In: Grassé PP, editor. *Structure et physiologie des sociétés animales*. Paris: CNRS. p 7–17.

Greene HW. 2005. Organisms in nature as a central focus for biology. *Trends Ecol Evol* 20:23–27.

Griffin AS, West SA. 2002. Kin selection: fact and fiction. *Trends Ecol Evol* 17:15–21.

Hamilton WD. 1964. The genetical evolution of social behaviour. I and II. *J Theor Biol* 7:1–52.

- Harrison MC, Jongepier E, Robertson HM, Arning N, Bitard-Feildel T, Chao H, Childers CP, Dinh H, Doddapaneni H, Dugan S, Gowin J, Greiner C, Han Y, Hu H, Hughes DST, Huylmans A, Kemena C, Kremer LPM, Lee SL, Lopez-Ezquerria A, Mallet L, Monroy-Kuhn JM, Moser A, Murali SC, Muzny DM, Otani S, Piulachs M, Poelchau M, Qu J, Schaub F, Wada-Katsumata A, Worley KC, Xie Q, Ylla G, Poulsen M, Gibbs RA, Schal C, Richards S, Belles X, Korb J, Bornberg-Bauer E. 2018. Hemimetabolous genomes reveal molecular basis of termite eusociality. *Nat Ecol Evol* 2:557-566.
- Howard KJ, Thorne BL. 2011. Eusocial Evolution in Termites and Hymenoptera. In: Bignell DE, Roisin Y, Lo N, editors. *Biology of Termites: a Modern Synthesis*. Springer Netherlands. p 97–132.
- Inward D, Vogler AP, Eggleton P. 2007a. A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. *Mol Phylogenet Evol* 44:953–67.
- Inward D, Beccaloni GW, Eggleton P. 2007b. Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biol Lett* 3:331–335.
- Johnstone RA, Cant MA, Field J. 2012. Sex-biased dispersal, haplodiploidy and the evolution of helping in social insects. *Proc Biol Sci* 279:787–793.
- Kapheim KM, Pan H, Li C, Salzberg SL, Puiu D, Magoc T, Robertson HM, Hudson ME, Venkat A, Fischman BJ, Others. 2015. Genomic signatures of evolutionary transitions from solitary to group living. *Science* 348:1139–1143.
- Kennedy JS. 1966. Some outstanding questions in insect behavior. *Symp R Entomol Soc London* 3:97–112.
- King H, Achiam M. 2017. The Case for Natural History. *Sci Educ* 26:125–139.
- Korb J. 2009. Termites: an alternative road to eusociality and the importance of group benefits in social insects. In: *Organization of Insect Societies. From Genome to Socio-complexity*. Harvard University Press, Cambridge, MA. p 128–147.
- Korb J, Heinze J. 2004. Multilevel selection and social evolution of insect societies. *Naturwissenschaften* 91:291–304.
- Korb J, Heinze J. 2008. The Ecology of Social Life: A Synthesis. In: Korb J, Heinze J, editors. *Ecology of Social Evolution*. Springer-Verlag Berlin Heidelberg. p 245–259.
- Korb J, Buschmann M, Schafberg S, Liebig J, Bagnères A-G. 2012. Brood care and social evolution in termites. *Proc Biol Sci* 279:2662–71.
- Korb J, Poulsen M, Hu H, Li C, Boomsma JJ, Zhang G, Liebig J. 2015. A genomic comparison of two termites with different social complexity. *Front Genet* 6:1–12.

502 Kukuk PF. 1994. Replacing the terms “primitive” and “advanced”: new modifiers for the term
503 “eusocial”. *Anim Behav* 47:1475–1478.

504 Lacey EA, Sherman PW. 2005. Redefining eusociality: concepts, goals and levels of analysis.
505 *Ann Zool Fenn* 42:573–577.

506 Lacy RL. 1980. The evolution of eusociality in termites: a haplodiploid analogy? *Am Nat*
507 116:449–451.

508 Legendre F, Condamine FL. 2018. When Darwin’s Special Difficulty Promotes
509 Diversification in Insects. *Syst Biol*:in press.

510 Legendre F, Grandcolas P. Order Dictyoptera: Blattodea. In: *Les Insectes du monde –*
511 *classification – clés pour la reconnaissance des principales familles* (Aberlenc, H-P. and
512 Delvare, G., Eds) (in press).

513 Legendre F, Pellens R, Grandcolas P. 2008a. A comparison of behavioral interactions in
514 solitary and presocial Zetoborinae cockroaches (Blattaria, Blaberidae). *J Insect Behav*
515 21:351–365.

516 Legendre F, Whiting MF, Bordereau C, Canello EM, Evans TA, Grandcolas P. 2008b. The
517 phylogeny of termites (Dictyoptera: Isoptera) based on mitochondrial and nuclear
518 markers: Implications for the evolution of the worker and pseudergate castes, and
519 foraging behaviors. *Mol Phylogenet Evol* 48:615–627.

520 Legendre F, Whiting MF, Grandcolas P. 2013. Phylogenetic analyses of termite post-
521 embryonic sequences illuminate caste and developmental pathway evolution. *Evol Dev*
522 15:146–157.

523 Legendre F, D’Haese CA, Deleporte P, Pellens R, Whiting MF, Schliep K, Grandcolas P.
524 2014. The evolution of social behaviour in Blaberid cockroaches with diverse habitats
525 and social systems: phylogenetic analysis of behavioural sequences. *Biol J Linn Soc*
526 111:58–77.

527 Legendre F, Nel A, Svenson GJ, Robillard T, Pellens R, Grandcolas P. 2015a. Phylogeny of
528 Dictyoptera: dating the origin of cockroaches, praying mantises and termites with
529 molecular data and controlled fossil evidence. *PLoS One* 10:e0130127.

530 Legendre F, Deleporte P, Depaertere M, Gasc A, Pellens R, Grandcolas P. 2015b. Dyadic
531 behavioural interactions in cockroaches (Blaberidae): ecomorphological and
532 evolutionary implications. *Behaviour* 152:1229–1256.

533 Lehmann L, Keller L. 2006. The evolution of cooperation and altruism - a general framework
534 and a classification of models. *J Evol Biol* 19:1365–1376.

535 Lin N, Michener CD. 1972. Evolution of sociality in insects. *Quarterly Rev Biol* 47:131–159.

536 Mahler DL, Ingram T, Revell LJ, Losos JB. 2013. Exceptional convergence on the
 537 macroevolutionary landscape in island lizard radiations. *Science* 341:292–5.
 538 Mahner M, Bunge M. 1997. Foundations of biophilosophy. Springer-Verlag Berlin
 539 Heidelberg.
 540 May RM. 1990. Taxonomy as destiny. *Nature* 347:129–130.
 541 McKittrick, F.A. 1964. Evolutionary study of cockroaches. Cornell University Agricultural
 542 Experiment Station Memoir, 389,1–197.
 543 Michener CD. 1969. Comparative social behavior of bees. *Annu Rev Entomol* 14:299–342.
 544 Moreau CS, Bell CD, Vila R, Archibald SB, Pierce NE. 2006. Phylogeny of the ants:
 545 diversification in the age of angiosperms. *Science* 312:101–4.
 546 Myles TG. 1988. Resource inheritance in social evolution from termites to man. In:
 547 Slobodchikoff CN, editor. The ecology of social behavior. San Diego, California:
 548 Academic Press. p 379–423.
 549 Myles TG, Nutting WL. 1988. Termite eusocial evolution: a re-examination of Bartz’s
 550 hypothesis and assumptions. *Quarterly Rev Biol* 63:1–23.
 551 Nalepa CA. 1984. Colony composition, protozoan transfer and some life history
 552 characteristics of the woodroach *Cryptocercus punctulatus* Scudder (Dictyoptera:
 553 Cryptocercidae). *Behav Ecol Sociobiol* 14:273–279.
 554 Nalepa CA. 1988. Cost of parental care in the woodroach *Cryptocercus punctulatus* Scudder
 555 (Dictyoptera: Cryptocercidae). *Behav Ecol Sociobiol* 23:135–140.
 556 Nalepa CA. 1994. Nourishment and the origin of termite eusociality. In: Hunt JH, Nalepa CA,
 557 editors. Nourishment and evolution in insect societies. Boulder, Colorado: Westview
 558 Press. p 57–104.
 559 Noirot C. 1985. Pathways of caste development in the lower termites. In: Watson JAL, Okot-
 560 Kotber BM, Noirot C, editors. Caste differentiation in social insects. Pergamon, Oxford.
 561 p 41–57.
 562 Noirot C, Pasteels JM. 1987. Ontogenetic development and evolution of the worker caste in
 563 termites. *Experientia* 43:851–952.
 564 Nonacs P. 2011. Kinship , greenbeards , and runaway social selection in the evolution of
 565 social insect cooperation. *PNAS* 108:10808–10815.
 566 Nowak MA, Tarnita CE, Wilson EO. 2010. The evolution of eusociality. *Nature* 466:1057–
 567 1062.
 568 Okasha S. 2003. Recent work on the levels of selection problem. *Hum Nat Rev* 3:349–356.

569 Okasha S. 2006. The levels of selection debate: philosophical issues. *Philos Compass* 1:74–
570 85.

571 Page LM. 2005. Organisms in nature as a central focus for biology. *Trends Ecol Evol* 20:361–
572 362.

573 Park YC, Grandcolas P, Choe JC. 2002. Colony composition, social behavior and some
574 ecological characteristics of the Korean wood-feeding cockroach (*Cryptocercus*
575 *kyebangensis*). *Zoolog Sci* 19:1133–1139.

576 Pellens R, Grandcolas P. 2003. Living in atlantic forest fragments: life habits, behaviour, and
577 colony structure of the cockroach *Monastria biguttata* (Dictyoptera, Blaberidae,
578 Blaberinae) in Espirito Santo, Brazil. *Can J Zool* 81:1929–1937.

579 Pellens R, Grandcolas P, Silva-Neto ID. 2002. A new and independently evolved case of
580 xylophagy and the presence of intestinal flagellates in the cockroach *Parasphaeria*
581 *boleiriana* (Dictyoptera, Blaberidae, Zetoborinae) from the remnants of the Brazilian
582 Atlantic forest. *Can J Zool* 80:350–359.

583 Pellens R, D’Haese CA, Bellés X, Piulachs M-D, Legendre F, Wheeler WC, Grandcolas P.
584 2007a. The evolutionary transition from subsocial to eusocial behaviour in Dictyoptera:
585 phylogenetic evidence for modification of the “shift-in-dependent-care” hypothesis with
586 a new subsocial cockroach. *Mol Phylogenet Evol* 43:616–26.

587 Pellens R, Legendre F, Grandcolas P. 2007b. Phylogenetic analysis of social behavior
588 evolution in [Zetoborinae + Blaberinae + Gyninae + Diplopterinae] cockroaches: an
589 update with the study of endemic radiations from the Atlantic forest. *Stud Neotrop Fauna*
590 *Environ* 42:25–31.

591 Perry J, Nalepa CA. 2003. A new mode of parental care in cockroaches. *Insectes Soc* 50:245–
592 247.

593 Rehan SM, Toth AL. 2015. Climbing the social ladder: the molecular evolution of sociality.
594 *Trends Ecol Evol* 30:426–433.

595 Robillard T, Höbel G, Gerhardt HC. 2006. Evolution of advertisement signals in North
596 American hylid frogs vocalizations as end-products of calling behavior. *Cladistics*
597 22:533–545.

598 Robinson GE. 1999. Integrative animal behaviour and sociogenomics. *Trends Ecol Evol*
599 14:202–205.

600 Robinson GE, Grozinger CM, Whitfield CW. 2005. Sociogenomics: social life in molecular
601 terms. *Nat Rev Genet* 6:257–270.

602 Roisin Y. 1994. Intragroup conflicts and the evolution of sterile castes in termites. *Am Nat*
 603 143:751–765.

604 Roisin Y. 1999. Philopatric reproduction, a prime mover in the evolution of termite sociality?
 605 *Insectes Soc* 46:297–305.

606 Roth LM. 1977. A taxonomic revision of the Panesthiinae of the world. I. The Panesthiinae of
 607 Australia (Dictyoptera: Blattaria: Blaberidae). *Aust J Zool Suppl Ser* 25:1–112.

608 Roth LM. 1981. The mother-offspring relationship of some Blaberid cockroaches
 609 (Dictyoptera: Blattaria: Blaberidae). *Proc Entomol Soc Washingt* 83:390–398.

610 Roth LM, Willis E. 1960. The Biotic Association of Cockroaches: Smithsonian Miscellaneous
 611 Collections, Vol. 141. Washingt Smithsonian Inst.

612 Rousset F, Lion S. 2011. Much ado about nothing: Nowak et al.'s charge against inclusive
 613 fitness theory. *J Evol Biol* 24:1386–92.

614 Schal C, Gautier JY, Bell WJ. 1984. Behavioural ecology of cockroaches. *Biol Rev* 59:209–
 615 254.

616 Shelford R. 1906. Studies of the Blattidae (continued). *Trans Entomol Soc London*:487–519.

617 Shellman-Reeve JS. 1997. The spectrum of eusociality in termites. In: Choe JC, Crespi BJ,
 618 editors. *The evolution of social behavior in Insects and Arachnids*. Cambridge University
 619 Press. p 52–93.

620 Sherman PW, Lacey EA, Reeve HK, Keller L. 1995. The eusociality continuum. *Behav Ecol*
 621 6:102–108.

622 Simola DF, Wissler L, Donahue G, Waterhouse RM, Helmkampf M, Roux J, Nygaard S,
 623 Glastad KM, Hagen DE, Viljakainen L, Reese JT, Hunt BG, Graur D, Elhaik E,
 624 Kriventseva EV, Wen J, Parker BJ, Cash E, Privman E, Childers CP, Munoz-Torres MC,
 625 Boomsma JJ, Bornberg-Bauer E, Currie CR, Elsik CG, Suen G, Goodisman MAD,
 626 Keller L, Liebig J, Rawls A, Reinberg D, Smith CD, Smith CR, Tsutsui N, Wurm Y,
 627 Zdobnov EM, Berger SL, Gadau J. 2013. Social insect genomes exhibit dramatic
 628 evolution in gene composition and regulation while preserving regulatory features linked
 629 to sociality. *Genome Res* 23:1235–1247.

630 Slobodchikoff CN. 1984. Resources and the evolution of social behavior. In: Price PW,
 631 Slobodchikoff CN, Gand WS, editors. *A new ecology: novel approaches to interactive*
 632 *systems*. New York: Wiley & Sons. p 227–251.

633 Sumner S. 2018. Determining the molecular basis of sociality in insects: progress, prospects
 634 and potential in sociogenomics. *Ann Zool Fennici* 43:423–442.

635 Terrapon N, Li C, Robertson HM, Ji L, Meng X, Booth W, Chen Z, Childers CP, Glastad
 636 KM, Gokhale K, Gowin J, Gronenberg W, Hermansen RA, Hu H, Hunt BG, Huylmans
 637 AK, Khalil SM, Mitchell RD, Munoz-Torres MC, Mustard JA, Pan H, Reese JT, Scharf
 638 ME, Sun F, Vogel H, Xiao J, Yang W, Yang Z, Zhou J, Zhu J, Brent CS, Elisk CG,
 639 Goodisman MA, Liberles DA, Roe RM, Vargo EL, Vilcinskas A, Wang J, Bornberg-
 640 Bauer E, Korb J, Zhang G, Liebig J. 2014. Molecular traces of alternative social
 641 organization in a termite genome. *Nat Commun* 5:3636.

642 Tewksbury JJ, Anderson JGT, Bakker JD, Billo TJ, Dunwiddie PW, Groom MJ, Hampton
 643 SE, Herman SG, Levey DJ, Machnicki NJ, Del Rio CM, Power ME, Rowell K, Salomon
 644 AK, Stacey L, Trombulak SC, Wheeler TA. 2014. Natural history's place in science and
 645 society. *Bioscience* 64:300–310.

646 Thompson, G.J, Kitade, O., Lo, N., & Crozier, R.H. 2000. Phylogenetic evidence for a single,
 647 ancestral origin of a “true” worker caste in termites. *Journal of Evolutionary Biology*,
 648 13,869–881.

649 Thompson, G.J, Kitade, O., Lo, N., & Crozier, R.H. 2004. On the origin of termite workers:
 650 weighing up the phylogenetic evidence. *Journal of Evolutionary Biology*, 17,217–220.

651 Thorne BL. 1997. Evolution of eusociality in termites. *Annu Rev Ecol Syst* 28:27–54.

652 Thorne BL, Traniello JFA. 2003. Comparative social biology of basal taxa of ants and
 653 termites. *Annu Rev Entomol* 48:283–306.

654 Toth AL, Varala K, Henshaw MT, Rodriguez-Zas SL, Hudson ME, Robinson GE. 2010.
 655 Brain transcriptomic analysis in paper wasps identifies genes associated with behaviour
 656 across social insect lineages. *Proc R Soc B* 277:2139–2148.

657 Trivers RL. 1971. The evolution of reciprocal altruism. *Quarterly Rev Biol* 46:35–57.

658 Troudet J, Grandcolas P, Blin A, Vignes-Lebbe R, Legendre F. 2017. Taxonomic bias in
 659 biodiversity data and societal preferences. *Sci Rep* 7:9132.

660 van Baaren J, Deleporte P, Grandcolas P, Biquand V, Pierre J-S. 2002. Measurement for
 661 Solitariness and Gregarism: Analysing Spacing, Attraction and Interactions in Four
 662 Species of Zetoborinae (Blattaria). *Ethology* 108:697–712.

663 van Baaren J, Bonhomme A-S, Deleporte P, Pierre J-S. 2003. Behaviours promoting grouping
 664 or dispersal of mother and neonates in ovoviviparous cockroaches. *Insectes Soc* 50:45–
 665 53.

666 Ware JL, Grimaldi DA, Engel MS. 2010. The effects of fossil placement and calibration on
 667 divergence times and rates: An example from the termites (Insecta : Isoptera). *Arthropod*
 668 *Struct Dev* 39:204–219.

669 Watson JAL, Sewell JJ. 1985. Caste development in *Mastotermes* and *Kalotermes*: which is
 670 primitive? In: Watson JAL, Okot-Kotber BM, Noirot C, editors. Caste differentiation in
 671 social insects. Pergamon, Oxford. p 27–40.

672 Wcislo W. 1997a. Are behavioral classifications blinders to studying natural variation? In:
 673 Choe JC, Crespi BJ, editors. The evolution of social behavior in insects and arachnids.
 674 Cambridge: Cambridge University Press. p 8–13.

675 Wcislo W. 1997b. Social terminology: what are words worth? Trends Ecol Evol 12:161.

676 Weinstock GM, Robinson GE, Gibbs RA, Worley KC, Evans JD, Maleszka R, Robertson
 677 HM, Weaver DB, Beye M, Bork P, Elsik CG, Hartfelder K, Hunt GJ, Zdobnov EM,
 678 Amdam G V., Bitondi MMG, Collins AM, Cristino AS, Michael H, Lattorff G, Lobo
 679 CH, Moritz RFA, Nunes FMF, Page RE, Simões ZLP, Wheeler D, Carninci P, Fukuda S,
 680 Hayashizaki Y, Kai C, Kawai J, Sakazume N, Sasaki D, Tagami M, Albert S,
 681 Baggerman G, Beggs KT, Bloch G, Cazzamali G, Cohen M, Drapeau MD, Eisenhardt D,
 682 Emore C, Ewing MA, Fahrbach SE, Forêt S, Grimmelikhuijzen CJP, Hauser F, Hummon
 683 AB, Huybrechts J, Jones AK, Kadowaki T, Kaplan N, Kucharski R, Leboulle G, Linial
 684 M, Littleton JT, Mercer AR, Richmond TA, RodriguezZas SL, Rubin EB, Sattelle DB,
 685 Schlipalius D, Schoofs L, Shemesh Y, Sweedler J V., Velarde R, Verleyen P, Vierstraete
 686 E, Williamson MR, Ament SA, Brown SJ, Corona M, Dearden PK, Dunn WA,
 687 Elekonich MM, Fujiyuki T, Gattermeier I, Gempe T, Hasselmann M, Kage E,
 688 Kamikouchi A, Kubo T, Kunieda T, Lorenzen M, Milshina NV., Morioka M, Ohashi K,
 689 Overbeek R, Ross CA, Schioett M, Shippy T, Takeuchi H, Toth AL, Willis JH, Wilson
 690 MJ, Gordon KHJ, Letunic I, et al. 2006. Insights into social insects from the genome of
 691 the honeybee *Apis mellifera*. Nature 443:931–949.

692 Wheeler WM. 1923. Social life among the insects. Hartcourt, Brace, New York. 375 p.

693 Willson MF, Armesto JJ. 2006. Is natural history really dead? Toward the rebirth of natural
 694 history. Rev Chil Hist Nat 79:279–283.

695 Wilson DS, Sober E. 1989. Reviving the Superorganism. J Theor Biol 136:337–356.

696 Wilson DS, Wilson EO. 2007. Rethinking the theoretical foundation of sociobiology. Q Rev
 697 Biol 82:327–348.

698 Wilson EO. 1971. The insect societies. Cambridge, Massachusetts: The Belknap Press of the
 699 Harvard University Press.

700 Wilson EO, Hölldobler B. 2005. The rise of the ants: a phylogenetic and ecological
 701 explanation. Proc Natl Acad Sci U S A 102:7411–4.

702 Woodard SH, Fischman BJ, Venkat A, Hudson ME, Varala K, Cameron SA, Clark AG,
703 Robinson GE. 2011. Genes involved in convergent evolution of eusociality in bees. *Proc*
704 *Natl Acad Sci* 108:7472–7477.

705 Xiao H, Hu Y, Lang Z, Fang B, Guo W, Zhang Q, Pan X, Lu X. 2017. How much do we
706 know about the breeding biology of bird species in the world? *J Avian Biol* 48:513–518.

707

708

FIGURE LEGENDS

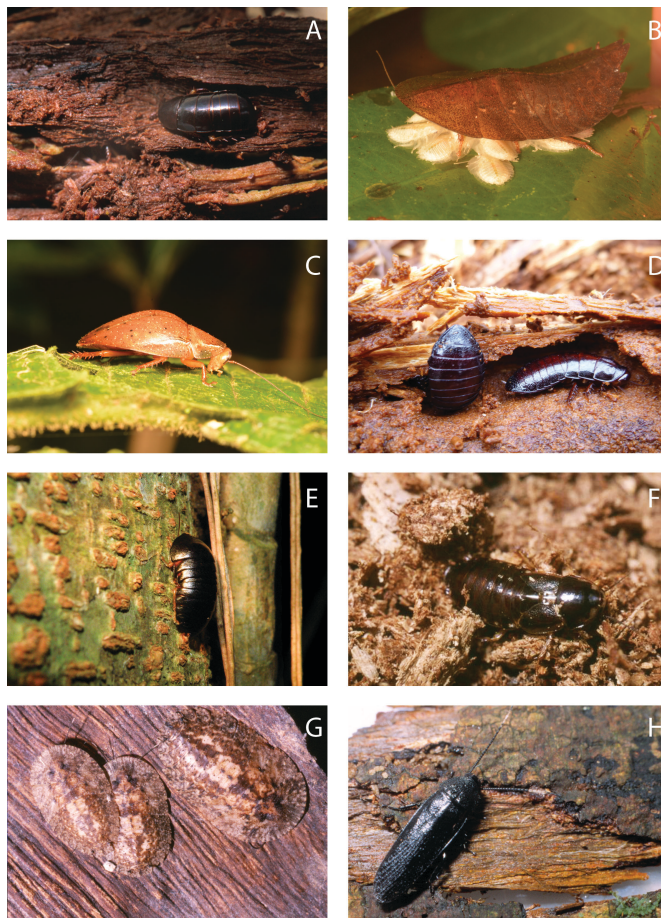


Fig. 1. Eight cockroach genera relevant for the investigation of the molecular basis of sociality in cockroaches and termites. A. *Lauraesilpha mearetoi* Grandcolas, 1997 excavated from its log in New Caledonia, B. Female of *Thanatophyllum akinetum* Grandcolas, 1991, solitary species, with its newborns, 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.)

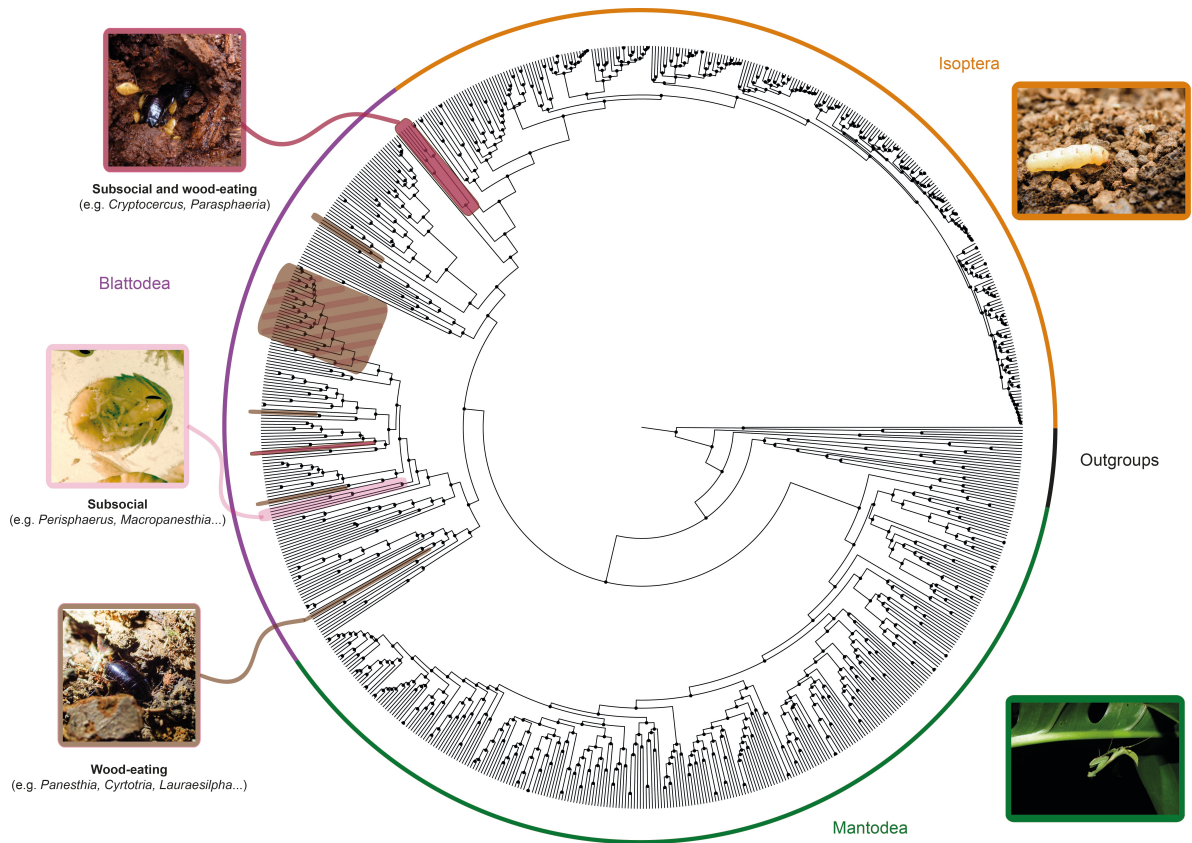


Fig. 2. Phylogenetic tree derived from the study in Legendre et al. (2015a) with subsocial and wood-eating lineages cited in the text highlighted. Obviously, only lineages sampled in this phylogeny are highlighted, meaning that other lineages have evolved wood-eating or subsociality. Stripes for the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