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SYSTEMATICS AND SOCIALITY EVOLUTION

Title

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

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).

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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 *Lamproblatt* 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. *Lamproblatt* Hebard, 1919, *Eurycanthablatta* Fritzsche and Zompro, 2008 and *Lamproglandifera* Roth, 2003) are scarce (Gautier and Deleporte, 1986; Grandcolas, 1994a; Grandcolas and Pellens, 2012). *Lamproblatt* 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

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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).