

The evolutionary transition from subsocial to eusocial behaviour in Dictyoptera: Phylogenetic evidence for modification of the “shift-in-dependent-care” hypothesis with a new subsocial cockroach

Roseli Pellens^a, Cyrille A. D’Haese^{a,b}, Xavier Bellés^c, Maria-Dolors Piulachs^c,
Frédéric Legendre^a, Ward C. Wheeler^b, Philippe Grandcolas^{a,*}

^a UMR 5202 CNRS, Département Systématique et Evolution, Muséum national d’Histoire naturelle, 45, rue Buffon, 75005 Paris, France

^b Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th St, New York, NY 10024, USA

^c Department of Physiology and Molecular Biodiversity, Institut de Biologia Molecular de Barcelona (CSIC), Jordi Girona 18, 0834 Barcelona, Spain

Received 28 April 2006; revised 13 November 2006; accepted 18 December 2006

Available online 31 December 2006

Abstract

Cockroaches have always been used to understand the first steps of social evolution in termites because they are close relatives with less complex and integrated social behaviour. Termites are all eusocial and ingroup comparative analysis would be useless to infer the origin of their social behaviour. The cockroach genus *Cryptocercus* was used as a so-called “prototermite” model because it shows key-attributes similar to the termites (except Termitidae): wood-feeding, intestinal flagellates and subsocial behaviour. In spite of these comparisons between this subsocial cockroach and eusocial termites, the early and remote origin of eusocial behaviour in termites is not well understood yet and the study of other relevant “prototermite” models is however needed. A molecular phylogenetic analysis was carried out to validate a new “prototermite” model, *Parasphaeria boleiriana* which shows a peculiar combination of these key-attributes. It shows that these attributes of *Parasphaeria boleiriana* have an independent origin from those of other wood-eating cockroaches and termites. The case of *P. boleiriana* suggests that a short brood care was selected for with life on an ephemeral wood resource, even with the need for transmission of flagellates. These new phylogenetic insights modify evolutionary hypotheses, contradicting the assumption made with *Cryptocercus* model that a long brood care is necessary for cooperation between broods in the “shift-in-dependent-care” hypothesis. An ephemeral wood resource is suggested to prompt generation overlap and the evolution of cooperation, even if brood care is shortened. © 2007 Elsevier Inc. All rights reserved.

Keywords: Origin of social behaviour; *Parasphaeria*; *Cryptocercus*; Termites; “Shift-in-dependent-care” hypothesis

1. Introduction

Societies of eusocial insects are the most complex and integrated cases of social behaviour. Although they have been studied in many aspects, their early and remote origin is not always well understood (Wilson, 1975; Choe and Crespi, 1997). This is especially true in the case of termites, all of which are eusocial (contrary to hymenopterans, aphids, and thrips). Ingroup comparative analysis is thus

useless to infer the early origin of their social behaviour (Thompson et al., 2000; Grandcolas and D’Haese, 2002). Only one cockroach group, the genus *Cryptocercus*, has been used as a “prototermite” model because it shows several key-attributes similar to the so-called “lower” termites, including wood-feeding, intestinal flagellates, and subsocial behaviour. Termites have evolved an impressive array of intestinal symbioses that are thought to play an important role in social evolution (Wilson, 1971; Abe et al., 2000). Intestinal flagellates are considered to be ancestral and to facilitate wood digestion. It has been assumed that the need for flagellate transmission from adult parents to brood larvae has led to a long and complex brood care. In turn, the

* Corresponding author. Fax: +33 1 40 79 56 79.
E-mail address: pg@mnhn.fr (P. Grandcolas).

long subsocial behaviour might have led to the selection of castes if the first broods take care of the second ones in the families, according to the “shift-in-dependent-care” hypothesis (Thorne, 1997; Nalepa, 1988).

This scenario has been traditionally linked to a particular phylogenetic hypothesis for the cockroach *Cryptocercus* that proposes that this genus clusters with termites, as an intermediate between primitively non-social cockroaches and eusocial termites (e.g., Lo et al., 2000; Maekawa et al., 2005a). Some other molecular phylogenetic trees have different topologies with *Cryptocercus* placed as a particular family within the cockroaches (Kambhampati, 1995; Maekawa and Matsumoto, 2000). Nevertheless, these phylogenetic hypotheses are controversial, given that other authors also consider that *Cryptocercus* is more properly placed among the Polyphagidae, between the Blattidae and Anaplectidae, based on morphology, peptides of corpora cardiaca and re-analysis of molecular data (Grandcolas, 1994a; Grandcolas and Deleporte, 1996; Gäde et al., 1997; Grandcolas and D’Haese, 2001; Grandcolas et al., 2001). Under any phylogenetic hypothesis and because it shows three key-attributes together, *Cryptocercus* is however an invaluable “prototermite” model. This term is hereafter used as a substitute for “taxon showing an analogous combination of the supposedly ancestral key-attributes of termites” (sensu Taylor, 1978). Indeed, even if *Cryptocercus* and termites are actually sister-groups (e.g., Lo et al., 2000), the ancestral states of some key-attributes remain ambiguous: it cannot be inferred whether their common ancestor was subsocial or eusocial, and we would need a phylogeny of flagellates to infer if they actually show co-cladogenesis with Dictyopteran insects (e.g., Gerbod et al., 2002). In addition, the main problem with using *Cryptocercus* as a “prototermite” model is that it shows behavioural traits incompatible with the “shift-in-dependent-care” hypothesis: the first brood borne remains with the female during several years but prevents it to have a second brood, precluding any shift in care from female to broods (Nalepa, 1988; Thorne, 1997).

Other cases of “prototermite” models are therefore needed to generalize or to modify the evolutionary scenario of social behaviour and to substantiate the “shift-in-dependent-care” hypothesis. These “prototermite” models should show the relevant combination of key attributes (wood-feeding, intestinal flagellates and social behaviour), with phylogenetic relationships clearly more distantly placed from *Cryptocercus* or any other wood-feeding cockroaches for sake of independence. The problem is that this combination of attributes was not known in any other cockroach until now. For example, some South-eastern Asian Panesthiinae wood-feeding cockroaches are subsocial but do not show associations with flagellates (Roth and Willis, 1960; Matsumoto, 1988; Maekawa et al., 2005b).

Intensive sampling of tropical areas, especially in areas of high biodiversity, during more than ten years (Grandcolas, 1994b,c, 1997, 1999a) has recently led to the discovery of a new cockroach—“prototermite” model, *P. boleiriana*

(Grandcolas and Pellens, 2002), in the Brazilian Atlantic forest. *Parasphaeria* fits the key attributes required to serve as a “prototermite” model. Indeed, first field and laboratory studies have shown that this cockroach feeds on rotten wood, displays brood care in wood chambers and permanently harbours intestinal flagellates (Grandcolas and Pellens, 2002; Pellens et al., 2002; Brugerolle et al., 2003). As another unique behavioural attribute, *P. boleiriana* feeds on a common fast-growing forest tree, *Joannesia princeps* Vellozo (Euphorbiaceae, called “boleira” in Espírito Santo) in the Brazilian Atlantic forest (Pellens et al., 2002), which has a low wood density (Castro et al., 1993). The first step to explore this new “prototermite” model was to carry out a multigene phylogenetic analysis in order to establish the phylogenetic position of *P. boleiriana* among cockroach families. The aim was to assess unambiguously whether this species is an independent case of evolution, thus phylogenetically unrelated to *Cryptocercus* or to any other previously known wood-feeding cockroach. The focus of our molecular phylogenetic analysis is especially to assess whether *P. boleiriana* is independent from other wood-feeding cockroaches of the family Blaberidae (Maekawa et al., 2003, 2005) where the genus *Parasphaeria* was always placed by systematists (e.g., Roth, 2003) and how did evolve the three key-attributes. We included any relevant species in the analysis, including *Cryptocercus* and termites to make our test more powerful even if we do not intend to solve the old-standing controversy of the *Cryptocercus* position which would need a specific taxon sampling with “basal” cockroach groups such as the family Polyphagidae.

It is now widely acknowledged that wood is a bonanza resource, food and habitat together, which is primarily important to explain social behaviour evolution (Crespi, 1994; Choe and Crespi, 1997; Myles, 1988; Roisin, 1999). For that reason, our second step was to examine how much the key-attributes of *P. boleiriana* (intestinal flagellates and subsocial behaviour) are influenced by the wood resource and by its availability and dynamics within the forest.

2. Materials and methods

2.1. Taxon and molecular sampling

Our sample comprised fifty-two taxa with thirty-seven exemplars representing all subfamilies of Blaberidae but Perisphaeriinae plus fifteen taxa used as outgroups. The latter were: a grasshopper (*Locusta*), an earwig (*Forficula*), five termites belonging to four different families (Termitidae, Mastotermitidae, Kalotermitidae and Rhinotermitidae), a mantid (*Mantis*), two Blattidae, two Blattellidae (usually considered sister group of Blaberidae), one Polyphagidae and two species of *Cryptocercus*. The trees were rooted with the grasshopper, *Locusta migratoria*. For these taxa, 18S rDNA, and mitochondrial 12S rDNA, 16S rDNA and Cytochrome Oxidase II (COII) were sequenced at the AMNH, New York and IBMB-CSIC, Barcelona.

Table 1
Primers sequences (5' to 3') used to generate 18S rDNA, 12SrDNA, 16S rDNA and Cytochrome Oxidase II sequences

Primer	Sequence	Reference
18S1F	TACCTGGTTGATCCTGCCAGT AG	Giribet et al. (1996)
18S5R	CTTGGCAAATGCTTTTCGC	Giribet et al. (1996)
18S3F	GTTTCGATTCCGGAGAGGGA	Giribet et al. (1996)
18SBI	GAGTCTCGTTCGTTATCGGA	Whiting et al. (1997)
18SA2.0	ATGGTTGCAAAGCTGAAAC	Whiting et al. (1997)
18S9R	GATCCTTCCGCAGGTTACCT AC	Giribet et al. (1996)
12SAI	AAACTAGGATTAGATACCCT ATTAT	AMNH
12SBI	AAGAGCGACGGGCGATGTGT	AMNH
16Sar	CGCCTGTTTATCAAAAACAT	Xiong and Kocher (1991)
16Sb	CTCCGGTTTGAACCTCAGATCA	Xiong and Kocher (1991)
A-tLEU	ATGGCAGATTAGTGCAATGG	Maekawa et al. (1999)
B-tLYS	GTTTAAGAGACCAGTACTTG	Liu and Beckenbach (1992)

The 18S rDNA was amplified in three overlapping fragments, using primer pairs 1F-5R, 3F-18Sbi and A2.0-9R (Giribet et al., 1996; Whiting et al., 1997). 12S rDNA was amplified with the primer pair 12SAI and 12SBI developed at the AMNH, in Ward Wheeler's lab. 16S rDNA was amplified with the primers 16Sar and 16Sb (Xiong and Kocher, 1991). Primers A-tLEU and B-tLYS (Liu and Beckenbach, 1992; Maekawa et al., 1999) were used for COII. A list with primers sequence is presented in Table 1. The protocols of PCR have followed those usually employed in the laboratories, e.g., available in Grandcolas et al. (2001) for CSIC of Barcelona, and in D'Haese (2002) for AMNH, New York. A total of 109 new sequences was obtained and deposited in GenBank; additional sequences were obtained from GenBank (see Appendix).

2.2. Phylogenetic analysis

Sequences were analyzed by means of Direct Optimization (Wheeler, 1996) implemented in the software POY designed by Wheeler, 2002 (Wheeler et al., 1996–2003) available at <ftp://ftp.amnh.org/pub/molecular.poy>. Direct Optimization avoids intermediate alignment steps by directly assessing the number of evolutionary events, i.e. DNA sequence transformations. This is accomplished through the generalization of existing character optimization procedures to insertion and deletion events (indels) and base substitutions, treating indels as real evolutionary processes as opposed to the patterns (i.e. gaps) implied by static sequence alignment. This method generates more efficient explanations of sequence variation than does standard multiple sequence alignment by producing more congruent results (shorter trees). The analysis was run using 30 replicates with branch swapping (SPR and TBR), ratcheting (Nixon, 1999) and treefusing (Goloboff, 1999). Then the resulting trees were submitted to another round of treefusing

to check if minimal tree length was reached. The influence of indel, transition, and transversion costs was studied through sensitivity analysis (Wheeler, 1995). The ratio of weights between indels and transversions ranged from 1 to 4, as did the ratio between transversions and transitions with an additional analysis with no transitions, resulting in six parameter sets (indel transversion transition): 111 (equal weighting), 211, 221, 421, 110, and 1641; extension gaps were weighted half the cost of an opening gap. The parameter set that minimized incongruence among the loci was considered optimal (D'Haese, 2002; Wheeler, 1995). Incongruence was assessed with the metric incongruence length distance (ILD) (Mickevich and Farris, 1981). This value is calculated by dividing the difference between overall tree length and the sum of its data components: $ILD = (\text{Length}_{\text{combined}} - \sum \text{length}_{\text{individual sets}}) / \text{length}_{\text{combined}}$. We illustrate how the tree topology varies among the different analyses by showing the optimal topology with Navajo rugs (non-interpolated Cartesian graphs of areas of the parameter space in which the strict consensus of the analysis whether recovered a monophyletic group or not, Wheeler, 1995). Here, the graphs report areas in which the analyses recover a monophyletic, paraphyletic or polyphyletic group. Jackknife and Bremer branch support were calculated using the line commands shown in Appendix.

To assess further whether this result stands independently of the method of analysis and alignment, we also carried out other analyses with maximum likelihood methods and static alignments. First, we made a maximum likelihood analysis under Direct Optimization on input topologies from parsimony analysis with default parameters coupled to treefusing and branch swapping (SPR and TBR). Second, a ML analysis was carried out more traditionally, without direct optimization. Sequences were aligned using Muscle 3.6 (Edgar, 2004) with the default parameters. The model GTR+I+G was selected using Modeltest v3.06 (Posada and Crandall, 1998). Phylogenetic analysis under maximum likelihood was performed with PHYML v2.4.4 (Guindon and Gascuel, 2003) with the following options: model of nucleotide substitution GTR; base frequency estimates ML; proportion of invariable sites estimated; number of substitution category rate 6; gamma distribution parameter estimated; input tree BIONJ; optimization of tree topology. The wood-eating behaviour

Table 2

Cladogram lengths and incongruence values for six different gap–transversion–transition parameters sets

g-tv-ts	Length 18S	Length 12S	Length 16S	Length COII	Total length	ILD
111	1232	1719	2032	3362	8544	0.0233
211	1477	1942	2263	3392	9288	0.0230*
221	1917	2732	3285	4765	13041	0.0262
421	2371	3143	3743	4836	14502	0.0282
110	644	969	1234	1382	4420	0.0432
1641	5621	6840	8018	7916	29640	0.0420

The analysis with the 211 (gap–transversion–transition) parameter set gives the lower ILD value (with an asterisk in the Table). This analysis maximizes the global congruence and is then retained as the best phylogenetic estimate.

was secondarily optimized on the molecular tree to assess the number of independent origins in the case of every different topology. The Australasian subfamilies Panesthiinae and Geoscaphinae are coded xylophagous as a whole, given that they have secondarily lost this behaviour and that this does not change anyway the optimization (Maekawa et al., 2003). The specific command lines, GenBank accession numbers and data files are provided in the Appendix.

2.3. Estimating the decay of dead wood

The decay rate of the dead wood used by *P. boleiriana*, *J. princeps* (“boleira”) (Grandcolas and Pellens, 2002; Pellens et al., 2002), and of the dead wood of other local tree species

was assessed by comparing the change of wood decay within two years. The study was conducted in remnants of the Brazilian Atlantic forest in Linhares and Sooretama, Espirito Santo. In October 1999, 60 pieces of “hard” dead wood of each category (“boleira” and “not boleira”) were selected haphazardly, marked with plastic label attached to a wire and left on the same place they were found. In October 2001, these trunks were retrieved and the evaluation of the wood hardness was repeated. The decay was assessed according to three categories: trunk intact (hard or more or less softened by decay), remains (the trunk is no more intact but in several pieces or partly disappeared), frass (the wood is completely destroyed and transformed into frass sometimes with some remaining pieces of bark).

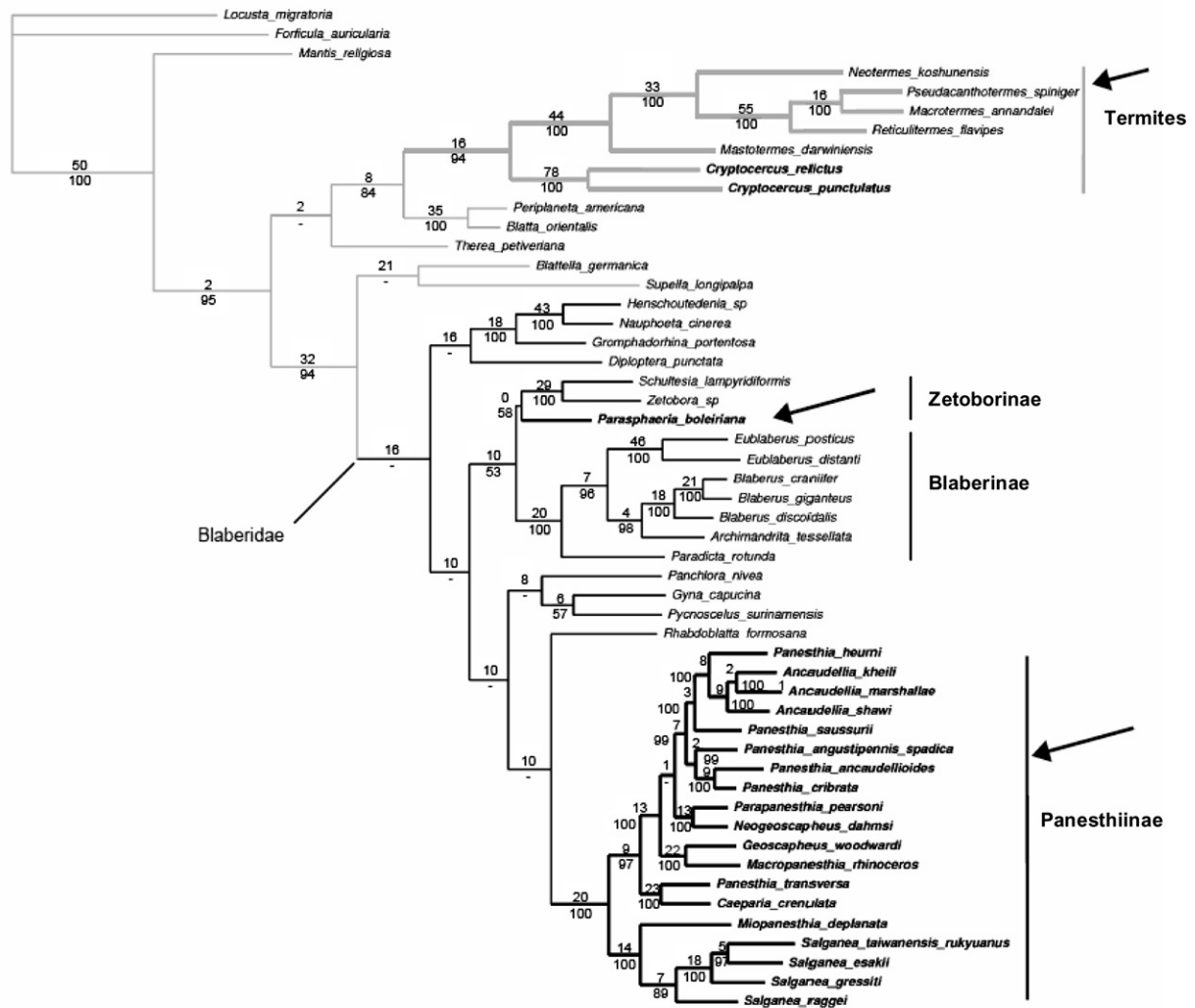


Fig. 1. Molecular phylogenetic tree showing the relationships of different wood-eating cockroaches (species names in bold characters pointed with arrows), based on large portions of genes 12S, 16S, 18S and COII from 44 cockroaches, 1 grasshopper, 1 earwig, 1 mantid and 5 termite species (tree length 9288, CI = 12, RI = 76). Analyses were carried out with Direct Optimization (Wheeler, 1996) implemented in POY. The whole set of analyses was used to state whether *Parasphaeria boleiriana* appears always unrelated to other wood-feeding cockroaches (*Cryptocercus* and Panesthiinae–Geoscaphinae) so that their xylophagy and subsocial behaviour (thick lines) appear convergent in the whole and wide space of parameters of sequence alignment. The single tree presented is one of the two resulting trees for the 211 parameter set analysis (transitions = 1, transversions = 1, gaps = 2) which minimized the incongruence among the loci. Bremer branch supports (steps) and Jackknife values (percentages) are given above and below the branches, respectively. Thick lines and arrows indicate xylophagous and subsocial species.

3. Results

The comparison of the values of the ILLD metrics for the six different gap–transversion–transition parameters sets indicated minimum incongruence for the parameters 211 (Table 2). Two optimal resulting trees were obtained with this set of parameters (tree length: 9288, CI = 12, RI = 76, Table 2). The topology of the optimal trees including non-closely related position of *P. boleiriana* to the Panesthiinae or *Cryptocercus* is supported by high values of Jackknife and Bremer branch support (Fig. 1). In the first tree, *P. boleiriana* is sister-group to the other sampled Neotropical Zetoborinae. In the second tree otherwise similar (not shown), *P. boleiriana* is sister-group to the closely related Neotropical subfamily Blaberinae, both together sister-group of the remaining Zetoborinae. In both cases, the East Asian Panesthiinae and Geoscaphinae appeared as a distant and monophyletic group. Also, *Cryptocercus* falls as a sister-group of termites, altogether sister-group of Blattidae cockroaches and being nested within the remainder of cockroaches. According to Navajo rugs, the node supporting the position of *Parasphaeria* and those supporting the largest splits within the tree appear to occur in most topolo-

gies recovered with the different parameter sets (Fig. 2). The multi-gene phylogenetic analyses (both optimal trees as well as in every tree obtained with any parameter set) indicate that *P. boleiriana* is an independently evolved case of wood-feeding behaviour, intestinal flagellates and female brood care in a wood chamber with respect to other wood-feeding cockroaches (Fig. 2). A similar result was found in a probabilistic framework both with prealigned (PHYML) (Fig. 3) or not prealigned (POY) data. The trees have similar topologies (log likelihood values, respectively, $\ln L = -39633.02$ and $\ln L = -42277.48$) and they let unchanged the most important features of the results obtained with parsimony analysis with respect either to relationships among the major groups or to the optimization of the characters of interest (wood-feeding, intestinal flagellates and female brood care in a wood chamber).

An independent origin of xylophagy for *P. boleiriana* and the Panesthiinae corresponds to a more parsimonious pattern than one involving a common origin. This latter scenario implies 5, 4 or 3 steps (Poy 211, Poy ML and PHYML, respectively) whereas an independent origin involves only 2 steps. Similarly a single origin of wood-eating behaviour in Blattaria (i.e. including *Cryptocercus*)

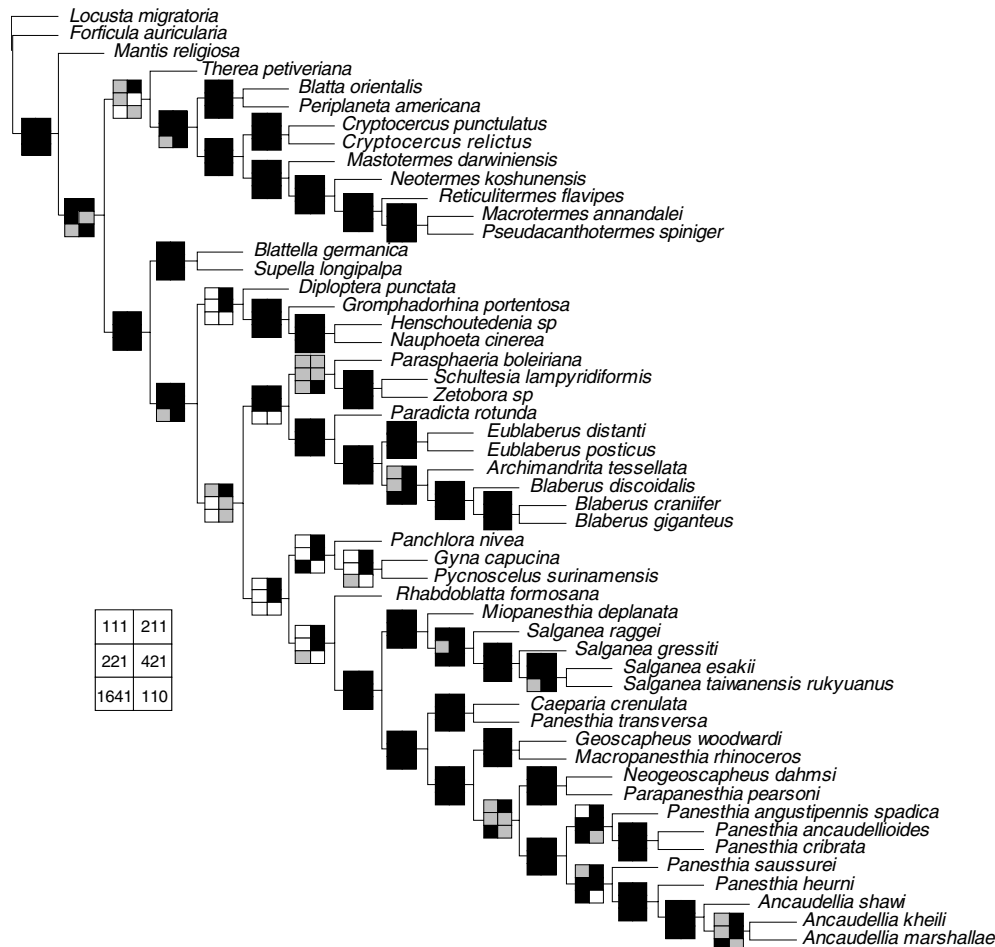


Fig. 2. The same tree presented in Fig. 1, with the results from the sensitivity analysis shown with Navajo rugs. Black boxes indicate monophyly; grey boxes, paraphyly; white boxes indicate polyphyly under the different parameter sets (gap, transversion, transition).



Fig. 3. Maximum likelihood phylogenetic tree showing the relationships of different wood-eating cockroaches (species names in bold characters pointed with arrows), based on large portions of genes 12S, 16S, 18S and COII from 44 cockroaches, 1 grasshopper, 1 earwig, 1 mantid and 5 termite species. The tree was produced with a maximum likelihood analysis with prealigned data and carried out with PHYML software (model GTR + I + G; ln L = -39633.02). Thick lines and arrows indicate xylophagous and subsocial species.

involves 9 steps in each case versus 3 steps for 3 independent origins of xylophagy, flagellates and brood care in a wood chamber. This new cockroach “prototermite” model, *P. boleiriana*, appears within the monophyletic Neotropical group of the subfamilies Zetoborinae and Blaberinae, nested itself in the family Blaberidae. Its behaviour is unique in that group and appears independently evolved according to any topology recovered with the different set of parameters. The study of the decay rate of the dead wood showed that dead trunks of boleira decompose faster

than the ones of other local trees (χ^2 test, $\chi^2 = 17.245$, $P < 0.001$, $df = 2$). In fact, 50% of the trunks of boleira partly disappeared or were transformed into frass within two years (Fig. 4).

4. Discussion

According to the present phylogenetic analyses, the wood-eating cockroach *P. boleiriana* can be used as one more independent and fully relevant “prototermite” model

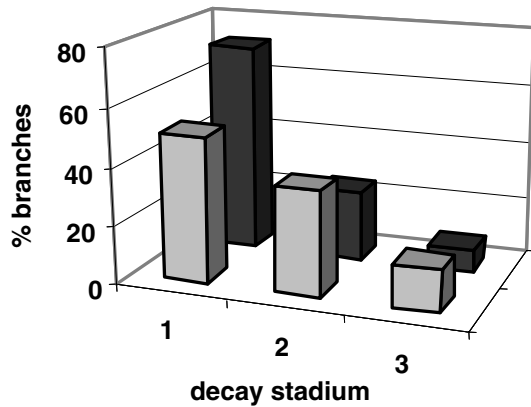


Fig. 4. Decay of dead wood of *Joannesia princeps* Vellozo, “boleira” (Euphorbiaceae) (grey bars), used by *Parasphaeria boleiriana* compared to the wood from other tree species (black bars). 60 trunks of each category were monitored within two years (1999–2001) in the Brazilian Atlantic forest from Linhares and Sooretama (State of Espírito Santo, Brazil). State 1 corresponds to complete dead trunks, state 2 to incomplete trunks already partly diminished by decay, state 3 to totally transformed trunks remaining only as frass with sometimes some pieces of bark.

in addition to *Cryptocercus* species because both show wood-feeding behaviour, brood care and intestinal flagellates, all behavioural key-attributes that evolved convergently. This is in agreement with previous morphological analyses (Grandcolas, 1993, 1998; Pellens et al., 2007) and with the South American geographical distribution of the genus *Parasphaeria* (Grandcolas and Pellens, 2002) which actually belongs to the well-known and diverse cockroach neotropical group, the group of subfamilies Zetoborinae and Blaberinae. All key-attributes of *Parasphaeria* have thus appeared in South America, in contrast with *Cryptocercus* species in North America and East Asia (Grandcolas, 1999b) and cockroaches of the subfamilies Panesthiinae and Geoscaphinae in Southeast Asia and Australia (Maekawa and Matsumoto, 2003; Maekawa et al., 2003). The study also retrieves the position of *Cryptocercus* sister-group of termites, both being nested within cockroaches (Lo et al., 2000). Therefore, the present analysis shows that at least three independent origins of wood-eating and subsocial behaviour occurred in Dictyoptera. The association with intestinal protista only appeared twice, in *Cryptocercus*-termites and in *Parasphaeria*. These results showed that the last two cases can be especially useful to study termite evolution because they show the combination of the three key-attributes by convergence. The first case, *Cryptocercus*, is presently inferred to be related to termites by descent with modification while the other case, *Parasphaeria*, is inferred to be a convergence. This second and convergent case can be especially useful since it shows traits possibly more explanatory with respect to termite evolution and to the “shift-in-dependent-care” hypothesis, as the first brood born does not remain with the female during several years, preventing it to have a second brood, and therefore precluding any shift in care from female to broods (Nalepa, 1988; Thorne, 1997).

In this respect, the comparison of *Parasphaeria* and *Cryptocercus* species suggests that the duration of brood care is more constrained by the quality of the wood resource and the short cockroach larval development and adult survival, than by the need for transmitting flagellates. *P. boleiriana* feeds on the peculiar softwood of boleira. Our monitoring of the wood decay showed that dead trunks of boleira can be completely decomposed in no more than two or three years. This period is very short when compared to the decomposition period of the wood used by *Cryptocercus* in temperate forests, which takes decades (Harmon et al., 1986). *P. boleiriana* develops and reproduces in a comparatively very short time, 2–3 years as a total (Pellens et al., 2002) compared to much more than 5 years for *Cryptocercus* (Nalepa, 1984; Park et al., 2002). It also shows a surprisingly short adult survival (one season) instead of several years for *Cryptocercus*. The brood care in *P. boleiriana* is also very short, 12 days as a mean (Pellens et al., 2002) compared to several years for *Cryptocercus* (Nalepa, 1988). In spite of fast development and short brood care in softwood trunks, *P. boleiriana* permanently harbours flagellates (Pellens et al., 2002; Brugerolle et al., 2003), which suggests the occurrence of mechanisms of flagellate transmission independent of a long social interaction, mechanisms which could be based on coprophagy, a behaviour that is widespread in cockroaches (Nalepa et al., 2001; Zhuzhikov, 2001). Whatever the transmission mechanism which remains to be identified and the actual role of intestinal flagellates, *P. boleiriana* shows that a long brood care is not needed to transmit and thus to harbour flagellates. The basic rationale of the “shift-in-dependent-care” hypothesis derived from *Cryptocercus* studies is not necessarily correct: the first termites may have evolved short brood care even if they harboured intestinal flagellates, just like *P. boleiriana*.

This modification of the common scenario for the first stages of social evolution in termites is important. If “prototermites” have not a long brood care, how could they evolve shift in brood care from female parent to an older brood? In this respect, it is worth noting that the fast dynamics of *P. boleiriana* colonies induced higher promiscuity between larvae of various ages, which interacted after the early spread from wood chambers in rotten branches (Pellens et al., 2002). Once again, this contrasts with *Cryptocercus*, which have long-lived adults and isolated groups of slow-developing larvae on hardwood trees in temperate forests (Park et al., 2002). The *Parasphaeria* “prototermite” model suggests that a longer and more elaborated brood care may have not been necessarily the path for caste emergence in termites. On the contrary, the long brood care of *Cryptocercus* precludes females to have a second brood when they care the first one and therefore prevent interactions among broods to occur (Nalepa, 1988). A shorter brood care could have allowed different cohorts of larval siblings to interact more, prompting the generation overlap necessary for altruism phenomena to occur (Wilson, 1975; Taylor and Irwin, 2000). In the

framework of the theory of cyclical inbreeding (Hamilton, 1972; Bartz, 1979), close prototermite colonies originating as different broods of the same parents whose larvae of different ages interact within the same rotten trunks could be part of an inbred sub-population, putting together necessary conditions for kinship selection and caste evolution (but see Roisin, 1999). This evolution is otherwise difficult to infer in the frame of the “shift-in-dependent-care” hypothesis, applied to the *Cryptocercus* “prototermite” model (Thorne, 1997).

As a basis to understand the dynamics of colonies that could have led to the evolution of a caste system, the *Parasphaeria* “prototermite” model drives the attention to the quality of wood used by termite ancestors. The kind of wood resource used could have determined the beginning of a complex evolution towards an eusocial system. This approach has never been made until now because it is counter-intuitive to suppose that long-lived societies could have originated on an ephemeral resource, a fast-decaying wood. In this respect, *P. boleiriana* is a surprising and important “prototermite” model for a better understanding of eusociality evolution in termites.

Acknowledgments

We are indebted to Laurence Packer and Jae Choe for their comments on this manuscript, which has been presented as a talk in the IUSSI meeting in Sapporo, Japan, 2002. Field work was made possible by a cooperation program between program of cooperation between the Conselho Nacional de Ciência e Tecnologia (Brazil) and Centre National de la Recherche Scientifique (France). Roseli Pellens has Post-Doctoral grant from CNPq, Brazil (Grant No. 200983/2004-0). Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) provided the authorization for fieldwork in Brazil. We thank Guanadir Gonçalves, chief of Biological Reserve of Sooretama, Renato de Jesus, administrator of Natural Reserve of Companhia Vale do Rio Doce, in Linhares, and the owners of several forest fragments, for authorizing the development of the research in the sites under their responsibility. Calculations were performed partly on the cluster developed at the AMNH by Ward Wheeler and on the cluster developed at the MNHN by Cyrille D’Haese.

Appendix A. Command lines used

A.1. POY

```
POY_OPTIONS='-parallel -jobspernode 2 -norandomizeoutgroup -holdmaxtrees 100 -fitchtrees -slop 5 -replicates 10 -buildsperreplicate 3 -ratchettbr 20 -ratchetpercent 10 -ratchetseverity 3 -ratchettrees 2 -treefuse -fuselimit 100 -fusemingroup 5 -fusemaxtrees 100 -check-slop 10 -indices'
```

```
#Data files
FILES_12S='12s.fas'
FILES_16S='16s.fas'
FILES_18S='18s.fas'
FILES_COII='coii.fas'
FILES_TOT='12s.fas 16s.fas 18s.fas coii.fas'
#Example of command line for the 111 parameter set
(extension gaps weighted half of opening gap cost)
poy $POY_OPTIONS -molecularmatrix 222.sank -extensiongap 1 $DATA_FILES -terminalsfile blab.taxa -minterminals 0 -printtree -plotfile BLB_111.tre > BLB_111.out 2> BLB_111.log
```

Where the *.fas files are the data files and *.sank the stepmatrices.

The resulting trees were submitted to TreeFusing to check if minimal tree lengths were reached:

```
POY_OPTIONS_TF='-parallel -jobspernode 1 -norandomizeoutgroup -molecularmatrix 222.sank extensiongap 1 $DATA_FILE -topofile $TOPO_FILE.tre -holdmaxtrees 100 -fitchtrees -replicates 0 -treefuse -fuselimit 100 -fusemingroup 5 -checkslop 10 -exact -indices'
```

Where *.tre are the files containing all the trees obtained for the various analyses under the different parameters sets for a given data set.

Analyses were performed on the AMNH cluster (280 nodes, 1024 M Ram per node, 560 CPU’s from 500Mhz PIII to 1 Ghz PIII, 100Mb Ethernet/ 10,4 Gb switch) and the MNHN cluster (13 nodes, 2 Go Ram per node, 22 AMDs 64 bits CPU’s for the slave nodes and 4 Xeon 32 bits CPU’s for the two master nodes).

A.2. ML – POY

```
TF_ML='-parallel -jobspernode 2 -likelihood -trullytallikelihood -norandomizeoutgroup -holdmaxtrees 200 -fitchtrees -replicates 0 -treefuse -fuselimit 200 -fusemingroup 5 -checkslop 20'
```

```
FILES_TOT='12sblab.fas 16sblab.fas 18sblab.fas coii-blab.fas'
```

```
poy $TF_ML $FILES_TOT -terminalsfile blab.taxa -minterminals 0 -topofile blbtot.arb > mltfblbtot.out 2> mltfblbtot.log
```

A.3. JACKNIFE

```
JACK='-parallel -jobspernode 2 -norandomizeoutgroup -holdmaxtrees 10 -fitchtrees -jackboot -replicates 100 -buildsperreplicate 2 -ratchetspr 1 -ratchetpercent 10 -ratchetseverity 3 -ratchettrees 2 -treefuse -fuselimit 100 -fusemingroup 5 -fusemaxtrees 40 -checkslop 5 -indices'
```

#Example of command line for the 211 parameter set (extension gaps weighted half of opening gap cost)

```
poy $JACK -molecularmatrix 211.sank -extensiongap 1 $FILES_TOT -terminalsfile blab.taxa -minterminals 0 -printtree -plotfile j2blbtot_211.tre -jackfpseudotrees j2blb_211.jpse -jackfpseudoconsensustrees j2blb_211.jcon -jackcharfile j2blb_211.char > j2blbtot_211.out 2> j2blbtot_211.log
```


A.4. BREMER

poy -parallel -jobspernode 2 -norandomizeoutgroup -molecularmatrix 211.sank -extensiongap 1 \$FILES_TOT-terminalsfile blab.taxa -minterminals 0 -topology “(Locusta migratoria_gb (Forficula auricularia (((Supella longipalpa Blattella germanica) ((Diptoptera punctata (Gromphadorrhina portentosa (Nauphoeta cinerea Henschoutedenia sp))) (((Pycnoscelus surinamensis Gyna capucina) Panchlora nivea) (((Salganea raggei_gb (Salganea gressiti_gb (Salganea esakii_gb (Salganea taiwanensis_rukyuanus_gb)))Miopanesthia deplanata_gb) ((Caeparia crenulata_gb Panesthia transversa_gb) ((Macropanesthia rhinoceros_gb Geoscaphheus woodwardi_gb) ((Neogeoscaphheus dahmsi_gb Parapanesthia pearsoni_gb) ((Panesthia cribrata Panes-

thia_ancaudellioides_gb) Panesthia angustipennis_spadica_gb) (Panesthia_saussurei_gb ((Ancaudellia shawi_gb (Ancaudellia_marshallae_gb Ancaudellia_kheili_gb)) Panesthia_heurni_gb)))))) Rhabdoblatta_formosana)) ((Parasphaeria_ boleiriana (Paradicta_rotunda ((Archimandrita_tessellata_gb (Blaberus_discoidealis (Blaberus_giganteus Blaberus_craniifer))) (Eublabeus_distanti Eublabeus_posticus)))) (Zetobora_sp Schultesia_lampyridiformis)))) (Therea_petiveriana ((Blatta_orientalis Periplaneta_ americana) ((Cryptocercus_punctulatus_gb Cryptocercus_relictus_gb) (Mastotermes_darwiniensis ((Reticulitermes_flavipes (Macrotermes_annandalei Pseudacanthotermes_spiniger)) Neotermes_koshunensis_gb)))))) Mantis religiosaFR))][9288];” -bremer -constrain tfblbtot_211 .con -exact > breblbtot_211.out 2> breblbtot_211.log

Taxonomic categories, exemplar species and genes used (with GenBank accession numbers for each data partition)

Genus species	Family	Sub-family	12S	16S	COII	18S
<i>Locusta migratoria</i>	Acrididae		NC_001712	NC_001712	NC_001712	AF370793
<i>Forficula auricularia</i>	Forficulidae		—	EF363255	AF140540	X89490
<i>Macrotermes annandalei</i>	Termitidae	Macrotermitinae	EF363284	EF363256	AB109527	EF363227
<i>Mastotermes darwiniensis</i>	Mastotermitidae		EF363285	EF363257	AB014071	EF363228
<i>Neotermes koshunensis</i>	Kalotermitidae	Neotermitinae	D89840	D89839	AB011408.1	AF220566
<i>Pseudacanthotermes spiniger</i>	Termitidae	Macrotermitinae	EF363286	EF363258	EF363203	EF363229
<i>Reticulitermes flavipes</i>	Rhinotermitidae	Heterotermitinae	EF363287	EF363259	EF363204	EF363230
<i>Mantis religiosa</i>	Mantidae	Mantinae	EF363288	EF363260	EF363226	EF363231
<i>Blatta orientalis</i>	Blattidae	Blattinae	EF363292	EF363264	—	EF363235
<i>Periplaneta americana</i>	Blattidae	Blattinae	EF363305	EF363277	EF363225	EF363248
<i>Blattella germanica</i>	Blattellidae	Blattellinae	EF363293	EF363265	EF363216	EF363236
<i>Supella longipalpa</i>	Pseudophyllodromiidae	Pseudophyllodromiinae	EF363309	EF363281	EF363224	EF363252
<i>Cryptocercus punctulatus</i>	Polyphagidae		U38402	U38403	AB005462	AF220571
<i>Cryptocercus relictus</i>	Polyphagidae		AF322490	AF322491	AB005908	AF220570
<i>Therea petiveriana</i>	Polyphagidae		EF363310	EF363282	—	EF363253
<i>Archimandrita tessellata</i>	Blaberidae	Blaberinae	U17762	U17761	AB014065	—
<i>Blaberus craniifer</i>	Blaberidae	Blaberinae	EF363289	EF363261	EF363218	EF363232
<i>Blaberus discoidealis</i>	Blaberidae	Blaberinae	EF363290	EF363262	EF363220	EF363233
<i>Blaberus giganteus</i>	Blaberidae	Blaberinae	EF363291	EF363263	EF363219	EF363234
<i>Eublabeus distanti</i>	Blaberidae	Blaberinae	EF363295	EF363267	EF363221	EF363238
<i>Eublabeus posticus</i>	Blaberidae	Blaberinae	EF363296	EF363268	EF363222	EF363239
<i>Paradicta rotunda</i>	Blaberidae	Blaberinae	EF363303	EF363275	EF363223	EF363246
<i>Diptoptera punctata</i>	Blaberidae	Diplopterinae	EF363294	EF363266	EF363211	EF363237
<i>Rhabdoblatta formosana</i>	Blaberidae	Epilamprinae	EF363307	EF363279	EF363215	EF363250
<i>Geoscaphheus woodwardi</i>	Blaberidae	Geoscaphinae	AB036132	AB036178	AB036092	AB036184
<i>Macropanesthia rhinoceros</i>	Blaberidae	Geoscaphinae	AB036131	AB036177	AB036091	AB036183
<i>Neogeoscaphheus dahmsi</i>	Blaberidae	Geoscaphinae	AB036134	—	AB036094	AB036186
<i>Parapanesthia pearsoni</i>	Blaberidae	Geoscaphinae	AB036133	—	AB036093	AB036185
<i>Gyna capucina</i>	Blaberidae	Gyninae	EF363298	EF363270	EF363217	EF363241
<i>Gromphadorrhina portentosa</i>	Blaberidae	Oxyhaloinae	EF363297	EF363269	EF363207	EF363240
<i>Henschoutedenia sp.</i>	Blaberidae	Oxyhaloinae	EF363299	EF363271	EF363205	EF363242
<i>Nauphoeta cinerea</i>	Blaberidae	Oxyhaloinae	EF363300	EF363272	EF363206	EF363243
<i>Panchlora nivea</i>	Blaberidae	Panchlorinae	EF363301	EF363273	EF363213	EF363244
<i>Ancaudellia kheili</i>	Blaberidae	Panesthiinae	AB036135	—	AB036095	AB036187
<i>Ancaudellia_marshallae</i>	Blaberidae	Panesthiinae	AB036136	—	AB036096	AB036188
<i>Ancaudellia shawi</i>	Blaberidae	Panesthiinae	AB036137	—	AB036097	AB036189
<i>Caeparia crenulata</i>	Blaberidae	Panesthiinae	AB036145	—	AB036103	AB036197
<i>Miopanesthia deplanata</i>	Blaberidae	Panesthiinae	AB036151	—	AB036105	AB036203
<i>Panesthia ancaudellioides</i>	Blaberidae	Panesthiinae	AB036143	—	AB036101	AB036195
<i>Panesthia angustipennis spadica</i>	Blaberidae	Panesthiinae	AB036138	AB036179	—	AB036190
<i>Panesthia cribrata</i>	Blaberidae	Panesthiinae	EF363302	EF363274	EF363209	EF363245
<i>Panesthia heurni</i>	Blaberidae	Panesthiinae	AB036141	—	AB036099	AB036193
<i>Panesthia saussurei</i>	Blaberidae	Panesthiinae	AB036140	—	AB036098	AB036192
<i>Panesthia transversa</i>	Blaberidae	Panesthiinae	AB036144	—	AB036102	AB036196
<i>Salganea esakii</i>	Blaberidae	Panesthiinae	AB036146	AB036180	AB007513-8	AB036198

Appendix A (continued)

Genus species	Family	Sub-family	12S	16S	COII	18S
<i>Salganea gressiti</i>	Blaberidae	Panesthiinae	AB036148	—	AB007528-9	AB036200
<i>Salganea raggei</i>	Blaberidae	Panesthiinae	AB036149	—	AB036206	AB036201
<i>Salganea taiwanensis rukyuanus</i>	Blaberidae	Panesthiinae	AB036147	AB036181	AB007521	AB036199
<i>Pycnoscelus surinamensis</i>	Blaberidae	Pycnoscelinae	EF363306	EF363278	EF363208	EF363249
<i>Parasphaeria boleiriana</i>	Blaberidae	Zetoborinae	EF363304	EF363276	EF363212	EF363247
<i>Schultesia lampyridiformis</i>	Blaberidae	Zetoborinae	EF363308	EF363280	EF363214	EF363251
<i>Zetobora</i> sp.	Blaberidae	Zetoborinae	EF363311	EF363283	EF363210	EF363254

References

- Abe, T., Bignell, D.E., Higashi, M. (Eds.), 2000. Termites: Evolution, Sociality, Symbioses, Ecology. Kluwer Academic Publishers, Dordrecht.
- Bartz, S.H., 1979. Evolution of eusociality in termites. Proc. Natl. Acad. Sci. USA 76, 5764–5768.
- Brugerolle, G., Silva-Neto, I.D., Pellens, R., Grandcolas, P., 2003. Electron microscopic identification of the intestinal protozoan flagellates of the xylophagous cockroach *Parasphaeria boleiriana* from Brazil. Parasitol. Res. 90, 249–256.
- Castro, F., Williamson, G.B., Moraes de Jesus, R., 1993. Radial variation in the wood specific gravity of *Joannesia princeps*: the roles of age and diameter. Biotropica 25, 176–182.
- Choe, J.C., Crespi, B.J. (Eds.), 1997. The Evolution of Social Behavior in Insects and Arachnids. Cambridge University Press, Cambridge.
- Crespi, B.J., 1994. Three conditions for the evolution of eusociality: are they sufficient? Ins. Soc. 41, 395–400.
- D'Haese, C., 2002. Were the first springtails semi-aquatic? A phylogenetic approach by means of 28S rDNA and optimization alignment. Proc. R. Soc. Lond. B 269, 1143–1151.
- Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucl. Acids Res. 32, 1792–1797.
- Gäde, G., Grandcolas, P., Kellner, R., 1997. Structural data on hypertrehalosaemic neuropeptides from *Cryptocercus punctulatus* and *Therea petiveriana*: how do they fit into the phylogeny of cockroaches? Proc. R. Soc. Lond. B 264, 763–768.
- Gerbod, D., Noël, C., Dolan, M.F., Edgcomb, V.P., Kitade, O., Noda, S., Dufernez, F., Ohkuma, M., Kudo, T., Capron, M., Sogin, M.L., Viscogliosi, E., 2002. Molecular phylogeny of parabasalids inferred from small subunit rRNA sequences, with emphasis on the Devescovinidae and Calonymphidae (Trichomonadea). Mol. Phyl. Evol. 25, 545–556.
- Giribet, G., Carranza, S., Bagui, J., Riutort, M., Ribera, C., 1996. First molecular evidence for the existence of a tardigrada + arthropoda clade. Mol. Biol. Evol. 13, 76–84.
- Goloboff, P.A., 1999. Analysing large data sets in reasonable times: solutions for composite optima. Cladistics 15, 415–428.
- Grandcolas, P., 1993. Monophylie et structure phylogénétique des [Blaberinae + Zetoborinae + Gyninae + Diplopterinae] (Dictyoptera: Blaberidae). Ann. Soc. Entomol. Fr. (N.S.) 29, 195–222.
- Grandcolas, P., 1994a. Phylogenetic systematics of the subfamily Polyphaginae, with the assignment of *Cryptocercus* Scudder, 1862 to this taxon (Blattaria, Blaberoidea, Polyphagidae). Syst. Entomol. 19, 145–158.
- Grandcolas, P., 1994b. Les Blattes de la forêt tropicale de Guyane Française: structure du peuplement (Insecta, Dictyoptera, Blattaria). Bull. Soc. Zool. Fr. 119, 59–67.
- Grandcolas, P., 1994c. Blattaria (Insecta: Dictyoptera) of Saudi Arabia: a preliminary report. In: Büttiker, W., Krupp, F. (Eds.), Fauna of Saudi Arabia, vol. 14, NCWCD, Pro Entomologia, Riyadh, Basle, pp. 40–58.
- Grandcolas, P., 1997. Systématique phylogénétique de la sous-famille des Tryonicinae (Dictyoptera, Blattaria, Blattidae). In: Najt J., Matile, L. (Eds.), Zoologia Neocaledonica, vol. 4, Mémoires du Muséum national d'Histoire naturelle, 171, Paris, pp. 91–124.
- 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., 1999a. El origen de la diversidad en las cucarachas: perspectiva filogenética de su gregarismo, reproducción, comunicación y ecología. In: Melic, A., De Haro, J.J., Mendez, M., Ribera, I. (Eds.), Evolucion y Filogenia de Arthropoda, Bol. S.E.A. 26, Zaragoza, pp. 397–420.
- Grandcolas, P., 1999b. Systematics, endosymbiosis, and biogeography of *Cryptocercus clevelandi* and *C. punctulatus* (Blattaria: Polyphagidae) from North America: a phylogenetic perspective. Ann. Entomol. Soc. Amer. 92, 285–291.
- Grandcolas, P., Deleporte, P., 1996. The origin of Protistan symbionts in termites and cockroaches: a phylogenetic analysis. Cladistics 12, 93–98.
- Grandcolas, P., D'Haese, C., 2001. The phylogeny of cockroach families: is the current molecular hypothesis robust? Cladistics 17, 48–55.
- Grandcolas, P., D'Haese, C., 2002. The origin of a 'true' worker caste in termites: phylogenetic evidence is not decisive. J. Evol. Biol. 15, 885–888.
- Grandcolas, P., Pellens, R., 2002. A new species of the cockroach genus *Parasphaeria* (Dictyoptera: Blattaria: Blaberidae) from the Atlantic forest in Brazil. Trans. Am. Entomol. Soc. 128, 23–29.
- Grandcolas, P., Park, Y.C., Choe, J.C., Piulachs, M.D., Bellés, X., D'Haese, C., Farine, J.P., Brossut, R., 2001. What does *Cryptocercus kyebangensis*, n.sp. from Korea reveal about *Cryptocercus* evolution? A study in morphology, molecular phylogeny and chemistry of tergal glands (Dictyoptera, Blattaria, Polyphagidae). Proc. Acad. nat. Sci. Phila. 151, 61–79.
- Guindon, S., Gascuel, O., 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Syst. Biol. 52, 696–704.
- Hamilton, W.D., 1972. Altruism and related phenomena mainly in social insects. Ann. Rev. Ecol. Syst. 3, 193–232.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Latting, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.
- Kambhampati, S., 1995. A phylogeny of cockroaches and related insects based on DNA sequence of mitochondrial ribosomal RNA genes. Proc. Natl. Acad. Sci. USA 92, 2017–2020.
- Liu, H., Beckenbach, A.T., 1992. Evolution of the mitochondrial cytochrome oxidase II gene among 10 orders of insects. Mol. Phylogenet. Evol. 1, 41–52.
- Lo, N., Tokuda, G., Watanabe, H., Rose, H., Slaytor, M., Maekawa, K., Bandi, C., Noda, H., 2000. Evidence from multiple gene sequences indicated that termites evolved from wood-feeding cockroaches. Curr. Biol. 10, 801–804.
- Maekawa, K., Matsumoto, T., 2000. Molecular phylogeny of cockroaches (Blattaria) based on mitochondrial COII gene sequences. Syst. Entomol. 25, 511–519.
- Maekawa, K., Matsumoto, T., 2003. Biogeography of Japanese wood-feeding cockroaches genus *Salganea* and *Panesthia* (Blaberidae: Panesthiinae). Mol. Phylogenet. Evol. 27, 156–159.
- Maekawa, K., Lo, N., Kitade, O., Miura, T., Matsumoto, T., 1999. Molecular phylogeny and geographic distribution of wood-feeding cockroaches in East Asian islands. Mol. Phylogenet. Evol. 13, 360–376.
- Maekawa, K., Lo, N., Rose, H., Matsumoto, T., 2003. The evolution of soil-burrowing cockroaches (Blattaria: Blaberidae) from wood-burrowing ancestors following an invasion of the latter from Asia into Australia. Proc. R. Soc. Lond. B 270, 1301–1307.

- Maekawa, K., Park, Y.C., Lo, N., 2005a. Phylogeny of endosymbiont bacteria harbored by the woodroach *Cryptocercus* spp. (Cryptocercidae: Blattaria): Molecular clock evidence for a late Cretaceous-early Tertiary split of Asian and American lineages. *Mol. Phylogenet. Evol.* 36, 728–733.
- Maekawa, K., Kon, M., Araya, K., 2005b. New species of the genus *Salganea* (Blattaria, Blaberidae, Panesthiinae) from Myanmar, with molecular phylogenetic analyses and notes on social structure. *Entomol. Sci.* 8, 121–129.
- Matsumoto, T., 1988. Colony composition of the wood-feeding cockroach, *Panesthia australis* Brunner (Blattaria, Blaberidae, Panesthiinae) in Australia. *Zool. Sci.* 5, 1145–1148.
- Mickevich, M.F., Farris, J.S., 1981. The implications of congruence in *Menidia*. *Syst. Zool.* 30, 351–370.
- Myles, T.G., 1988. Resource inheritance in social evolution from termites to man. In: Slobodchikoff, C.N. (Ed.), *The Ecology of Social Behavior*. Academic Press, San Diego, California, pp. 379–423.
- Nalepa, C.A., 1984. Colony composition, protozoan transfer and some life history characteristics of the woodroach *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae). *Behav. Ecol. Sociobiol.* 14, 273–279.
- Nalepa, C.A., 1988. Cost of parental care in the woodroach *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae). *Behav. Ecol. Sociobiol.* 23, 135–140.
- Nalepa, C.A., Bignell, D.E., Bandi, C., 2001. Detritivory, coprophagy, and the evolution of digestive mutualisms in Dictyoptera. *Ins. Soc.* 48, 194–201.
- Nixon, K.C., 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15, 407–414.
- Park, Y.C., Grandcolas, P., Choe, J.C., 2002. Colony composition, social behavior and some ecological characteristics of the Korean wood-feeding cockroach (*Cryptocercus kyebangensis*). *Zool. Sci.* 19, 1133–1139.
- Pellens, R., Grandcolas, P., Silva-Neto, I.D., 2002. A new and independently evolved case of xylophagy and the presence of intestinal flagellates in cockroaches: *Parasphaeria boleiriana* (Dictyoptera, Blaberidae, Zetoborinae) from the remnants of Brazilian Atlantic Forest. *Can. J. Zool.* 80, 350–359.
- Pellens, R., Legendre, F., Grandcolas, P., 2007. Phylogenetic analysis of social behavior evolution in [Zetoborinae + Blaberinae + Gyninae + Diplopterinae] cockroaches: an update with the study of endemic radiations from the Atlantic forest. *Stud. Neotr. Fauna Environ.* 42, 25–31.
- Posada, D., Crandall, K.A., 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14, 817–818.
- Roisin, Y., 1999. Philopatric reproduction, a prime mover in the evolution of termite sociality? *Ins. Soc.* 46, 297–305.
- Roth, L.M., 2003. Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). *Oriental Insects* 37, 1–186.
- Roth, L.M., Willis, E.R., 1960. The biotic associations of cockroaches. *Smithson. Misc. Coll.* 141, 1–470.
- Taylor, V.A., 1978. A winged élite in a subcortical beetle as a model for a prototermite. *Nature* 276, 73–75.
- Taylor, P.D., Irwin, A.J., 2000. Overlapping generations can promote altruistic behavior. *Evolution* 54, 1135–1141.
- Thompson, G.J., Kitade, O., Lo, N., Crozier, R.H., 2000. Phylogenetic evidence for a single, ancestral origin of a 'true' worker caste in termites. *J. Evol. Biol.* 13, 869–881.
- Thorne, B.L., 1997. Evolution of eusociality in termites. *Ann. Rev. Ecol. Syst.* 28, 27–54.
- Wheeler, W.C., 1995. Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data. *Sys. Biol.* 44, 321–331.
- Wheeler, W.C., 1996. Optimization alignment: the end of multiple sequence alignments in phylogenetics? *Cladistics* 12, 1–9.
- Wheeler, W.C., Gladstein, D.S., De Laet, J. 1996–2003. POY version 3.0. American Museum of Natural History.
- Whiting, M., Carpenter, J., Wheeler, Q., Wheeler, W., 1997. The Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. *Syst. Biol.* 46, 1–68.
- Wilson, E.O., 1971. *The Insect Societies*. Belknap Press, Cambridge, Massachusetts.
- Wilson, E.O., 1975. *Sociobiology: The New Synthesis*. Belknap Press, Cambridge, Massachusetts.
- Xiong, B., Kocher, T.D., 1991. Comparison of mitochondrial DNA sequences of seven morphospecies of black flies (Diptera: Simuliidae). *Genome* 34, 306–311.
- Zhuzhikov, D.P., 2001. Autocoprophagy is a precursor of proctodeal trophallaxis in cockroaches and termites. *Zool. Zh.* 80, 403–411.