

## Review article

# Termites and trees: a review of recent advances in termite phylogenetics

*Dedicated to Professor Ch. Noirot*

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**Summary.** Modern termite phylogenetics is critically reviewed, with an emphasis on tree topologies as phylogenetic hypotheses. Studies have especially concentrated on (1) the position of Isoptera among the Dictyoptera and (2) the family group relationships within the Isoptera. The first of these problems is still controversial; although the weight of evidence now suggests that termites are nested within the cockroaches, thus making “Blattaria” as presently constituted paraphyletic. The exact position of termites within the cockroaches is uncertain, although *Cryptocercus* is the most plausible sister group.

Family groups relationships are rather better resolved. Mastotermitidae is now generally accepted to be the most basal termite group. Termopsidae, Hodotermitidae and Kalotermitidae are all basal to (Termitidae + Serritermitidae + Rhinotermitidae), although their relative positions within that part of the tree are disputed. Most recent studies support a sister group relationship for Serritermitidae and (Termitidae + Rhinotermitidae). However, no study has yet unambiguously found the Rhinotermitidae monophyletic. The Termitidae are well established as monophyletic and as the most apical termite family. However, within the Termitidae the monophyly of none of the subfamilies is well established, making subfamily level analyses unreliable.

A number of problem areas are identified: (1) poor taxon sampling is a universal problem, (2) higher taxonomic groupings are often assumed to be monophyletic *a priori* without adequate support, (3) datasets are collected from different taxa and character systems without consideration of the overall international effort.

**Key words:** Isoptera, cladistics, molecular systematics, morphological systematics, Dictyoptera.

## Termite trees: introduction

Termites are studied by biologists for a number of reasons. They are eusocial insects with extraordinarily complex social

systems, and they represent the only major non-hymenopteran fully-social arthropods. They are also very important ecological players in tropical ecosystem, having been described as “ecosystem engineers” due to their important role in providing soil ecosystem services. These services include: distribution, protection and stabilisation of organic matter, increasing microsite heterogeneity, the genesis of soil microaggregates and porosity, humification, the release of immobilised N and P, the improvement of drainage and aeration, and an increase in exchangeable cations (Lavelle et al., 1997; Holt and Lepage, 2000; Donovan et al., 2001).

Several theories have been proposed to explain such disparate elements of termite biology as the role of gut symbionts, the structure of soldier defence strategies, nest-architecture, and the origin of eusociality. None of these theories, however, have the element that would allow their testing – a robust tree of evolutionary relationships.

In this paper I critically review recent attempts that have been made to provide rigorous phylogenetic trees for (1) the position of termites within the Dictyoptera, and (2) the internal phylogeny of the termites.

In order to simplify what follows I will discuss here only studies with explicit tree topologies or those that have a direct potential bearing on tree topology (see Table 1). I attempt no major criticism of cladistic methodologies or methods of sequence alignment. My comments come entirely from my knowledge of termite systematics and are inevitably biased by my own background as a morphological systematist and global ecologist whose aim is a generic level phylogeny for termites.

## Roots: relationships within Dictyoptera

Termites are uncontroversially placed within the Orthopteroid group of insect orders (Boudereaux, 1979; Hennig, 1981). Also generally accepted is that termites, mantids and cockroaches form a monophyletic group, the Dictyoptera. Mantids and termites are also both almost certainly monophyletic

**Table 1.** Summary of recent phylogenetic studies involving tree reconstruction that are discussed in the text

Subject	Reference	Data used	Method of analysis
Morphological phylogenetics of Dictyoptera (7 family-level taxa)	Thorne and Carpenter (1992)	70 behavioural and developmental characters	Maximum parsimony
Molecular phylogenetics of Dictyoptera (36 species)	Kambhampati (1995)	~ 415 bps, 16s rRNA ~ 430 bps, 12s rRNA	Maximum parsimony
Molecular phylogenetics of Dictyoptera (16 species)	Lo et al. (2000)	~ 1700 bps, 18s rRNA ~ 670 bps, COII ~ 1000 bps, endo- $\beta$ -1,4-glucanase	Maximum likelihood
Morphological phylogenetics across the Isoptera (49 species)	Donovan et al. (2000)	96 worker characters 93 soldier characters 7 biological characters	Maximum parsimony
Molecular phylogenetics of termite families (10 species)	Kambhampati et al. (1996)	~ 415 bps, 16s rRNA	Maximum parsimony Neighbour joining
Molecular phylogenetics of termite families (20 species)	Kambhampati and Eggleton (2000)	~ 430 bps, ND5	Maximum parsimony (with successive character weighting)
Molecular phylogenetics of termites families (12 species in most relevant analysis)	Thompson et al. (2000)	~ 610 bps, COII ~ 880 bps, 16s rRNA	Maximum likelihood
Molecular phylogenetics of Termitidae (15 species)	Miura et al. (1998)	~ 680 bps, COII Translated amino acid sequences	Unweighted parsimony and neighbour joining using bps and translated amino acid sequences
Molecular phylogenetics of Pacific <i>Nasutitermes</i> (17 species)	Miura et al. (2000)	~ 680 bps, COII ~ 790 bps, 16S rRNA	Maximum parsimony Neighbour joining
Molecular phylogenetics of Australian Kalotermitidae (25 species)	Thompson et al. (2000)	~ 620 bps, COII gene ~ 1060 bps, Cytb gene	Maximum likelihood

groups. The relationships of the three orders within the Dictyoptera clade, however, have been vigorously debated.

There are presently three plausible but divergent hypothesis concerning dictyopteran relationships (Fig. 1):

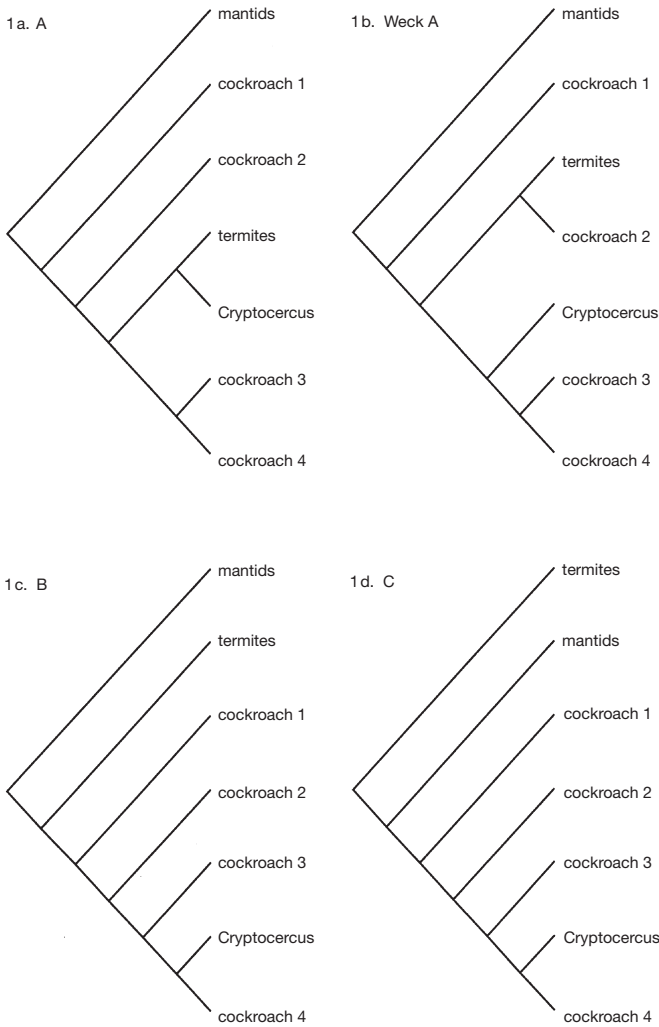
1. *Cryptocercus* is the sister group of the termites and so cockroaches as presently constituted are paraphyletic. I will call this hypothesis A. Cleveland et al. (1934) (Fig. 1 a) first suggested that termites might be closely related to the social wood-feeding cockroach *Cryptocercus* on the basis of similar behaviours, shared flagellate gut symbionts and a striking morphological similarity between lower termite pseudergates and *Cryptocercus* nymphs. A weaker version of this hypothesis is that the sister group of the termites is a, as yet unspecified, cockroach taxon (Fig. 1 b).

2. Cockroaches and termites are sister groups and so cockroaches are monophyletic. I will call this hypothesis B (Fig. 1 c – this one of two topologies proposed in Hennig, 1981).

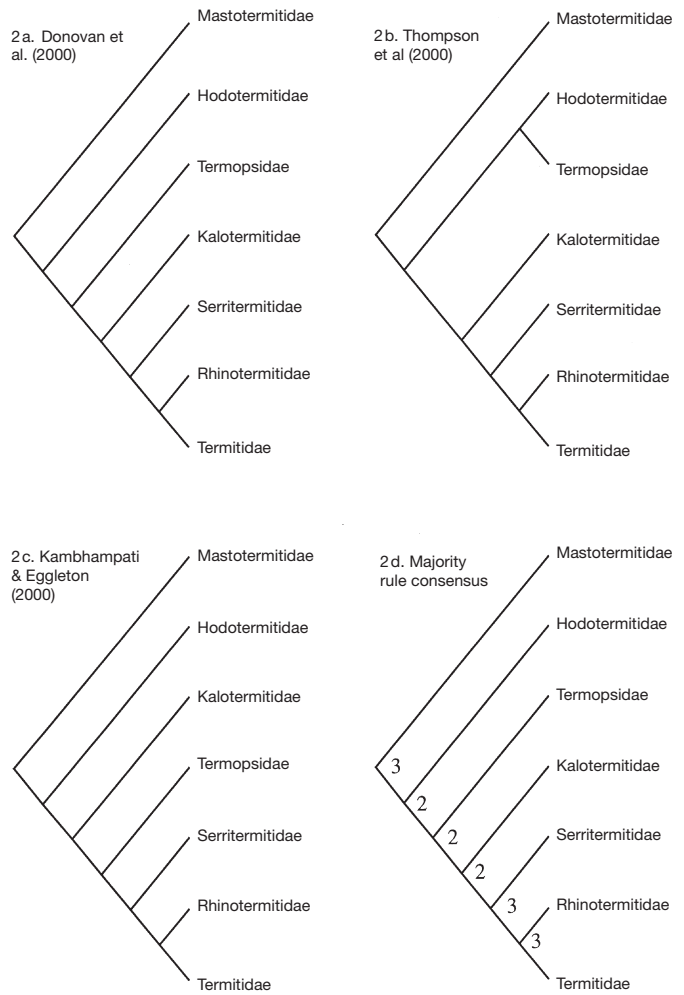
3. Termites are the sister group of a mantid + cockroach clade and *Cryptocercus* is nested within a cockroach clade (Fig. 1 d). I will refer to this hypothesis C (as suggested by Boudreaux, 1979). The exact position of *Cryptocercus* is debated (e.g. Grandcolas and Deleporte, 1996) but if distantly related to termites its exact position is not relevant here.

Until 1990 the, largely untested, sister group relationship between *Cryptocercus* and the Isoptera was generally accepted (although see Nalepa and Bandi, 2000 for a discussion of other views). However, Thorne (1990) proposed that the similarity in morphology between termites and *Cryptocercus* was convergent, and, perhaps most importantly, that the gut flagellates of termites may have been acquired by feeding on cadavers of *Cryptocercus* living in the same woody substrates – a process known as transfaunation. This idea was supported by the finding that naturally sympatric species of *Zootermopsis* (Termopsidae) and *Cryptocercus* show aggressive behaviour to each other involving feeding on the dead bodies of those killed during the encounters. This feeding, and experimental work showing that the flagellates could pass from one species to another, gave a counter argument against one set of putative synapomorphies supporting the proposed *Cryptocercus*/termite sister group relationship in hypothesis A.

Along with this argument based on evolutionary plausibility, Thorne and Carpenter (1992) conducted a phylogenetic analysis of the main Dictyoptera groupings using morphological and behavioural characters. They found support for the topology of hypothesis C, with a monophyletic Blattaria including *Cryptocercus*, a sister group relationship between this Blattaria and the mantids, and a sister group



**Figure 1.** Alternative Dictyopteran phylogenies. See text for full details. Numbers after cockroach names indicates separate (unspecified) cockroach clades



**Figure 2.** Family level phylogenies for termites. Final tree shows majority rule consensus tree for the three studies with numbers indicating the number of studies supporting a particular node

relationship between this Blattaria+mantid group and the Isoptera (but see re-evaluation in Kristensen, 1991 that appears to support hypothesis B). In addition, and again in line with the transfaunation scenario, the Termopsidae were found to be the most basal termite family (of only three discussed). Molecular sequences (16S and 12S rRNA) analysed in Kambhampati (1995) supported this topology, although bootstrap values were low for some important nodes (i.e. see Fig. 2 of that paper) and only three termite species were included. In many entomologists' minds, especially in the US, this apparently emphatic support for topology C seemed to be the last word and has now found its way into textbooks (e.g. Gullen and Cranston, 2000, where it is cited as a classic example of convergence).

Advocates for hypothesis A (at least in its weaker form, Fig. 1b), however, were quick to provide data that apparently contradicts hypothesis C. A series of papers published since Nalepa's (1991) response to Thorne (1990), have shown that there are a number of apparent synapomorphies

between cockroaches and termites in addition to the shared flagellate protozoa. These include: the structure of the proventriculus (Klass, 1998b) and ovipositor (Klass, 1998a), the presence of *Blattabacterium* in bacteriocytes (Bandi and Sacchi, 2000), and the structure of the oothecae and elements of oviposition biology (Nalepa and Lenz, 2000). Note that many of these synapomorphies are really only apparent when *Mastotermites* is assumed to be the most basal termite (see below). In addition, many morphological characters are difficult to polarise within the Dictyoptera due to paedomorphosis in termites and key groups of cockroaches (Nalepa and Bandi, 2000) and the highly derived nature of such characters in the entirely predatory mantids.

Two recent papers using similar molecular datasets (Mackawa et al., 1999; Lo et al., 2000) have concluded that termites are nested within the cockroaches. The most relevant of these studies to termite phylogenetics, the Lo study, used 18s rRNA, COII, and endogenous endo-β-1,4-glucanase (EG)

sequences, and showed strong statistical support for a sister group relationship between *Cryptocercus* (two species) and the study group termites (six species) for both a combined 18S RNA/COII analysis and the EG sequences. Note, however, that the EG gene was not found in mantids and so does not in fact contradict the possibility of, for example, a termite + mantid or *Cryptocercus* + mantid clade, although other relevant data makes this result seem very unlikely. The Lo study clearly contradicts hypotheses B and C, but taxon sampling is too scanty to discount the weaker form of hypothesis A.

After all this work, much still remains uncertain. However, my present interpretation of the evidence presented above is that termites probably *are* eusocial cockroaches but that their exact position has not yet been firmly established (i.e. I support some version of hypothesis A). The growing weight of morphological and molecular evidence appears to make a (mantids + cockroaches) sister to (termites) relationship a more remote possibility than was previously thought. However, some workers have suggested that the divergence rate of cockroaches, mantids and termites was so rapid that resolution of the branching order of the taxa may, in any case, be extremely difficult (Nalepa and Bandi, 2000).

This conclusion does not necessarily have a bearing on the transfaunation question. Until a more representative and comprehensive set of cockroaches is added to the dictyopteran sequence dataset transfaunation must remain a formal possibility; this time postulated as transfer between relatively closely related “cockroach” species. It certainly seems premature to suggest that “horizontal transfer of cellulolytic symbionts between the ancestors of termites and *Cryptocercus*... (appears) ... untenable” (Lo et al., 2000). However, two of the main requirements of the transfaunation *phylogenetic* scenario, (a) distant relatedness between *Cryptocercus* and Isoptera and (b) that the most basal termite is a wood nesting termopsid (see below), are not now strongly supported.

It is perhaps unfortunate that so much controversy has accumulated over the placement of *Cryptocercus*. If *Cryptocercus* did not exist, with its tantalising “missing link” characteristics, the weight of evidence for the monophyly of (Blattaria + Isoptera) would still be considerable.

### Major trunks: termite families

Termite family relationships have been discussed since the time of pioneer termite systematists, especially by the early 20<sup>th</sup> Century termitologist, Holmgren. However, it is only recently that modern systematic methodology has been used to address the question.

There have been a number of recent partial phylogenetic treatments. Noirot's (1995) detailed analysis of the gut structure of the non-termitid families indicated numerous potential synapomorphies within and between families. However, he did not present a formal cladistic analysis and his phylogenetic conclusions were intended to be provisional. Other studies (e.g. Thorne and Carpenter, 1992; Vawter, 1991; Kambhampati et al., 1996) did not include a full complement of families.

There are three studies that have a full complement of families. These are: Kambhampati and Eggleton (2000), using the mitochondrial NADH 5 dehydrogenase gene; Thompson et al. (2000), using mitochondrial 16S rRNA and CO II genes; and Donovan et al. (2000) using morphological characters of soldiers and workers. Encouragingly, although these studies used different sets of character systems, they give broadly similar results (Fig. 2). I think it is fair to say that a consensus has now emerged concerning most of the family-level tree, although some areas of uncertainty remain. Figure 2d shows a majority rule consensus tree for the three studies. However, this consensus tree has only heuristic utility, as the resolution of complex patterns of interactions between the datasets will only become apparent when they are (hopefully) combined in a total evidence analysis. However, such an analysis is not yet possible with any degree of accuracy, due to the different exemplar taxa that were chosen for each study. A number of interesting points arise from these studies.

*Mastotermitidae*. It is now well established that *Mastotermes* is the most basal termite group. Its mixture of apparently “primitive” and apparently “advanced” features has proven confounding in the past, and the Termopsidae have often been regarded as phylogenetically most “primitive” (e.g. see Thorne and Carpenter, 1992). However, the molecular evidence seems convincing, and additional morphological analyses using cockroaches as outgroups (Donovan et al., unpublished data – the original analysis used *Mastotermes* as an outgroup) unambiguously show the same relationships.

*Termopsidae and Hodotermitidae*. Thompson et al. find these families to be sister groups while the other two studies find Hodotermitidae to be basal to the Termopsidae. Note that Noirot's (1995) paper on sternal glands provides additional support for a Termopsidae + Hodotermitidae clade. However, the Kambhampati and Eggleton, and Donovan, trees reverse the positions of the Termopsidae and Kalotermitidae.

The Thompson study uses statistical likelihood measures to judge support for a number of alternative phylogenetic hypotheses (including Figs. 2a and 2b). This cannot completely resolve relationships (as is perhaps implied in that paper) as all the likelihoods are judged against the Thompson study sequence data alone. This argument is circular and it inevitable that alternative hypotheses will be statistically less favoured. This reasoning seems based on the implicit assumption that the gene sequences employed in the Thompson paper inevitably contain a reliable signal of the true phylogeny, and that all that is required is an efficient way to recover that signal. Similar arguments could be used to assert the statistical superiority of the other datasets (e.g. those of Figs. 2a and 2b) by testing the Thompson topology against them and finding it statistically “inferior”. What is needed is a combined analysis on an agreed shared group of taxa (such data do not yet exist).

*Kalotermitidae*. Two out of three of the studies show the Kalotermitidae as the sister group of the Rhinotermitidae + Serritermitidae + Termitidae (Fig. 2). The Kalotermitidae + Mastotermitidae clade proposed by earlier workers (e.g. Krishna, 1970) is not supported on any of the three sets of trees.

*Serritermitidae*. All three of the critical datasets show the Serritermitidae as the sister group of the (Rhinotermitidae + Termitidae) (Fig. 2). This differs from earlier hypotheses of relationships which have placed the family within (or as sister to) the Rhinotermitidae (e.g. Noirot, 1995) or as sister to Termitidae (Krishna, 1970). However, poor taxon sampling within the Rhinotermitidae makes this position provisional, especially given doubts concerning the monophyly of the Rhinotermitidae (see below).

*Serritermitidae, Rhinotermitidae and Termitidae*. There is an almost universal consensus throughout the termite systematics literature that Serritermitidae + Rhinotermitidae + Termitidae form a monophyletic group. The exact relationships within the group are, however, still open to debate (see below).

*Monophyly of families*. Although the basic relationships between particular indicative taxa show similar patterns throughout the recent studies, the monophyly of at least one of the presently recognised families is open to doubt: none of the existing studies have sufficiently comprehensive taxon sampling to test the monophyly of the Rhinotermitidae. This family is extremely heterogenous morphologically and has no clearly defined morphological synapomorphies (e.g. see Kambhampati and Eggleton, 2000). The COII subset of Thompson's data (for which a greater number of rhinotermitid taxa were sequenced than for the other gene that was used) finds the Rhinotermitidae to be polyphyletic. Although the authors point out that a topology with the Rhinotermitidae constrained to be monophyletic is statistically just as likely, I think it quite probable that the group is not monophyletic.

Morphological and molecular work suggest that the following families are almost certainly monophyletic: Hodotermitidae, Termopsidae (but see Klass et al., 2000, regarding the Stolotermitinae), Kalotermitidae, and Termitidae.

### The main bough: subfamily relationships within Termitidae

Only two recent studies, Miura et al. (1998) and Donovan et al. (2000) have examined sub-family level relationships within the Termitidae.

The Donovan study (which was also discussed above at the family level) has the best taxon sampling (for the Termitidae) of any study so far attempted. However, it suffers from a number of serious flaws. First, the tree produced is well resolved, but poorly supported at most nodes. This was because the worker and soldier characters produced strongly

incongruent topologies. Second, even here the taxon sampling is poor for some groups (e.g. the Hodotermitidae is represented by only one taxon, the Kalotermitidae and Rhinotermitidae by only two). Third, the characters chosen for the study were based on characters used in polyclave (i.e. multiple entry) computer keys and relatively little effort was put into re-examining them in a phylogenetic context.

Worker mandible characters perhaps best exemplify the problem of phylogenetic incongruence and this problem is most apparent with the Termitidae, as the family has the widest range of trophic specialisations. Although used extensively in some of the earliest phylogenetic studies (e.g. Ahmad, 1950) and forming a substantial part of the Donovan dataset, there is growing evidence that mandible characters are not good phylogenetic markers. Similar mandibular forms appear to have evolved numerous times (e.g. the *Nasutitermes*-group Nasutitermitinae in Madagascar and South-east Asia show strikingly similar parallel diversification in feeding strategies and associated mandible structure, Eggleton and Davies, in press). In any phylogenetic analysis these ecologically correlated characters will clearly add considerable noise to tree reconstructions within the Termitidae.

The Miura study is the first to use molecular sequence data for termitid subfamilies. However it lacks a number of key taxa and assumes monophyly of subfamilies. There is, for example, uncertainty about the monophyly of Termitinae (critical taxa: *Foraminitermes*, *Labritermes* and the *Amitermites*-group), Nasutitermitinae (critical taxon: the *Cornitermes*-group), and Macrotermitinae (critical taxon: *Sphaerotermites*). This problem is emphasised by the difficulty of proving monophyly even in the relatively well taxon-sampled Donovan study, where monophyly was not established for any of the presently constituted sub-families. Relationships in the Miura study may therefore simply indicate the positions of individual members of paraphyletic (or even polyphyletic) groups.

Overall, then, it seems that the subfamily classification is not yet stable enough to allow an analysis of sub-families and that analyses should be conducted at the generic level or below to allow proper tests of monophyly. Neither of the two existing studies takes us very far.

### Some branches: species-level studies within families

*Pacific Nasutitermes*. Miura et al. (2000) present a phylogenetic analysis of a sample of the highly speciose pantropical genus *Nasutitermes* from the Oriental, Neotropical, Australasian and Papuan regions using COII and 16S rRNA sequences. They conclude that the Australian and South American species form monophyletic groups, but that the New Guinea and Asian species are polyphyletic, with one set of Asian/New Guinea species (those close to *N. matangensis*) being most closely related to the Neotropical clade.

Although revealing a number of interesting patterns, the major problem with the study is that *Nasutitermes* is clearly not a monophyletic group, and that it is becoming obvious that many presently recognised nasute genera (e.g. all Ma-

lagasy nasutes, many south-east Asian genera including *Bulbitermes*) are probably nested within the genus. Given this, the choice of the species within the grade labelled *Nasutitermes* is inevitably arbitrary and due to accidents of nomenclatural history. One good example of this exists in the Miura study taxa: *Nasutitermes longinasus* does not have the defining characteristics of *Nasutitermes* and is clearly derived from a paraphyletic Asian assemblage of “*Nasutitermes*” (Gathorne-Hardy, pers. comm.). Had this species already been split taxonomically from *Nasutitermes*, it would have been automatically excluded from the Miura study.

*Other studies.* A few other studies have examined smaller scale phylogenetic patterns, generally as part of taxonomic revisions. These include: Miller (1986) for the basal Nasutitermitinae, Miller (1991) for Australian *Termes*-group species, Constantino (1995) for *Syntermes*, Cancellato and Myles (2000) for mandibulate nasutes, Roisin et al. (1996) for Antillean Nasutitermitinae, Thompson et al. (in press) for Australian Kalotermitidae and Sands (1999) for *Amicotermes*. None of these have had major consequences for the phylogenetics of the Isoptera as a whole.

### Trees and leaves: taxon sampling as a major problem

All studies of termite phylogenetics have a major taxon-sampling problem. This problem is most pronounced for molecular studies, but also besets the present morphological studies.

The recent batch of studies using the COII gene nicely illustrates the problem of taxon sampling. There are at least seven papers that use this gene to investigate Dictyopteran relationships (including some cockroach papers not listed in Table 1). In total there are ~80 species-level gene sequences spread over all the papers – an average of only ~11 species per paper. It seems clear that these data would have been better analysed as a single dataset by an international consortium. However, increasing pressure on researchers to publish tends to work against such time consuming concerted efforts.

Morphological work, although in many ways more time consuming, can generally tackle a wider taxon sample than analogous molecular work. Molecular work requires material stored in particular ways, of not more than a certain age, and even then obtaining a sequence is never certain. Clearly in multi-gene studies a shortage of material will tend to limit the comprehensiveness of the research. For termites, a wide range of taxa are required to develop a meaningful phylogeny, but we already know that morphological data alone are unlikely to fully resolve relationships (Donovan et al., 2000). These limitations must be overcome if termite phylogenetics is to proceed further. I believe that only by developing truly international collaborative projects will they be addressed.

A related problem within termite phylogenetics is the need to attach external significance to taxon sampling choices in order to ensure publication in high impact journals. Such external factors have included: the evolution of

the “true” worker cast (Thompson et al., 2000a), the evolution of feeding/defence strategies (Thompson et al., in press), and biogeographical considerations (Miura et al., 2000). One consequence of this has been a desire to resolve relationships at very high taxonomic levels (e.g. families and sub-families). This in itself has led to innate taxon sampling deficiencies as many of the basal families have very few species and the most apical family (Termitidae) has about 60% of all species. In addition, as I commented earlier in the paper, the monophyly of many higher taxonomic groupings has not been satisfactorily proven.

### Conclusions

1. The last ten years has seen an enormous increase in the number of termite phylogenetics papers. Many previously uncertain hypotheses of relationships are now much more firmly established. These include: the relationship between termites and cockroaches, the position of *Mastotermes*, and the monophyly of both the [Serritermitidae + Rhinotermitidae + Termitidae] and the Termitidae.

2. Inadequate taxon sampling has had a major influence on the findings of papers reviewed here: in every study so far attempted, phylogenetically key taxa are missing. My view is that future research into termite phylogenetics should concentrate more fully on taxon sampling across the whole phylogenetic range of the group, and should construct plausible large scale phylogenies before general questions of biological significance are asked.

3. Intimately linked to 2., *a priori* assumptions of monophyly of groups have led to a number of serious problems with interpretation of trees. Much more bottom-up analyses of taxa at (at least) the generic level are required to resolve these monophyly problems, before higher taxonomic level analyses are attempted. Note that this problem is exacerbated by the absence of good modern works on termite morphological systematics. For example, the present Termitidae subfamily classification is implicitly based on Sands (1972), a revisionary monographic work that was intended to be only a preliminary step towards a stable classificatory system.

4. Morphological and molecular studies are not being integrated. There is a pressing need for studies that employ as wide a range of both morphological and molecular character systems as possible. As importantly, an internationally agreed set of taxa for analysis is vital. Without such an agreed “core set” any attempts at combined analyses will be problematical.

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