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Phylogeny

Invited reply

Response to Lo *et al.*

There is a constant tension between the findings of phylogenetic analyses and the expression of those findings in a classification. This is predominantly because the Linnean system was not designed to accommodate the multiple ranks necessary for groups with large numbers of clades. This problem is compounded by the tendency of earlier taxonomists to emphasize large within-clade differences in their classification, so that groups like birds and tetrapods were given an inflated taxonomic rank, because there were large phenotypic differences between those groups and their sister taxa. In modern systematic practice, sister groups (i.e. those of the same age) should be given the same taxonomic rank, although in reality it has proven to be very difficult to achieve. This tension has led some taxonomists to propose the abandonment of the Linnean system completely, to be replaced with a system of rank-free clade names (Cantino & DeQueiroz 2006).

Termites represent a particularly good example of this problem. Their extraordinary social structures, nest architecture and ecological impact make them appear very distinctly different from other Dictyoptera. However, it is clear now, from our work and several others, that these differences are all anagenetic, that is they have occurred entirely within the termite lineage, and that these differences are linked predominantly to a shift to eusociality. The closest living relative of the termites is the woodroach, *Cryptocercus*, which is very clearly a cockroach. Termites are therefore derived from cockroaches, and in phylogenetic terms, they *are* cockroaches. The real question then becomes (as highlighted by Lo *et al.* 2007), what is the best rank and name for termites within the cockroaches?

We attempted to answer this question in our recent paper (Inward *et al.* 2007), and it is perhaps worth reiterating the logic behind our proposal here:

(i) Because termites are clearly nested phylogenetically within cockroaches, they cannot be assigned an ordinal rank, as this would mean that one order was a subset of another.
(ii) Given this, it is necessary to fit the classification of the contained group (termites) into the classification of the containing group (cockroaches).
(iii) Within the cockroach classification, the sister group of the termites (*Cryptocercus*) is widely recognized as a family (Cryptocercidae).
(iv) Sister taxa should ideally be given the same rank; therefore, termites must be assigned a familial rank.
(v) The only available family name for termites is Termitidae, based on the oldest available termite generic name, *Termes* Linnaeus, 1758.
(vi) Given this, all taxonomic rankings within the termites must be shifted down a rank (e.g. families become subfamilies). The internal elements within the termites remain otherwise the same. This represents purely an exercise in renaming.

The above argument is based solely on the fact that *Cryptocercus* is the sister group of the termites, which is the case regardless of whether the topology in Klass & Meier (2006) or Inward *et al.* (2007) is true.

We believe that, beyond this systematic logic, there are other general advantages in a classification that places termites as a family of cockroaches. The main one is that it stresses the very close phylogenetic relatedness of all termites (family Termitidae), a situation directly analogous to the ants (family Formicidae). The similarities between the two groups are then striking: two relatively small insect families nested within a larger, generally solitary, group of species, but having an enormous ecological impact because they have developed eusociality. The conceptual value of having the same taxonomic rank for the two groups is therefore considerable.

Weighed against these considerations are the legitimate, if somewhat narrowly focused, concerns expressed in the response to Inward *et al.* Of particular concern to Lo *et al.* 2007. is the reclassification of termites as the family Termitidae, which would confuse the long-standing use of 'Termitidae' for the largest clade of termites. It would also cause confusion because the other families and their nominate subfamilies would go down a rank (e.g. Rhinotermitidae and Rhinotermitinae become Rhinotermitinae and Rhinotermitini). From a more general biological perspective, the difficulties caused to termitologists may not really weigh very heavily against the gain of clarity. However, it is the termitologists who will decide which system prevails, by their constant use of a particular classification, and this is the major reason why we feel it is sensible to try to find a compromise.

Lo *et al.* 2007 have three main proposals. Their preferred one is to retain Isoptera as an unranked name within Blattodea. However, we believe that this is both unnecessary and unsatisfactory, since *Cryptocercus* is both a cockroach and the sister group to the termites, so the two lineages should have a name whose rank is subordinate to order. The second proposal is to treat the lineages as superfamilies, but this would merely inflate all the cockroach names by one rank, which is undoubtedly not desirable. The third proposal, the use of the epifamily rank, however, overcomes all these problems by assigning a rank to termites between family and superfamily and has the advantage of having minimal impact on either the termite or the cockroach classification (figure 1). We therefore propose the new epifamily Termitoidae for the termites (type genus *Termes* Linnaeus, 1758), and the new epifamily Cryptocercoidae (type genus *Cryptocercus* Scudder, 1862) for the *Cryptocercus* lineage (figure 1). Additionally, we propose the new epifamily Blattoidae (type genus *Blatta* Linnaeus, 1758) for the lineage which includes the Blattidae, since otherwise this would be the only one of the three lineages in the superfamily Blattoidea in our cladogram without a name.

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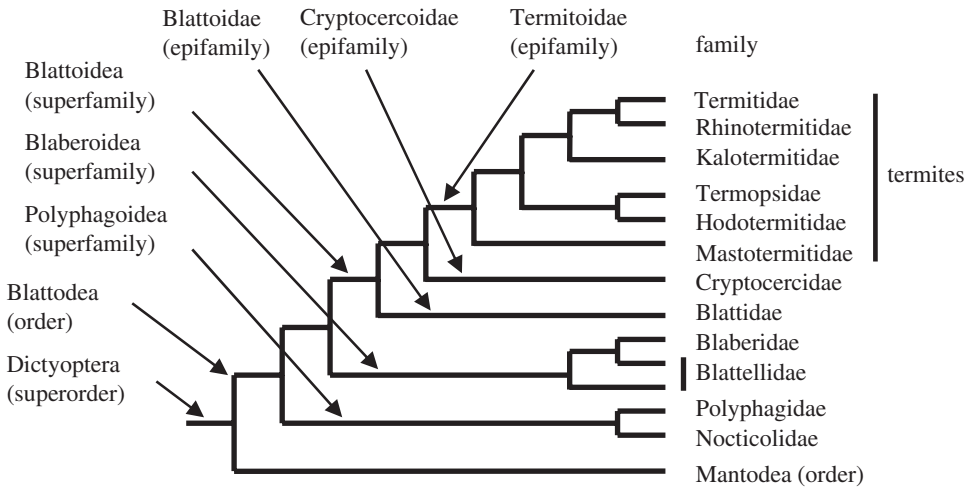

Figure 1. Proposed epifamily classification shown on the tree topology from Inward *et al.* (2007).

We hope that this response to Lo *et al.*'s 2007 critique and the new classification we propose will lay the foundation for classificatory stability, while emphasizing the strongly corroborated hypothesis that termites are eusocial cockroaches.

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