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Integrating molecular phylogenetic results into ant taxonomy (Hymenoptera: Formicidae)

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Abstract

The ongoing molecular revolution in ant systematics, of which Ross Crozier was an early proponent and practitioner, has led to remarkable progress in our understanding of ant phylogeny. In this review I consider the interplay between molecular and morphological evidence, and the integration of molecular phylogenetic results into ant classification. New phylogenetic findings indicate that most ant subfamilies and genera are monophyletic, but there are some significant exceptions, including the subfamily Cerapachyinae and several large and species-rich ant genera (*Amblyopone*, *Aphaenogaster*, *Camponotus*, *Cerapachys*, *Messor* and *Pachycondyla*, among others). These non-monophyletic groups are manifestations of two different phenomena: (1) convergence in morphology and (2) heterogeneity in rates of morphological evolution. Granivorous ants in the genus *Messor* are an example of the former: molecular phylogenetic analysis indicates that the New World and Old World *Messor* are separate lineages that independently evolved similar derived morphology. Heterogeneity in rates of evolution is exemplified by highly divergent army ants and certain other dorylomorphs – currently assigned to different genera, tribes and subfamilies – that are nested phylogenetically within a group of morphologically plesiomorphic species, most of which are placed in a single genus (*Cerapachys*). This presents a classificatory conundrum if we wish to maintain a Linnaean (i.e., ranked) classification system in which all named taxa are monophyletic and easily diagnosed. Nevertheless, despite the conceptual appeal of a rank-free classification (as embodied in the PhyloCode), there are practical advantages to maintaining a ranked phylogenetic taxonomy, at least for groups such as ants that are in relatively recent and species-rich branches of the tree of life. These benefits include explicit information about the inclusivity and exclusivity of clades, and identification (through binomial nomenclature) of those taxa that are considered to represent species. It is important to recognize that the assignment of family-group or genus-group rank to clades is arbitrary and that ant taxa of a given rank are not equivalent, except in a very approximate sense. A new *modus operandi* is emerging in ant taxonomy above the species level, wherein molecular (DNA sequence) data from multiple nuclear genes are used to generate a well supported phylogeny, and the resulting tree serves as a framework for evaluating the informativeness of morphological traits and for identifying (and naming) clades that can be diagnosed morphologically. In following this protocol an attempt should be made to maintain continuity in nomenclature and taxon concepts with the preexisting classification, to the extent that this is possible. A similar set of principles has been followed by plant systematists developing a ranked phylogenetic classification of flowering plants (Angiosperm Phylogeny Group system).

Key words: Formicidae, systematics, phylogeny, monophyly, paraphyly, convergence, rate heterogeneity, Linnaean classification, rank-free classification, phylogenetic nomenclature, review.

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Introduction

The goals of systematics include the discovery and delimitation of clades and species, the estimation of phylogenetic relationships among taxa, and the establishment of a classification reflecting this information. In the middle of the last century there was considerable debate about methods of classification, as "evolutionary" systematists battled with pheneticists and cladists (MAYR 1982, HULL 1988), but there is now a broad consensus that biological classifications should be phylogenetic, i.e., that the groups recognized in a classification should be monophyletic (DE QUEIROZ & GAUTHIER 1994, BACKLUND & BREMER 1998, NIXON & CARPENTER 2000, JUDD & al. 2007, ANGIOSPERM PHYLOGENY GROUP 2009). Taxonomy and nomenclature have been somewhat eclipsed by other areas of systematics, however, especially the spectacular advances in phylogenetics. In his book *Inferring Phylogenies* FELSENSTEIN (2004) declared himself a founder of the "It-Doesn't-Matter-Very-Much" school of taxonomy, in a section of the book provocatively entitled "The irrelevance of classification". Yet there are compelling practical reasons for continuing to maintain and improve biological classifications. A stable, informative and universal nomenclature is important in fields as diverse as conservation, biodiversity research, collections management, and bioinformatics (GODFRAY & KNAPP 2004, MACE 2004, FRANZ 2005, PATTERSON & al. 2006, GODFRAY & al. 2007). If the main objec-

Tab. 1: Examples of non-monophyletic ant genera revealed by recent molecular phylogenetic studies. Non-monophyly due to convergence refers to the circumscription of a genus on the basis of similarities now believed to have evolved independently in more than one lineage. Non-monophyly due to plesiomorphy involves the recognition of a paraphyletic subset of species within a clade on the basis of ancestral similarities. This occurs when there is heterogeneity in rates of morphological evolution within the clade, and the more divergent taxa are assigned to different genera. "Ant AToL (unpubl.)" refers to work in progress in the Ant AToL (Assembling the Tree of Life) Project. Other, more trivial examples of non-monophyletic genera that have emerged from the Ant AToL Project include *Pheidole* (which contains the monotypic *Anisopheidole*) and *Tetramorium* (which contains the derivative taxon *Decamorium*).

Subfamily	Genus	Cause	Reference
Myrmicinae	*Messor*	convergence	BRADY & al. (2006)
Myrmicinae	*Aphaenogaster*	plesiomorphy	BRADY & al. (2006)
Myrmicinae	*Monomorium*	plesiomorphy?	Ant AToL (unpubl.)
Myrmicinae	*Cyphomyrmex*	plesiomorphy	SCHULTZ & BRADY (2008)
Myrmicinae	*Trachymyrmex*	plesiomorphy	SCHULTZ & BRADY (2008)
Formicinae	*Camponotus*	convergence	BRADY & al. (2006)
Formicinae	*Paratrechina* (old sense)	convergence	LAPOLLA & al. (2010)
Cerapachyinae	*Cerapachys*	plesiomorphy	Ant AToL (unpubl.)
Cerapachyinae	*Sphinctomyrmex*	convergence	Ant AToL (unpubl.)
Pseudomyrmecinae	*Tetraponera*	plesiomorphy	WARD & DOWNIE (2005)
Ponerinae	*Pachycondyla*	plesiomorphy	SCHMIDT (2009)
Amblyoponinae	*Amblyopone*	plesiomorphy	Ant AToL (unpubl.)

tive is to infer phylogenies then taxonomy is arguably inconsequential, but for many other downstream applications classifications provide a valuable framework for organizing information, communicating ideas, and developing public policy.

In this paper I review the recent advances that have occurred in ant systematics – specifically in the area of molecular phylogenetics – and I consider how this new knowledge can be integrated into the more traditional morphology-based system of ant classification. There are challenges in reconciling these two areas, especially when it comes to retention of a ranked (Linnaean) classification system (BENTON 2000, SCHUH 2003). The experience of plant systematists in honing a ranked phylogenetic classification of flowering plants (ANGIOSPERM PHYLOGENY GROUP 2009) offers an interesting comparison. This review addresses higher (supraspecific) classification only. There are many issues associated with the integration of morphological and molecular evidence in the species-level taxonomy of ants (WARD 2009) but they are not considered here.

Current state of knowledge

Our understanding of ant evolutionary history has improved substantially in the last decade, thanks in large part to the application of molecular approaches pioneered by Ross Crozier. The use of DNA sequence data, in conjunction with a comprehensively revised higher classification of ants (BOLTON 2003) and new fossil finds (ENGEL & GRIMALDI 2005, PERRICHOT & al. 2008), has brought increasing clarity to the major features of ant evolution (CROZIER 2006, WARD 2007, MOREAU 2009). Earlier work based on morphology had failed to deliver a clear consensus on the relationships among the major ant lineages, but the application of sequence data from multiple nuclear genes has provided unprecedented resolution.

These molecular phylogenetic studies yield consistent and strong support for a group of ants known as the formicoid clade (WARD & BRADY 2003, SAUX & al. 2004, WARD & DOWNIE 2005, BRADY & al. 2006, MOREAU & al. 2006). This clade contains about 90% of all described ant species and 14 of the 21 extant subfamilies (BOLTON & al. 2007, RABELING & al. 2008, WARD 2009). Formicoids encompass many familiar kinds of ants, including the members of three large subfamilies, Myrmicinae, Formicinae and Dolichoderinae, as well as army ants and relatives (dorylomorphs), bulldog ants and their kin (Myrmeciinae), big-eyed arboreal ants (Pseudomyrmecinae), and the ectaheteromorphs (ants in the subfamilies Ectatomminae and Heteroponerinae, that had been previously associated incorrectly with the Ponerinae). Accompanying this taxonomic diversity there is a wide range of nesting and feeding behaviors among the formicoids, from generalized omnivory to specialized predation, seed-harvesting, and fungus-cultivation. Many species are avid tenders of hemipterans and extrafloral nectaries. There is also great variation in levels of social organization among different taxa within this group (WARD 2006).

The internal phylogeny of the formicoids is reasonably well resolved at the subfamily level and above (BRADY & al. 2006, MOREAU 2009). Recent studies have also clarified relationships within the Dolichoderinae (WARD & al. 2010), the Pseudomyrmecinae (WARD & DOWNIE 2005), the *Prenolepis* genus-group of formicines (LAPOLLA & al. 2010), the myrmicine tribes Attini (SCHULTZ & BRADY 2008) and Myrmicini (JANSEN & SAVOLAINEN 2010), and the dorylomorphs (S.G. Brady B.L. Fisher, T.R. Schultz & P.S. Ward, unpubl.). There have also been species-level molecular phylogenetic studies of some of the more diverse formicoid genera, including the myrmicine genera *Pheidole* (MOREAU 2008), *Cardiocondyla* (HEINZE & al. 2005), *Tetramorium* (SCHLICK-STEINER & al. 2006) and *Myrmica* (JANSEN & al. 2010), the bulldog ants of the genus *Myrmecia* (HASEGAWA & CROZIER 2006), the dolichoderine genus *Linepithema* (WILD 2009) and the army ant genus *Dorylus* (KRONAUER & al. 2007).

Outside the formicoid clade there are several groups of ants whose relationships to one another and to the formicoids are less clear (WARD 2009). These include the subfamilies Leptanillinae and Martialinae, and a cluster of five subfamilies known collectively as poneroids (Agroecomyrmecinae, Amblyoponinae, Paraponerinae, Proceratiinae, and Ponerinae). The poneroids form either a clade that is sister to the formicoids or a paraphyletic group within which the formicoids originate (BRADY & al. 2006, MOREAU & al. 2006, RABELING & al. 2008). In some phylogenetic analyses the subfamily Leptanillinae is positioned as sister to {poneroids + formicoids} but factors such as long-branch attraction and base frequency heterogeneity may be pulling leptanillines artificially to the base of the ant tree (BRADY & al. 2006). An analysis based on three nuclear genes placed the monotypic and enigmatic Martialinae as sister to all other ants, with robust statistical support (RABELING & al. 2008). This is an intriguing result that merits further evaluation with additional genes and more comprehensive taxon sampling.

Many of these non-formicoid ants are somewhat cryptic, living underground and having workers with weakly pigmented bodies and poor vision. The preponderance of such hypogeic habits in these early branching lineages could be interpreted as indicating that the ancestral ant was similarly subterranean. It seems more plausible, however, that the surviving members of these old clades have simply retreated to underground habitats, in the face of competition from the more derived formicoid ants (RABELING & al. 2008, WARD 2009).

Concordance between traditional classification and phylogeny

How well has the conventional classification of ants fared under the onslaught of new phylogenetic information? One measure of this is the proportion of higher ant taxa, originally recognized and defined on the basis of morphology, that are supported as monophyletic groups when tested with molecular data. At the level of subfamilies, the results are quite favorable. Of the 21 subfamilies of extant ants (BOLTON 2003, RABELING & al. 2008) there is good support for monophyly of 19 of them, the exceptions being Cerapachyinae (BRADY & al. 2006, MOREAU & al. 2006) and Amblyoponinae (WARD 2007). If we exclude the three subfamilies that have only a single living species (Martialinae, Paraponerinae, Aneuretinae) then the numbers are 16 / 18 or 89%. This pleasing concordance of morphology and molecules is testimony to the comprehensiveness and insightfulness of BOLTON's (2003) morphology-based monograph on the higher classification of ants.

We can see in retrospect, however, that the relationships *among* subfamilies of ants were not well resolved with morphology, both as expressed in informal groups of subfamilies (BOLTON 2003) and in explicit cladistic analyses of morphological data (BARONI URBANI & al. 1992, GRIMALDI & al. 1997). For example, the formicoid clade, one of the best supported supra-subfamilial groups, does not emerge as a clade in any morphological study. Another striking discordance involves the ant genus *Tatuidris*. Together with two fossil genera it comprises a group which was treated as a tribe (Agroecomyrmecini) within the subfamily Myrmicinae (BOLTON 1995, BARONI URBANI & DE ANDRADE 2007) or as a subfamily (Agroecomyrmecinae) closely related to Myrmicinae (BOLTON 2003). This was supported by morphological similarity between the two groups including the presence of a postpetiole, tergosternal fusion of the second abdominal segment, and similarities in mandibular structure with a specific subgroup of myrmicines (BARONI URBANI & DE ANDRADE 2007). Yet DNA sequence data show conclusively that *Tatuidris* (and by implication the two similar fossil genera) is not at all closely related to Myrmicinae. In fact it is not even a member of the formicoid clade; rather it is a poneroid, appearing as sister to the monotypic Paraponerinae in some rooted trees but joining next to Amblyoponinae in some other analyses (BRADY & al. 2006, MOREAU & al. 2006, RABELING & al. 2008). In this instance morphological convergence between two distantly related taxa strongly misled earlier taxonomic judgment.

How well do ant genera and tribes hold up? Here there is less information but the frequency of non-monophyletic groups appears to be greater than at the subfamily level. Based on molecular phylogenetic evidence WARD (2009) estimated that 43 of 55 ant tribes are monophyletic, given their current composition. (This statistic excludes subfamilies containing only a single tribe.) Ant genera have received more taxonomic scrutiny than tribes and it seems likely that most of them represent clades (WARD 2007) but there are some glaring exceptions, including a number of well known and species-rich taxa (Tab. 1). An example that was uncovered in the Ant AToL (Assembling the Tree of Life) Project is the seed-harvesting ant genus *Messor*. These ants are found in arid habitats in the Nearctic, Palearctic and Afrotropical regions. They have long been considered related to *Aphaenogaster*, but they were separated by several distinctive and apparently apomorphic traits, including polymorphic workers, a broad head, robust mandibles (presumably for milling seeds), and the presence of a psammophore (specialized curved setae on the underside of the head) (BOLTON 1982). It is now known that the New World and Old World *Messor* represent separate lineages, independently evolved from *Aphaenogaster*-like relatives (BRADY & al. 2006). The apomorphic features are apparently convergent adaptations for a granivorous lifestyle in dry environments. The genus *Aphaenogaster* is also non-monophyletic (BRADY & al. 2006) but not because of convergence: It is essentially the plesiomorphic counterpart of *Messor*, having no obviously derived features of its own (cf. BOLTON 1982: 342).

The *Aphaenogaster* / *Messor* example highlights the two major factors leading to the occurrence of non-monophyletic groups in ant taxonomy: (1) convergent evolution and (2) retention of ancestral similarities in a subset of taxa within a larger diversifying clade (Tab. 1). In the former case, once the phenomenon has been brought to light, monophyly can be restored by recognizing each independent lineage as a separate taxon. Of course the situation also highlights the need for identification of new morphological features to diagnose each clade. In the case of genera defined on the basis of plesiomorphic similarity, morphology alone (if appropriately interpreted) could signal probable paraphyly, but previous taxonomic practices – especially the idea that genera should show a sufficient "degree of difference" from one another – led to the persistence of such paraphyletic taxa in ant taxonomy (WARD 2007). It must be admitted that these paraphyletic genera are sometimes morphologically coherent. They reflect an underappreciated phenomenon in ants: substantial heterogeneity in rates of phenotypic evolution, such that some clades contain both highly divergent taxa *and* species that have undergone much more limited morphological (and social) evolution.

Consider the ant genus *Cerapachys*: Molecular phylogenetic analyses reveal that the species currently assigned to this genus comprise at least nine different lineages, scattered across the dorylomorph tree (S.G. Brady B.L. Fisher, T.R. Schultz & P.S. Ward, unpubl.). The taxa placed in this genus have retained similar generalized morphology – presumably close to the ancestral condition for the dorylomorphs – while other ants in this clade, such as *Cylindromyrmex*, *Acanthostichus*, leptanilloidines and army ants, have experienced much greater directional change in morphology and behavior. As a consequence they have been regarded as separate genera, tribes, or even (in the case of army ants) subfamilies. A similar, if less extreme, level of paraphyly applies to "*Pachycondyla*" within the Ponerinae (SCHMIDT 2009) and to "*Amblyopone*" within the Amblyoponinae (P.S. Ward & B.L. Fisher, unpubl.). In the face of such variability in rates of morphological evolution it may prove challenging to parse these paraphyletic genera into mutually exclusive and phenotypically distinct clades (see below).

Nevertheless there are some instances where molecular work has confirmed previous morphological circumscriptions of genera. A recent study of the subfamily Dolichoderinae based on 10 nuclear genes generated a strongly supported and well resolved tree (WARD & al. 2010). Fourteen of the 26 genera were represented by multiple species, and these were chosen in such a way as to maximize within-genus diversity. All of these 14 genera proved to be monophyletic, with very high support (Bayesian posterior probabilities 1.00, maximum likelihood bootstraps 0.94 - 1.00). In this case there had been an earlier generic revision of the subfamily (SHATTUCK 1992), based solely on morphology, which evidently cleaved the subfamily in a phylogenetically accurate way. On the other hand previous attempts to resolve the relationships among dolichoderine genera using morphology (SHATTUCK 1995, BRANDÃO & al. 1999) yielded poorly supported trees and topologies that do not agree with the new molecular phylogeny.

Thus, careful morphological studies have been quite successful at identifying some ant clades, as exemplified by BOLTON's (2003) subfamily classification and SHATTUCK's (1992) revision of dolichoderine genera. Taxa assigned to the ranks of subfamily and genus hold up well in these two cases, but relationships among them do not. Perhaps certain nodes in the ant tree of life will prove to be more amenable to diagnosis by morphology than others, specifically those corresponding to clades that arose in the Cretaceous (subfamilies) and the Tertiary (genera), during periods of evolutionary innovation. But the paraphyly documented above indicates that morphological diagnoses of higher taxa will not always be straightforward because rapid morphological divergence in one group can be accompanied by relative stasis in others.

What role now for morphology?

A long-standing issue in systematics has been the question of whether and how to combine morphological and molecular data in phylogenetic analysis (WORTLEY & SCOTLAND 2006). Given that morphological convergence and heterogeneity in rates of morphological evolution are prevalent in ants we should be wary of a "total evidence" approach when exploring formicid relationships. It is far from clear that adding morphology to molecular data matrices would improve the accuracy of phylogenetic inference.

A study of pseudomyrmecine ants (WARD & DOWNIE 2005), that employed both morphological and molecular data, affords an opportunity to evaluate the phylogenetic efficacy of the two kinds of data. The morphology matrix comprised 144 characters (142 parsimony-informative); the DNA data set was based on five nuclear genes for a total of 5,191 base pairs (974 parsimony-informative). The results were clear-cut, if unsurprising: For ingroup clades the morphology bootstrap values were consistently lower than those based on molecular data. Moreover, when the morphological characters were added to the molecular data matrix this tended to reduce bootstrap values of most groups, except those that were already well supported (compare figures 2 and 4 in WARD & DOWNIE 2005). In other words, morphology reinforced the support for those groups whose monophyly was in little doubt, but it appeared to add more noise than phylogenetic signal for more difficult-to-resolve parts of the tree.

The point to emphasize is not that morphology is phylogenetically uninformative, but that its usefulness varies widely and somewhat unpredictably among characters and taxa. As it turns out, most of the *Pseudomyrmex* species-groups previously established on the basis of morphology were strongly supported as monophyletic by the molecular data (WARD & DOWNIE 2005). In one of the instances where there was conflict between the two sources of data a retrospective evaluation, in light of the new phylogeny, revealed an example of convergent evolution of worker morphology in two independent lineages of ant-plant specialists that had been placed incorrectly in a single species-group. Thus, there is a salutary interplay between the two sources of data, with molecular (DNA sequence) data providing the phylogenetic framework whereby morphology can be better understood and more accurately employed for diagnosis and identification of clades. Because it is so much more convenient and less expensive, it seems likely that morphology will continue to play a major role in identification of ants, in species delimitation, and in guiding the choice of exemplar species for molecular studies. Knowledge of morphology also remains essential for incorporation of fossil taxa into a revised classification because it is highly unlikely that molecular data will be available for such specimens.

For species-rich taxa such as ants, containing tens of thousands of species, many still undescribed and / or of uncertain delimitation, molecular studies will never achieve "complete" taxon sampling. It will probably always be necessary to associate some species or specimens with clades on the basis of inferences from morphology. Thus, the process of refining morphological diagnoses, with the assistance of a phylogenetic scaffold, remains a crucially important component of ant systematics.

Which clades should be named?

Most myrmecologists would probably not favor a classification system in which all nodes on the (still incompletely known) ant tree of life are given formal names. Taxonomies should serve as summaries of biological diversity, broad-scale road maps for navigating and organizing information about the world's biological riches. But which of the many clades in our estimated phylogenies merit formal recognition in a classification? Practical considerations suggest that we name those ant taxa that (1) are strongly supported as monophyletic groups by molecular data, and (2) have distinctive phenotypic features that allow them to be distinguished from related taxa. For groups that meet only the first of these two criteria – but about which we would like to communicate – informal names can be adopted (e.g., formicoid clade). Perhaps in the future the use of molecular characters in ant systematics will be so routine that the absence of distinctive morphological traits will not be considered problematic. For the moment, however, I suspect that most users of a classification would prefer that groups with a formal name are relatively easily and inexpensively recognized from external morphology.

In identifying clades that are well supported by molecular evidence one's confidence is enhanced if the results are based on multiple independent genes, with appropriate levels of variability in the focal taxon. For exploring the ant tree of life it is increasingly feasible – and in some instances arguably necessary – to target a moderately large number of nuclear genes (10 - 15 or more) for these purposes. The mode of analysis of these data also bears scrutiny. Because of better statistical performance, model-based approaches (maximum likelihood, Bayesian inference) have all but replaced parsimony in phylogenetic analysis (HUELSENBECK & al. 2001, FELSENSTEIN 2004, PHILIPPE & al. 2005). The results can be sensitive to model assumptions, however, so the choice of an appropriate substitution model is a key part of any phylogenetic analysis. Potential complicating factors, such as long-branch attraction, heterotachy, base-frequency heterogeneity, outgroup composition, and gene tree / species tree discord should also receive careful assessment.

Let us assume that due consideration has been given to these matters, and that we have a robustly supported ant clade. In seeking to characterize this clade morphologically there is inherent interest in identifying one or more derived (apomorphic) traits. With the availability of molecular phylogenies, however, morphology no longer carries the burden of proof of monophyly. That role is now being appropriated by molecular data, and as a result greater practical value lies in morphological features that reliably *diagnose* a clade, irrespective of their apomorphic credentials, especially given that there is often uncertainty about character polarity anyway. For example, ants in the genus *Myrmica* are largely recognized by morphological features that are considered plesiomorphic (BOLTON 1988, RADCHENKO & al. 2007). The monophyly of *Myrmica* is now well established from DNA sequence data (JANSEN & al. 2010), so if these features consistently permit recognition of the genus then they retain some utility – although it behooves us to continue to search for ostensibly apomorphic traits, and to be cautious when placing fossil taxa. Moreover morphology, like DNA, continues to evolve so there is no reason to expect that changes occurring in the common ancestor of a clade – whether they involve morphology or nucleotides – will always persist in recognizable form in all descendants (HILLIS 2006). Thus, for some ant genera and tribes it seems inevitable that it will be necessary to employ morphological definitions that involve unique (and conditional) *combinations* of traits rather than clear and unequivocal synapomorphies. As with tree building, statistical approaches are being used increasingly in ancestral state reconstruction (CUNNINGHAM & al. 1998, RONQUIST 2004). But inferences about the ancestral morphological states of a clade may be of limited value for a utilitarian diagnosis – at the very least, only a subset of such ancestral features is likely to persist in a form that makes them useful for identification purposes.

A further consideration is that not all groups meeting the requirements of monophyly (as judged by molecular evidence) and morphological diagnosability will necessarily merit a name. There will be many instances where two morphologically distinct clades will be each other's sister group (e.g., *Aenictogiton* and *Dorylus*; *Manica* and *Myrmica*), and together form a distinct clade, yet for practical reasons (stability of nomenclature, avoidance of a cumbersome classification) we would opt for either two names or a single name for the larger clade, but not both. The choice to be made in these and similar cases will often be arbitrary, but can be tempered by the desirability of maintaining nomenclatural continuity and of applying names to those clades that are most phenotypically distinct.

Linnaean (ranked) versus rank-free classification

There has been heated debate between proponents (e.g., DE QUEIROZ & GAUTHIER 1994, BRYANT & CANTINO 2002, DONOGHUE & GAUTHIER 2004, BERTRAND & HÄRLIN 2006, DE QUEIROZ 2006, LAURIN & al. 2006) and opponents (e.g., BENTON 2000, CARPENTER 2003, NIXON & al. 2003, MOORE 2003, DUBOIS 2006, STEVENS 2006) of a recently introduced system of phylogenetic nomenclature known as the PhyloCode (http://www.ohio.edu/phylocode/) which, in contrast to the Linnaean system, is rank-free and dispenses with binomial names for species and typification of taxa. The PhyloCode has not yet seen widespread application, but there is justifiable concern about the confusion that would ensue from the adoption of two parallel systems of nomenclature (SLUYS & al. 2004, GODFRAY & KNAPP 2004, DUBOIS 2007).

A rank-free phylogenetic classification is conceptually appealing, but there are distinct practical advantages to employing a ranked classification in shallower branches of the tree of life. The rules of zoological nomenclature apply only to family-, genus- and species-group names (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1999), and this is perhaps fortunate because application of ranked classifications at deeper levels within the tree of life becomes increasingly awkward and difficult to justify – it encourages the fallacious view that there are "phylum-level" traits or ground-plans (FITCH & SUDHAUS 2002) and it runs up against the challenge of maintaining coordinate ranks for the unicellular eukaryotes, within which metazoans, fungi and plants arose. When discussing (or teaching students about) the phylogenetic relationships of major groups of organisms such as arthropods or vertebrates, I find that the use of ranks often serves no useful purpose and interferes with tree-based thinking. But when engaged in more practical activities such as teaching insect identification, curating a collection of ants, or rough-sorting field samples of insects into bins, I am grateful for the convenience of a ranked classification. It is perhaps no coincidence that those plant systematists whose focus is specimen-based research and curation (especially herbarium work) have opted for a ranked phylogenetic classification of their organisms (ANGIOSPERM PHYLOGENY GROUP 2009), whereas those of a more conceptual or theoretical bent tend to be PhyloCode enthusiasts.

What are the practical benefits of a ranked classification? For a focal group, such as ants, all taxa of a given rank are *mutually exclusive* (CARPENTER 2003) and collectively they contain all known species in the focal clade. The rank of taxa is self-evident, because of distinctive suffixes for families (-idae), subfamilies (-inae) and tribes (-ini) and because genera are italicized, so the relative inclusiveness of taxa is explicit. In addition the system of binomial nomenclature identifies which taxa are species and illuminates species relationships by placing related forms in the same genus. Of course these advantages apply only if the classification system is truly phylogenetic and, as documented above, we are not there yet in ant systematics. Nevertheless progress is being made, and as examples of non-monophyletic groups arise they are being flagged and targeted for reconfiguration.

A recent exemplary study of this kind involved the reevaluation of relationships and generic limits among formicine ants related to *Prenolepis* and *Paratrechina* (LAPOLLA & al. 2010). The authors showed convincingly from DNA-sequence data that the genus *Paratrechina* (as then defined) was not monophyletic; they overhauled the classification and established new genera, whose monophyly was strongly supported in a multi-gene molecular phylogenetic analysis; and they uncovered distinctive morphological features for each of the newly defined higher taxa. In this instance the new findings from molecular phylogenetics were well accommodated within a revised Linnaean classification.

Opponents of the Linnaean system have criticized its artificiality, especially the lack of equivalency of taxa of the same rank (ERESHEVKSY 2001). Even when we have reached the point that all recognized ant genera are monophyletic (and therefore mutually exclusive) they can be expected to show considerable variation in terms of age, diversity and morphological disparity – and they cannot be compared, except in a very approximate way, with one another or with the genera of other insect groups. For example, dating of the dolichoderine phylogeny revealed that the constituent genera of the subfamily have crown-group ages that vary by an order of magnitude, from approximately 5 million years ago (mya) to 50 mya (WARD & al. 2010). An Australian clade of these ants that diversified in the last ~ 20 million years has been divided into nine genera. In contrast there are other dolichoderine clades, as old as or older than the Australian radiation, that are assigned to single genera, such as *Tapinoma* and *Dolichoderus*, with the latter dating back to the early Eocene. This circumstance reflects the uneven rates of morphological evolution in the group, with the Australian clade undergoing excessive divergence compared to other species in the subfamily.

Comparable discrepancies in ages of genera occur in other ant subfamilies and tribes (BRADY & al. 2006, SCHULTZ & BRADY 2008). In the end what can we say about ant genera? Once we have rectified the problem of non-monophyletic groups, ant genera are simply clades of morphologically similar and mutually exclusive species that arose sometime within the last 60 million years. The genera may be a rough proxy for morphological disparity but generic limits are also a function of idiosyncratic taxonomic histories and varying personal tastes. As such they should be used cautiously (if at all) in metrics of biodiversity.

Phylogenetic thinking has also introduced useful distinctions between stem- (or branch-), node- and apomorphy-based definitions of clades, and between crown-groups and stem-groups (HENNIG 1966, DE QUEIROZ & GAUTHIER 1994, DE QUEIROZ 2006). The stem-group / crown-group distinction is crucial when calibrating molecular phylogenies (MAGALLÓN 2004), and it helps to clarify discussions about the time of origin of taxa (DOYLE & DONOGHUE 1993), including ants (WARD 2007). The crown-clade concept is node-based: the most recent common ancestor of the extant members of a clade and all descendants. Such a node-based definition requires reference to two or more taxa that are thought to span the root node. For example, if *Martialis heureka* is the sister to all other extant ants (RABELING & al. 2008), crown Formicidae could be defined as the clade originating from the most recent common ancestor of that species and any formicoid ant (say, *Myrmica rubra*). But such an abstract definition provides little guidance on the placement of fossil taxa in a tree. In order to use fossil specimens for calibration purposes in a molecular phylogeny – or to place them in a phylogenetic classification – we are dependent upon explicit character evidence to make inferences about their clade membership. In turn this requires character-based definitions of the subclades of interest within any given crown clade. For fossil ants this can only come from morphological characters – not from the molecular data on which the phylogenies of extant taxa are built. As a result it is essential to ant taxonomy that there is continued growth in our knowledge and understanding of morphological variation, a point that needs to be emphasized given that molecular phylogenetics is garnering an increasing share of resources in systematics.

If heterogeneity in rates of morphological evolution is widespread in ants – as is suggested by the examples discussed above – it will be difficult or impossible to establish a ranked phylogenetic classification in which all taxa of a given rank are monophyletic and show comparable morphological distinctness. One can envisage situations where, in order to maintain monophyly and mutual exclusivity, it will be necessary to recognize either a single large and heterogeneous taxon (the lumping alternative) or a plethora of small genera, some showing only subtle distinctions (the splitting alternative). Once again *Cerapachys* provides an illustrative example. If we fold all those derivative dorylomorphs into *Cerapachys*, we recover monophyly but at the expense of a huge, unwieldy genus, essentially equivalent to all dorylomorphs. This is hardly an acceptable solution, but note that the only other viable option – given the morphological distinctness of other dorylomorph genera – is to split *Cerapachys* into a series of at least nine separate monophyletic units and identify diagnostic morphological features of each. In fact such a revision of "cerapachyine" genera is currently underway (M. Borowiec, pers. comm.), and Chris Schmidt and Steve Shattuck are similarly engaged in a major classification overhaul of the tribe Ponerini to deal with the "*Pachycondyla*" problem.

A final concern with a ranked classification of ants – or any other species-rich taxon – is the adequacy of the number of available ranks, in this case between family Formicidae and individual species. Four ranks have been traditionally used in higher ant classification: subfamily, tribe, genus and subgenus. Although judicious use of prefixes could increase this number, one can imagine the need for interposition of unranked named clades in parts of the classification. This was an improvement to the Linnaean system proposed by NIXON & al. (2003) and it has already seen informal use in some classifications (ANGIOSPERM PHYLOGENY GROUP 2009). In ant taxonomy an informal category between genus and tribe, "genus group", has gained some currency (BOLTON 2003, LAPOLLA & al. 2010).

Concluding remarks

Application of molecular phylogenetic methods has led to unprecedented progress in our understanding of ant evolutionary history. The prospects for further enlightenment are promising, especially as whole ant genomes become available for study (BONASIO & al. 2010). Recent phylogenetic work has also illuminated two striking phenomena in ants: (1) Instances of morphological convergence are more common than was previously appreciated, and (2) there is marked variation in rates of phenotypic evolution, with divergent taxa often nested within clades whose other species show much greater stasis. As a result, the use of morphology alone can lead to incorrect inferences about phylogenetic relationships, and the addition of morphological characters to molecular data sets may add more noise than useful information.

Given these realities a new protocol is beginning to emerge in ant systematics that combines molecular phylogenetics and morphology-based taxonomy (e.g., LAPOLLA & al. 2010). It involves the following steps:

- Obtain estimates of phylogeny from multiple nuclear genes and comprehensive sampling of taxa, with choice of exemplars being guided by the existing taxonomy
- Reexamine the status of named supraspecific taxa (previously established on the basis of morphological differences) and reconfigure where necessary to ensure monophyly
- Develop reliable morphology-based diagnoses of the named clades

Thus, during initial sampling in a molecular phylogenetic study the current classification provides useful guidance for taxon sampling. This is a necessary step for species-rich groups such as ants, where complete species sampling is not feasible. It is also important to base phylogenetic inferences on a sufficient number of independent genes, of appropriate levels of variability. Phylogenies derived from only a few genes are less likely to provide a solid foundation for reassessing and modifying existing classifications. Ultimately we would like to be in a position where a robust molecular phylogeny – estimated using statistical methods and models of appropriate complexity – can be used as a framework for reevaluating morphological characters and determining those that are most informative about clade membership.

The basic goal, then, is the identification of clades that are *well-supported by molecular evidence* and *phenotypically distinct*. This provides the basis for a stable and informative phylogenetic classification. At the same time, most taxonomists would agree that it is desirable to minimize nomenclatural changes and modifications of taxon concepts (morphological definitions), insofar as this is compatible with the new phylogenetic information. A similar set of principles for the transformation of phylogenies into ranked classifications has been adopted by plant systematists (BACKLUND & BREMER 1998, ANGIOSPERM PHYLOGENY GROUP 2009), and it will be instructive in the years ahead to see them applied more comprehensively in ant taxonomy.

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References

ANGIOSPERM PHYLOGENY GROUP 2009: An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. – Botanical Journal of the Linnean Society 161: 105-121.

BACKLUND, A. & BREMER, K. 1998: To be or not to be – principles of classification and monotypic plant families. – Taxon 47: 391-401.

BARONI URBANI, C., BOLTON, B. & WARD, P.S. 1992: The internal phylogeny of ants (Hymenoptera: Formicidae). – Systematic Entomology 17: 301-329.

BARONI URBANI, C. & DE ANDRADE, M.L. 2007: The ant tribe Dacetini: limits and constituent genera, with descriptions of new species. – Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova) 99: 1-191.

BENTON, M.J. 2000: Stems, nodes, crown clades, and rank-free lists: Is Linnaeus dead? – Biological Reviews 75: 633-648.

BERTRAND, Y. & HÄRLIN, M. 2006: Stability and universality in the application of taxon names in phylogenetic nomenclature. – Systematic Biology 55: 848-858.

BOLTON, B. 1982: Afrotropical species of the myrmicine ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus* (Formicidae). – Bulletin of the British Museum (Natural History). Entomology 45: 307-370.

BOLTON, B. 1988: A new socially parasitic *Myrmica*, with a reassessment of the genus (Hymenoptera: Formicidae). – Systematic Entomology 13: 1-11.

Bolton, B. 1995: A new general catalogue of the ants of the world. – Harvard University Press, Cambridge, MA, 504 pp.

Bolton, B. 2003: Synopsis and classification of Formicidae. – Memoirs of the American Entomological Institute 71: 1-370.

Bolton, B., Alpert, G., Ward, P.S. & Naskrecki, P. 2007: Bolton's catalogue of ants of the world. – Harvard University Press, Cambridge, Massachusetts, CD-ROM.

Bonasio, R., Zhang, G., Ye, C., Mutti, N.S., Fang, X., Qin, N., Donahue, G., Yang, P., Li, Q., Li, C., Zhang, P., Huang, Z., Berger, S.L., Reinberg, D., Wang, J. & Liebig, J. 2010: Genomic comparison of the ants *Camponotus floridanus* and *Harpegnathos saltator*. – Science 329: 1068-1071.

Brady, S.G., Fisher, B.L., Schultz, T.R. & Ward, P.S. 2006: Evaluating alternative hypotheses for the early evolution and diversification of ants. – Proceedings of the National Academy of Sciences of the United States of America 103: 18172-18177.

Brandão, C.R.F., Baroni Urbani, C.,Wagensberg, J. & Yamamoto, C.I. 1999: New *Technomyrmex* in Dominican amber (Hymenoptera: Formicidae), with a reappraisal of Dolichoderinae phylogeny. – Entomologica Scandinavica 29: 411-428.

Bryant, H.N. & Cantino, P.D. 2002: A review of criticisms of phylogenetic nomenclature: Is taxonomic freedom the fundamental issue? – Biological Reviews 77: 39-55.

Carpenter, J.M. 2003: Critique of pure folly. – The Botanical Review 69: 79-92.

Crozier, R.H. 2006: Charting uncertainty about ant origins. – Proceedings of the National Academy of Sciences of the United States of America 103: 18029-18030.

Cunningham, C.W., Omland, K.E. & Oakley, T.H. 1998: Reconstructing ancestral character states: a critical reappraisal. – Trends in Ecology & Evolution 13: 361-366.

de Queiroz, K. 2006: The PhyloCode and the distinction between taxonomy and nomenclature. – Systematic Biology 55: 160-162.

de Queiroz, K. & Gauthier, J. 1994: Toward a phylogenetic system of biological nomenclature. – Trends in Ecology & Evolution 9: 27-31.

Donoghue, M.J. & Gauthier, J.A. 2004: Implementing the PhyloCode. – Trends in Ecology & Evolution 19: 281-282.

Doyle, J.A. & Donoghue, M.J. 1993: Phylogenies and angiosperm diversification. – Paleobiology 19: 141-167.

Dubois, A. 2006: Naming taxa from cladograms: a cautionary tale. – Molecular Phylogenetics and Evolution 42: 317-330.

Dubois, A. 2007: Naming taxa from cladograms: some confusions, misleading statements, and necessary clarifications. – Cladistics 23: 390-402.

Engel, M.S. & Grimaldi, D.A. 2005: Primitive new ants in Cretaceous amber from Myanmar, New Jersey, and Canada (Hymenoptera: Formicidae). – American Museum Novitates 3485: 1-23.

Ereshevksy, M. 2001: The poverty of the Linnaean hierarchy. A philosophical study of biological taxonomy. – Cambridge University Press, Cambridge, UK, X + 316 pp.

Felsenstein, J. 2004: Inferring phylogenies. – Sinauer Associates, Sunderland, MA, XX + 664 pp.

Fitch, D. & Sudhaus, W. 2002: One small step for worms, one giant leap for "Bauplan"? – Evolution & Development 4: 243-246.

Franz, N.M. 2005: On the lack of good scientific reasons for the growing phylogeny / classification gap. – Cladistics 21: 495-500.

Godfray, H.C.J., Clark, B.R., Kitching, I.J., Mayo, S.J. & Scoble, M.J. 2007: The web and the structure of taxonomy. – Systematic Biology 56: 943-955.

Godfray, H.C.J. & Knapp, S. 2004: Taxonomy for the twenty-first century. Introduction. – Philosophical Transactions of the Royal Society B-Biological Sciences 359: 559-569.

Grimaldi, D., Agosti, D. & Carpenter, J.M. 1997: New and rediscovered primitive ants (Hymenoptera: Formicidae) in Cretaceous amber from New Jersey, and their phylogenetic relationships. – American Museum Novitates 3208: 1-43.

Hasegawa, E. & Crozier, R.H. 2006: Phylogenetic relationships among species groups of the ant genus *Myrmecia*. – Molecular Phylogenetics and Evolution 38: 575-582.

Heinze, J., Trindl, A., Seifert, B. & Yamauchi, K. 2005: Evolution of male morphology in the ant genus *Cardiocondyla*. – Molecular Phylogenetics and Evolution 37: 278-288.

Hennig, W. 1966: Phylogenetic systematics. (Transl. by Davis, D.D. & Zangerl, R.). – University of Illinois Press, Urbana, IL, 263 pp.

Hillis, D.M. 2006: Constraints in naming parts of the tree of life. – Molecular Phylogenetics and Evolution 42: 331-338.

Huelsenbeck, J.P., Ronquist, F., Nielsen, R. & Bollback, J.P. 2001: Bayesian inference of phylogeny and its impact on evolutionary biology. – Science 294: 2310-2314.

Hull, D.L. 1988: Science as a process. An evolutionary account of the social and conceptual development of science. – University of Chicago Press, Chicago, IL, xiii + 586 pp.

International Commission on Zoological Nomenclature 1999: International Code of Zoological Nomenclature, Fourth edition. – International Trust for Zoological Nomenclature, London, XXIX + 306 pp.

Jansen, G. & Savolainen, R. 2010: Molecular phylogeny of the ant tribe Myrmicini (Hymenoptera: Formicidae). – Zoological Journal of the Linnean Society 160: 482-495.

Jansen, G., Savolainen, R. & Vepsäläinen, K. 2010: Phylogeny, social parasite-host relationships, divergence time estimation and biogeography of the Holarctic ant genus *Myrmica*. – Molecular Phylogenetics and Evolution 56: 294-304.

Judd, W.S., Campbell, C.S., Kellogg, E.A., Stevens, P.F. & Donoghue, M.J. 2007: Plant systematics. A phylogenetic approach. Third edition. – Sinauer Associates, Sunderland, MA, XV + 611 pp.

Kronauer, D.J.C., Schöning, C., Vilhelmsen, L.B. & Boomsma, J.J. 2007: A molecular phylogeny of *Dorylus* army ants provides evidence for multiple evolutionary transitions in foraging niche. – BioMed Central Evolutionary Biology 7: 56. (doi: 10.1186/1471-2148-7-56)

LaPolla, J.S., Brady, S.G. & Shattuck, S.O. 2010: Phylogeny and taxonomy of the *Prenolepis* genus-group of ants. – Systematic Entomology 35: 118-131.

Laurin, M., de Queiroz, K. & Cantino, P.D. 2006: Sense and stability of taxon names. – Zoologica Scripta 35: 113-114.

Mace, G.M. 2004: The role of taxonomy in species conservation. – Philosophical Transactions of the Royal Society B-Biological Sciences 359: 711-719.

Magallón, S. 2004: Dating lineages: molecular and paleontological approaches to the temporal framework of clades. – International Journal of Plant Science 165(4 Suppl.): S7-S21.

Mayr, E. 1982: The growth of biological thought. Diversity, evolution and inheritance. – Belknap Press, Cambridge, MA, IX + 974 pp.

Moore, G. 2003: Should taxon names be explicitly defined? – The Botanical Review 69: 2-21.

Moreau, C.S. 2008: Unraveling the evolutionary history of the hyperdiverse ant genus *Pheidole* (Hymenoptera: Formicidae). – Molecular Phylogenetics and Evolution 48: 224-239.

MOREAU, C.S. 2009: Inferring ant evolution in the age of molecular data (Hymenoptera: Formicidae). – Myrmecological News 12: 201-210.

MOREAU, C.S., BELL, C.D., VILA, R., ARCHIBALD, S.B. & PIERCE, N.E. 2006: Phylogeny of the ants: diversification in the age of angiosperms. – Science 312: 101-104.

NIXON, K.C. & CARPENTER, J.M. 2000: On the other "phylogenetic systematics". – Cladistics 16: 298-318.

NIXON, K.C., CARPENTER, J.M. & STEVENSON, D.W. 2003: The PhyloCode is fatally flawed, and the "Linnaean" system can easily be fixed. – The Botanical Review 69: 111-120.

PATTERSON, D.J., REMSEN, D., MARINO, W.A. & NORTON, C. 2006: Taxonomic indexing – extending the role of taxonomy. – Systematic Biology 55: 367-373.

PERRICHOT, V., LACAU, S., NÉRAUDEAU, D. & NEL, A. 2008: Fossil evidence for the early ant evolution. – Naturwissenschaften 95: 85-90.

PHILIPPE, H., ZHOU, Y., BRINKMANN, H., RODRIGUE, N. & DELSUC, F. 2005: Heterotachy and long-branch attraction in phylogenetics. – BioMed Central Evolutionary Biology 5: 50. (doi:10.1186/1471-2148-5-50)

RABELING, C., BROWN, J.M. & VERHAAGH, M. 2008: Newly discovered sister lineage sheds light on early ant evolution. – Proceedings of the National Academy of Sciences of the United States of America 105: 14913-14917.

RADCHENKO, A.G., DLUSSKY, G. & ELMES, G.W. 2007: The ants of the genus *Myrmica* (Hymenoptera, Formicidae) from Baltic and Saxonian amber (Late Eocene). – Journal of Paleontology 81: 1494-1501.

RONQUIST, F. 2004: Bayesian inference of character evolution. – Trends in Ecology & Evolution 19: 475-481.

SAUX, C., FISHER, B.L. & SPICER, G.S. 2004: Dracula ant phylogeny as inferred by nuclear 28S rDNA sequences and implications for ant systematics (Hymenoptera: Formicidae: Amblyoponinae). – Molecular Phylogenetics and Evolution 33: 457-468.

SCHLICK-STEINER, B.C., STEINER, F.M., MODER, K., SEIFERT, B., SANETRA, M., DYRESON, E., STAUFFER, C. & CHRISTIAN, E. 2006: A multidisciplinary approach reveals cryptic diversity in western Palearctic *Tetramorium* ants (Hymenoptera: Formicidae). – Molecular Phylogenetics and Evolution 40: 259-273.

SCHMIDT, C.A. 2009: Molecular phylogenetics and taxonomic revision of ponerine ants. – Ph.D. Dissertation, University of Arizona, Tucson, AZ, 279 pp.

SCHUH, R.T. 2003: The Linnaean System and its 250-year persistence. – The Botanical Review 69: 59-78.

SCHULTZ, T. & BRADY, S.G. 2008: Major evolutionary transitions in ant agriculture. – Proceedings of the National Academy of Sciences of the United States of America 105: 5435-5440.

SHATTUCK, S.O. 1992: Generic revision of the ant subfamily Dolichoderinae (Hymenoptera: Formicidae). – Sociobiology 21: 1-181.

SHATTUCK, S.O. 1995: Generic-level relationships within the ant subfamily Dolichoderinae (Hymenoptera: Formicidae). – Systematic Entomology 20: 217-228.

SLUYS, R., MARTENS, K. & SCHRAM, F.R. 2004: The PhyloCode: naming of biodiversity at a crossroads. – Trends in Ecology & Evolution 19: 280-281.

STEVENS, P.F. 2006: An end to all things? – plants and their names. – Australian Systematic Botany 19: 115-133.

WARD, P.S. 2006: Ants. – Current Biology 16: R152-R155.

WARD, P.S. 2007: Phylogeny, classification, and species-level taxonomy of ants (Hymenoptera: Formicidae). – Zootaxa 1668: 549-563.

WARD, P.S. 2009 [2010]: Taxonomy, phylogenetics and evolution. In: LACH, L., PARR, C.L. & ABBOTT, K. (Eds.): Ant ecology. – Oxford University Press, Oxford, pp. 3-17.

WARD, P.S. & BRADY, S.G. 2003: Phylogeny and biogeography of the ant subfamily Myrmeciinae (Hymenoptera: Formicidae). – Invertebrate Systematics 17: 361-386.

WARD, P.S., BRADY, S.G., FISHER, B.L. & SCHULTZ, T.R. 2010: Phylogeny and biogeography of dolichoderine ants: effects of data partitioning and relict taxa on historical inference. – Systematic Biology 59: 342-362.

WARD, P.S. & DOWNIE, D.A. 2005: The ant subfamily Pseudomyrmecinae (Hymenoptera: Formicidae): phylogeny and evolution of big-eyed arboreal ants. – Systematic Entomology 30: 310-335.

WILD, A.L. 2009: Evolution of the Neotropical ant genus *Linepithema*. – Systematic Entomology 34: 49-62.

WORTLEY, A.H. & SCOTLAND, R.W. 2006: The effect of combining molecular and morphological data in published phylogenetic analyses. – Systematic Biology 55: 677-685.