

Molecular data confirm family status for the *Tryonicus*–*Lauraesilpha* group (Insecta: Blattodea: Tryonicidae)

Jérôme Murienne^{a,b,*}

^aDepartment of Organismic and Evolutionary Biology & Museum of Comparative Zoology, Harvard University,
26 Oxford Street, 02138 Cambridge, MA, USA

^bUMR 5202 CNRS, Département Systématique et Évolution, Muséum national d'Histoire naturelle, CP50 – 45 rue Buffon,
75005 Paris, France

Received 25 July 2008; accepted 31 October 2008

Abstract

Family status was recently proposed for the *Tryonicus*–*Lauraesilpha* group (Insecta: Blattodea: Tryonicidae), which had been assigned to Blattidae before. In order to test this hypothesis, a molecular phylogenetic analysis of Blattodea was conducted using the 12S and H3 genes. The results show that Tryonicidae indeed form a lineage distinct from Blattidae. The results are compared to the previous classifications and phylogenetic hypotheses (morphology- and molecular-based). It is suggested that the Polyzosteriinae tribe Methanini should remain in Polyzosteriinae (Blattodea: Blattidae).

© 2008 Gesellschaft für Biologische Systematik. Published by Elsevier GmbH. All rights reserved.

Keywords: Blattodea; Tryonicidae; Tryonicinae; New Caledonia

Introduction

In recent years, phylogenetic relationships among the principal lineages of Blattodea (or even Dictyoptera; see [Lo et al. 2007](#)) have been subject to many debates. There is conflict not only between morphological ([Klass and Meier 2006](#)) and molecular studies, but also between the various molecular studies themselves ([Inward et al. 2007](#); [Lo et al. 2007](#); [Pellens et al. 2007](#)). It seems that the results are not only affected by the choice of outgroup taxa and markers, but also by the taxon sampling ([Ware et al. 2008](#)). In this framework,

I present a molecular phylogeny of Blattodea, for the first time including the *Tryonicus*–*Lauraesilpha* group, which has been proposed to constitute another principal lineage ([Klass and Meier 2006](#)).

The genus *Tryonicus* was originally described by [Shaw \(1925\)](#) and placed within the subfamily Blattinae (Blattodea: Blattidae). [McKittrick and Mackerras \(1965\)](#) considered the genus as representing a separate subfamily (Blattodea: Blattidae: Tryonicinae), a point of view accepted in most subsequent studies ([Mackerras 1968](#); [Roth 1987](#)), though not by [Princis \(1966\)](#). In his revision of the Tryonicinae, [Grandcolas \(1997\)](#) split *Tryonicus* in two genera: *Tryonicus* (comprising species endemic to Australia and others endemic to New Caledonia) and *Lauraesilpha* (endemic to New Caledonia). He considered the morpho-anatomical as well as life-habit differences (*Lauraesilpha* being xylophagous) as

*Corresponding author at: Department of Organismic and Evolutionary Biology & Museum of Comparative Zoology, Harvard University,
26 Oxford Street, 02138 Cambridge, MA, USA.

E-mail address: murienne@mnhn.fr (J. Murienne).

justifying the distinction of two genera. In addition, he held that the tribe Methanini (Blattidae: Polyzosteriinae) as well as several newly described genera resembling Polyzosteriinae (pers. obs.) – *Angustonicus*, *Punctulonicus*, *Rothisilpha*, *Pallidionicus*, and *Pellucidonicus* – should be placed with the *Tryonicus*–*Lauraesilpha* group within Tryoniceinae. Klass (2001) provided arguments that only *Tryonicus* and *Lauraesilpha* should be placed within Tryoniceinae. Murienne et al. (2008) studied the molecular phylogeny of *Lauraesilpha* species on New Caledonia, without questioning the phylogenetic position of the genus.

From a phylogenetic point of view, *Tryonicus* was considered as belonging to Blattidae in Grandcolas' (1996) morphological study, a position again asserted (see the discussion below) with a molecular study using 12S and 16S rRNA (Grandcolas et al. 2002). In contrast, *Tryonicus* was considered as an isolated lineage of Blattodea by Klass (1995, 1997, 2001), based mainly on male genital morphology. This was confirmed by the morphology-based phylogenetic analysis of Klass and Meier (2006), who therefore proposed separate family status for the *Tryonicus*–*Lauraesilpha* group (Blattodea: Tryoniceidae). The group has not been included in the recent molecular-based phylogenetic studies of Blattodea by Inward et al. (2007), Lo et al. (2007), and Pellens et al. (2007). It has recently been included in a combined (molecular and morphological) analysis of Dictyoptera (Ware et al. 2008), but no sequences were available for *Tryonicus* or *Lauraesilpha*, and results were inconclusive regarding placement of the group.

Because some sequences are now available for *Tryonicus* and *Lauraesilpha* (Murienne et al. 2008), I decided to conduct a molecular phylogenetic analysis of Blattodea in order to test three hypotheses: (i) the *Tryonicus*–*Lauraesilpha* group is the sole member of a high-rank clade in Blattidae, probably sister to the remaining Blattidae (then to be classified as Blattodea: Blattidae: Tryoniceinae) (McKittrick and Mackerras 1965); (ii) the group is most closely related to certain Polyzosteriinae and subordinate in Blattidae (corresponding to placement within a Tryoniceinae subfamily of Blattidae together with some former Polyzosteriinae) (Grandcolas 1997); and (iii) the group is the sole member of a high-rank clade in Blattodea for which either no relationship to other Blattidae or even a relationship to another blattodean lineage is supported (then to be classified as Blattodea: Tryoniceidae) (Klass and Meier 2006).

Throughout this paper, I will use the terms 'Blattodea' for the clade comprising both cockroaches and termites (following Hennig 1969, 1981; Inward et al. 2007; Ware et al. 2008), 'Cryptocercoidae' for the genus *Cryptocercus*, and 'Termitoidae' for termites (following Eggleton et al. 2007).

Material and methods

In order to avoid missing data, I chose to use the mitochondrial 12S rRNA gene (12S hereafter) and the nuclear protein-encoding histone 3 gene (H3 hereafter), which both had been used for Inward et al.'s (2007) comprehensive molecular study on Dictyoptera and for Murienne et al.'s (2008) study on *Lauraesilpha*. Accordingly, most of the non-tryoniceine species in the dataset are those already sampled by Inward et al. (2007). Sequences were downloaded from GenBank (Table 1), and I tried as much as possible to include representatives of most families and subfamilies of Blattodea. I paid particular attention to the Blattidae family and for the first time included both *Drymaplaneta* and *Angustonicus*, considered as members of Tryoniceinae by Grandcolas (1997). Because of the relatively fast evolution observed in the chosen genes, I chose to root the phylogeny with members of Mantodea in order to avoid the effect of random outgrouping. Mantodea has been considered as the sister-group to Blattodea in morphological (Klass 1995; Klass and Meier 2006) and molecular studies (Maekawa et al. 1999; Lo et al. 2000, 2003; Terry and Whiting 2005; Kjer et al. 2006; Inward et al. 2007; Pellens et al. 2007; Ware et al. 2008), though not by Lo et al. (2007; with very weakly supported blattodean paraphyly). Even if the choice of outgroup has been shown to be critical for resolving the phylogeny of Dictyoptera (Ware et al. 2008), I consider that the dataset is sufficient to test the present study's hypotheses (see the introduction above).

Sequences were aligned using MUSCLE 3.6 (Edgar 2004). Ambiguous regions were removed using Gblocks' 0.91b default parameters (Castresana 2000), allowing gap position to be retained. Phylogenetic hypotheses were obtained using PhyML 3.0 (Guindon and Gascuel 2003), with the best-fitted model of evolution chosen by MrAIC.pl (Nylander 2004). The last version of PhyML implements new methods of subtree pruning and regrafting (SPR) topological rearrangements (Hordijk and Gascuel 2005), allowing for better exploration of tree space than with NNI alone. Nodal support was measured using 1000 bootstrap replicates. Analyses were conducted for separate datasets as well as in combination. Concatenation of the separate data was performed using Phytily (Smith and Dunn 2008). A Bayesian phylogenetic analysis was performed with MrBayes 3.1 (Huelsenbeck and Ronquist 2001), using 2 runs of 1 million generations, applying the best-fitted models to the different partitions.

Even though Maximum Likelihood is less prone to Long Branch Attraction than Parsimony (Swofford et al. 1996; Huelsenbeck 1997) it is not immune to this phenomenon (Brinkmann and Philippe 1999; Sanderson et al. 2000; Omilian and Taylor 2001). In order to check whether the position of the *Tryonicus*–*Lauraesilpha* group

Table 1. List of taxa included in the analyses, and GenBank accession numbers.

Order	Family	Subfamily	Species	12S	H3
Blattodea	Blaberidae	Blaberinae	<i>Eublaberus posticus</i>	DQ874044 (I)	DQ873967 (I)
Blattodea	Blaberidae	Diplopterinae	<i>Diploptera punctata</i>	DQ874037 (I)	DQ873959 (I)
Blattodea	Blaberidae	Epilamprinae	<i>Aptera fusca</i>	DQ874025 (I)	DQ873945 (I)
Blattodea	Blaberidae	Geoscapheinae	<i>Macropanesthia rhinoceros</i>	DQ874065 (I)	DQ873985 (I)
Blattodea	Blaberidae	Gyninae	<i>Gyna lurida</i>	DQ874052 (I)	DQ873973 (I)
Blattodea	Blaberidae	Oxyhaloinae	<i>Rhyparobia maderae</i>	DQ874098 (I)	DQ874016 (I)
Blattodea	Blaberidae	Panchlorinae	<i>Panchlora azteca</i>	DQ874076 (I)	DQ873995 (I)
Blattodea	Blaberidae	Panesthiinae	<i>Panesthia cribrata</i>	DQ874078 (I)	DQ873997 (I)
Blattodea	Blaberidae	Perisphaeriinae	<i>Perisphaerus</i> sp.	DQ874085 (I)	DQ874003 (I)
Blattodea	Blaberidae	Pycnoscelinae	<i>Pycnoscelus surinamensis</i>	DQ874097 (I)	DQ874015 (I)
Blattodea	Blaberidae	Zetoborinae	<i>Phortioeca phoraspoides</i>	DQ874087 (I)	DQ874005 (I)
Blattodea	Blattellidae	Blattellinae	<i>Paratemnopteryx coultoniana</i>	DQ874079 (I)	DQ873998 (I)
Blattodea	Blattellidae	Ectobiinae	<i>Ectobius lapponicus</i>	DQ874039 (I)	DQ873961 (I)
Blattodea	Blattellidae	Nyctiborinae	<i>Paratropes</i> sp.	DQ874080 (I)	DQ873999 (I)
Blattodea	Blattellidae	Pseudophyllodromiinae	<i>Euthlastoblatta</i> sp.	DQ874049 (I)	DQ873971 (I)
Blattodea	Blattidae	Archiblattinae	<i>Archiblatta hoeveni</i>	DQ874026 (I)	DQ873946 (I)
Blattodea	Blattidae	Blattinae	<i>Blatta orientalis</i>	DQ874031 (I)	DQ873951 (I)
Blattodea	Blattidae	Blattinae	<i>Deropeltis</i> cf. <i>paulioni</i>	DQ874036 (I)	DQ873958 (I)
Blattodea	Blattidae	Blattinae	<i>Deropeltis erythrocephala</i>	DQ874035 (I)	DQ873957 (I)
Blattodea	Blattidae	Blattinae	<i>Deropeltis</i> sp.	DQ874034 (I)	DQ873956 (I)
Blattodea	Blattidae	Blattinae	<i>Periplaneta australasiae</i>	DQ874081 (I)	DQ874000 (I)
Blattodea	Blattidae	Blattinae	<i>Periplaneta brunnea</i>	DQ874082 (I)	DQ874001 (I)
Blattodea	Blattidae	Blattinae	<i>Pseudoderopeltis</i> sp.	DQ874092 (I)	DQ874010 (I)
Blattodea	Blattidae	Polyzosteriinae	<i>Drymaplaneta</i> cf. <i>semivitta</i>	DQ874038 (I)	DQ873960 (I)
Blattodea	Blattidae	Polyzosteriinae	<i>Eurycotis floridana</i>	DQ874046 (I)	DQ873968 (I)
Blattodea	Blattidae	Polyzosteriinae	<i>Eurycotis pluto</i>	DQ874047 (I)	DQ873969 (I)
Blattodea	Blattidae	Polyzosteriinae	<i>Angustonicus amieuensis</i>	AJ870995 (M)	EU486056 (M)
Blattodea	Cryptoceridae		<i>Cryptocercus punctulatus</i>	DQ441677 (I)	DQ873955 (I)
Blattodea	Nocticolidae		<i>Nocticola australiensis</i>	DQ874070 (I)	–
Blattodea	Polyphagidae	Euthyrrhaphinae	<i>Euthyrrhapha pacifica</i>	DQ874050 (I)	–
Blattodea	Polyphagidae	Holocompsinae	<i>Holocompsa</i> sp.	DQ874056 (I)	–
Blattodea	Polyphagidae	Polyphaginae	<i>Eremoblatta subdiaphana</i>	DQ874043 (I)	DQ873965 (I)
Blattodea	Polyphagidae	Polyphaginae	<i>Ergaula capucina</i>	–	DQ873966 (I)
Blattodea	Polyphagidae	Polyphaginae	<i>Polyphaga aegyptiaca</i>	DQ874089 (I)	DQ874007 (I)
Blattodea	Polyphagidae	Polyphaginae	<i>Therea</i> sp.	DQ874103 (I)	–
Blattodea	Polyphagidae	Tiviinae	<i>Tivia</i> sp.	DQ874104 (I)	DQ874021 (I)
Blattodea	Termitidae	Termitinae	<i>Nasutitermes similis</i>	DQ441765 (I)	AY125226
Blattodea	Tryonicidae		<i>Tryonicus</i> sp. 1	EU486010 (M)	EU486057 (M)
Blattodea	Tryonicidae		<i>Tryonicus</i> sp. 2	EU486011 (M)	EU486058 (M)
Blattodea	Tryonicidae		<i>Lauraesilpha</i> sp. 1	EU486012 (M)	EU486059 (M)
Blattodea	Tryonicidae		<i>Lauraesilpha</i> sp. 3	EU486013 (M)	EU486060 (M)
Blattodea	Tryonicidae		<i>Lauraesilpha chazeaui</i>	EU486015 (M)	EU486062 (M)
Blattodea	Tryonicidae		<i>Lauraesilpha koghiensis</i>	EU486017 (M)	EU486064 (M)
Blattodea	Tryonicidae		<i>Lauraesilpha heteroclita</i>	EU486018 (M)	EU486065 (M)
Blattodea	Tryonicidae		<i>Lauraesilpha</i> sp. 5	EU486020 (M)	EU486067 (M)
Blattodea	Tryonicidae		<i>Lauraesilpha antiqua</i>	EU486021 (M)	EU486068 (M)
Blattodea	Tryonicidae		<i>Lauraesilpha</i> sp. 2	EU486024 (M)	EU486071 (M)
Blattodea	Tryonicidae		<i>Lauraesilpha dogniensis</i>	EU486026 (M)	EU486073 (M)
Blattodea	Tryonicidae		<i>Lauraesilpha mearetoi</i>	EU486027 (M)	EU486074 (M)
Blattodea	Tryonicidae		<i>Lauraesilpha</i> sp. 4	EU486030 (M)	EU486076 (M)
Mantodea	Hymenopodidae	Epaphroditinae	<i>Phyllocrania paradoxa</i>	DQ874088 (I)	DQ874006 (I)
Mantodea	Hymenopodidae	Hymenopodinae	<i>Pseudocreobotra wahlbergii</i>	DQ874091 (I)	DQ874009 (I)
Mantodea	Iridopterygidae	Tropidomantinae	<i>Ichromantis dichroica</i>	DQ874058 (I)	DQ873978 (I)
Mantodea	Mantidae	Mantinae	<i>Tenodera sinensis</i>	DQ874102 (I)	DQ874020 (I)
Mantodea	Mantidae	Miomantinae	<i>Miomantis</i> sp.	DQ441740 (I)	DQ873987 (I)
Mantodea	Metallyticidae		<i>Metallyticus violacea</i>	DQ874067 (I)	DQ873986 (I)

Systematics based on Roth (2003), Inward et al. (2007) and the present results (regarding Blattidae and Tryonicidae). Sequences from Inward et al. (2007) indicated by (I), from Murienne et al. (2005, 2008) by (M).

could be linked to a Long Branch Attraction artifact, I performed a long branch extraction test (see Bergsten 2005) as proposed by Siddall and Whiting (1999) and Pol and Siddall (2001), sequentially removing the *Tryonicus*–*Lauraesilpha* group and its sister-group.

Results

The 12S analysis produced an alignment of 400 characters (77% of the original 518 positions), 229 of them parsimony informative. MrAIC identified the GTR + Γ model as the best-fitting one. The H3 analysis produced an alignment of 228 characters with no gaps (60% of the original 376 positions) comprising 88 parsimony informative characters. MrAIC identified the K2P + I + Γ model as the best-fitting one. For the combined dataset, the best-fitting model was GTR + Γ .

When all the available data were analyzed in combination under Maximum Likelihood, I found a topology of $\text{loglk} = -10391.01$ (Fig. 1). Final parameter estimates were base frequencies $A = 0.27$, $C = 0.17$, $G = 0.21$, $T = 0.34$; $\alpha = 0.381$. The tree shows the monophyly of

Tryonicidae (Klass and Meier 2006) supported by very high bootstrap frequency (BF hereafter; 99%). The family includes the genera *Tryonicus* and *Lauraesilpha* only, for both of which monophyly is confirmed (100% and 95% BF, respectively). Tryonicidae appears as a lineage distinct from Blattidae sensu Klass and Meier (2006) (i.e. not including *Tryonicus* and *Lauraesilpha*), which also appears as a monophyletic group with very high bootstrap support (99%). Tryonicidae appears as sister to the Cryptocercoidae + Termitoidae group (68% BF). The monophyly of Polyphagoidea is retrieved, with Nocticolidae sister to Polyphagidae. Blaberoidea appears as paraphyletic (though monophyletic if *Euthlastoblatta* is excluded). Results from Bayesian analysis of the combined data (Fig. 2) are largely congruent with those obtained from Maximum Likelihood.

When I performed the long branch extraction test, sequentially removing from the analysis Tryonicidae and the Cryptocercoidae + Termitoidae group, the topologies obtained remained identical (not shown). This result strongly suggests that the placement of Tryonicidae as sister to the Cryptocercoidae–Termitoidae group is not the result of a long branch attraction artifact.

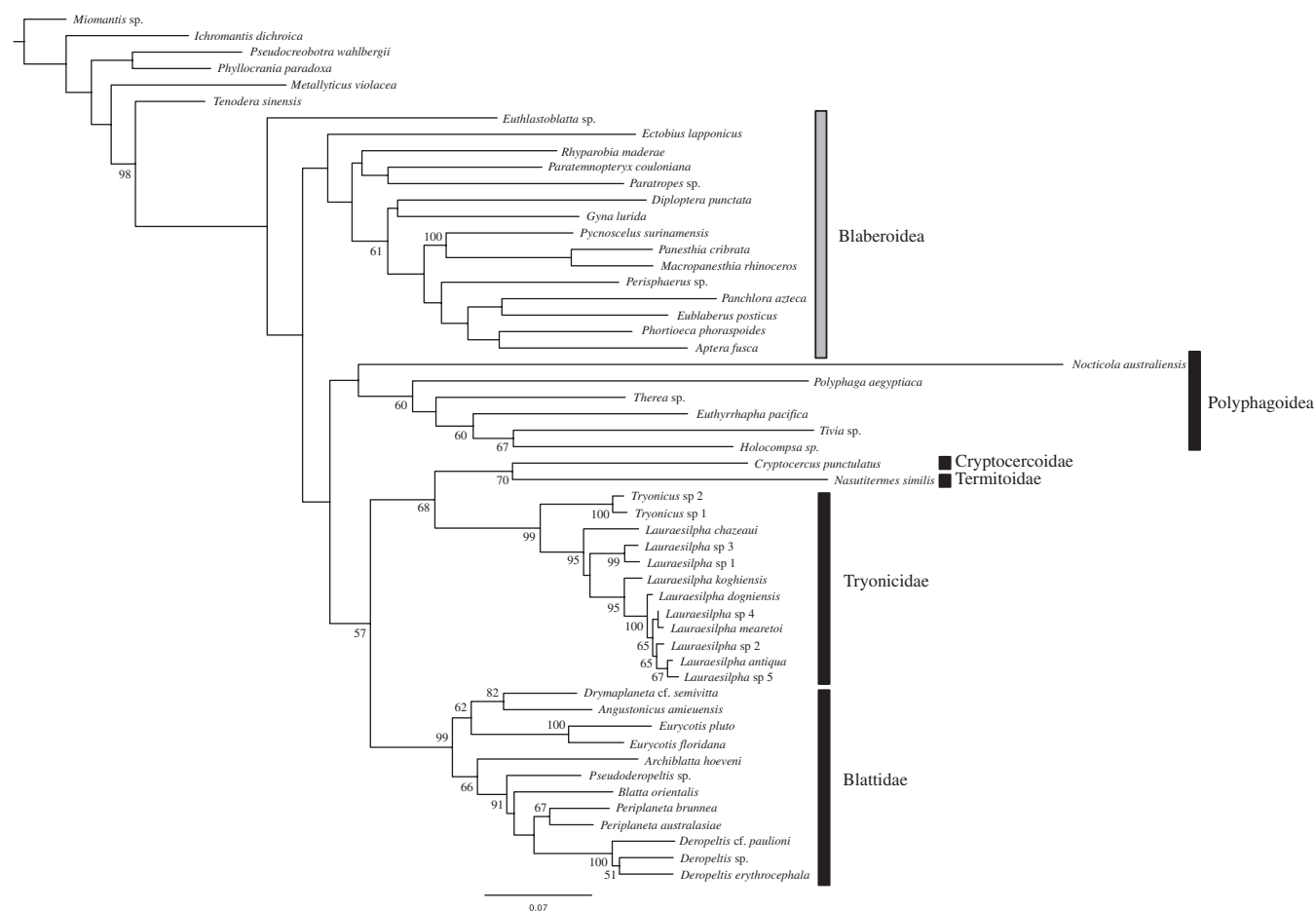


Fig. 1. Maximum Likelihood topology obtained from 12S and H3 analyzed in combination. Bootstrap frequencies indicated at nodes. Black bars indicate monophyly, grey bars paraphyly.

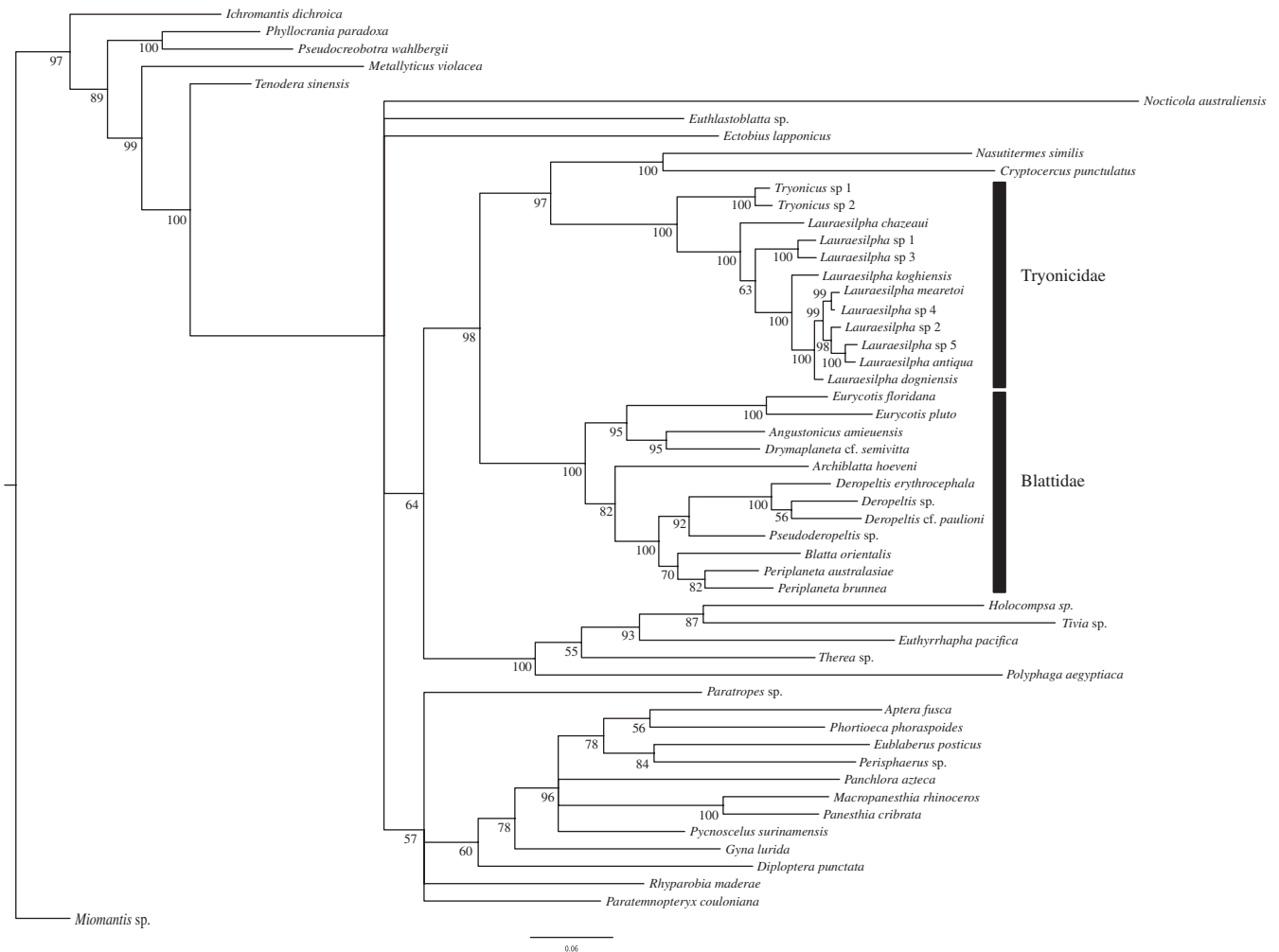


Fig. 2. Bayesian topology obtained from 12S and H3 analyzed in combination. Posterior probabilities of clades indicated at nodes. Black bars indicate monophyly.

Although I take the total tree resulting from the combined analysis of all available data as the best estimate of the phylogeny, I present the results of the separate analyses for the record. When 12S was analyzed alone under Maximum Likelihood, I found a topology of $\log_{10} L = -7028.48$ (Fig. 3). The final parameter estimates were base frequencies $A = 0.31$, $C = 0.09$, $G = 0.18$, $T = 0.43$; $\alpha = 0.466$. The topology shows monophyly for Tryonicidae (93% BF), *Tryonicus* (99% BF), and *Lauraesilpha* (67% BF). The monophyly of Blattidae (sensu Klass and Meier 2006) is retrieved with 92% bootstrap support. In this topology, the *Tryonicus*–*Lauraesilpha* group does not form a monophyletic group with *Drymaplaneta* and *Angustonicus* (contra Grandcolas 1997). It is compatible with McKittrick and Mackerras' (1965) hypothesis, with *Tryonicus*–*Lauraesilpha* as sister to the remaining Blattidae. However, this relationship is supported by very low bootstrap frequency (42). In addition, the branches connecting Tryonicidae and Blattidae are

among the longest in the tree, suggesting family status for each of the two groups.

When H3 was analyzed alone, I found a topology of $\log_{10} L = -2957.56$ (Fig. 4). The final parameter estimates were gamma shape parameter 1.550, proportion on invariant 0.588. The topology shows monophyly for Tryonicidae (89% BF), *Tryonicus* (96% BF), and *Lauraesilpha* (67% BF). Blattidae appears as a paraphyletic group due to the position of *Polyphaga* as sister to *Archiblatta*. Once again, Tryonicidae (Klass and Meier 2006) appears as a lineage distinct from Blattidae (contra McKittrick and Mackerras 1965) and from *Drymaplaneta*–*Angustonicus* (contra Grandcolas 1997).

Discussion

The results contradict Grandcolas et al.'s (2002) conclusions from their molecular results. In that study, the authors conducted a molecular phylogenetic analysis

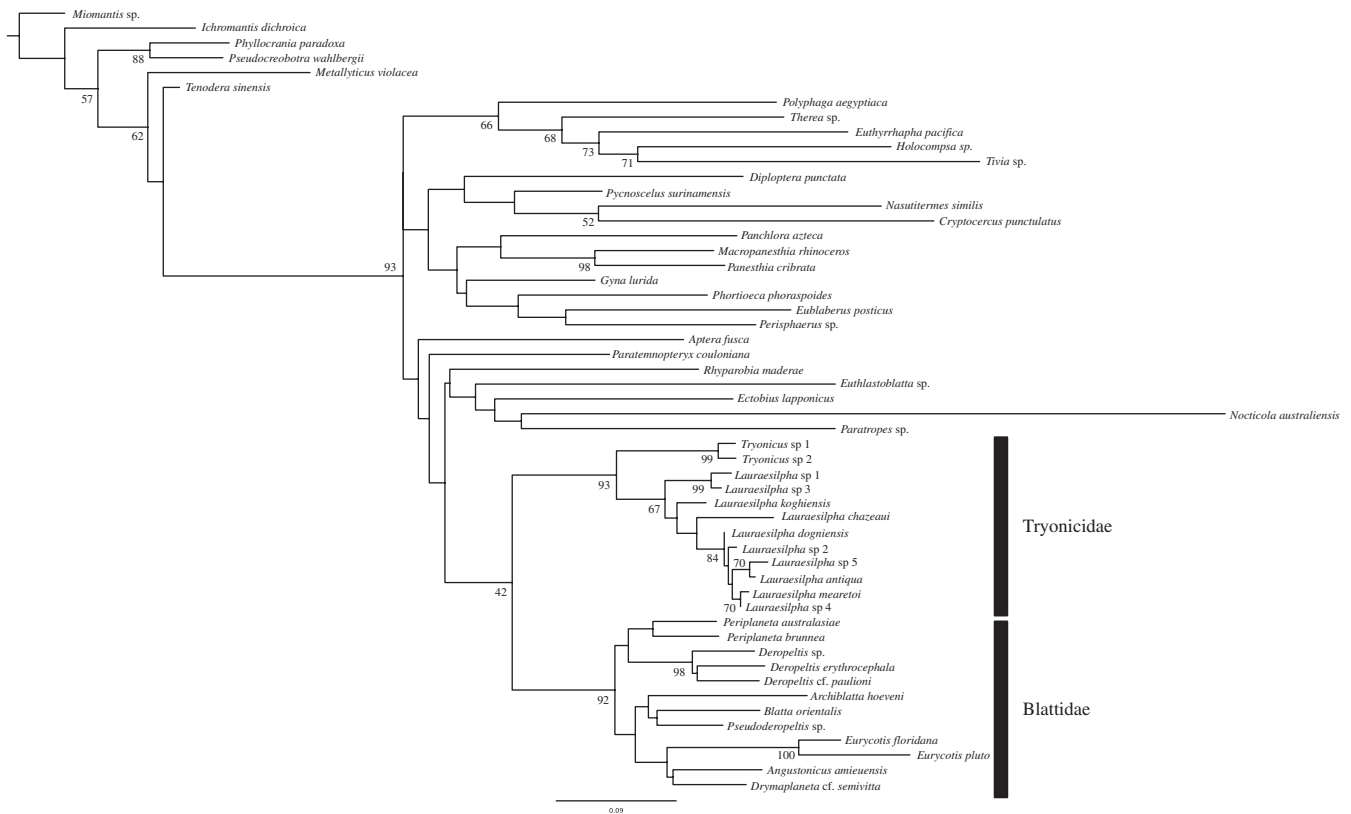


Fig. 3. Maximum Likelihood topology from 12S analyzed alone. Bootstrap frequencies indicated at nodes.

of Blattidae using 12S and 16S genes, including *Lauraesilpha*, one Polyzosteriinae (*Melanozosteria*), and 6 Blattinae (from the genera *Blatta*, *Periplaneta*, and *Shelfordella*). As previously noted by Klass and Meier (2006), Grandcolas et al. (2002) used only one outgroup (the polyphagid *Therea petiveriana*), which is insufficient to test the monophyly of a group. Furthermore, the topology obtained, with *Lauraesilpha* sister to the remaining Blattidae, is compatible with the present topology considering their insufficient taxon sampling. Their conclusion that the data on *Lauraesilpha* 'confirm its belonging to the Blattidae family' is thus based on an obvious rooting problem. Moreover, despite their statement that the sequences obtained 'are similar to those of other Blattidae', a standard Blast search using their 16S sequence of *Lauraesilpha mearetoi* (GenBank accession number AJ308734) shows higher similarity to Blattellidae (*Blattella germanica*, *B. nipponica*, *B. vaga*) than to Blattidae. There is a 98% identity score between the AJ308734 sequence and the *Blattella germanica* sequence (EF363265) obtained in the same laboratory. The facts that the 12S sequence can be assigned to *Lauraesilpha* and that the original voucher is correctly identified (pers. obs.) indicate that this result is not due to a mislabeling problem. Independent sequencing of *Lauraesilpha mearetoi* by Murienne et al. (2008) (GenBank accession number EU486050; only 79% identity with AJ308734) suggests that the sequence used

by Grandcolas et al. (2002) is a contamination, likely from the German cockroach pest *Blattella germanica*.

The results of the present study clearly show that the *Tryonicus*–*Lauraesilpha* group does not form a monophyletic group with *Angustonicus* and *Drymaplaneta* (contra Grandcolas 1997). Like Klass (2001), I therefore suggest that the Polyzosteriinae tribe Methanini (here represented by *Drymaplaneta*), considered as a part of Tryonicinae by Grandcolas (1997), should remain in Polyzosteriinae (Blattodea: Blattidae). *Angustonicus*, also placed in Tryonicinae by Grandcolas (1997), clearly groups with *Drymaplaneta* and *Eurycotis* (Blattidae, Polyzosteriinae) in the present study. Morphological analysis is still needed to formally assign *Angustonicus* (as well as *Punctulonicus*, *Rothsilpha*, *Pallidionicus*, and *Pellucidonicus*) to Polyzosteriinae (author's work in progress).

The results confirm the separate family status proposed by Klass and Meier (2006) for the *Tryonicus*–*Lauraesilpha* group (Blattodea: Tryonicidae). However, the results of the combined analysis indicate that this family is sister to the Cryptocercoidae–Termitoidae group, whereas it was retrieved as sister to the remaining Blattodea (excluding Blattidae) in Klass and Meier's (2006) morphological analysis. These results remain compatible with those of Ware et al.'s (2008), due to the unresolved position of Tryonicidae and Blattidae. It is now well established that the phylogeny of Blattodea is highly sensible to the choice of genes, taxon coverage

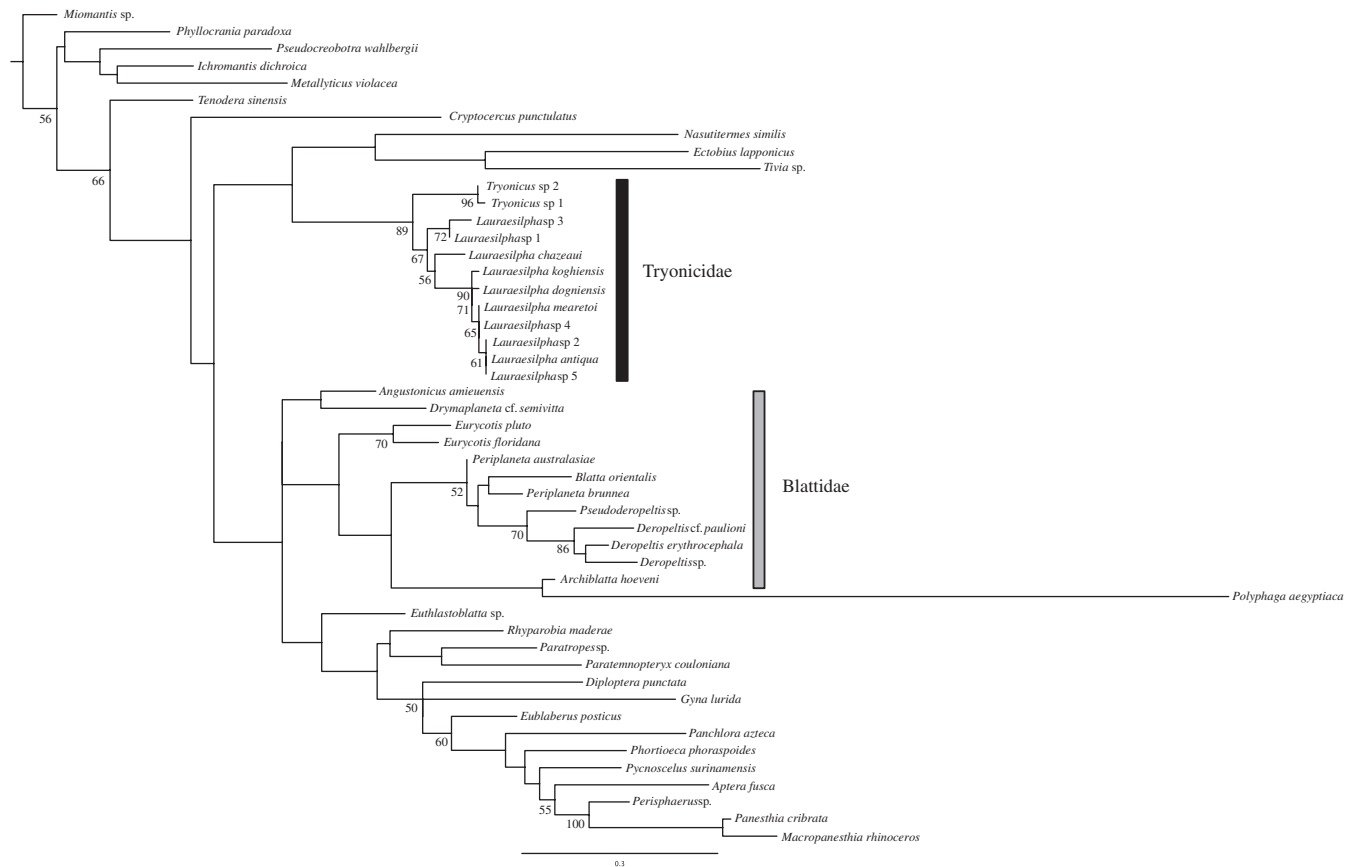


Fig. 4. Maximum Likelihood topology from H3 analyzed alone. Bootstrap frequencies indicated at nodes. Black bar indicates monophyly, grey bar paraphyly.

and outgroups (Ware et al. 2008). The present study was limited by available genes (with influence on taxon sampling), but was sufficient to test whether the *Tryonicus*–*Lauraesilpha* group is a member of the family Blattidae. The results indicate that this group forms a lineage independent from Blattidae, but more work (including more genes and more species) is needed to resolve the position of Tryonicidae within Blattodea.

From a biogeographical point of view, Tryonicidae appears as an excellent group to study the origin of biodiversity in New Caledonia, especially in the context of the submersion of this territory after the breakup of Gondwana (Murienne et al. 2005, 2008; Murienne in press). In addition, Tryonicidae appears as a lineage distinct from Blattidae taxa endemic to New Caledonia. Unfortunately, only Tryonicidae species endemic to New Caledonia have been sequenced. It still remains to sequence some *Tryonicus* species endemic to Australia in order to study the origin of the group in the region.

Acknowledgments

A Lavoisier Fellowship from the French Ministry of Foreign Affairs supported the author. Presently, he is

holding a Marie Curie Fellowship from the European Commission. The author would like to thank the two reviewers, who helped improve the manuscript.

References

- Bergsten, J., 2005. A review of long branch attraction. *Cladistics* 21, 163–193.
- Brinkmann, H., Philippe, H., 1999. Archaea sister group of bacteria? Indications from tree reconstruction artefacts in ancient phylogenies. *Mol. Biol. Evol.* 16, 817–825.
- Castresana, J., 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Mol. Biol. Evol.* 17, 540–552.
- Edgard, R.C., 2004. MUSCLE: a multiple sequence alignment method with high accuracy and high throughput. *Nucleic Acids Res.* 32, 1792–1797.
- Eggleton, P., Beccaloni, G., Inward, D., 2007. Response to Lo et al. *Biol. Lett.* 3, 564–565.
- Grandcolas, P., 1996. The phylogeny of cockroach families: a cladistic appraisal of morpho-anatomical data. *Can. J. Zool.* 74, 508–527.
- Grandcolas, P., 1997. Systématique phylogénétique de la sous-famille des Tryonicinae (Dictyoptera, Blattaria, Blattidae). In: Najt, J., Matile, L. (Eds.), *Zoologia Neocaledonica*, vol. 4, pp. 91–124 (Mém. Mus. Natl. Hist. Nat. 171).

- Grandcolas, P., Bellés, X., Piulachs, M.-D., D'Haese, C., 2002. Le genre *Laurasilpha* Grandcolas, 1997: nouvelles espèces, endémisme, séquences d'ARN ribosomique et caractères d'appartenance aux Blattidae (Insectes, Dictyoptères, Blattidae, Tryonicinae). In: Najt, J., Grandcolas, P. (Eds.), *Zoologia Neocaledonica*, vol. 5. Systématique et Endémisme en Nouvelle-Calédonie, pp. 117–131 (Mém. Mus. Natl. Hist. Nat. 187).
- Guindon, S., Gascuel, O., 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Syst. Biol.* 52, 696–704.
- Hennig, W., 1969. *Die Stammesgeschichte der Insekten*. Waldemar Kramer, Frankfurt.
- Hennig, W., 1981. *Insect Phylogeny*. Wiley, Chichester.
- Hordijk, W., Gascuel, O., 2005. Improving the efficiency of SPR moves in phylogenetic tree search methods based on maximum likelihood. *Bioinformatics* 21, 4338–4347.
- Huelsenbeck, J.P., 1997. Is the Felsenstein zone a fly trap? *Syst. Biol.* 46, 69–74.
- Huelsenbeck, J.P., Ronquist, F., 2001. MrBayes: Bayesian inference of phylogeny. *Bioinformatics* 17, 754–755.
- Inward, D., Beccaloni, G., Eggleton, P., 2007. Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biol. Lett.* 3, 331–335.
- Kjer, K.M., Gillespie, J.J., Ober, K.A., 2006. Structural homology in ribosomal RNA, and a deliberation on POY. *Arthropod Syst. Phyl.* 64, 71–76.
- Klass, K.-D., 1995. *Die Phylogenie der Dictyoptera*. PhD thesis, L.-M.-University Munich, Cuvillier, Göttingen.
- Klass, K.-D., 1997. The external male genitalia and the phylogeny of Blattaria and Mantodea. *Bonn. Zool. Monogr.* 42, 1–341.
- Klass, K.-D., 2001. Morphological evidence on blattarian phylogeny: “phylogenetic histories and stories” (Insecta, Dictyoptera). *Dt. Entomol. Z.* 2, 223–265.
- Klass, K.-D., Meier, R., 2006. A phylogenetic analysis of Dictyoptera (Insecta) based on morphological characters. *Entomol. Abh.* 63, 3–50.
- Lo, N., Tokuda, G., Watanabe, H., 2000. Evidence from multiple gene sequences indicates that termites evolved from wood-feeding cockroaches. *Curr. Biol.* 10, 801–804.
- Lo, N., Bandi, C., Watanabe, H., Nalepa, C., Beninati, T., 2003. Evidence for cocladogenesis between diverse dictyopteran lineages and their intracellular endosymbionts. *Mol. Biol. Evol.* 20, 907–913.
- Lo, N., Beninati, T., Stone, F., Walker, J., Sacchi, L., 2007. Cockroaches that lack *Blattabacterium* endosymbionts: the phylogenetically divergent genus *Nocticola*. *Biol. Lett.* 3, 327–330.
- Mackerras, M.J., 1968. Australian Blattidae (Blattoidea). IX. Revision of Polyzosteriinae tribe Methanini, Tryonicinae, and Blattinae. *Aust. J. Zool.* 16, 511–575.
- Maekawa, K., Kitade, O., Matsumoto, T., 1999. Molecular phylogeny of orthopteroid insects based on the mitochondrial cytochrome oxidase II gene. *Zool. Sci.* 16, 175–184.
- McKittrick, F.A., Mackerras, M.J., 1965. Phyletic relationships within the Blattidae. *Ann. Entomol. Soc. Am.* 58, 224–230.
- Murienne, J., in press. New Caledonia: biology. In: Gillespie, R.G., Clague, D. (Eds.), *Encyclopedia of Islands*. University of California Press, Berkeley.
- Murienne, J., Grandcolas, P., Piulachs, M.-D., Bellés, X., D'Haese, C., Legendre, F., Pellens, R., Guilbert, E., 2005. Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? *Cladistics* 21, 2–7.
- Murienne, J., Pellens, R., Budinoff, R.B., Wheeler, W.C., Grandcolas, P., 2008. Phylogenetic analysis of the endemic New Caledonian cockroach *Laurasilpha*. Testing competing hypotheses of diversification. *Cladistics* 24, 802–812.
- Nylander, J.A.A., 2004. MrAIC.pl. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- Omilian, A.R., Taylor, D.J., 2001. Rate acceleration and long-branch attraction in a conserved gene of cryptic daphniid (Crustacea) species. *Mol. Biol. Evol.* 18, 2201–2212.
- Pellens, R., D'Haese, C.A., Bellés, X., Piulachs, M.-D., Legendre, F., Wheeler, W.C., Grandcolas, P., 2007. 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. *Mol. Phyl. Evol.* 43, 616–626.
- Pol, D., Siddall, M.E., 2001. Biases in maximum likelihood and parsimony: a simulation approach to a 10-taxon case. *Cladistics* 17, 266–281.
- Princis, K., 1966. Blattariae: subordo Blattoidea; fam. Blattidae, Nocticolidae. In: Beier, M. (Ed.), *Orthopterorum Catalogus*, pars 8. W. Junk, s'Gravenhage, pp. 401–614.
- Roth, L.M., 1987. The genus *Tryonicus* Shaw from Australia and New Caledonia (Blattaria: Blattidae: Tryonicinae). *Mem. Queensl. Mus.* 25, 151–167.
- Roth, L.M., 2003. Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). *Orient. Insects* 37, 1–186.
- Sanderson, M.J., Wojciechowski, M.F., Hu, J.M., Khan, T.S., Brady, S.G., 2000. Error, bias, and long-branch attraction in data for two chloroplast photosystem genes in seed plants. *Mol. Biol. Evol.* 17, 782–797.
- Shaw, E., 1925. New genera and species (mostly Australian) of Blattidae, with notes, and some remarks on Tepper's types. *Proc. Linn. Soc. N.S.W.* 50, 171–213.
- Siddall, M.E., Whiting, M.F., 1999. Long-branch abstractions. *Cladistics* 15, 9–24.
- Smith, S.A., Dunn, C.W., 2008. Phyutility: a phyloinformatics tool for trees, alignments, and molecular data. *Bioinformatics* 24, 715–716.
- Swofford, D.L., Olsen, G.J., Waddell, P.J., Hillis, D.M., 1996. Phylogenetic inference. In: Hillis, D.M., Moritz, C., Mable, B.K. (Eds.), *Phylogenetic Inference*. Sinauer Associates, Sunderland, MA, pp. 407–514.
- Terry, M.D., Whiting, M.F., 2005. Mantophasmatodea and phylogeny of the lower neopterous insects. *Cladistics* 21, 240–257.
- Ware, J.L., Litman, J., Klass, K.-D., Spearman, L.A., 2008. Relationships among the major lineages of Dictyoptera: the effect of outgroup selection on dictyopteran tree topology. *Syst. Entomol.* 33, 429–450.