Phylogeny of the Dictyoptera Re-examined (Insecta)

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Abstract. This work presents a critical evaluation of the currently available morphological and biological data base relevant to reconstructing phylogeny in Dictyoptera. In 1992, B.L. Thorne and J.M. Carpenter (Systematic Entomology 17: 253–268) published a widely acknowledged phylogenetic analysis of Dictyoptera that gave the relationships (Mantodea + (*Blattaria + Cryptocercidae)) + ((Mastotermitidae + Kalotermitidae) + Termopsidae) [*Blattaria = Blattaria excluding Cryptocercidae]. The present study uses that work as a starting point to demonstrate the importance of a thorough treatment of characters in phylogenetic reconstruction. Repeating the analysis of Thorne and Carpenter without disputable polarity assumptions produced Mantodea + ((*Blattaria + Cryptocercidae) + ((Mastotermitidae + Kalotermitidae) + Termopsidae)). Analyses after a careful revision of the characters as well as analyses including seven additional characters produced Mantodea + (*Blattaria + (Cryptocercidae + (Mastotermitidae + (Kalotermitidae + Termopsidae)))). The latter result, indicating paraphyly of Blattaria with respect to Isoptera, is in strong contrast to the findings of Thorne and Carpenter, but concurs with some recent morphological and molecular studies. It includes a single acquisition of both symbiotic fat body *Blattabacterium* and hindgut flagellates within Dictyoptera, and the homology of sociality in Cryptocercidae and Isoptera.

Key words. Blattaria, Mantodea, Isoptera, *Cryptocercus*, phylogenetic analysis, cladistic analysis, evolution, sociality.

1. Introduction

WILLI HENNIG (1969) was the first to discuss thoroughly the evolution of Dictyoptera (his Blattopteroidea: cockroaches, mantids, and termites) on the grounds of phylogenetic systematics. He proposed a sistergroup relationship between Mantodea and Blattodea, the latter including Blattaria and Isoptera. HENNIG (1969) recognized the prominent role of the wingless cockroaches of the family Cryptocercidae (which includes only *Cryptocercus*) in the discussion of the relationships between Blattaria and Isoptera. Cryptocercidae and Isoptera share xylophagy and some aspects of sociality and behavior, and they are unique in harbouring a diverse fauna of flagellates of the groups Oxymonadida and Hypermastigida in their hindguts, which they pass to young individuals by anal trophallaxis (proctodeal feeding).

Nonetheless, based on the structure of the hindwing vein PCu (=A1=1A=AA$_{3+4}$ of various authors), HENNIG (1969: 191) preferred to consider Isoptera as the sister group of Blattaria rather than nested within Blattaria as the sister group of Cryptocercidae. Within Isoptera, HENNIG (1969: 326f) regarded as undisputed a basal dichotomy between the Mastotermitidae (which includes only *Mastotermes*) and the remaining termites.

In recent years the Dictyoptera have generated much interest among biologists. This is mainly due to the many biological and morphological distinctions that have evolved within this taxon. Examples include the above cited sociality and the association with oxymonadid and hypermastigid flagellates in Cryptocercidae and lower Isoptera, but also the occurrence of symbiotic Eubacteria (*Blattabacterium*) in the fat body of Mastotermitidae and Blattaria, and symmetry changes in the proventriculus (gizzard) and the male genitalia (KLASS 1997, 1998b; K.-D. Klass & R. Meier in prep.: A cladistic analysis of Blattaria and Mantodea based on the male genitalia). Evolutionary scenarios for these characters and others are of great interest for a variety of disciplines within the biological sciences, but they require a well-corroborated phylogenetic tree for the Dictyoptera. Consequently, a great number of morphology- and molecule-based analyses of Dictyoptera phylogeny have been published during the last decade.

The monophyly of the Dictyoptera is now generally accepted (e.g., KRISTENSEN 1991, 1995; KLASS 1995; BEUTEL & GORB 2001; WHEELER et al. 2001), as is the monophyly of both the Mantodea and Isoptera. However, the phylogenetic relationships among Mantodea, Blattaria, and Isoptera as well as those within the Blattaria have remained highly controversial, and Blattaria are variously considered monophyletic or paraphyletic with respect to Isoptera. Prominent issues in the debate are the phylogenetic placement of Cryptocercidae and Isoptera and the relationships between these two taxa.

In terms of the relationships among the three major subgroups of the Dictyoptera, the work of THORNE & CARPENTER (1992) (abbreviated T&C hereafter) has been most influential. T&C reviewed previous literature on Dictyoptera and analyzed phylogenetic relationships among six 'key' taxa. They defined 70 morphological, biological, and behavioral characters, though 18 of these were uninformative in their analysis. Using the implicit enumeration option of HENNIG86 (FARRIS 1988), they obtained the topology (Mantodea + (*Blattaria + Cryptocercidae)) + (Termopsidae + (Mastotermitidae + Kalotermitidae)) [herein, *Blattaria denotes 'Blattaria except Cryptocercidae']. The tree was rooted to a hypothetical ancestor plesiomorphic in all characters (as perceived by T&C).

While some workers disagreed with T&C's results (e.g., KRISTENSEN 1995; KLASS 1995, 1998a, b, 2001a, c; LO et al. 2000; EGGLETON 2001; HAAS & KUKALOVÁ-PECK 2001), others have accepted them (KUKALOVÁ-PECK & PECK 1993; NOIROT 1995a; KAMBHAMPATI 1995; GRANDCOLAS 1996; GRIMALDI 1997). Some have even combined new molecular data with T&C's data to infer the phylogeny of Dictyoptera (DESALLE et al. 1992; DESALLE 1994). Recent editions of major entomology textbooks have variously adopted (GULLAN & CRANSTON 2000) or rejected (BOHN & KLASS 2003) T&C's phylogenetic results.

In his own re-examination of T&C's data, KRISTENSEN (1995) reasonably recoded five characters and obtained Mantodea + ((*Blattaria + Cryptocercidae) + ((Mastotermitidae + Kalotermitidae) + Termopsidae [as 'Termitidae'])), demonstrating that T&C's results were less robust than they had indicated.

KLASS (1995, 1997, 1998a, b, 2001a) studied in detail the male and female genitalia and the proventriculus of Mantodea, Blattaria, and *Mastotermes*. He revised many previous morphological descriptions, homology hypotheses, and polarity assumptions, partly by outgroup comparison with various Pterygota, Zygentoma (= Thysanura sensu stricto), and Archaeognatha (= Microcoryphia). His revisions relate to many of T&C's characters and cast doubt on their topology. KLASS (1995) proposed Mantodea + (*Blattaria + (Cryptocercidae + (Mastotermitidae + remaining Isoptera))), with the Cryptocercidae-Isoptera clade deeply subordinate within Blattaria.

A recent review of work on isopteran phylogeny and origins (EGGLETON 2001) also concluded that termites are likely nested within Blattaria, *Cryptocercus* then being the most plausible sister group of Isoptera. In a recent analysis of pterygote wing structure, HAAS & KUKALOVÁ-PECK (2001) proposed the topology Mantodea + (Blattaria + Isoptera).

While the phylogenetic relationships within the Mantodea have so far received little attention (but see KLASS 1995, 1997), and work on termite phylogeny has increased only recently (KAMBHAMPATI et al. 1996; MIURA et al. 1998; THOMPSON et al. 2000; DONOVAN et al. 2000; EGGLETON 2001), the phylogeny of the Blattaria has been strongly disputed between GRANDCOLAS (1994, 1996, 1999b) and KLASS (1995, 1997, 2001c; see also Klass & Meier in prep.). One prominent matter in this dispute is the position of *Cryptocercus*. According to GRANDCOLAS this genus is deeply subordinate within the cockroach family Polyphagidae, but KLASS retrieved it as the sister group of Polyphagidae + Lamproblattinae.

This controversy on the placement of *Cryptocercus* is intimately correlated with the question of the phylogenetic placement of the Isoptera. With GRANDCOLAS' hypothesis *Cryptocercus* cannot be the sister group of the Isoptera, because the splitting event between *Cryptocercus* and its surmised polyphagid sister group must have occurred long after the first appearance of termites in the fossil record (see GRANDCOLAS 1999a). However, no direct contradiction to *Cryptocercus* and Isoptera being sister groups results from KLASS' placement of *Cryptocercus*, discussed above.

Molecular data have provided conflicting topologies for Dictyoptera. VAWTER (1991: nuclear 18S rDNA of Dictyoptera and other Neoptera) found Rhinotermitidae + (Cryptocercidae + (Mastotermitidae + Blattidae)). DESALLE et al. (1992: 18S rDNA from a Miocene *Mastotermes*, five extant Dictyoptera, and three outgroup taxa) retrieved Blattaria + (Mantodea + (Termitidae + (Mastotermitidae + Termopsidae))); only when they combined their DNA data with T&C's data did Isoptera appear as the sister group of Blattaria + Mantodea. A later inclusion of DNA data from *Cryptocercus* (DESALLE 1994) did not alter these relations, *Cryptocercus* appearing as the sister group of the sole additional included representative of Blattaria. KAMBHAMPATI (1995: mitochondrial 12S and 16S rDNA) found Isoptera + (Mantodea + Blattaria), with *Cryptocercus* appearing as the sister group of the remaining Blattaria (represented by a large taxon sample). Both MAEKAWA et al. (1999: mitochondrial cytochrome oxidase II gene) and WHITING et al. (2003: nuclear 18S and 28S rDNA and histone 3 gene) obtained Mantodea + (Blattaria + Isoptera); neither study included *Cryptocercus*. BANDI et al. (1995: 16S rDNA from

Blattabacterium in fat body, absent in Mantodea and most Isoptera) found a sistergroup relationship between the symbionts of *Mastotermes* and those of Blattaria (including *Cryptocercus*). LIEBRICH et al. (1995: neuropeptides) obtained Mantodea + (Blattaria + Isoptera). Hence, while the relationships between Mantodea, Blattaria, and Isoptera vary among these studies, none that included Cryptocercidae retrieved the Isoptera as the sister group of this taxon or as otherwise subordinate within Blattaria. Still one should note that most of the studies mentioned have used a small and hence inadequate taxon sample.

On the other hand, three recent molecular studies do recover a monophyletic Cryptocercidae + Isoptera as a subordinate clade within the Blattaria. Lo et al. (2000), analyzing nuclear 18S rDNA, mitochondrial cytochrome oxidase subunit II genes, and endo-β-1,4-glucanase genes, found Cryptocercidae + Isoptera as the sister group of the Blattidae. More recently, Lo et al. (2003) demonstrated cocladogenesis in dictyopterans and their *Blattabacterium* endosymbionts; data from four insect genes (nuclear 18S rDNA, mitochondrial 12S and 16S rDNA, and cytochrome oxidase II gene) gave the topology Mantidae + (((Blattellidae + Blaberidae) + Polyphagidae) + (Blattidae + (Cryptocercidae + (Mastotermitidae + other Isoptera)))), and the topology for the endosymbionts (based on 16S rDNA) was strongly correlated with that of their hosts. In a so far unpublished study, R. Meier and K.-D. Klass reanalyzed available 12S and 16S rDNA sequence data using direct optimization (as implemented in POY: GLADSTEIN & WHEELER 1997), which is known to yield shorter trees than those resulting from fixed alignment and subsequent cladistic analysis (WHEELER 1996, 2000); with most analytic settings *Cryptocercus* and Isoptera were obtained as sister groups, though the position of this clade within the Blattaria varied with the settings.

Regarding basal termite phylogeny, the topology of KAMBHAMPATI et al. (1996: mitochondrial 16S rDNA), Mastotermitidae + (Termopsidae + (Kalotermitidae + (Termitidae + Rhinotermitidae))), is in contrast to that of T&C.

In light of the extreme differences among these findings, the need for additional work on reconstructing dictyopteran phylogeny is indisputable. Of particular uncertainty is the phylogenetic position of the Isoptera. Are they the sister group of Blattaria + Mantodea, of Blattaria, or of the Cryptocercidae? This is the most important point addressed by T&C and by the present study.

Spurred by the continuing lively debate on dictyopteran phylogeny and by the increasing molecular evidence (from multiple genes) contradicting T&C's phylogenetic result, we here examine critically the existing morphological, biological, and behavioral evidence on this issue. In order to specify weak points in T&C's work, we use their study as a starting point and in a three-stage approach first omit disputable polarity assumptions, then revise characters, and finally add further characters. We also incorporate recent data that was not available to T&C, notably, a significant body of new morphological evidence obtained by KLASS (1995, 1998a, b, 2001a).

2. Methods

2.1. General approach: 3 stages

Using T&C's work as the starting point, our study consists of three sequential stages: (A) omission of polarity assumptions that are disputable, including those revised in the next stage; (B) revision of characters with regard to the reliability and reasonability of published data, of definitions of

states, of scorings of taxa, of topographic homologization (as defined by KLASS 2001c), and of polarization; (C) incorporation of additional characters. Each stage builds on the previous one as summarized in Tabs. 3 and 4. Phylogenetic analyses were completed at each stage.

2.2. Terminal taxa

Ingroup taxa. We work with the same six ingroup taxa as delimited and used by T&C: Mantodea, *Blattaria (= Blattaria exclusive of Cryptocercidae = Blattodea sensu T&C), Cryptocercidae, Mastotermitidae, Kalotermitidae, and Termopsidae. 'Blattaria' is used, as by T&C, to comprise *Blattaria and Cryptocercidae, but not Carboniferous fossils representing the stem-group of Dictyoptera (inclusion of the latter, as in, e.g., CARPENTER 1992: 134, implicitly places mantids and termites within Blattaria). For each terminal ingroup taxon the assumed groundplan condition is scored.

We explicitly note that two of the terminal taxa may be paraphyletic in terms of others. *Blattaria may be paraphyletic in terms of Cryptocercidae and in terms of the isopteran families (for controversy on the phylogenetic placement and family level status of *Cryptocercus* see: GÄDE et al. 1997; GRANDCOLAS 1996, 1997, 1999a, b; GRANDCOLAS & DELEPORTE 1992, 1996; KAMBHAMPATI 1995, 1996; KLASS 1995, 1997, 2001c; NALEPA & BANDI 1999, 2000). Ideally, one would avoid this situation by scoring exemplars of the major clades of *Blattaria separately (PRENDINI 2001). First, however, this would require much new data not likely to be gathered for many years. Second, in the reconstruction of blattarian phylogeny the male and female genitalia are two key character systems (with 107 male genitalic characters in a recent matrix by Klass & Meier, unpublished data), but both systems are greatly or entirely reduced in the Isoptera.

Treatment of *Blattaria as a single terminal taxon (together with scoring the assumed groundplan condition for each taxon) has the consequence that potential apomorphies shared by Isoptera or Cryptocercidae (or both) and subgroups of *Blattaria are not recognized. Hence, support for paraphyly of *Blattaria in terms of Cryptocercidae or Isoptera (or both) is a priori excluded; support for paraphyly of Blattaria in terms of Isoptera may be weakened. Affected characters are, for example, those of the proventriculus listed in KLASS (1998b: 37; 2001a: tab. 2; characters not considered herein) and, possibly, character 18 (see chapter 3).

Termopsidae – if including Stolotermitinae and Porotermitinae – are possibly another paraphyletic terminal taxon (in terms of Kalotermitidae and the isopteran families not considered herein). This is indicated by features of, e.g., the internal genitalia (KLASS et al. 2000), the Malpighian tubules (see NOIROT 1995a), and the tarsi (see WEIDNER 1970: 18f). Thus, our scorings of Termopsidae are based, as far as our sources allowed, on the Termopsinae.

Outgroup/Ancestor. According to KRISTENSEN (1991, 1995), the Neoptera fall into 10 major lineages whose phylogenetic relationships are unresolved. Besides the Dictyoptera these are the Orthoptera, Phasmatodea, Notoptera, Embioptera, Dermaptera, Plecoptera, Zoraptera, Acercaria (hemipteroid orders), and Endopterygota (= Holometabola). An 11th lineage is constituted by the recently described Mantophasmatodea (KLASS et al. 2002; see also TILGNER 2002 and KLASS 2002).

Three extensive all-insect phylogenetic analyses have been published in recent years (WHITING et al. 1997; WHEELER et al. 2001; BEUTEL & GORB 2001); nonetheless, a solution of basal splitting events within Neoptera is not in sight. The many character revisions in BEUTEL & GORB (2001) have demonstrated that the scoring of many morphological characters in WHITING et al. (1997) and WHEELER et al. (2001) is highly problematic, and the reliability of the phylogenetic results in these contributions is thus limited.

BEUTEL & GORB's revised set of morphological characters, which at present is surely the most elaborate, supports a clade (Dictyoptera + Phasmatodea) + Notoptera (= Grylloblattodea). However, in their analysis few characters contribute to resolving the relationships among the major neopteran lineages, and a notable percentage of these characters display a high degree of homoplasy (e.g., characters 2, 38, 46, 50, 106 in BEUTEL & GORB 2001, related to ocelli, tarsomeres, costal cross veins, forewing tegminization, and arolium, respectively). In this context the few questionable groundplan scorings, e.g., Mantodea having the forewings tegminized (compare character 17 herein), could have a significant misleading influence. More importantly, some generally known characters not included in BEUTEL & GORB's data set are no less useful than those included, but in part provide contradictory evidence: the presence of styli on abdominal segment 9 in males, the position of the genital opening and type of subgenital lobe in females (e.g., KLASS 2001b: 273), the location, structure, and musculature of abdominal spiracles (e.g., KLASS 2001a: 246f), and the variety of fusions in the postabdominal ganglia (e.g., NESBITT 1941) are among these. In sum, though in terms of character evaluation it constitutes an important step, BEUTEL & GORB's analysis cannot be considered as providing a strong hypothesis for relationships among the major lineages of Neoptera.

Due to these circumstances, outgroup taxa for our analysis could be arbitrarily recruited from among the 11 major neopteran lineages listed above. Notably, the selection would to some extent influence the polarization of characters and thus the result of our analysis. We therefore decided to reconstruct a hypothetical Ancestor that presumably corresponds to the most recent ancestor common to all Dictyoptera; this reconstruction is based on broad outgroup comparison that considers various 'lower' Pterygota, Zygentoma, and Archaeognatha – depending on the availability of data on and applicability of characters to the various taxa. The amount of subjectivity involved in this procedure does not appear to be greater than that of feigning the selection of a discrete outgroup taxon (or taxa). One implication of this procedure is that polarity may be discussed for a character prior to the cladistic analysis.

Limitations. As noted above, the present study, like T&C's, has two unavoidable shortcomings. (1) The lack of data in many characters for a sufficient sample of blattarian taxa and analytical concerns with missing data (WIENS 1998) resulted in scoring *Blattaria as a single terminal taxon. (2) The lack of well-founded hypotheses on the phylogenetic relationships of the Dictyoptera with other major lineages of the Neoptera precludes the consistent use of a discrete outgroup taxon. Instead, a hypothetical Ancestor is reconstructed. The procedures applied herein with respect to these two limitations follow T&C.

2.3. Use of cladistic symbols and terms

In each character, discrete states are represented by [0], [1], [2], and so forth; [?] indicates that the state is unknown; [-] indicates either that the character is not applicable because the assessed element is absent (e.g., wing venation in an apterous taxon) or that the character is excluded (only in Stages B and C).

In polarized characters, [0] stands for the state assumed to be most plesiomorphic within Dictyoptera (exception: in character 44 only, [1] designates the plesiomorphic state to facilitate an ordered character treatment); [1], [2], etc. stand for apomorphic states. The ancestral scoring of a character may be: [0], if the character is believed applicable to the Ancestor and a polarity is assumed; [-], if inapplicable to the Ancestor; or [?], if a polarity is not assumed.

A character is specified as uninformative if it is not phylogenetically informative in the framework of the present analyses and as invariant if it shows the same state in all taxa that can be reasonably scored (i.e., excluding [?] and [-]). Unless otherwise noted, characters relate to conditions in adults (winged males or females in Isoptera). If a character relates to one sex only, this is noted in the character definition.

2.4. Phylogenetic analysis

Parismony-based analyses were performed using PAUP* 4.0b8 (SWOFFORD 1999). In each stage, we used the implicit enumeration option (alltrees) to find the most parsimonious tree(s), first treating all characters as unordered and, second, treating as ordered all characters with the Ancestor scored as [0] as well as, in Stages B and C, character 44. All analyses were rooted to the Ancestor, and we optimized the characters on the trees using ACCTRAN. We used MacClade 3.04 (MADDISON & MADDISON 1992) to calculate tree length for T&C's topology under the character conditions used in our partially ordered analyses of Stages A–C. Decay indices (= Bremer support values; BREMER 1988) were computed using the software TreeRot 2 (SORENSON 1999) to assess support for individual clades in the cladogram resulting from the partially ordered analysis of Stage C.

2.5. Stage A: omission of disputable polarity assumptions

The goal here was to test to what extent T&C's polarity assumptions alone influenced the outcome of their analysis. T&C treated all characters except two (41 and 49) as polarized and all except seven (25, 28, 34, 41, 45, 51, 64) as ordered, but in many characters their assumptions on polarity or transformation series (in multistate characters) are questionable or in need of revision (see Stage B). To exclude the effects of these assumptions, we scored the Ancestor as indefinite [? or -] in 31 characters. This included some characters for which revisions in State B show that a polarity does not exist because the character is actually invariant, or the data are too confused for a reasonable treatment.

In Stage A, we also simplified or clarified the definitions of characters, or their states, or both, yet endeavored to maintain the original intent. Apart from minor rewordings, modifications made in Stage A are explicitly mentioned in the List of Characters (chapter 3).

2.6. Stage B: revision of characters

A re-examination of the characters treated by T&C revealed, for certain characters, several problems: (1) redundant information occurs in 11 multistate characters; (2) inconsistencies occur between scorings and data in the literature (works cited by T&C as well as others), or ambiguity in the literature was not considered; (3) differences in the terminology or interpretation of elements were mistak-

en as differences in structure and defined as different states; (4) assumptions on homology (topographic homologization as defined by KLASS 2001c) or character polarity were included that are disputable or cannot be upheld. Additionally, (5) relevant information is given in more recent literature. Much revision was thus required.

Redundant information. We first eliminated the redundancies in T&C's multistate characters 29, 56–61, 63, and 68–70, each of which embodies a hidden character. T&C consistently coded these with a state [0] that did not match the respective character definition, e.g., **Soldier ocelli**: [0] soldiers primitively absent, [1] ocelli present, [2] ocelli absent (character 57). T&C assumed polarity (Ancestor scored as [0]) and linear order [0]→[1]→[2] (p. 257), and they scored terminal taxa lacking the soldier caste (Mantodea, *Blattaria, and Cryptocercidae) as [0]. Each of these characters actually consists of two characters, which in the chosen example are 'presence of a soldier caste' and 'presence of ocelli in the soldiers'. The former character and its scoring are 'hidden', because only the treatment of the latter is evident from the character definition. One accurate coding conveying the original content would be **Soldiers and their ocelli**: [0] both absent, [1] both present, [2] soldiers present, soldier ocelli absent.

As a consequence of redundant scorings for the 'presence of soldiers' in characters 56–61 (hidden) as well as 67 (stated), the change from 'soldier primitively absent' to 'soldier present' costs 7 steps in T&C's analyses, instead of 1. Further redundant characters are 'presence of workers' (hidden in character 63, stated in 67), 'presence of nest' (hidden in 68–70, not stated separately), and 'presence of wing basal suture' (hidden in 29, stated in 28). T&C considered castes, nests, and wing basal sutures all as present only in the isopteran taxa. Hence, their codings introduced artificially strong support for isopteran monophyly into the analysis (which, nonetheless, is undisputed).

We eliminated the redundancies by formulating the offending characters as simple binary characters that refer only to the content actually indicated by T&C's definition (in our example only to the presence of ocelli in the soldiers; thus, **Soldier ocelli**: [0] present, [1] absent) and by reductive character coding (STRONG & LIPSCOMB 1999), in which terminal taxa lacking the assessed element (for example, soldier caste) are scored as [-]. We retained each of the former hidden characters only once in our analyses (see chapter 3): in characters 28 (presence of wing basal suture), 67 (with the presence of soldiers and workers/pseudergates implicit in "alloparental brood care"), and 70 (to retain "presence of a nest", we preserved T&C's coding of 70).

In contrast to the above, T&C's treatment of characters 62 and 64 – which also refer to structures of workers (midgut caeca, sternal glands) – included no state "workers primitively absent". In these, however, T&C disregarded their own definitions by scoring the respective structures also in *Blattaria and Cryptocercidae, which have no workers (or pseudergates). Here we restricted these characters to workers and scored terminal taxa lacking workers as [-] (alternatively, one could reformulate the characters based only on adults/alates).

Evaluation of data base. Earlier descriptions and interpretations of dictyopteran morphology and the respective terminologies vary greatly, especially regarding the proventriculus, wing venation, and female genitalia, which are among the more important character systems for reconstructing phylogeny in Dictyoptera. When comparing contributions of various workers, it is often difficult to distinguish among differences in terminology, differences in interpretation, and genuine differences in structure.

This is particularly true for the characters relating to 'sterna' of the female genital region. Abdominal 'sterna' are composed of a true sternum (eusternum) plus limb base sclerotizations (SNODGRASS 1935: 251). In the literature, the limb base sclerotizations of the female genital segments are usually specified as such in Blattaria and Mantodea (e.g., valvifers, gonangulum) but referred to as 'sterna' in Isoptera. In addition to this nomenclatural problem, the interpretation of most elements differs among authors. Hence, homologous elements have many synonyms, and non-homologous elements may bear the same name.

The situation is similarly confused regarding the wing venation. Our discussions of wing characters largely follow KUKALOVÁ-PECK (1991; personal communication), KUKA-LOVÁ-PECK & PECK (1993), and HAAS & KUKALOVÁ-PECK (2001); however, we made no attempt to examine all 47 wing characters that HAAS & KUKALOVÁ-PECK (2001: tabs. 6F–G) listed as relevant to dictyopteran relationships (see chapter 5). Tabs. 1 and 2 give a comparison of the forewings of various Dictyoptera and present our reinterpretation of T&C's characters 19–27 (some observations are based on crude illustrations and further detailed investigations are warranted).

Our discussions on the proventriculus, postabdomen, and female genitalia, relating to T&C's characters 30–34, 36–40, and 42–47, follow KLASS (1997, 1998a, b, c, 2001a, b, c; see also KLASS & KRISTENSEN 2001). Much of the data on life history and behavior were drawn from publications of Nalepa and co-authors (see References). As documented by these citations and by notes in chapter 3, our scorings in many characters are based on direct examination of specimens by the authors, using material at the North Carolina State University Insect Collection, the Zoological Museum of the University of Copenhagen, and other institutes. We did not list many additional observations that simply confirmed T&C's scorings.

Technical procedure. We revised the characters in light of the mentioned problems and new evidence. All modifications, except minor rewordings, are mentioned in or evident from the character discussions in chapter 3. The character or character state definitions were often corrected in Stage B, or the states redefined, and some multistate characters were reformulated as binary. In terms of character definitions, unless alternate definitions are given at the beginning of "Stage A" and "Stages B–C", those given in the headings of the character discussions are valid throughout all Stages A–C. In terms of character state definitions, unless new definitions are given in "Stages B–C", those given in "Stage A" are valid throughout all Stages A–C.

We provided references supplementary to those in T&C, in some instances using secondary literature sources to document information that is generally established. We excluded all invariant characters from analysis but generally retained uninformative characters (YEATES 1992). We are aware that certain characters are strongly interdependent (e.g., association with particular hindgut symbionts, anal trophallaxis, and sub/eusociality, see characters 67 and 75; NALEPA 1991, 1994) and that certain characters may act as an evolutionary constraint on others (e.g., eusociality on associated behaviors; BARONI URBANI 1989).

2.7. Stage C: incorporation of additional characters

We used T&C's characters 1–70 as revised in our Stage B and added 7 further characters, 71–77. Stages B and C are thus identical in terms of characters 1–70 and are treated together in the discussion of these characters.

3. List of characters

3.1. Characters used by THORNE & CARPENTER (1992): 1–70

Character 1: shape of antenna. S t a g e A . [0] filiform; [1] moniliform. We limited the character to antenna shape. — S t a g e s B – C . We scored Cryptocercidae as [1] because the antennae of *Cryptocercus punctulatus* Scudder, 1862 are somewhat moniliform (SCUDDER 1862; our unpublished observations) as in *Mastotermes*. Mantodea and *Blattaria score as [0] (BALDERSON & KEY 1991: 348; ROTH 1991: 320; RAMSAY 1990: 14, 25; ROY 1999: 20, 24, 35), the isopteran taxa [1] (WATSON & GAY 1991: 331).

Character 2: number of antennomeres. S t a g e A . [**0**] ≥35; [**1**] 30–31; [**2**] 23–27; [**3**] 11–21. — S t a g e s B – C . [**0**] ≥44; [**1**] 29–42; [**2**] ≤27. While aware of the subjectivity in defining states in a character relating to a continuous range, we redefined the states to reflect apparent natural gaps: Mantodea (many, up to 134 antennomeres: SLIFER 1968: 106; RAMSAY 1990: figs. 3–6; ROY 1999: 24) and *Blattaria (many, up to 178: GUTHRIE & TINDALL 1968: 98) score as [0], Cryptocercidae (31–42: NALEPA et al. 1997: 417) and Mastotermitidae (29–32: WATSON & GAY 1991: 342) as [1], Kalotermitidae (11–22: WATSON & GAY 1991: 342) and Termopsidae (21–27: EMERSON 1933: 167–179) as [2]. Because the number of antennomeres in Blattaria and Isoptera increases during postembryonic development (BEIER 1974: 20; WEIDNER 1970: 78), reduction may be interpreted as paedomorphosis.

Character 3: separation of compound eyes on vertex. S t a g e A . [**0**] narrow; [**1**] broad. We clarified the definitions of states and note that scoring "stereoscopic vision" is problematic due to the lack of physiological evidence in some terminal taxa (e.g., Cryptocercidae, Mastotermitidae). — S t a g e s B – C . *Excluded*. The eyes in *Cryptocercus* (small, flat) and alate Isoptera (small, semi-globular) are very widely separated on the vertex. Separation is somewhat less wide in Mantodea with their very large, semi-globular eyes (e.g., *Choeradodis* and *Mantoida*), the only taxon scored as [1] by T&C. In *Blattaria the flat, somewhat kidney-shaped eyes frequently approach each other on the vertex. Thus, e.g., *Ergaula* (Polyphagidae) and *Leucophaea* (Blaberidae) display a very narrow separation. However, the eyes remain much more widely separated in, e.g., *Symploce* (Blattellidae), *Diploptera*, and *Phoetalia* (Blaberidae). The width of separation can vary strongly even within a genus (much greater in *Periplaneta fuliginosa* than in *P. americana*; Blattidae). Due to the considerable variation in *Blattaria and the interdependence of the character with the relative size of the eyes, we do not consider this character useful and excluded it.

Character 4: number of ocelli. S t a g e A . [**0**] 3; [**1**] 2; [**2**] 0. — S t a g e s B – C . We scored Cryptocercidae as [2], finding no external evidence of ocelli (SCUDDER 1862: 420; BEÎ-BIENKO 1935: 132; our unpublished observations). ROY (1999: 24) gave data on Mantodea.

Character 5: number of marginal teeth of left mandible. S t a g e s A – C . [**0**] ≥3; [**1**] 2. We simplified the character states. *Blattaria have up to 4 (YUASA 1920: 264; AHMAD 1950: fig. 5); for Mantodea a condition with 2 marginal teeth is reported (incisor processes except the apical one: LEVEREAULT 1936: 212). AHMAD's (1950) work indicates that reductions occurred independently in several clades of Isoptera (see KLASS 1995: 183).

Tab. 1. Reinterpretation of forewing venation for selected figures of Dictyoptera. Based largely on KUKALOVÁ-PECK (1991, personal communication), KUKALOVÁ-PECK & PECK (1993), and HAAS & KUKALOVÁ-PECK (2001). Original labels for veins are given in [square brackets]. **1** = based on unpublished observations of Kukalová-Peck (personal communication).

Taxon and source figure	Venational nomenclature followed here									
	CP	**ScA**	**ScP**	**RA**	**RP**	**MA**	**MP**	**CuA**	**CuP**	**AA & AP**
Dictyoptera stem-group	CP short	ScA short	ScP moderately long, branched	RA, RP & MA fused basally			MP branched	CuA branched	CuP absent (arching vein = AA_1)	AA_1–AA_4 & AP veins
HAAS & KUKALOVÁ-PECK 2001: fig. 20A (Archimylacridae)	[CP]	[ScA]	[ScP]	[RA]	[RP]	[MA]	[MP]	[CuA]	[CuP in claval fold]	[$CuP+AA_1$, AA_2–AA_4, AP]
Mantodea	?	ScA short[1]	ScP long (simple?)	RA, RP, & MA apparently fused for a greater distance (frequently this entire complex unbranched)			MP branched	CuA branched	CuP absent (arching vein = AA_1; fused distally with other AA branches in some higher Mantodea)[1]	AA_1, AA_2, AA_{3+4} & AP veins[1]
SMART 1956: fig. 1	–	–	[Sc]		[R]		[M]	[Cu_1]	[Cu_2] = AA_1	[Cu_2, Pcu, 1V & unlabeled veins]
RAMSAY 1990: fig. 12	–	–	[Sc]		[R_1 & Rs]		[MA_1, MA_2, & MP]	[Cu_{1a} & Cu_{1b}]	[Cu_2] = AA_1	[Cu_2+PCu+1V, 2V–4V]
Blattaria	?	ScA short[1]	ScP moderately long, branched	RA, RP & MA fused basally			MP branched	CuA branched	CuP absent (arching vein = AA_1; fused distally with other AA branches)[1]	AA_1–AA_4 & AP veins[1]
BOUDREAUX 1979: fig. 78	–	–	[c-sc cross-veins & Sc]	[c-r cross-veins in part]	[c-r cross-veins in part]	[c-r cross-veins, R & Rs]	[M]	[CuA]	[CuP] = AA_1	[CuP, A]
Isoptera: Mastotermitidae	?	ScA short	ScP short (simple?)	RA, RP & MA fused basally			MP branched	CuA branched	CuP absent (arching vein = AA_1)[1]	AA_1, AA_2, AA_{3+4} & AP veins[1]
BOUDREAUX 1979: fig. 77A	–	–	–	[c-sc cross-veins in part]	[c-sc cross-veins in part & Sc]	[c-r cross-veins in part, R & Rs]	[M]	[CuA]	–	[CuP]
KUKALOVÁ-PECK & PECK 1993: fig. 20 (wing base)	–	[ScA]	[ScP]	[RA]	[RP]	[MA]	[MP]	[CuA]	[$CuP+AA_{1+2}$] = AA_1	[$CuP+AA_{1+2}$, AA_{3+4}, AP]

Tab. 2. Interpretation of wing structures (characters 19–27). Unless otherwise indicated, sources for interpretation as in Tab. 1. **1** = surmised groundplan condition of Dictyoptera as reconstructed from some Palaeozoic fossils and outgroup comparison. **2** = based on KUKALOVÁ-PECK (1991: fig. 6.19C,D) and HAAS & KUKALOVÁ-PECK (2001: fig. 20A). **3** = based on SCHNEIDER (1984) and HAAS & KUKALOVÁ-PECK (2001: fig. 20B). **4** = based on SMART (1956: 549, *Chaeteessa*). **5** = based on SMART (1956: fig. 1), RAMSAY (1990: fig. 16; "Pcu" represents AA₃₊₄ , according to KUKALOVÁ-PECK, personal communication), and HAAS & KUKALOVÁ-PECK (2001: fig. 13). **6** = based on ROTH (1991: fig. 19.2C; "CuP" represents AA₃₊₄), REHN (1951: fig. 76), and HAAS & KUKALOVÁ-PECK (2001: fig. 11A,B). **7** = based on KUKALOVÁ-PECK & PECK (1993: figs. 20–22) and HAAS & KUKALOVÁ-PECK (2001: fig. 12). **8** = based on GRASSÉ (1986: fig. 282Aa,Ba,Ea,Ep) and KUKALOVÁ-PECK (personal communication). **9** = based on EMERSON (1933: fig. 15), GRASSÉ (1986: fig. 270E,F), IMMS (1919: figs. 16, 17), WEESNER (1969: fig. 8E), and KUKALOVÁ-PECK (personal communication).

Taxon or Ancestor	Forewing characters: 19–24						Hindwing characters: 25–27		
	19: RA branching *(excluded)*	20: ScP length	21: MP position	22: MP branching	23: Clavus size	24: Jugum size *(excluded)*	25: ScP length (25)	26: AA₃₊₄ branching	27: Anojugal area size
Ancestor (Stages B+C)[1]	2-branched[2]	moderately long	about midway between MA and CuA (scored [?])	branched	large	uncertain: small? (scored [?])	moderately long[3]	many-branched[3] (scored [?])	moderately large[3]
Mantodea	uncertain: RA, RP & MA fused for a considerable distance	long	about midway between MA and CuA	branched (at least forked)	large	small[4]	long[5]	unbranched[5]	large[5]
*Blattaria	uncertain: RA, RP & MA fused basally	moderately long	about midway between MA and CuA	branched	large	small	moderately long[6]	unbranched or 2- or 3-branched[6]	large[6]
Mastotermitidae[7]	branched	short	about midway between MA and CuA	branched	small	small	moderately long	many-branched	moderately large
Kalotermitidae[8]	unbranched	short	closer to MA than to CuA distally	branched	small	uncertain: small?	short	probably absent	small or absent
Termopsidae[9]	unbranched	short	closer to MA than to CuA distally	branched	small	uncertain: small?	short	probably absent	small or absent

Tab. 3. Data matrix for characters in Stage A of present study. Corresponding to original matrix of Thorne & Carpenter (1992), but amended ancestor of present paper additionally included: 'Ancestor (Stage A)', amended as described in chapters 2.5 and 3. In our partially ordered analysis, characters with the Ancestor scored [0] were treated as ordered, all others were treated as unordered. (T&C's analysis – also partially ordered – treated only characters 25, 28, 34, 41, 45, 51, and 64 as unordered.) **u**, **i** = uninformative and informative characters, respectively, in partially ordered analysis.

	1---5	6--10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50
Ancestor (original)	00000	00000	00000	00000	00000	00000	00000	00000	?0000	000?0
Ancestor (Stage A)	00?00	?0???	0?000	0??0?	?00??	?000?	????0	??000	??0??	??0?0
Mantodea	0010?	0??00	01010	01?11	10011	10000	1??20	00000	1?002	?00?0
*Blattaria	00010	00010	01000	01?10	10000	10001	1?110	10100	11002	100?0
Cryptocercidae	00010	01110	01000	1????	?????	????1	10111	10110	11002	100?1
Mastotermitidae	11011	00011	10100	00100	10100	01210	01000	11101	00110	01100
Kalotermitidae	13011	00001	10101	00210	11102	02210	0?000	11103	2?10?	00110
Termopsidae	12020	10001	10100	00000	00100	02100	00000	11102	2?001	00110
original character content	iiuii	uuuii	iiiuu	uiiiu	iuiuu	iiiii	iuiiu	iiiui	iiiui	iuiuu
stage A character content	iiuii	uuuii	iiiuu	uiuiu	uuiuu	iiiii	iuiiu	uiiui	iuiuu	iuiuu

	51-55	56-60	61-65	66-70
Ancestor (original)	00000	00000	00000	00000
Ancestor (Stage A)	00?0?	00000	000??	00000
Mantodea	0?10?	00000	0?0?1	?0000
*Blattaria	00100	00000	00011	00000
Cryptocercidae	0?100	00000	00021	00000
Mastotermitidae	21110	21222	20200	11222
Kalotermitidae	11121	22132	11110	01111
Termopsidae	01001	12111	10110	01111
original character content	uiiii	iiiii	iuiii	uiiii
stage A character content	iiuii	iiiii	iuiui	uiiii

Tab. 4. Data matrix for characters in Stages B (characters 1–70) and C (characters 1–77) of present study. 'Ancestor (Stages B+C)' established as described in chapters 2.2, 2.6, and 3. In our partially ordered analysis, characters with the Ancestor (Stages B+C) scored [0] and character 44 were treated as ordered; all others were treated as unordered. **a** = character added in Stage C; **c** = character constant (= invariant = only one state present); **i** = character informative in partially ordered analyses of Stages B and C; **n** = character not modified in Stages B and C; **r** = character reformulated (including reversal of polarity assumption) and rescored in Stages B and C; **s** = one or more scorings of character changed in Stages B and C, but character and its states essentially as defined in Stage A; **u** = character uninformative in partially ordered analyses in Stages B and C; **x** = character excluded in Stages B and C.

	1---5	6--10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50
Ancestor (stages B+C)	00-00	?0??-	0?000	0??-0	?-0-0	?00-0	00-?0	--000	0--1-	0?0-0
Mantodea	00-01	???0-	01110	0??-0	0-0-0	100-0	00-00	--000	1--2-	000-0
*Blattaria	00-10	??01-	01000	01?-0	0-0-0	100-0	00-00	--100	1--1-	000-0
Cryptocercidae	11-20	?111-	01?00	1----	-----	----0	01-01	--110	1--1-	000-1
Mastotermitidae	11-11	0000-	10000	001-1	0-1-0	001-1	11-10	--100	1--0-	111-0
Kalotermitidae	12-11	0000-	10001	001-1	1-1-1	211-1	11-10	--101	0--?-	??1-0
Termopsidae	12-20	1??0-	10000	000-1	1-1-1	211-1	11-10	--101	0--?-	??1-0
data modifications	srxss	ssssx	nnrnn	nsrxr	rxnxr	rrrxr	rrxrn	xxnnr	rxxrx	rsnxn
character content	iicii	uuui-	iiuuu	uuu-i	icici	iii-i	ii-iu	cciui	iccuc	uui-u

	51-55	56-60	61-65	66-70	71---77
Ancestor (stages B+C)	00-00		----?	00--0	00?0000
Mantodea	00-00	-----	----1	00--0	0000000
*Blattaria	00-01	-----	----1	00--0	1000011
Cryptocercidae	?0-11	-----	----1	01001	1100111
Mastotermitidae	21-11	10101	10100	12112	1111111
Kalotermitidae	11-10	01011	01010	02001	11211?1
Termopsidae	11-10	01000	0002?	02001	11211?1
data modifications	ssxrr	rrrrr	rrrrs	rrrrr	aaaaaaa
character content	iicii	uuuuu	uuuui	uiuui	iiiiiii

Character 6: subsidiary tooth on 1st marginal tooth of right mandible. S t a g e A . [**0**] absent; [**1**] present. We reworded the states and scored the Ancestor as [?]. — S t a g e s B – C . A homologue in *Blattaria, Cryptocercidae, and Mantodea (all scored as [?]) is uncertain and polarity is ambiguous (AHMAD 1950: compare pp. 51 and 53; WEIDNER 1970: 17, regarded presence as plesiomorphic).

Character 7: mandibular glands. S t a g e A . [**0**] present; [**1**] absent. Polarity [0]→[1] is supported by the presence of mandibular glands in the same position in Archaeognatha and Zygentoma (BRUNTZ 1908: 205, as 'glandes céphaliques antérieures'; DENIS & BITSCH 1973: ceglm in fig. 56; CHAUDONNERET 1950: ceglm in fig. 55; compare BROSSUT 1973: 1 in fig. 1). — S t a g e s B – C . BROSSUT (1973: 44, tab. 1) found the glands in Mastotermitidae and Kalotermitidae. The conditions in Termopsidae (Termopsinae not studied: BROSSUT studied *Anacanthotermes*, which belongs to Hodotermitidae), Mantodea (the glands treated by SUSLOV 1912: oe in fig. 1 are likely inferior hypostomial glands; compare BROSSUT 1973: fig. 2) and *Blattaria are scored here as uncertain [?]. Absence in the ground plan of Blattaria is indicated by BROSSUT's observation of the glands only in the subordinate clade Blattellidae + Blaberidae; however, outgroup comparison suggests otherwise. Thus, state [1] is clear only for Cryptocercidae. BROSSUT (1973) and MILLER (1989) gave data on various head glands that may be phylogenetically useful.

Character 8: hypopharyngeal glands. S t a g e A . [**0**] present; [**1**] absent. We scored the Ancestor as [?]. — S t a g e s B – C . We scored Termopsidae as [?] (no Termopsinae studied, see character 7). As far as known (BROSSUT 1973), many *Blattaria (Polyphagidae, Blaberidae), Cryptocercidae, and those isopteran families not included here lack these glands. Homologies with non-Dictyoptera need further investigation.

Character 9: expansion of pronotum over head. S t a g e A . [**0**] absent; [**1**] present. We scored the Ancestor as [?] because the expansion is absent in extant outgroups but present in members of the stem-group of Dictyoptera (or of the 'Blattoid assemblage': KUKALOVÁ-PECK 1991: 166); for further arguments see HENNIG (1969: 187f) and KLASS (1995: 164). — S t a g e s B – C . We scored Mastotermitidae as [0], because, as in basal Mantodea (at least *Mantoida, Eremiaphila;* Klass, unpublished observations), the pronotum covers only the posteriormost part of the head.

Character 10: meso/metathoracic ventropleurites. S t a g e A . [**0**] present; [**1**] absent. — S t a g e s B – C . *Excluded.* In Isoptera the absence of ventropleurites appears fairly clear (MATSUDA 1960: 718). In Blattaria ventropleurites were noted by MATSUDA (1960: 718), but not by MATSUDA (1970: 151). In Mantodea, MATSUDA (1960: 720) indicated ventropleurites that are fused to the pre-episterna, but later (1970: 163) regarded the latter sclerites as the pre-episterna proper, not mentioning a ventropleurite portion, which, in addition, he claimed to be "absent in related orders". In view of these confused data and clear need for re-examination, we excluded character 10.

Character 11: mesothoracic alary muscles. S t a g e s A – C . [**0**] present; [**1**] absent. We limited the character to these muscles (for which data are clear: NUTTING 1951: 530–532).

Character 12: segmental arteries in abdomen. S t a g e s A – C . [**0**] absent; [**1**] present. We scored the Ancestor as [?] (KLASS 1995: 165). We retain Mantodea scored as [1], noting that only members of the highly derived Mantidae have been studied and arteries were found only in Mantinae, but not in Amelinae and Thespinae (NUTTING 1951: 511, 529).

Character 13: abdominal neuromeres (segmental ganglia) fused to metathoracic neuromere. S t a g e A . [**0**] none; [**1**] 1st+2nd. We reworded the character. — S t a g e s B – C . [**0**] 1st only; [**1**] 1st+2nd+3rd. We corrected the state definitions and scorings. Abdominal neuromere 1 is fused with the metathoracic neuromere in apparently all Dictyoptera (NESBITT 1941: 67 [Blaberidae: *Blaberus*; Termopsidae: *Termopsis*]; ENGELMANN 1963: 2 [Blaberidae: *Leucophaea*]; SHANKLAND 1965: 361 [Blattidae: *Periplaneta*]; STRIEBEL 1960: 237 [Kalotermitidae: *Kalotermes*]; Klass, unpublished observations [Mastotermitidae: *Mastotermes*; Polyphagidae: *Polyphaga*]; note: we have no data on *Cryptocercus*). In *Mantoida* and in species of Mantidae, representing the two basalmost sister groups within Mantodea (KLASS 1995: 315) – and therefore probably in the mantodean ground plan – abdominal neuromeres 2 and 3 are additionally fused with this complex, and 4 free abdominal ganglia are thus recognized (KLASS 1999: fig. 2 and unpublished observations [*Mantoida, Creobroter, Sphodromantis*]; STEINMANN 1962: 155 [*Mantis*]; NESBITT 1941: 67 [*Mantis*]; KERRY & MILL 1987 [*Hierodula*]). The literature on Mantodea includes contradictory numbers, but in most cases the sources and the manner of counting are not indicated (HILTON 1937 [5 free abdominal ganglia in a "Mantid"]; ILLIES 1962: 140 [7]; BEIER 1968: 28 [7]; MATSUDA 1976: 105 [4–5]; GRASSÉ 1975: 455 [5–6]; BALDERSON & KEY 1991: 350 [7]).

Character 14: forelegs. S t a g e s A – C . [**0**] not raptorial; [**1**] raptorial.

Character 15: number of tarsomeres. S t a g e s A – C . [**0**] 5; [**1**] 4. Kalotermitidae show, like the termite families not considered herein, state [1] (WEIDNER 1970: 14ff). Mastotermitidae and Termopsinae have 5 tarsomeres, though in the latter the second is reduced and visible only from below (this applies to all legs in extant species but only to fore- and midlegs in the Oligocene *Termopsis*: EMERSON 1933: 169–170; WEIDNER 1970: 17). Still, it seems possible that state [1] has evolved from a condition as found in Termopsinae.

Character 16: wings. S t a g e s A – C . [**0**] present; [**1**] absent.

Character 17: tegminization of forewings. S t a g e A . [**0**] absent; [**1**] present. We reworded the character, and we scored the Ancestor as [?] because tegminized forewings are found in many Neoptera (e.g., Orthoptera, Dermaptera). — S t a g e s B – C . We scored Mantodea as [?], because in at least Mantoididae and Chaeteessidae, the most basal clades of Mantodea (KLASS 1995, 1997; Klass & Meier in prep.), the forewings are membranous and similar in texture to the hindwings (SMART 1956). This condition may or may not represent the mantodean ground plan.

Character 18: pimpules of wings. S t a g e A . Wing microsculpturing: [**0**] only papillae; [**1**] papillae and pimpules; [**2**] papillae, pimpules, and tubercles. We scored the Ancestor as [?] due to the lack of clear outgroup data. — S t a g e s B – C . Pimpules of wings: [**0**] absent; [**1**] present. We emended "papillae" (present in all states of T&C) and "tubercles" (presumably apomorphic presence only in Kalotermitidae and hence uninformative), limiting the character to "pimpules" and reformulating it as binary. We left *Blattaria scored as [?], but note that *Supella*, the one blattarian genus ROONWAL & RATHORE (1983) examined, has pimpules.

Character 19: forewing radius anterior (preradius in T&C). S t a g e A . [**0**] 2-branched; [**1**] absent. — S t a g e s B – C . *Excluded.* In Mantodea and Blattaria the presence and thus the condition of RA (and of RP) are difficult to

ascertain with confidence because R and MA are fused for some distance, and RA and RP thus appear as two successive basal, anteriorly directed 'branches' of MA. Branching sequence is here a major criterion for distinguishing RA, RP, and MA, but could easily be confounded by the loss or basal fusion of one or more 'branches' (RA and RP). There is thus little or no basis for T&C's scorings of RA being absent in Mantodea, *Blattaria, and Kalotermitidae.

Character 20: length of forewing subcosta posterior (subcosta in T&C). S t a g e A . [0] short; [1] long. We scored the Ancestor as [?]. — S t a g e s B – C . [0] longer than 1/3 of wing length; [1] shorter than 1/3 of wing length. We reversed the polarity (Boudreaux 1979: 217, as subcosta; Kukalová-Peck 1991: fig. 6.19C) and scored the Ancestor and *Blattaria as (moderately) long [0] (Tabs. 1, 2).

Character 21: position of forewing media posterior (media in T&C). S t a g e A . [0] closer to cubitus anterior (= Cu in T&C) than to media anterior (= Rs in T&C); [1] about midway between cubitus anterior and media anterior, or closer to media anterior. We scored the Ancestor as [?] (see Stages B–C). — S t a g e s B – C . [0] about midway between MA and CuA; [1] largely closer to MA than to CuA. Because MP is apparently not closer to CuA than to MA in the ground plan of any terminal taxon treated, we abandoned T&C's state [0]; however, we split their state [1] into two states. We thus scored Kalotermitidae and Termopsidae as [1] (Weesner 1969: fig. 8E [RP+MA is labeled R$_{2+3}$; MP is labeled R$_{4+5}$; CuA is labeled M]; Grassé 1986: fig. 282Aa,Ba,Ea), the Ancestor as [?], and the remaining winged taxa as [0] (Tab. 2).

Character 22: branching of forewing media posterior (media in T&C). S t a g e A . [0] branched; [1] simple (without branches). — S t a g e s B – C . *Excluded* (probably invariant). MP is probably branched in the ground plan of all taxa with winged forms, including Kalotermitidae (Tabs. 1, 2).

Character 23: size of forewing clavus. S t a g e s A – C . [0] large; [1] small or absent. We limited the character to claval size noting that wing veins (part of T&C's state [0]) are present in the small clavus of Mastotermitidae (Kukalová-Peck & Peck 1993: fig. 20) (Tab. 2).

Character 24: size of forewing jugum (jugal lobe). S t a g e A . [0] small; [1] slightly enlarged. We scored the Ancestor as [?]; Kukalová-Peck (1991) indicated the presence of a small jugum in some outgroup taxa (Protodonata and a member of the orthopteroid stem-group: figs. 6.15B,I, 6.18C), but no jugum in others (including a member of the Dictyoptera stem-group: fig. 6.19C). — S t a g e s B – C . *Excluded*. Although a slightly enlarged jugum occurs in the forewing of some Mantodea (Ramsay 1990: fig. 12, jugum proximal to "3V"), the groundplan mantodean jugum appears to be small (Smart 1956: 549, *Chaeteessa*, a presumed basal group). The character is thus invariant among the winged taxa for which we have information (Tabs. 1, 2).

Character 25: length of hindwing subcosta posterior (subcosta in T&C). S t a g e A . [0] short; [1] long; [2] absent. We scored the Ancestor as [?]. — S t a g e s B – C . [0] longer than 1/3 of wing length; [1] shorter than 1/3 of wing length. We reversed the polarity, formulated the character as binary (ScP occurs in the ground plan of all taxa with winged forms), and scored Mantodea, *Blattaria, and Mastotermitidae as [0] and Kalotermitidae and Termopsidae as [1] (Tab. 2). This scoring differs from Haas & Kukalová-Peck (2001: tab. 6F), who applied a different subdivision of the range and categorized ScP to be short in Blattaria and Mastotermitidae.

Character 26: branching of hindwing anal anterior 3+4 (postcubitus PCu or A1 in T&C). S t a g e A . [0] with many branches; [1] simple. We clarified the character and scored the Ancestor as [?]. — S t a g e s B – C . [0] ≥4 branches; [1] ≤3 branches; [2] absent. We redefined the states because *Blattaria can have up to 3 distal branches (e.g., *Arenivaga*: Rehn 1951: fig. 76). Furthermore, Termopsidae (Emerson 1933: fig. 15; Grassé 1986: 270F) and Kalotermitidae (Grassé 1986: 282Ep) seem to entirely lack AA$_{3+4}$ (Kukalová-Peck, personal communication) (Tab. 2). In Mantodea AA$_{3+4}$ is simple throughout (Smart 1956: PCu in figs. 1–4; Kukalová-Peck, personal communication). Polarity is disputable: Schneider (1984) found state [0] in all Palaeozoic Dictyoptera. Kukalová-Peck (1991: fig. 6.19D) found state [0] in *Puknoblattina*, which she (1991: 166) apparently regards as a stemgroup representative of, and hence an outgroup to Dictyoptera (see also Haas & Kukalová-Peck 2001: fig. 20B). On the other hand, Kristensen (1995: 123) considered state [1] plesiomorphic due to outgroup comparison with extant lower Neoptera. We thus scored the Ancestor as [?].

Character 27: size of hindwing anojugal area. S t a g e A . [0] enlarged; [1] reduced; [2] essentially or totally absent. — S t a g e s B – C . [0] large or moderately large; [1] small or absent. We reformulated the character as binary by combining the former states [0] and [1] into one state [0] (Tab. 2; review by Klass 1995).

Character 28: distinctness of forewing basal suture. S t a g e A . [0] absent; [1] weak; [2] pronounced. T&C implicitly limited the character to the forewing based on their definition of state 2 (pronounced in forewing, weak in hind). — S t a g e s B – C . [0] absent; [1] present. We reformulated the character as binary by emending T&C's state [1]. According to Emerson (1933), not only T&C's state [1] (p. 175, fig. 14: *Archotermopsis*) but also state [2] (fig. 31: *Zootermopsis*) seems to occur in Termopsidae. By comparison with Mastotermitidae (Kukalová-Peck & Peck 1993: fig. 20) and Kalotermitidae (Grassé 1986: fig. 282Aa,Ba,Ea), T&C's state [2] appears to be plesiomorphic for Termopsidae. Thus all isopteran terminal taxa share the same groundplan state.

Character 29: curvature of forewing basal suture. S t a g e A . [0] primitively absent; [1] slight; [2] distinct. — S t a g e s B – C . *Excluded*. T&C's state [2] is not listed in their matrix, but clearly occurs in some Termopsidae (Emerson 1933: 168) and Kalotermitidae (Grassé 1986: fig. 282Aa,Ba,Ea), as well as in Mastotermitidae (Kukalová-Peck & Peck 1993: fig. 20). Because the character is inapplicable for Mantodea, *Blattaria, and Cryptocercidae, and ambiguous for the other taxa except Mastotermitidae (state [2]), we excluded it.

Character 30: symmetry of proventriculus. S t a g e A . [0] radial; [1] bilateral. We scored the Ancestor as [?]. — S t a g e s B – C . [0] bilateral; [1] radial. We reversed the polarity (based on outgroups: Lepismatidae and Corduliidae nymphs in Klass 1998b; the phasmid *Timema* in Tilgner et al. 1999: 160), scoring Mantodea (Ramme 1913; Klass 1998b: fig. 5) as well as the Ancestor as [0]. The evolution from bilateral to radial was gradual, involving various elements whose features could be coded as several characters (Klass 1998b: 36ff).

Character 31: secondary denticles of proventriculus. S t a g e A . Primary and secondary teeth of proventriculus: [0] similar; [1] dissimilar. We note that T&C's "teeth" refer to plicae in general. We simplified the character states and scored the Ancestor as [?]. — S t a g e s B – C . Secondary denticles of proventriculus: [0] absent; [1] present. We reformulated the character based on Klass' (1998b) work and revised terminology. Secondary plicae (more or less folds)

are present in the dictyopteran ground plan. Secondary sclerites (on the plicae) are present only in Blattaria and Isoptera (see character 71). Cryptocercidae and Isoptera share the condition that the secondary sclerites are similar to the primary sclerites in size and shape (see character 72). Secondary denticles (tooth-like bulges on the sclerotized parts of the plicae) are present only in Isoptera (state [1] of character 31; LEBRUN & LEQUET 1983; MCKITTRICK 1964; KLASS 1998b).

Character 32: primary pulvilli of proventriculus. S t a g e A . [**0**] expanded anteriorly, partially overlapping associated teeth; [**1**] not expanded. We clarified the character and scored the Ancestor as [?]. — S t a g e s B – C . [**0**] not expanded; [**1**] expanded anteriorly, partially overlapping associated sclerites. We reversed the polarity and scored the Ancestor, Mantodea, and *Blattaria as [0] (KLASS 1998b) and Kalotermitidae and Mastotermitidae as [1] (in T&C scored [?] and "not expanded", respectively, but their pulvilli are distinctly expanded: LEBRUN & LEQUET 1985: pl. I, fig. 1; KLASS 1998b: 37).

Character 33: secondary pulvilli of proventriculus. S t a g e A . [**0**] bulbous; [**1**] flat. We scored the Ancestor as [?]. — S t a g e s B – C . *Excluded*. T&C scored Isoptera as "bulbous" (surmised as the plesiomorphic state), *Blattaria and Cryptocercidae as "flat", and Mantodea as [?]. KLASS (1998b), however, noted that the secondary pulvilli of both *Cryptocercus* and *Mastotermes* are flat and much less prominent than those of, e.g., many Blattellidae and Blaberidae. We excluded the character because of the problems regarding the polarity and the definitions and distribution of its states.

Character 34: quaternary plicae of proventriculus. S t a g e A . Proventricular intercalaries: [**0**] longitudinal folds between teeth; [**1**] intercalary plate (sclerotizations of phragmata between denticles and interdentiaries); [**2**] anastomosing ridges. We scored the Ancestor as [?]. — S t a g e s B – C . Quaternary plicae of proventriculus: [**0**] present; [**1**] absent. We reformulated the character based on KLASS' (1998b) work. Quaternary plicae are groundplan elements of Blattaria (including Cryptocercidae) and Mantodea but are not reported for Isoptera (*Mastotermes* clearly lacks them). Polarity is unclear (outgroup comparison currently not possible). The absence in Isoptera may be plesiomorphic, or apomorphic (as in the cockroaches *Anaplecta* and *Plectoptera*: MCKITTRICK 1964). If the latter, absence may be related to the small size of the proventriculus.

Character 35: extension of abdominal tergum 7. S t a g e s A – C . [**0**] not entirely covering more posterior parts of abdomen; [**1**] entirely covering more posterior parts of abdomen dorsally. We clarified this character.

Character 36: composition of abdominal 'tergum 10'. S t a g e A . [**0**] only tergum 10; [**1**] tergum 10 plus more posterior sclerotization. We reworded the character. — S t a g e s B – C . *Excluded* (invariant). KLASS (1997: 20–22) rejected the statements by MATSUDA (1976) on which this character was based in T&C. The adult morphology of the respective area (exoskeleton and muscles) is very similar in Blattaria, Mantodea, and *Mastotermes* (KLASS 2001a and unpublished observations) and does not indicate any difference in the composition of 'tergum 10'; it is probably a composite structure in all Dictyoptera.

Character 37: number of abdominal sterna. S t a g e A . [**0**] 11; [**1**] 10. — S t a g e s B – C . *Excluded* (invariant). Based on T&C's sources, the character must relate to the postabdomen. In most contributions on termite morphology (e.g., BROWMAN 1935; ROONWAL 1956), the paraprocts are regarded as abdominal sternum 10. In contrast, SNODGRASS (1937) regarded the paraprocts of Blattaria and Mantodea as sternum 11. This, however, reflects a difference not in

structure but in interpretation. The paraprocts of Isoptera and Blattaria / Mantodea are certainly homologous (KLASS 2001a; CRAMPTON 1920: 142 assigned the paraprocts of *Mastotermes* to segment 11). For a discussion of the problems in the interpretation of paraprocts in insects see KLASS (2001b: 294ff).

Character 38: length of ovipositor (female). S t a g e s A – C . [**0**] reaching or exceeding posterior end of sternum 7; [**1**] not reaching posterior end of sternum 7 (ending within vestibulum). We reformulated the character. Data are in part from MCKITTRICK (1964: figs. 10, 22, 26, 40), KEY (1970: fig. 16.3), and personal observations. State [0] is regarded as plesiomorphic because the ovipositor is very long in Zygentoma and Archaeognatha as well as in stem-group representatives of Dictyoptera.

Character 39: small moveable spines on gonapophyses 8 (first pair of ovipositor valves in T&C) (female). S t a g e s A – C . [**0**] absent; [**1**] present, numerous. We clarified the definitions (MARKS & LAWSON 1962: 155–156). This uninformative character (state [1] only in Cryptocercidae) needs reinvestigation.

Character 40: gonapophyses 9 and gonoplacs (female). S t a g e A . Ovipositor gonapophyses and gonoplacs (ovipositor valves in T&C): [**0**] well developed; [**1**] reduced; [**2**] highly reduced; [**3**] only gonapophyses 8 (= ventral valves) present (plus membranous elevations). — S t a g e s B – C . Gonapophyses 9 and gonoplacs: [**0**] well developed to moderately reduced; [**1**] highly reduced or vestigial. We reformulated the character as binary, scoring Mastotermitidae as moderately reduced [0]. Data are from BROWMAN (1935: 126), MARKS & LAWSON (1962: 142), MATSUDA (1976: 181), WATSON & GAY (1991: 332), ROY (1999: 33), and KLASS (1998a). We note that characters 38 and 40 could be combined as a single multistate character.

Character 41: ootheca (female). S t a g e A . Egg deposition: [**0**] in mass, 2 rows, with secretory envelope; [**1**] in ootheca with discrete outer case; [**2**] singly. — S t a g e s B – C . Ootheca (= group of eggs in mass with tanned outer coating): [**0**] absent (eggs laid singly); [**1**] present. We reformulated the character as binary by combining T&C's states [0] and [1] in one state [1]. Indeed, T&C do not explain the difference between these states, i.e., between "secretory envelope" and "discrete outer case". Micrographs and behavioral evidence (NALEPA & LENZ 2000) confirm the close resemblance (and thus the plausible homology) between oothecae of *Mastotermes* (scored here as [1]) and Blattaria (see also WATSON & GAY 1991: 342; KLASS 1995: 126f; KRISTENSEN 1995: 123). We scored the Ancestor as [0] because outgroup comparison indicates that this state is plesiomorphic: no potential outgroup taxa build comparable egg cases by using secretions from the true 9th-segmental accessory glands (see KLASS 1995: 127 for comparison with Caelifera, which do not use the accessory glands). KLASS (1995: 127) noted, however, that the presence of nest building and eusociality (both apomorphic) in all terminal taxa showing state [0] makes the assumption that state [0] is apomorphic within the Dictyoptera equally reasonable.

Character 42: laterogonocoxae of abdominal segment 8 (extensions of laterosternal shelf in T&C) (female). S t a g e A . [**0**] absent; [**1**] present. We reworded the character and its states and scored the Ancestor as [?]. — S t a g e s B – C . *Excluded* (invariant). KLASS (1998a) demonstrated homology of these elements with the 'laterosternites' of Ensifera (ANDER 1939, 1956) and the laterogonocoxae 8 of Archaeognatha (BITSCH 1974, as 'laterocoxite'; see also KLASS 2001b). Thus, polarity must be reversed with 'present' as plesiomorphic. The elements are

present in Mantodea, *Blattaria (absent in some, e.g., *Eurycotis*), Cryptocercidae, and Mastotermitidae (KLASS 1998a: figs. 5–10). Reliable data for Kalotermitidae and Termopsidae are not available.

Character 43: laterosternal shelf of abdominal segment 7 (sternum 8 in T&C) (female). S t a g e A. [**0**] entire; [**1**] divided. We clarified the definition of the character. — S t a g e s B – C. *Excluded* (invariant). We tried to identify the element that T&C referred to as 'sternum 8'. Their source for scoring Termopsidae as having 'sternum 8' entire must be IMMS (1919: text fig. 11) because BROWMAN (1935: fig. 6), the other possible source, shows division for what he terms 'sternum 8'. 'Sternum 8' of IMMS is the laterosternal shelf, since it has the same position as the shelf of *Mastotermes* and other Dictyoptera (KLASS 1998a: figs. 4, 10), which is probably a posterior element of abdominal segment 7 (KLASS 1998a: 90). The scoring of various Isoptera as [0] or [1] being the crucial point in T&C, we relate character 43 to the laterosternal shelf (T&C seem to relate it to other elements in the other taxa). The shelf is entire in Termopsidae (BROWMAN 1935: I in fig. 6), Mastotermitidae, and Cryptocercidae (KLASS 1998a: figs. 8, 10). Both *Blattaria and Mantodea range from no trace of division to complete longitudinal division (KLASS 1998a: figs. 5, 6, 7, 9, 20), with an undivided or partially divided (notched) condition in the ground plan. In Kalotermitidae the shelf is strongly reduced (BROWMAN 1935: fig. 11) and thus hardly assessable. Hence, probably no taxon has the derived state [1] in its ground plan.

Character 44: lateral separation between anterior arch and posterior lobes of second valvifer ring (female). S t a g e A. Sternum 9: [**0**] entire; [**1**] divided. We scored the Ancestor as [?]. — S t a g e s B – C. Lateral separation between anterior arch and posterior lobes of second valvifer ring: [**0**] broad (= sclerites widely separated); [**1**] narrow (= sclerites articulated; plesiomorphic); [**2**] absent (= sclerites fused). The only possible sclerite division on abdominal venter 9 to which T&C's character could refer (no source given) is a division of the 'second valvifer ring', and we redefined the character in this sense. The division is established by a wide membrane in *Mastotermes* (KLASS 1998a: between anterior arch aa and posterior lobes pl in fig. 4; aa = medisternite M, pl+pm = secondary medisternite of BROWMAN 1935: 118, 119) but is likewise present, as an articulation, in some *Blattaria, in Cryptocercidae, and in, e.g., Ensifera (outgroup); Mantodea show state [2], with apparent vestiges of a former articulation (KLASS 1998a: articulation A6 in figs. 11, 14, 15, 17, 25). The division is probably present in the dictyopteran ground plan, but the wide separation may be an apomorphy of *Mastotermes*. Reliable data for Kalotermitidae and Termopsidae are not available (scored [?]).

Character 45: position of spermathecal opening (female). S t a g e A. [**0**] between sterna 8 and 9; [**1**] on sternum 9; [**2**] through pore midline of sternum 8. We scored the Ancestor as [?] because both [0] and [2] represent the plesiomorphic state (see Stages B–C). — S t a g e s B – C. *Excluded* (invariant). We note that 'sterna' comprises true sterna and limb base sclerotizations (gonocoxae and laterogonocoxae in KLASS 1998a). T&C's states relate, first, to different descriptions of the same position: The opening is in Dictyoptera on the membrane midline of 'sternum' 8 (as in state [2]) as well as shortly anterior to 'sternum' 9 (which includes the spermathecal plate) and thus between 'sterna' 8 and 9 (as in state [0]) (KLASS 1998a: figs. 2–4). Second, T&C's states are based on different interpretations of sclerites: The position on 'sternum' 9 (state [1]) scored for Termopsidae must come from IMMS (1919: 100).

It is not immediately clear what IMMS meant by 'sternum' 9 because the genital area is only vaguely outlined. IMMS' text fig. 11 shows that his 'sternum' 8 is the laterosternal shelf (compare character 43) – which BROWMAN (1935: 117, 120) regarded in Termopsidae as a sclerotization of the intersegmental fold 7–8, his 'sternum' 8 lying in the dorsal wall of the genital chamber. IMMS' 'sternum' 9 reaches the anterior end of the genital chamber, thus comprising the areas assigned to 'sterna' 8 and 9 by BROWMAN (1935). Hence, the area containing the spermathecal opening is 'sternum' 9 of IMMS but 'sternum' 8 of BROWMAN (and others). State [1] thus corresponds with the states [2] and [0]. In the ground plans of the dicondylian insects (see, e.g., SNODGRASS 1935: 566) and of all taxa here scored, the opening is on the unsclerotized posterior rim of 'sternum' 8 or, better, venter 8 (Mantodea, *Blattaria, Cryptocercidae, Mastotermitidae: KLASS 1998a: figs. 2–4; MCKITTRICK 1965: 19, 6 in figs. 5–7; Termopsidae, Kalotermitidae: BROWMAN 1935: S in figs. 6, 11; GEYER 1951: fig. 39; therein, medisternite mster = anterior arch aa of KLASS 1998a). We note that apomorphic states are present in Blattellidae and Blaberidae (MCKITTRICK 1964; GUPTA 1948).

Character 46: Antecostal ridge of paratergal extension of abdominal segment 9 (female). S t a g e A. Form of paratergites (erroneously termed 'paraprocts' in T&C) in cross-section: [**0**] flat; [**1**] V-shaped. T&C refer to MCKITTRICK (1965: 19), where the form of the paratergites (not paraprocts) is given for Cryptocercidae and *Blattaria (both V-shaped in section) and for Mastotermitidae (flat). We scored the Ancestor as [?]. — S t a g e s B – C. Antecostal ridge of abdominal paratergal extension 9: [**0**] well-developed; [**1**] reduced. We clarified the character. The relevant structures are extensions of the paratergites, which form a fulcrum for the ovipositor (KLASS 1998a: 83–85, paratergal extensions tg and te in figs. 2–4). They are lateral parts of tergum 9 and include the respective part of the antecosta and a narrow acrotergal rim (tergum 8 may additionally contribute). The antecosta (KLASS 1998a: ac) forms an internal ridge (V-shaped in section), which strengthens the extensions and serves for muscle attachment. We reversed the polarity because the ridge is present also in other insects with a well-developed ovipositor, e.g., Ensifera (SNODGRASS 1933: 56, fig. 18) and Notoptera (WALKER 1943: 684, 'lateral apodeme'). The ridge is well developed in *Blattaria, Cryptocercidae, and Mantodea, but vestigial in *Mastotermes* (KLASS 1998a: ac in fig. 4). We do not know T&C's source for scoring Kalotermitidae and Termopsidae (no data in MCKITTRICK 1965).

Character 47: connection of tergum and paratergal extensions in abdominal segment 9 (female). S t a g e A. Fused paratergites: [**0**] absent; [**1**] present. We scored the Ancestor as [?]. — S t a g e s B – C. Connection of tergum 9 and paratergal extensions 9: [**0**] absent; [**1**] present. We revised the character for clarity, scored the Ancestor as [?] (outgroup comparison is ambiguous; KLASS 1998a), Mantodea, *Blattaria, and Cryptocercidae as [0], Mastotermitidae as [1], and the other Isoptera as [?] (reliable data not available). We note that *Lamproblatta* (Blattaria: Lamproblattinae), like *Mastotermes*, shows a broad connection (KLASS 1998a: figs. 11–18).

Character 48: external genitalia (male). S t a g e s A – C. [**0**] very complex; [**1**] very simple. We simplified the states. In Mantodea, *Blattaria, and Cryptocercidae the male genitalia (phallomere complex) show a very complicated structure throughout, with many sclerites, projections, and muscles, and with a strong asymmetry; KLASS (1995, 1997) demonstrated the homology of genitalic sub-structures and asymmetry in Blattaria and Mantodea. In Isoptera a simply

structured, symmetrical lobe with a pair of ventral sclerites (*Mastotermes*: KLASS 2001a; *Stolotermes*: KLASS et al. 2000) represents the most elaborate structure observed, while other termites have only a small membranous papilla or lack any differentiations (ROONWAL 1970).

Character 49: opening of vasa deferentia into ampullar part of genital ducts (ejaculatory duct in T&C) (male). S t a g e A . [**0**] ventral; [**1**] dorsal. We reworded the character (see KLASS 2001a for terminology related to genital ducts). — S t a g e s B – C . *Excluded*. In *Mastotermes* the vasa deferentia open into the ampullar part laterally, not ventrally (KLASS 2001a: fig. 17, vd and ac). The opening is dorsal in the Termopsidae (MATSUDA 1976: fig. 53B; dorso-lateral in *Stolotermes*: KLASS et al. 2000) and seems to vary in Kalotermitidae from dorsal (as scored by T&C) to lateral (WALL 1971: fig. 2; MATSUDA 1976: fig. 53D). Based on SNODGRASS (1937: figs. 9B, 15D, 16A), in the few examined Mantodea and Blattaria, both scored [?] by T&C, the opening is lateral (Mantodea) or dorsal (Blattaria). In light of this situation, we consider character 49 to be without merit and excluded it.

Character 50: extension of abdominal sternum 7 (male). S t a g e s A – C . [**0**] not entirely covering more posterior parts of abdomen; [**1**] entirely covering more posterior parts of abdomen ventrally. We clarified the character. Data are from MCKITTRICK (1964: 68), ROONWAL (1970: 41–42), BALDERSON & KEY (1991: 350), ROTH (1991: 321), WATSON & GAY (1991: 332), and KLASS (1997: 104).

Character 51: number of flagella per sperm cell (male). S t a g e A . [**0**] 1; [**1**] 0; [**2**] many. We reworded the character. — S t a g e s B – C . We scored Termopsidae as [1] (BACCETTI et al. 1981: 87; JAMIESON et al. 1999: 130, 135). Cryptocercidae score as [?]: JAMIESON et al. (1999: 118) gave no indication that *Cryptocercus* had been examined; in observations using light microscopy, P. Luykx (personal communication) indicated that the sperm are probably biflagellate; in studies using transmission electron microscopy, K.J. Mullins (personal communication) observed both single and paired flagellar cross-sections. Data on Mantodea are from IWAIKAWA & OGI (1985: 2).

Character 52: sperm cell acrosome (male). S t a g e A . [**0**] present; [**1**] absent. — S t a g e s B – C . We scored Mantodea (BACCETTI 1987: 14–17; IWAIKAWA & OGI 1985: 1; JAMIESON et al. 1999: 129) and *Cryptocercus* (K.J. Mullins, personal communication) as [0].

Character 53: styli of abdominal segment 9 (female). S t a g e A . [**0**] present; [**1**] absent. We scored the Ancestor as [?]. — S t a g e s B – C . *Excluded* (invariant). In Termopsidae, the only terminal taxon T&C scored as [0], both states [0] (*Zootermopsis*: BROWMAN 1935: fig. 6) and [1] (*Archotermopsis*: IMMS 1919: 100, as subanal styles) are reported; by outgroup comparison with other Dictyoptera, [1] appears plesiomorphic for Termopsidae. All scored taxa thus share the same ground plan [1]. The presence of styli in some adult female Termopsidae seems to be, as in certain Blattaria and Orthoptera (MATSUDA 1979: 145, 161), an apomorphic, paedomorphic condition.

Character 54: number of cercomeres. S t a g e A . [**0**] ≥6; [**1**] 3–5; [**2**] ≤2. — S t a g e s B – C . [**0**] ≥10; [**1**] ≤8. Character 54 is problematic because reduction may result from either fusion (probable in *Cryptocercus* and *Mastotermes*) or loss of articles, and because in cases of incomplete fusion scoring is arbitrary. Because very low numbers do thus not necessarily represent comparable conditions, we redefined the states and formulated the character as binary. The ground plan is presumably 10 or more in Mantodea (RAMSAY 1990: 18, 25, 30; ROY 1999: 33) and *Blattaria (MURRAY 1967: 13; CORNWELL 1968: 226;

GUTHRIE & TINDALL 1968: 98; RICHARDS & DAVIES 1977: 594; ROTH 1991: 320). Cryptocercidae have 1 (FAUCHEUX 1990: figs. 2–3; NALEPA et al. 1997: figs. 1, 2, 6, 7). Termopsidae have 4–8 (EMERSON 1933: 167, 175; BROWMAN 1935: 126); Mastotermitidae could be considered as having either 5 cercomeres or 1 composite cercomere (KLASS 2001a); Kalotermitidae have 2 (KRISHNA 1961: 315; WATSON & GAY 1991: 342).

Character 55: *Blattabacterium* in specialized cells of fat body. S t a g e A . [**0**] present; [**1**] absent. We clarified the character and scored the Ancestor as [?]. — S t a g e s B – C . [**0**] absent; [**1**] present. We reversed the polarity based on outgroup comparison. DNA sequence data (BANDI et al. 1994) show that the endosymbiotic *Blattabacterium* belong to the lineage informally known as the *Cytophaga-Flavobacterium-Bacteroides* assemblage (LO et al. 2003). DNA sequence analyses of BANDI et al. (1995) and LO et al. (2003), and the ultrastructural studies of SACCHI et al. (1998) confirm homology of the symbiosis in various cockroaches and *Mastotermes*. We scored Mantodea as [0] (C. Bandi and L. Sacchi, personal communication; based on electron microscopy and molecular marker tests of *Mantis religiosa*).

Character 56: head size and shape (soldier). S t a g e A . Size and head shape (soldier): [**0**] soldiers primitively absent; [**1**] large/elongate (flat); [**2**] not large/not elongate. — S t a g e s B – C . Head size and shape (soldier): [**0**] large and elongate; [**1**] not large and elongate. We clarified the character and reformulated it as binary (taxa lacking soldiers scored as [-]) and scored Kalotermitidae as [0] (WEESNER 1969: 31; WEIDNER 1970: 15).

Character 57: ocelli (soldier). S t a g e A . [**0**] soldiers primitively absent; [**1**] present (but vestigial); [**2**] absent. — S t a g e s B – C . [**0**] vestigial; [**1**] absent. We reformulated the character as binary (taxa lacking soldiers scored as [-]).

Character 58: bladelike forecoxa protuberance (soldier). S t a g e A . [**0**] soldiers primitively absent; [**1**] absent; [**2**] present. — S t a g e s B – C . [**0**] absent; [**1**] present. We reformulated the character as binary (taxa lacking soldiers scored as [-]).

Character 59: number of cercomeres (soldier). S t a g e A . [**0**] soldiers primitively absent; [**1**] 5–7 (length 2x length of stylus); [**2**] 5 (length subequal to stylus); [**3**] 2 (slightly shorter than stylus). We reworded the character. — S t a g e s B – C . [**0**] 5–7; [**1**] 2. We reformulated the character as binary (taxa lacking soldiers scored as [-]).

Character 60: soldier neotenics. S t a g e A . [**0**] soldiers primitively absent; [**1**] present in both sexes; [**2**] absent (gonads reduced or vestigial). We reworded the character (THORNE 1997: 30; ROISIN 2000). — S t a g e s B – C . [**0**] present; [**1**] absent. We reformulated the character as binary (taxa lacking soldiers scored as [-]). We note that state [0] occurs also in some Kalotermitidae and data are lacking for most Termopsidae (MYLES 1986: 294–295, 298). Although we retained this character, additional study is desirable to establish that soldier neotenics are homologous among various groups. In general, the recognition of soldier neotenics ("reproductive soldiers" of T&C) is problematic; morphological traits that otherwise distinguish soldiers possibly occur in termite neotenics as a side effect of hormonal surges during reproductive development (ROISIN 2000). Furthermore, NOIROT & BORDEREAU (1989) stated that soldier neotenics (fertile soldiers) are intercastes (intermediate between soldiers and neotenics).

Character 61: chemical defense (soldier). S t a g e A . [**0**] soldiers primitively absent; [**1**] absent; [**2**] present. We simplified the definitions. — S t a g e s B – C . [**0**] absent; [**1**] present. We formulated the character as binary (taxa lacking

soldiers scored as [-]). Defensive secretions arose independently in various termite families and consist of entirely different chemicals (MOORE 1969: 419). This lack of similarity is not of concern here only because state [1] occurs in our taxon sample just in Mastotermitidae.

Character 62: anterior caeca of mesenteron (worker/ pseudergate). S t a g e A. Anterior caeca of mesenteron: [**0**] present; [**1**] absent. This formulation conforms to T&C's character scorings. — S t a g e s B – C. Anterior caeca of mesenteron (worker/pseudergate): [**0**] present; [**1**] absent. We restricted the character as explicit in T&C's original definition and scored taxa lacking workers/pseudergates as [-]. Data are from NOIROT & NOIROT-TIMOTHÉE (1969: 73; Termopsidae) and NOIROT (1995a: 207f).

Character 63: reversionary molts (worker/pseudergate). S t a g e A. [**0**] caste primitively absent; [**1**] present; [**2**] absent. We simplified the character. — S t a g e s B – C. [**0**] present; [**1**] absent. We reformulated the character as binary (taxa lacking workers / pseudergates scored as [-]). We note that character 63 is related to foraging strategy (ABE 1987; NOIROT & PASTEELS 1988; HIGASHI et al. 1991). We retained T&C's scoring of Mastotermitidae as 'absent' (here state [1]) (WATSON et al. 1977), but note that reversionary molts have not been ruled out in *Mastotermes* (ROISIN 2000).

Character 64: abdominal segments bearing sternal glands (worker/pseudergate). S t a g e A. Number of abdominal segments with sternal glands: [**0**] 3; [**1**] 1; [**2**] 0. This formulation conforms to T&C's character scorings. We scored the Ancestor as [?]. — S t a g e s B – C. Abdominal segments bearing sternal glands (worker / pseudergate): [**0**] III+IV+V; [**1**] V; [**2**] IV. We restricted the character to workers/pseudergates (as explicit in T&C's original definition) and scored taxa lacking these as [-]. Furthermore, we dropped T&C's state [2], which is not found in any sampled taxa having workers/pseudergates, and we split T&C's state [1] into two states (our [1] and [2]), because it included two conditions that are not comparable: the single gland is on segment V in Kalotermitidae, but on IV in Termopsidae. Mastotermitidae, with glands on segments III, IV, and V, score as [0]. Our data are from NOIROT (1995b), who found the number and location of sternal glands phylogenetically informative within the Isoptera; this, however, is not the case within our restricted sample.

Character 65: chromosomal sex determination. S t a g e A. [**0**] XX/XY; [**1**] XX/XO. Because the polarity is disputed (WHITE 1976: v, 19; LUYKX 1990: 87; BLACKMAN 1995: 68; KRISTENSEN 1995: 123), we scored the Ancestor as [?]. — S t a g e s B – C. Mantodea score as [1] (only Mantinae and Iridopteryginae have more apomorphic sex determination systems; WHITE 1976: 19; BLACKMAN 1995: 68–69; ROY 1999: 37, 40). Blattaria are invariably [1] (WHITE 1976: 5; BLACKMAN 1995: 68), including Cryptocercidae (LUYKX 1983: 518). We scored Mastotermitidae (BEDO 1987: 78; with X and Y undifferentiated) and Kalotermitidae (LUYKX 1990; with XX/XY apparently in the ground plan) as [0]. For Termopsidae data are not available; we score them as [?] (*Stolotermes* with state [1], studied by LUYKX 1990, is likely not a termopsid: KLASS et al. 2000).

Character 66: diploid chromosome number. S t a g e A. [**0**] ≤52; [**1**] 98. — S t a g e s B – C. [**0**] ≤93; [**1**] 98. Character 66 is uninformative (state [1] only in Mastotermitidae) and arbitrary in that just the highest number observed is separated from the rest. Much variation occurs within cockroach families and even genera (ROTH 1970: 91); 2n exceeds 52 in some *Blattaria and Kalotermitidae (H. Rose, personal communication: 2n=93 in a *Macropanesthia* [Blaberidae]; COHEN & ROTH 1970: 1523–1524;

WHITE 1976: 5; LUYKX et al. 1990: 390). In Mantodea, scored as [?] by T&C, 2n=16–40 (WHITE 1976: 15–17; ROY 1999: 34). Polarity [0]→[1] is supported by comparison to, e.g., Zygentoma (2n=36–58), Odonata (18–26), and Plecoptera (10–46) (MAKINO 1951; MAKINO & MOMMA 1956).

Character 67: care of juveniles. S t a g e A. Eusociality: [**0**] absent; [**1**] highly developed with caste system. — S t a g e s B – C. Care of juveniles: [**0**] absent (solitary or gregarious); [**1**] parental (subsocial); [**2**] alloparental = care of young by individuals other than the mother or father (eusocial). The evolution of eusociality was a stepwise process that likely involved aggregation, care of juveniles, and caste formation. Because of arguments concerning the semantics of 'eusociality' (e.g., COSTA & FITZGERALD 1996), we formulated character 67 based on stages in the evolution of care of juveniles, rather than caste formation. Although the ground plan for *Blattaria is [0], a number of species exhibit parental care (NALEPA & BELL 1997: 36–38). Data are from NOIROT (1985), NALEPA (1988), and ROISIN (1990).

Character 68: inquilines. S t a g e A. [**0**] nest primitively absent; [**1**] absent; [**2**] fully integrated. We simplified the states. — S t a g e s B – C. [**0**] absent; [**1**] present. We formulated the character as binary (taxa lacking a nest scored as [-]). The term 'inquiline' embraces a vast array of organisms (KISTNER 1969: 527). To be a meaningful phylogenetic character, 'inquilines' must refer to a monophyletic taxon. This would be of concern here, but state [1] occurs only in Mastotermitidae (as in character 61). Related to characters 68–70, nest-building occurs in certain *Blattaria (NALEPA & BELL 1997: 37–38), but is not in the taxon's ground plan.

Character 69: foraging away from nest. S t a g e A. [**0**] nest primitively absent; [**1**] absent; [**2**] present. We simplified the definitions. — S t a g e s B – C. [**0**] absent; [**1**] present. We reformulated the character as binary (taxa lacking a nest scored as [-]) and scored Cryptocercidae, which forage within a wood nest, as [0] (CLEVELAND et al. 1934: 189–190; NALEPA 1984: 274). Data for Isoptera are from IMMS (1919), NOIROT (1970), and ABE (1991).

Character 70: nest architecture. S t a g e A. [**0**] nest primitively absent; [**1**] excavation of wood, no extensive gallery network; [**2**] nest away from or within host wood. — S t a g e s B – C. [**0**] absent; [**1**] simple galleries within wood; [**2**] complex galleries within and away from wood. We reworded the states to reduce ambiguity (IMMS 1919; CLEVELAND et al. 1934; NOIROT 1970; WATSON & GAY 1991) and scored Cryptocercidae as [1] (CLEVELAND et al. 1934).

3.2. Supplementary characters of Stage C: 71–77

Character 71: secondary sclerites of proventriculus. S t a g e C. [**0**] absent; [**1**] present. We scored the Ancestor and Mantodea as [0], and *Blattaria, Cryptocercidae, and the isopteran taxa as [1] (see character 31; KLASS 1998b).

Character 72: similarity of primary and secondary sclerites of proventriculus. S t a g e C. [**0**] secondary sclerites much narrower than primary sclerites and of different shape; [**1**] secondary sclerites not much narrower than primary sclerites and of similar shape. Mantodea and – based on comparison with Zygentoma and many Pterygota (KLASS 1998b) – the Ancestor lack secondary sclerites (see characters 31, 71) and are scored as [0] (lacking secondary sclerites = extreme dissimilarity). In the many *Blattaria studied by MCKITTRICK (1964: figs. 142ff) and KLASS (1998b) the secondary sclerites are less than half the width of the primary ones (unless gizzard sclerites are altogether

reduced as in, e.g., Polyphaginae) and display a different shape (much more slender, and frequently forked anteriorly; e.g., KLASS 1998b: figs. 4, 14, 15); *Blattaria are thus scored as [0]. Cryptocercidae and the isopteran taxa are scored as [1], as their secondary sclerites have a width distinctly more than half of that of the primary sclerites (MCKITTRICK 1964: figs. 135, 139, 141) and essentially have the same shape.

Character 73: number of Malpighian tubules. S t a g e C . [**0**] ≥17; [**1**] 12–16; [**2**] ≤10. We scored Mantodea (BALDERSON & KEY 1991: 350), *Blattaria (ROTH 1991: 322), and Cryptocercidae (Deitz & Nalepa, unpublished observations) as [0], Mastotermitidae as [1], and Kalotermitidae and Termopsidae as [2] (NOIROT 1995a: 208–210). Four tubules are present in most Termitidae (WEIDNER 1970: 93; NOIROT 1995a: 210) as well as in early ontogenetic stages of all Dictyoptera (Mantodea, embryo: GÖRG 1959: 421; *Blattaria, Kalotermitidae, and Termopsidae, 1st instar nymphs: NOIROT 1995a: 210). Because some Zygentoma likewise have 4 tubules (BARNHART 1961: 186), this pattern seems to represent some developmental archetype of Insecta. Nevertheless, higher numbers are found in Archaeognatha (ca. 20; BITSCH & BITSCH 1998), some Zygentoma (8, 12; BITSCH & BITSCH 1998), and many Pterygota (e.g. Plecoptera: ZWICK 1973: 84), as well as in all Dictyoptera except higher termites. We therefore score the Ancestor [?], assuming the ground plans of both Insecta and Dictyoptera to have either state [0] or [1]. Reduction in Isoptera may be due to paedomorphosis.

Character 74: number of mitochondrial derivatives in sperm cell (male). S t a g e C . [**0**] 2 (additional mitochondria absent); [**1**] 0 (several to many small mitochondria present). We scored the Ancestor, Mantodea, *Blattaria, and Cryptocercidae as [0] and the isopteran taxa as [1] (BACCETTI 1987: 14–15; JAMIESON et al. 1999: 119, 129, 464–465; K.J. Mullins, personal communication: *Cryptocercus*).

Character 75: 'protozoan' hindgut symbionts, Hypermastigida and Oxymonadida. S t a g e C . [**0**] absent; [**1**] present. We scored the Ancestor, Mantodea, and *Blattaria as [0] and Cryptocercidae and the isopteran taxa as [1] (BOBYLEVA 1975; INOUE et al. 2000). We note that a few members of apparently 'basal' subgroups of both flagellate taxa occur in the guts of cockroaches other than *Cryptocercus* (Hypermastigida: *Lophomonas*) and even in non-dictyopteran insects and vertebrates (Oxymonadida: *Monocercomonoides*, *Polymastix*) (e.g., PARKER 1982: 500f, 506; LORENC 1939). The remaining subgroups of both taxa, however, are restricted to *Cryptocercus* and termites, with several genus- and family-level flagellate subgroups shared between the two (Oxymonadida: *Oxymonas*; Hypermastigida: *Trichonympha*, *Leptospironympha*, Staurojoeninidae, Eucomonymphidae, Spirotrichosomidae – according to PARKER's 1982 classification). Hypermastigida and Oxymonadida are not closely related (MORIYA et al. 2001) and have surely independently evolved their association with *Cryptocercus* and Isoptera. Therefore, character 75 should actually be coded as two or possibly several characters, one character for each evolutionary origin of an association with *Cryptocercus* and Isoptera in the tree of Hypermastigida and Oxymonadida. The presence of a diverse, highly interdependent hindgut fauna that includes oxymonadid and hypermastigid flagellates is related to the advent of direct transmission of gut microbes between host generations via proctodeal trophallaxis and is correlated with social structure (character 67) (NALEPA et al. 2001).

Character 76: pair of longitudinal folds dorsally on subgenital lobe (female). S t a g e C . [**0**] absent; [**1**] present.

These are the 'intersternal folds' in MCKITTRICK (1964) and KLASS (1998a). We scored Mantodea as [0], *Blattaria, Cryptocercidae, and Mastotermitidae as [1] (KLASS 1998a: 76), and Kalotermitidae and Termopsidae as [?] (data not available; absence seems likely in both because the folds work as a casting mold in ootheca production: MCKITTRICK 1964: 48). The subgenital lobe is established by a strong development in abdominal segment 7 of the ventral 'intersegmental' fold; the latter is present on all abdominal segments in many insects and corresponds to the coxal lobes in Archaeognatha. We score the Ancestor as [0], because on the subgenital lobe of Dermaptera (KLASS in press), which like in Dictyoptera is constituted by an enlarged sternum 7, as well as on the normally developed 'intersegmental' fold of segment 7 of other insects, folds comparable to those here considered are absent.

Character 77: cardiac (stomodaeal) valve of proventriculus. S t a g e C . [**0**] short funnel; [**1**] long tube. We scored the Ancestor and Mantodea as [0], and *Blattaria, Cryptocercidae, and the isopteran taxa as [1] (NOIROT 1995a: 204; KLASS 1998b: 37, with outgroup data).

4. Results: most parsimonious trees

Each stage A–C, consisting of an unordered and a partially ordered analysis, produced a single minimal length tree.

Stage A, with the omission of disputable polarity assumptions, produced the cladogram in Fig. 2 (unordered length = 100 steps; partially ordered length = 104). Under the conditions of Stage A, T&C's topology (Fig. 1) requires one additional step (unordered length = 101; partially ordered length = 105).

Stage B, with the revision of characters, produced the cladogram in Fig. 3 (unordered and partially ordered lengths = 70). Under the partially ordered conditions of Stage B, T&C's topology (Fig. 1) requires 11 additional steps (length = 81).

Stage C, with the incorporation of additional characters, produced also the cladogram in Fig. 3 (unordered and partially ordered lengths = 78). Under the partially ordered conditions of Stage C, T&C's topology (Fig. 1) requires 16 additional steps (length = 94).

Tree statistics for our partially ordered analyses at each stage are given in the caption of Figs. 1–3. Fig. 4 gives the character state changes (mapped on the tree using ACCTRAN optimization) and the Bremer support values for the most parsimonious tree from our partially ordered analysis of Stage C (see Fig. 3).

As shown in Fig. 4, it would take 6 additional steps in the analysis to break up the clade Blattaria + Isoptera (Bremer support value = 6), 7 to break up the clade Cryptocercidae + Isoptera, 10 to break up a monophyletic Isoptera, and 6 to break up the clade Kalotermitidae + Termopsidae. With an overall tree length of 78 steps, this indicates strong support for all clades shown in Fig. 4.

The matrix used in Stage C (Tab. 4) best reflects the current knowledge on the morphological and life history characters in the Dictyoptera, and the cladogram in Figs. 3 and 4 is thus the preferable hypothesis of phylogenetic relationships in the Dictyoptera. We note, however, that with our scoring of *Blattaria as a single terminal taxon our analyses leave open whether the clade comprising Cryptocercidae and Isoptera is a subgroup or the sister group of *Blattaria.
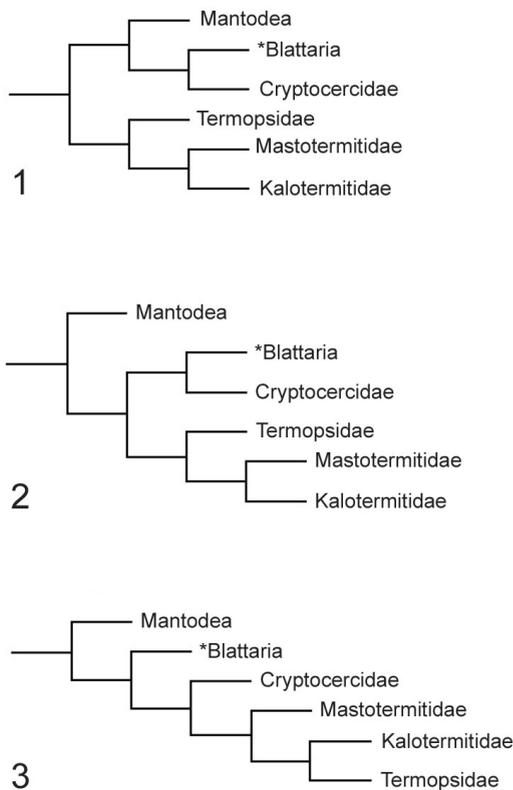
Figs. 1–3. Hypotheses of relationships among the dictyopteran taxa used as terminal taxa in Thorne & Carpenter (1992) and herein. **1**: Result of Thorne & Carpenter's original analysis; length = 109 steps, consistency index CI = 0.881; retention index RI = 0.842. **2**: Result of Stage A of present paper (disputed polarity assumptions removed), with partially ordered analysis; length = 104 steps, CI = 0.923, RI = 0.897. **3**: Result of Stages B (corrections and revisions) and C (like B, but with additional characters) of present paper, with partially ordered analysis; Stage B: length = 70 steps, CI = 0.914, RI = 0.887; Stage C: length = 78 steps, CI = 0.923, RI = 0.878.

5. Discussion and conclusions

In contrast to the perceived importance of T&C's study as a seminal work on dictyopteran phylogeny, it has likely had an influence beyond its real merits. Though we based our analyses on the data set of T&C, our phylogenetic result differs diametrically from theirs (compare cladograms in Figs. 1 and 3). We performed our study in three stages (A–C) to show where differences in the results were predominantly rooted: (A) disputable polarity assumptions, (B) inadequate treatment of characters, or (C) the lack of some relevant characters.

First, in Stage A, we only omitted disputed polarity assumptions from T&C's original data. The resulting cladogram (Fig. 2) differs from T&C's (Fig. 1) in showing Isoptera as the sister group of Blattaria rather than of Blattaria + Mantodea. This result has little merit except to illustrate that T&C's phylogeny is not robust even with their treatment of characters (see also Kristensen 1995) and that the subjectivity involved in polarizing characters may significantly influence the outcome of a phylogenetic analysis. Nonetheless, even though a different most parsimonious tree results, the effect of inadequate polarity assumptions is not overwhelming in this particular instance, since under the conditions of our Stage A T&C's topology requires only

one additional step, i.e., 1% of tree length in partially ordered analysis (see chapter 4).

In Stage B we revised many characters, character states, and scorings, in part because much of the morphological literature on the Dictyoptera used by T&C was flawed by inconsistencies and errors in the description, terminology, and interpretation of structures. In this way our analyses in Stage B were more rigorous than T&C's, based on more complete, representative, and reliable data, a great deal of which was assembled by specimen-based work of the authors or close cooperation with other specialists. Analyses in Stage B consistently resulted in the cladogram in Fig. 3, which shows Blattaria as paraphyletic with respect to Isoptera, Cryptocercidae as the sister group of the Isoptera, and Mastotermitidae as the sister group of Kalotermitidae + Termopsidae. This result differs fundamentally from that of T&C, whose topology under the conditions of our Stage B requires 11 additional steps, i.e., 15.7% of tree length. Thus, the character revisions in Stage B have a strong influence on the outcome of the phylogenetic analysis.

Finally, adding seven characters in Stage C resulted in a cladogram unaltered compared to Stage B (Fig. 3). That T&C's topology in Stage C requires 16 additional steps (i.e., 20.5% of tree length; instead of 11 steps in Stage B) is explained by the addition of these characters. This addition had no great effect, but confirmed the Stage B analyses.

The enormous influence of the character revisions in Stage B on the result of the analysis clearly demonstrates that an accurate and critical treatment of morphological and life history characters is essential to meaningful phylogenetic reconstruction.

While T&C's data seem to form an impressive basis for a phylogenetic analysis of the Dictyoptera, only 49 of the 70 original characters (Tab. 3) were phylogenetically informative in their analysis (i.e., the others have no effect on the branching patterns within cladograms). After our revisions in Stage B the number of informative characters decreased to 29. This was partly due to the elimination of characters in which T&C coded different descriptions or interpretations of structures as different character states (e.g., characters 22, 36, 37, 43, 45). After the addition of 7 characters in Stage C, our final matrix still included only 36 informative characters (Tab. 4). Of these (Fig. 4), only 21 confer information on the relationships among Mantodea, Blattaria, and Isoptera, while the others are informative only in terms of the monophyly of the Isoptera and the relationships among its families.

Thus of the many characters considered here, relatively few are phylogenetically useful for inferring relationships among the Mantodea, Blattaria, and Isoptera. Because difficulties exist in the treatment of some of these, other researchers may well differ with some of our codings and polarity assumptions, and the phylogeny of the Dictyoptera is not likely set to rest with the present study. Further reliable data on dictyopterans and potential outgroups are crucial to improved understanding of evolutionary relationships within the Dictyoptera.

On one hand, in many of the characters used here data must be acquired for representatives of the principal clades of Blattaria (see Klass 1995, 1997, 2001c), for 'basal' members of Mantodea (Mantoididae and Chaeteessidae), and for a broad selection of outgroup taxa (preferably various 'lower' Pterygota and Zygentoma). On the other hand, the discovery of additional characters depends upon a closer examination of a variety of character systems. Notably, much information can still be drawn from comparative studies of the female genitalia (see McKittrick 1964; Klass 1998b) and the musculature and nervous system of
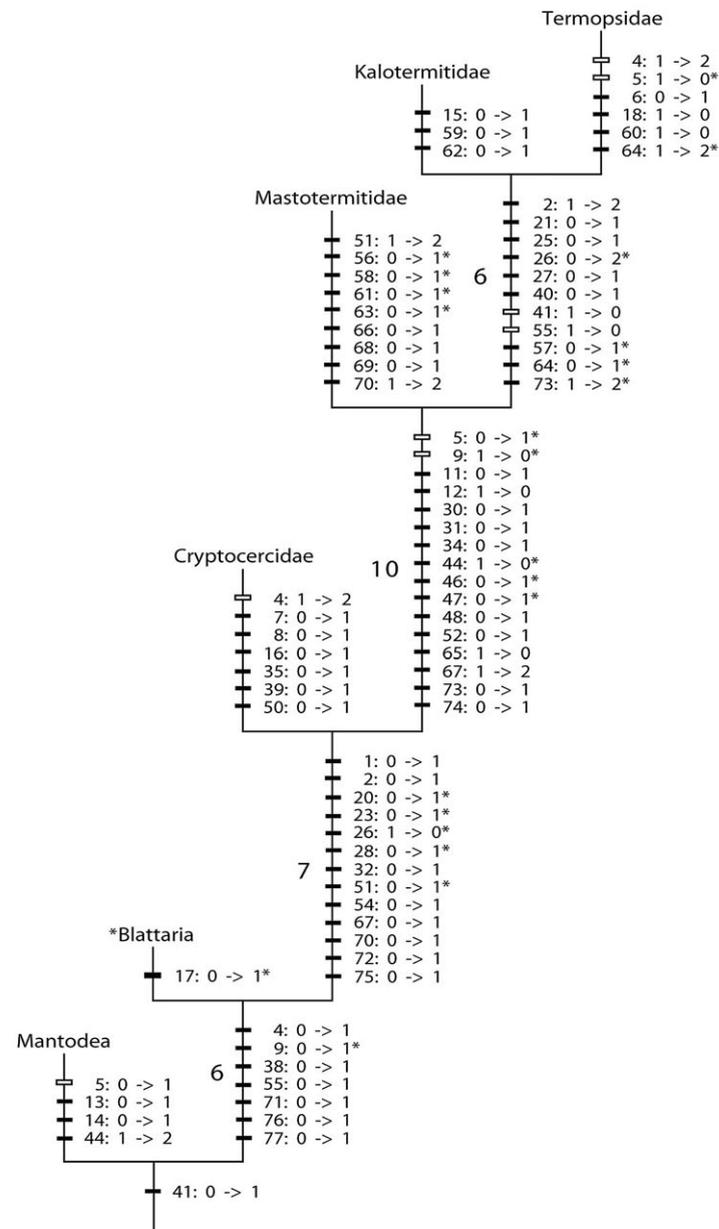
Fig. 4. Cladogram from partially ordered analysis in Stage C (see Fig. 3). Character state changes (character number: state change) mapped using ACCTRAN optimization at right of clades; Bremer support values (= decay indices) at left of clades. Homoplastic changes and reversals indicated by white bars, unique changes by black bars. Changes with ambiguous placement on the tree indicated by an asterisk*.

the Dictyoptera (KLASS 1999). Also, further assessment is needed of 47 wing characters that HAAS & KUKALOVÁ-PECK (2001: tabs. 6F–G) listed as strongly supporting the topology Mantodea + (Blattaria + Isoptera); however, wing characters are not useful with the several apterous 'key' taxa included in the Blattaria, such as *Cryptocercus*, *Lamproblatta*, and *Tryonicus* (see KLASS 1997, 2001c).

The debate on Dictyoptera phylogeny over the past decade has focused on the phylogenetic positions of *Cryptocercus* and Isoptera. The predominant view has followed T&C's (1992) topology – Isoptera + (Mantodea + Blattaria including *Cryptocercus*) – as well as GRANDCOLAS' (1994) proposal that *Cryptocercus* is deeply subordinate within the Polyphagidae and thus only distantly related to Isoptera. This view gained support as it was congruent with the results of the majority of early molecular analyses.

However, comparative studies of the male genitalia and other structures (KLASS 1997: 327ff; 2001c) show that

GRANDCOLAS' placement of *Cryptocercus* must be rejected. His analyses were flawed by unparsimonious topographic homology hypotheses (i.e., alignment of morphological structures), which led to spurious character definitions and scorings (KLASS 2001c; see also NALEPA & BANDI 1999). Indeed, studies of the phallomere exoskeleton and musculature and a numerical cladistic analysis (KLASS 1997; Klass & Meier's work in progress) provide strong support for *Cryptocercus* as the sister group of a clade comprising the polyphagid and lamproblattine cockroaches (Isoptera were not included due to their simplified male genitalia). In contrast to GRANDCOLAS' placement of *Cryptocercus*, the latter phylogenetic position does not a priori exclude a sistergroup relationship between *Cryptocercus* and Isoptera (the latter then being a subgroup of Blattaria).

Moreover, some recent molecular analyses obtained a monophyletic clade *Cryptocercus* + Isoptera as a subgroup of Blattaria. This relationship is strongly supported by

LO et al.'s (2000) analysis of three genes; by an unpublished reanalysis by Meier & Klass of available 12S and 16S rDNA sequence data using direct optimization (see chapter 1); and by LO et al.'s (2003) analysis of 4 genes in 17 dictyopteran taxa, which is the most comprehensive molecular study to date. Nonetheless, the exact placement of *Cryptocercus* + Isoptera within Blattaria has remained controversial among morphological and molecular analyses.

The strong support in our phylogenetic analysis of a sistergroup relationship between *Cryptocercus* and Isoptera (Fig. 4) is thus congruent with the most extensive molecular analyses, and it is not in conflict with current morphological evidence on blattarian phylogeny.

Within Isoptera our analysis supports the relationship Mastotermitidae + (Kalotermitidae + Termopsidae), which contradicts the results of T&C (compare Figs. 1 and 3), but corresponds with the traditional view (HENNIG 1969; KLASS 1995) and is in accord with recent molecular (KAMBHAMPATI et al. 1996; LO et al. 2003) and morphological (DONOVAN et al. 2000) analyses. The monophyly of Isoptera was never seriously disputed.

Thus, the phylogenetic relationships shown in Figs. 3 and 4 are supported by a majority of the most recent evidence. According to this phylogenetic hypothesis, *Cryptocercus* may well be compared with Isoptera in a strict phylogenetic perspective and be used to test assumptions on early termite evolution by (potential) homology (in contrast to GRANDCOLAS 1997: 240, 246). The aspects of behavior, physiology, and social structure common to *Cryptocercus* and Isoptera are most parsimoniously explained as autapomorphies of a clade *Cryptocercus* + Isoptera[2]. The same applies to the shared presence of a diversity of oxymonadid and hypermastigid flagellates in the hindgut of *Cryptocercus* and lower Isoptera and to the related behavior of anal trophallaxis in both groups. This is in contrast to advocates of a lateral transfer of the flagellates between the two dictyopteran taxa (THORNE 1990, 1991; GRANDCOLAS & DELEPORTE 1996; see KLASS 2001c: 262 for difficulties in the lateral transfer hypothesis as specified by the latter authors), but concurs with a recently proposed hypothesis on the origins of hindgut mutualisms (NALEPA et al. 2001).

Our results also confirm homology for the presence of *Blattabacterium* endosymbionts in the fat body of Blattaria (including *Cryptocercus*) and *Mastotermes* (see BANDI et al. 1995; SACCHI et al. 2000; LO et al. 2003). The absence of *Blattabacterium* in higher termites is surely secondary (if the monophyly of Isoptera is accepted), while its lack in Mantodea is most parsimoniously considered primary.

Lastly, our results provide a context for better understanding patterns of behavioral and morphological paedomorphosis within termites and certain cockroaches, including *Cryptocercus* (NALEPA & BANDI 2000).

Indeed, the enormous biological diversity observed among the Dictyoptera demands the soundest possible phylogenetic hypothesis, which can explain with confidence the evolution of the many complex patterns of ecology, behavior, sociality, and other aspects of life history exhibited within the group. The likelihood that the termites – a spectacular lineage of social animals – are nested within the cockroaches makes the study of these insects extraordinarily intriguing.

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[2] We note that characters of the protozoan and bacterial symbioses, behavior, and sociality were used in our cladistic analyses and contributed to our phylogenetic result. Here we view the evolution of these characters as subsets of our result, considering it legitimate to describe how certain characters behave within the framework of the entire hypothesis. This approach does not infer conclusions beyond the phylogenetic result and is thus not circular (see also LUCKOW & BRUNEAU 1997).

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