

A phylogenetic analysis of Dictyoptera (Insecta) based on morphological characters

KLAUS-DIETER KLASS¹ & RUDOLF MEIER²

¹ Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde, Königsbrücker Landstraße 159, 01109 Dresden, Germany [klaus.klass@snsd.smwk.sachsen.de] – ² National University of Singapore, Department of Biological Sciences and University Scholars Programme, 14 Science Dr 4, Singapore 117543 [dbsmr@nus.edu.sg]

Abstract. A cladistic analysis of Dictyoptera is presented based on a data set comprising 27 ingroup taxa and 175 characters from morphology and life history (3 relating to symbiotic relationships). The focus is on the asymmetrical male genitalia (phallomeres; 107 characters), which are well developed only in Blattaria and Mantodea. For the ingroup we obtained a single most-parsimonious tree based on the entire data set and under exclusion of symbiosis characters. The result is independent on whether we used six discrete outgroup taxa or a hypothetical ancestor. Analyses using the phallomere characters alone essentially gave the same tree but did not clearly resolve relationships among "higher" Blattellidae and Blaberidae. The Mantodea are the sister group of Blattaria + Isoptera, and Isoptera are deeply nested in Blattaria as the sister group of Cryptocercidae. The basal split in Blattaria is between Blattidae and the remaining taxa, with the latter also including Lamproblattidae (new status) and Tryonicidae (new status). A placement of Cryptocercidae + Isoptera outside (but near) the Polyphaginae is strongly supported. In the clade Blattellidae + Blaberidae, the Anaplectinae are most basal, the 'Plectopterinae' (= 'Pseudophyllodromiinae') are paraphyletic, and the ovoviparous Blaberidae are deeply subordinate. In Mantodea we obtain Mantoididae and, then, Chaeteessidae as the basalmost branches. The phylogenetic trees are then used to test scenarios for the evolution of reproductive biology and sociality. Ootheca rotation originated once and preceded ootheca retraction and ovoviviparity in Blaberidae. Eusociality in Isoptera and subsociality in Cryptocercidae go back to a common origin. Side-switches of phallomere asymmetry have likely undergone single and two-fold reversals. In the dictyopteran proventriculus an unusual evolution of six fairly different plcae into identical ones is proposed.

Key words. Blattaria, Mantodea, Isoptera, asymmetry, ovoviviparity, phallomeres, phylogeny, proventriculus, sociality, symbiosis, symmetry

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1. Introduction

Dictyoptera comprises the Blattaria (cockroaches, ca 4.000 species), Mantodea (praying mantises, ca 2.300 species), and Isoptera (termites, ca 3.000 species), and its monophyly is now generally accepted (e.g., KRISTENSEN 1991, 1995; KLASS 1995, 2003a; BEUTEL & GORB 2001; WHEELER et al. 2001; MAEKAWA et al. 1999; BOHN & KLASS 2003; KJER 2004). Striking dictyopteran autapomorphies are the perforation in the tentorium (HUDSON 1945, 1947) and the presence of oothecae (eggs assembled within a case produced by asymmetrical accessory glands; HENNIG 1981; KLASS 1995; NALEPA & LENZ 2000).

However, the phylogenetic relationships between the dictyopteran subgroups have remained highly controversial. The relationships between Blattaria, Isoptera, and Mantodea as well as those between the various '(sub)families' of Blattaria have been strongly disputed in the literature throughout the past 15 years (THORNE & CARPENTER 1992; DESALLE et al. 1992; KAMBHAMPATI 1995, 1996; GRANDCOLAS 1994, 1996, 1997a, 1999a,b; GRANDCOLAS & DELEPORTE 1992, 1996; GRANDCOLAS & D'HAESE 2001; KLASS 1995, 1997, 1998a,b, 2000, 2001b, 2003a; BANDI et al. 1995; GRIMALDI 1997, 2003; GÄDE et al. 1997; BELLÉS et al. 1999; MAEKAWA & MATSUMOTO 2000; DEITZ et al. 2003; LO et al. 2000, 2003; LO 2003; MUKHA et al. 2002; BOHN & KLASS 2003). The phylogeny of the Mantodea and Isoptera has only recently received increasing attention (KLASS 1995, 1997; SVENSON & WHITING 2004; GRIMALDI 2003; KAMBHAMPATI et al. 1996; DONOVAN et al. 2000; EGGLETON 2001; MIURA et al. 1998; THOMPSON et al. 2000). Most prominent in the debate on Dictyoptera phylogeny are the positions of the Isoptera and of the cockroach genus *Cryptocercus*.

1.1. Evolutionary questions

The great interest in the phylogenetic relationships of Dictyoptera has also been driven by the desire to propose and test evolutionary scenarios for some interesting biological features. The main issues are whether the sociality in *Cryptocercus* (subsocial) is homologous with that in termites (eusocial) and whether the unique association of *Cryptocercus* and lower-grade Isoptera with a rich diversity of hindgut flagellates of the Oxymonadida and Hypermastigida has been inherited from a common ancestor (NALEPA 1991; KLASS 2001b; DEITZ et al. 2003) or is the result of an interspecific transfer between Isoptera and *Cryptocercus* (THORNE 1990, 1991; GRANDCOLAS & DELEPORTE 1996; see HENNIG 1981: 200). Another question concerns the symbiosis found in Blattaria and the basal termite *Mastotermes darwiniensis* in form of Eubacteria (genus *Blattabacterium*) that are harboured in specialized cells of the fat body (bacteriocytes), play an important role in the nitrogen metabolism, and are maternally inherited through transovarian transmission between generations (SACCHI et al. 1998a,b, 2000). For *Blattabacterium* and its dictyopteran hosts, co-cladogenesis has meanwhile been demonstrated (LO et al. 2003).

Furthermore, because of its reproductive biology there is much interest in the clade Blattellidae + Blaberidae. All Blaberidae and most Blattellidae rotate their completed ootheca by 90°, from a vertical into a horizontal orientation. All Blaberidae and few Blattellidae furthermore retract the rotated ootheca into a brood pouch, which extends from the vestibulum (the space above the outer subgenital plate, coxosternum VII) far anteriad into the body. In addition, a few other Blattellidae perform such a retraction without a preceding rotation (ROTH 1967, 1970, 1995, 1997; NALEPA & BELL 1997). The storage of the ootheca in the brood pouch is associated with ovoviviparity or, rarely, viviparity. While ootheca retraction has surely originated several times, it depends on the phylogenetic hypothesis whether ootheca rotation is assumed to have evolved once or several times (ROTH 1970; GRANDCOLAS 1996; KLASS 2001b).

Lastly, several interesting questions in Dictyoptera relate to evolutionary changes in symmetry relations, which are potentially interesting for developmental biologists. One concerns the highly complex and strongly asymmetrical male genitalia (phallomeres). Phallomeres in Blaberidae, several subgroups of Blattellidae, and some Mantidae are mirror-images of those in other Blattellidae resp. Mantidae. They have obviously undergone a side-switch (BALDERSON 1978; BOHN 1987; KLASS 1997: 271ff), but it remains unclear how often this has occurred, and whether the normal phallomere orientation in some Blattellidae is primary or a character reversal due to a second side-switch (KLASS 1997: 316).

Another symmetry change is found in the proventriculus (gizzard, a part of the fore gut; KLASS 1998b). In the Blattidae this organ shows a hexaradial symmetry component (with six sclerites and denticles) that is superimposed by a strong bilateral symmetry component (due to differences between the single sclerites/denticles). Bilateral symmetry is weak in Cryptocercidae and some other Blattaria, and it is absent in Isoptera with their completely radial proventriculus. On the other hand, in some basal insects (Zygentoma: Lepismatidae) whose proventriculus strongly resembles that of Blattidae, bilateral symmetry is dominant over radial symmetry (KLASS 1998b). Thus, originally very different components of the proventriculus have perhaps evolved to become identically shaped parts within a radial symmetry (KLASS 1998b: 39).

1.2. Dictyoptera phylogenetics

Interordinal relationships. The abovementioned evolutionary questions can only be answered based on a well-founded phylogenetic hypothesis for the Dictyoptera. For the three major subgroups of Dictyoptera, THORNE & CARPENTER (1992) suggested the relationships Isoptera + (Blattaria + Mantodea). Their work was based on data from the literature and has gained fairly wide acceptance (e.g., DESALLE et al. 1992; KUKALOVÁ-PECK & PECK 1993; KAMBHAMPATI 1995; GRANDCOLAS 1996), although it includes inaccuracies in the treatment of the characters

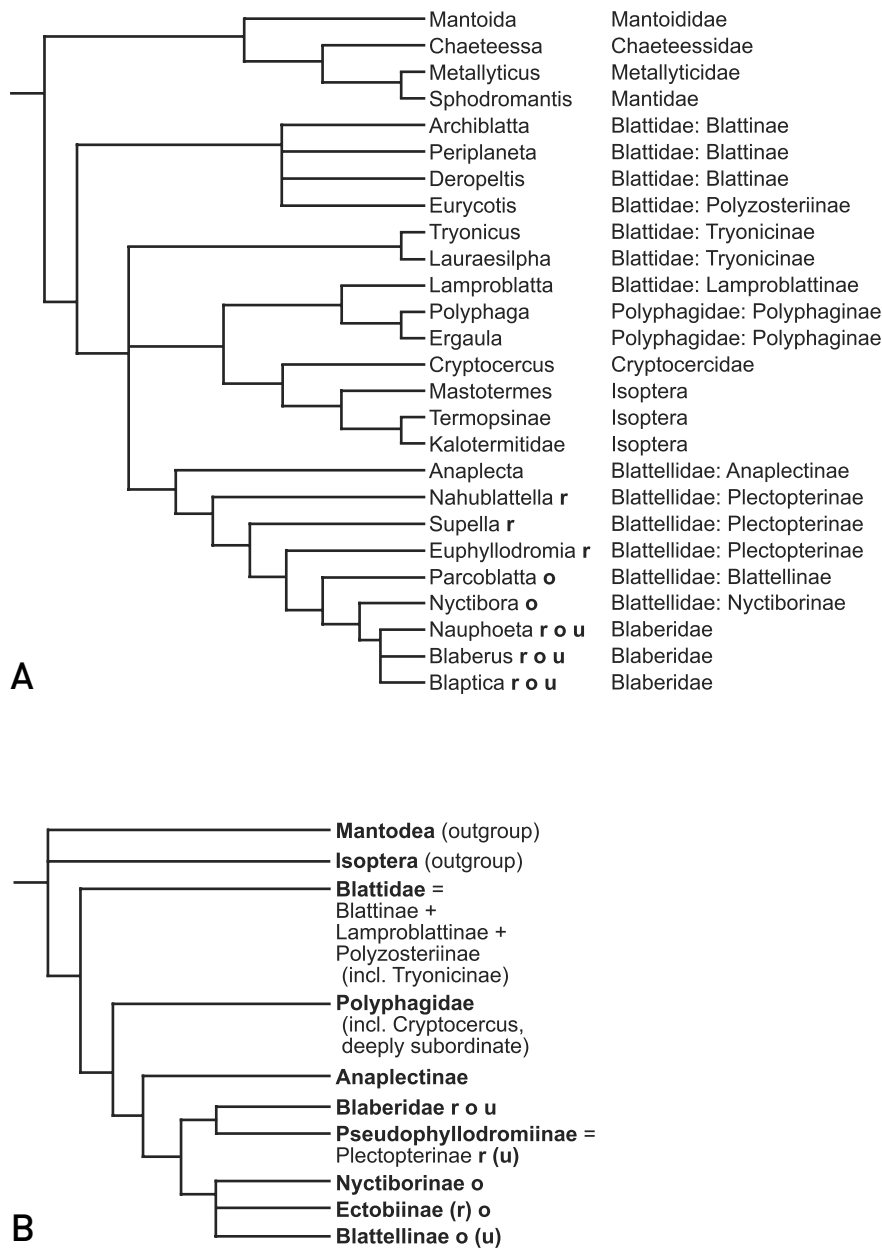


Fig. 1. Phylogenetic hypotheses for Dictyoptera; **r** and **(r)** indicate side-reversed phallomeres in all resp. some members of a taxon; **o** indicates ootheca rotation; **u** and **(u)** indicate ootheca retraction into brood pouch (uterus) in all resp. some members of a taxon. **A:** Hypothesis of KLASS (1995, 1997). Suprageneric classification according to MCKITTRICK (1964), MCKITTRICK & MACKERRAS (1965), and BEIER (1968a). **B:** Hypothesis of GRANDCOLAS (1996), with *Cryptocercus* and Tryonicinae deeply subordinate within the respective terminal taxa according to GRANDCOLAS (1994, 1997a); subfamily status retained for Anaplectinae and Pseudophyllodromiinae = Plectopterinae.

and their states. In particular, many assumptions on topographic homology (identification of corresponding parts in different taxa; see KLASS 2001b: 230f) and character polarity are questionable, and misscorings occur (see KLASS 1995, 1998a,b). A complete revision and cladistic re-examination of THORNE & CARPENTER'S (1992) data set, with further characters added, recovers a monophyletic Isoptera + *Cryptocercus* as the sister group or a subgroup of Blattaria, and Blattaria + Isoptera are sister to Mantodea (DEITZ et al. 2003). In earlier years,

the DNA-sequence analyses of Dictyoptera and their *Blattabacterium* symbionts that included non-dictyopteran/non-*Blattabacterium* outgroup taxa (KAMBHAMPATI 1995; BANDI et al. 1995) contradicted a sistergroup relationship between *Cryptocercus* and Isoptera. However, the recent studies of LO et al. (2000, 2003) supported a clade Isoptera + *Cryptocercus*, subordinate within Blattaria, based on combined analyses of sequences from several genes (see also LO 2003). Hence, a monophyletic Isoptera + *Cryptocercus* as the sister group or a subgroup

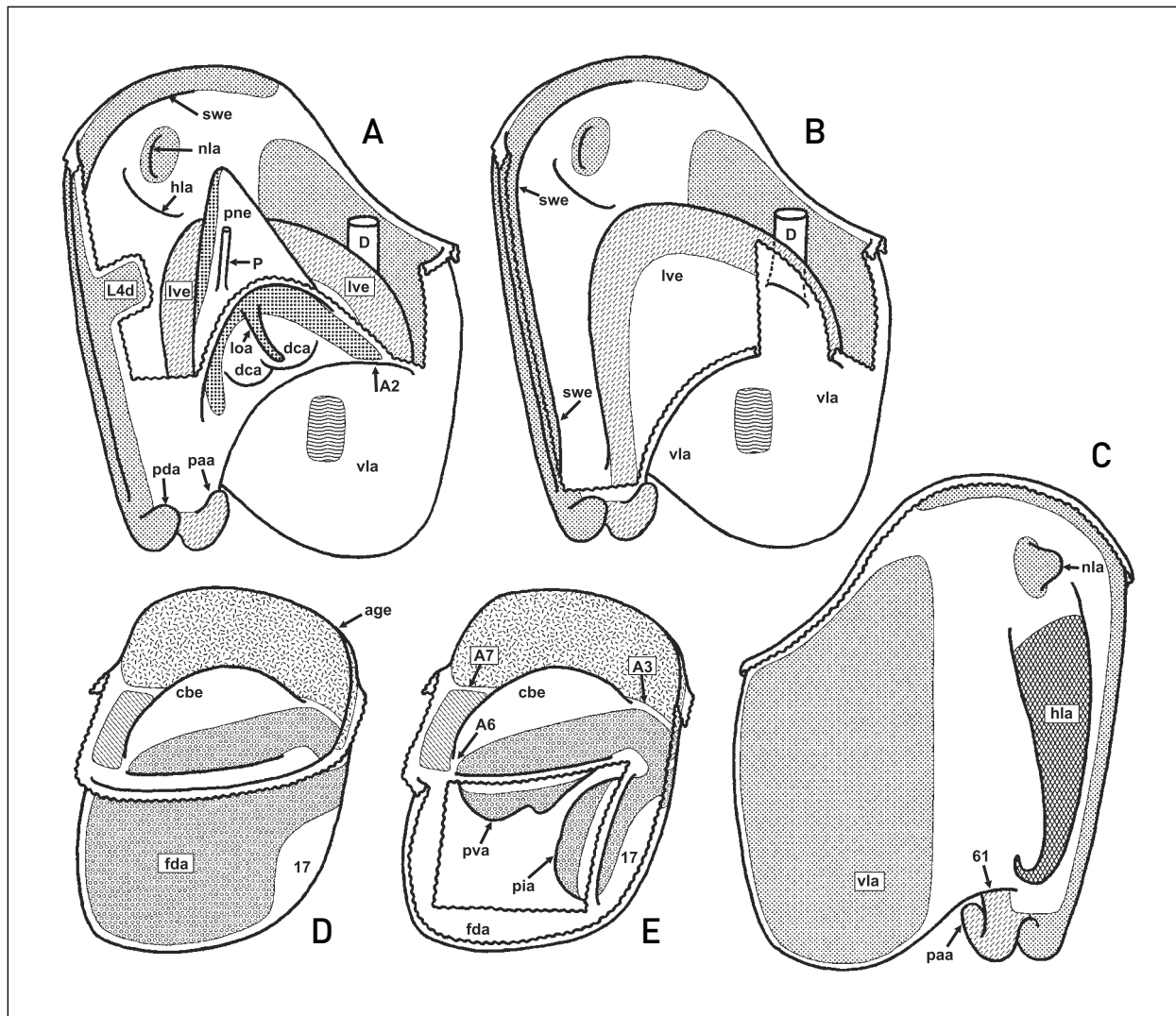
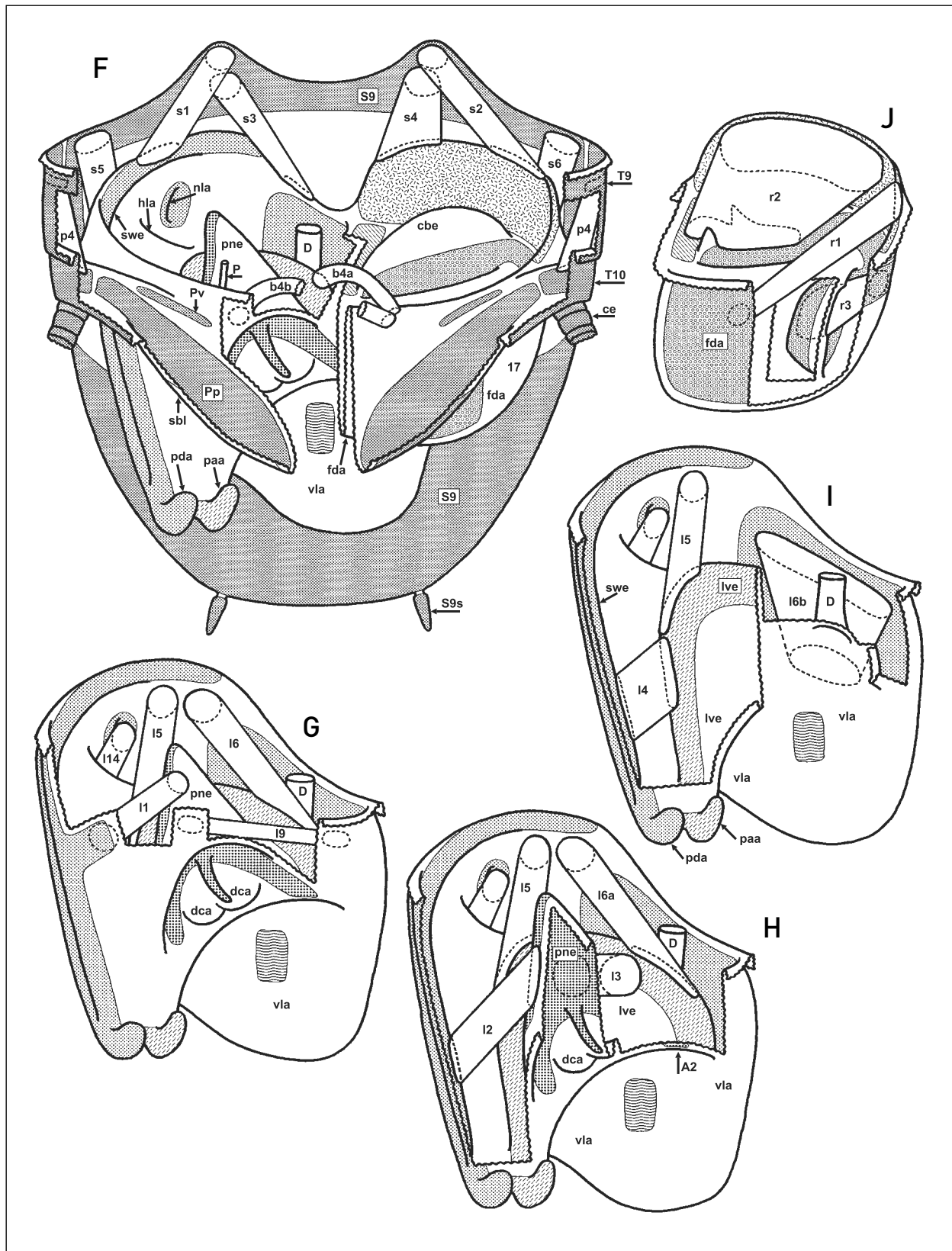


Fig. 2. Generalized scheme of exoskeleton and musculature of male genitalia in Blattaria and Mantodea, showing the ground plan as reconstructed in KLASS (1997). Orientation: ↑ anterior. Undulate lines represent cut cuticle. Major phallomere sclerites L1, L2, L3, L4 and R1, R2, R3 shaded differently (see explanations for Fig. 3); in Fig. 2F additional surrounding non-phallomere sclerites shaded by puncture: coxosternum IX = S9, styli IX = S9s, tergum IX = T9, tergum X = T10, paraproct = Pp, Pv-sclerites = Pv, cerci = ce. A2, A3, A6, A7 are sclerite articulations; dca, sbl, cbe, fda, hla, loa, lve, nla, paa, pda, pia, pne, pva, swe, vla are formative elements; D = ejaculatory duct; P = phallomere gland. **A, B:** Left part of male genitalia (= left complex = left + ventral phallomeres) in a dorsal view, with some dorsal parts removed in Fig. 2B. **C:** Left part of male genitalia in a ventral view. **D, E:** Right part of male genitalia (= right phallomere) in a dorsal view, with dorsal and ventral walls of lobe fda removed in Fig. 2E to show teeth pia and pva. **F:** Entire male genitalia in a dorsal view, with some surrounding sclerites and all extrinsic phallomere muscles and muscles connecting left and right phallomeres. **G, H, I:** Left part of male genitalia in a dorsal view, with its intrinsic muscles, and with dorsal parts successively removed. **J:** Right part of male genitalia in a dorsal view, with its intrinsic muscles.

of Blattaria appears presently best supported through morphological, biological, and molecular evidence. This is congruent with a single origin of sociality and of the diverse oxymonadid and hypermastigid flagellate 'fauna' in Isoptera and *Cryptocercus*.

Blattarian relationships. Modern phylogenetic work in Blattaria has been initiated by MCKITTRICK (1964); she was the first to reconstruct the phylogenetic relationships of the (sub)families through extensive morphological work, with a focus on the male and female genitalia and the proventriculus. In recent years P. Grandcolas and K.-D. Klass have revisited blattarian phylogeny using morphological characters. GRANDCOLAS (1994, 1996, 1997a) in his numerical cladistic analyses used characters of the female genitalia, wings, and some other

organs, but focused on phallomere morphology (tree in Fig. 1B). KLASS (1995, 1997) inferred a phylogenetic hypothesis for Blattaria and Mantodea using a large number of phallomere characters (tree in Fig. 1A). At first glance Grandcolas' and Klass' phylogenetic hypotheses are similar: the basal dichotomy is between Blattidae and the remaining Blattaria; *Cryptocercus* is nested within Blattaria close to Polyphaginae; Blattellidae are paraphyletic with respect to Blaberidae, and Anaplectinae constitute the basal-most blattellid clade. However, in the details there are important differences: Tryonicinae and Lamproblattinae are assigned to Blattidae by Grandcolas but to the other principal blattarian clade by Klass, and *Cryptocercus* is considered deeply subordinate within the Polyphaginae by Grandcolas but more distantly related



to these by Klass. The proposed relationships within the Blattellidae + Blaberidae are also very different. Furthermore, upon closer inspection, the identical clades in Grandcolas and Klass are surprisingly largely based on different apomorphies (see KLAS 2001b). This is mainly rooted in different hypotheses on topographic homologies,

i.e., which structural components of the phallomeres (e.g., sclerites, projections) correspond among different taxa and should be compared within the same character ('alignment' of structural components). This issue, which is the basis for most of the controversy, is extensively documented in KLAS (2001b). Of course, especially

Tab. 1. Dictyoptera included in this study, with systematic assignment (2nd column) and abbreviation (3rd column) here used. MG and DG mark mono- and digeneric (sub-)families. Tryoninae and Lamproblattinae are elevated to family rank in this paper (Tryonidae, Lamproblattidae). Plectopterinae = Pseudophyllodromiinae. See GRANDCOLAS (1997a) and KLASS (2001b) for the definition of Tryoninae; *Lauraesilpha angusta* (Chopard, 1924) in this paper is identical with *Tryonicus angustus* (Chopard, 1924) in KLASS (1995, 1997); *Lauraesilpha* was erected in GRANDCOLAS (1997a). Genus and species names according to EHRMANN (2002; Mantodea) and PRINCIS (1962–1971; Blattaria).

<i>Sphodromantis</i> Stål, 1871 (sp. indet.)	Mantodea: Mantidae	Sph
<i>Metallyticus violacea</i> (Burmeister, 1838)	Mantodea: Metallyticidae (MG)	Met
<i>Chaeteessa caudata</i> Saussure, 1871	Mantodea: Chaeteessidae (MG)	Cha
<i>Mantoida schraderi</i> Rehn, 1951	Mantodea: Mantoididae (MG)	Man
<i>Archiblatta hoeveni</i> Sn. v. Vollenhoven, 1862	Blattaria: Blattidae: Blattinae	Arc
<i>Deropeltis</i> Burmeister, 1838 (sp. indet.)	Blattaria: Blattidae: Blattinae	Der
<i>Periplaneta americana</i> (Linné, 1758)	Blattaria: Blattidae: Blattinae	Per
<i>Eurycotis floridana</i> (Walker, 1868)	Blattaria: Blattidae: Polyzosteriinae	Eur
<i>Tryonicus parvus</i> (Tepper, 1895)	Blattaria: Blattidae: Tryoninae (DG)	Try
<i>Lauraesilpha angusta</i> (Chopard, 1924)	Blattaria: Blattidae: Tryoninae (DG)	Lau
<i>Polyphaga aegyptiaca</i> (Linné, 1758)	Blattaria: Polyphagidae: Polyphaginae	Pol
<i>Ergaula capensis</i> (Saussure, 1893)	Blattaria: Polyphagidae: Polyphaginae	Erg
<i>Ergaula capucina</i> (Brunner v. W., 1893)	Blattaria: Polyphagidae: Polyphaginae	Erg
<i>Lamproblatta albipalpus</i> Hebard, 1919	Blattaria: Blattidae: Lamproblattinae (MG)	Lam
<i>Cryptocercus punctulatus</i> Scudder, 1862	Blattaria: Cryptocercidae (MG)	Cry
<i>Anaplecta</i> Burmeister, 1838 (sp. indet.)	Blattaria: Blattellidae: Anaplectinae	Ana
<i>Nahublattella</i> Bruijning, 1959 (sp. indet.)	Blattaria: Blattellidae: Plectopterinae	Nah
<i>Supella longipalpa</i> (Fabricius, 1798)	Blattaria: Blattellidae: Plectopterinae	Sup
<i>Euphyllodromia angustata</i> (Latreille, 1811)	Blattaria: Blattellidae: Plectopterinae	Eup
<i>Parcoblatta lata</i> (Brunner v. W., 1865)	Blattaria: Blattellidae: Blattellinae	Par
<i>Nyctibora</i> Burmeister, 1838 (sp. indet.)	Blattaria: Blattellidae: Nyctiborinae	Nyc
<i>Nauphoeta cinerea</i> (Olivier, 1789)	Blattaria: Blaberidae: Oxyhaloinae	Nau
<i>Blaberus craniifer</i> Burmeister, 1838	Blattaria: Blaberidae: Blaberinae	Blb
<i>Blaptica</i> Stål, 1874 (sp. indet.)	Blattaria: Blaberidae: Blaberinae	Blp
<i>Phoetalia pallida</i> (Brunner v. W., 1865)	Blattaria: Blaberidae: Epilamprinae	Pho
<i>Mastotermes darwiniensis</i> Froggatt, 1896	Isoptera: Mastotermitidae (MG)	Mas
Kalotermitidae	Isoptera: Kalotermitidae	Kal
Termopsinae	Isoptera: Termopsidae	Ter

for *Cryptocercus* a well-supported placement would be highly desirable, given its significance for understanding the origin of termites. GRANDCOLAS' (1994) arguments for assigning *Cryptocercus* to the Polyphaginae have been refuted on grounds of comparative morphology in KLASS (1995, 1997: 327ff). However, KLASS (1995, 1997: 314) also considered his own placement of the genus (Fig. 1A) only weakly supported. For the different views with respect to the further issues of dispute see GRANDCOLAS (1996, 1997a, 1999b: 304) and KLASS (1997, 2001b). Molecular studies including non-dictyopteran/non-*Blattabacterium* outgroup taxa (KAMBHAMPATI 1995; BANDI et al. 1995; GADE et al. 1997; BELLÉS et al. 1999; LO et al. 2000, 2003) could so far not resolve the problematical nodes in Blattaria. While all studies have corroborated Blattellidae + Blaberidae, the dichotomies within this clade remain controversial; Lamproblattinae, Tryoninae, and Anaplectinae have yet to be included in molecular work, and the placement of Cryptocercidae varies considerably.

Mantodean relationships. Here the genera *Metallyticus* and especially *Mantoida* and *Chaeteessa* are of particular interest because compared to all other Mantodea they display some unique plesiomorphic conditions (SMART 1956; BEIER 1968a; ROY 1999). The phallomere studies of KLASS (1995, 1997), which included these three genera

and a species of the derived genus *Sphodromantis*, led to the hypothesis *Mantoida* + (*Chaeteessa* + (*Metallyticus* + *Sphodromantis*)). The important study of GRIMALDI (2003) includes an excellent revision of early fossil Mantodea, but it could not provide a clear picture of the basal relationships among extant mantodeans. The molecular study of SVENSON & WHITING (2004) confirms the basal position of *Mantoida* and reveals that the current family-level classification of higher Mantodea (e.g., EHRMANN 2002) needs extensive revision. However, since *Chaeteessa* and *Metallyticus* were not included, the core issue of basal mantodean relationships is not addressed. WIELAND's (2006) comparative study of the cervical sclerites in many Mantodea, which includes the three abovementioned basal genera, provides no clear indications on basal phylogenetic relationships in Mantodea.

Isopteran relationships. In the termites, *Mastotermes* has traditionally been considered the sister group of all other Isoptera (e.g., HENNIG 1981), because in numerous characters of, e.g., the female genitalia and wings, it is clearly more plesiomorphic than all other termites. THORNE & CARPENTER's (1992) result of *Mastotermes* + Kalotermitidae being sister to the Termopsidae – only these three taxa were included in their analysis – was thus intriguing. Nonetheless, all subsequent studies, whether

molecular- or morphology-based, have unambiguously supported the traditional view (KLASS 1995, 1998b; KAMBHAMPATI et al. 1996; EGGLETON 2001; DEITZ et al. 2003; KJER 2004).

1.3. Useful morphological character systems and data sets

The male and female genitalia and to a minor extent the proventriculus and the wing venation are the most suitable character systems in the morphology-based phylogeny reconstruction of Dictyoptera. This is due to their great structural complexity and diversity.

The male genitalia (phallomeres) of Blattaria and Mantodea are asymmetrical ventral projections of abdominal segment IX (or possibly X) that surround the gonopore, serve for copulation, and are covered ventrally by a subgenital lobe sclerotized by coxosternum IX, the subgenital plate (basic design shown in Fig. 2). Their complexity is due to the presence of many sclerites, extrinsic and intrinsic muscles, and formative elements (discrete in- and evaginations and thickenings of the body wall: hooks, lobes, pouches, apodemes, ridges, tendons). Phallomere asymmetry is so strong that homonomies between right- and left-side elements have so far not been convincingly demonstrated (see KLASS 1997: 326f, 332f). Their structural diversity is exemplified in Fig. 3 for the exoskeleton of the left half of the phallomeres. For the phallomeres an extensive data set is available from the studies of KLASS (1995, 1997).

In contrast, the structure of the female genitalia and proventriculus has remained insufficiently documented, and recent studies in few exemplary Dictyoptera (KLASS 1998a,b) have revealed that many structural data and topographic homology hypotheses in the literature need revision (see also DEITZ et al. 2003; KLASS 2001b). Similarly, in the wing venation the only systematically broad account (REHN 1951) does not include the wing base, which is important for analysing vein homologies (e.g., KUKALOVÁ-PECK 1991; HAAS & KUKALOVÁ-PECK 2001). Consequently, only few characters from these character systems can presently be used – but their use is important to facilitate the inclusion of Isoptera.

The Isoptera are peculiar among dictyopteran subgroups since male genitalia and – with the exception of *Mastotermes* – female genitalia are highly reduced. Male genitalia are simple papillae or completely missing (ROONWAL 1955, 1970; KLASS 2000); only in *Stolotermes inopinus* Gay, 1969 they are large and heavily sclerotized, but yet very simply structured (KLASS et al. 2000). The few phallic components in Isoptera cannot at present be homologized with phallic components in Blattaria and Mantodea (KLASS et al. 2000), and phallomere characters are thus not applicable to Isoptera. Collecting characters from a variety of body parts and life history is thus needed in order to place Isoptera in the dictyopteran tree. The character set in DEITZ et al. (2003), which was built on that of THORNE & CARPENTER (1992), fulfils this requirement. It includes characters from the

female genitalia, proventriculus, wing venation and microsculpture, Malpighian tubules, ganglionic chain, ocelli, antennae, head glands, dentition of mandible, life history, sociality, and symbiotic organisms (hindgut flagellates, *Blattabacterium*). This character set was specifically coined for analysing relationships among Blattaria, Isoptera, and Mantodea, and for that sake six terminal taxa were defined: Mantodea, Cryptocercidae, remaining Blattaria, Mastotermitidae, Kalotermitidae, and Termopsinae. As explained in DEITZ et al. (2003: 71), the next important step in the development of this data set will be scoring the characters separately for those blattarian and mantodean exemplars for which data on the male genitalia are available.

1.4. Scope of the present study

Our study has several unique features. Firstly, we combine the two major morphological data sets established in the previous literature and develop them further in order to arrive at a more comprehensive hypothesis on dictyopteran phylogeny. Secondly, we code the phallomere characters from KLASS (1995, 1997) into an explicit matrix and subject this data for the first time to a numerical cladistic analysis; we also complement KLASS' (1995, 1997) data by providing additional information for taxa incompletely studied therein. Thirdly, we score many of the characters in DEITZ et al.'s (2003) data set for the taxa represented in the phallomere data set, either by own examination or by extracting data from the literature. Few additional characters were adopted from GRANDCOLAS (1996), but most of the characters used therein could not be included here for the problems explained in the character discussions in KLASS (2001b; e.g., incompatible homology hypotheses).

The data set thus assembled is the presently most extensive one available for a morphology-based cladistic analysis of Dictyoptera. Based on the phylogenetic results derived from it we test evolutionary scenarios for reproductive biology, sociality, symbiosis, and symmetry changes.

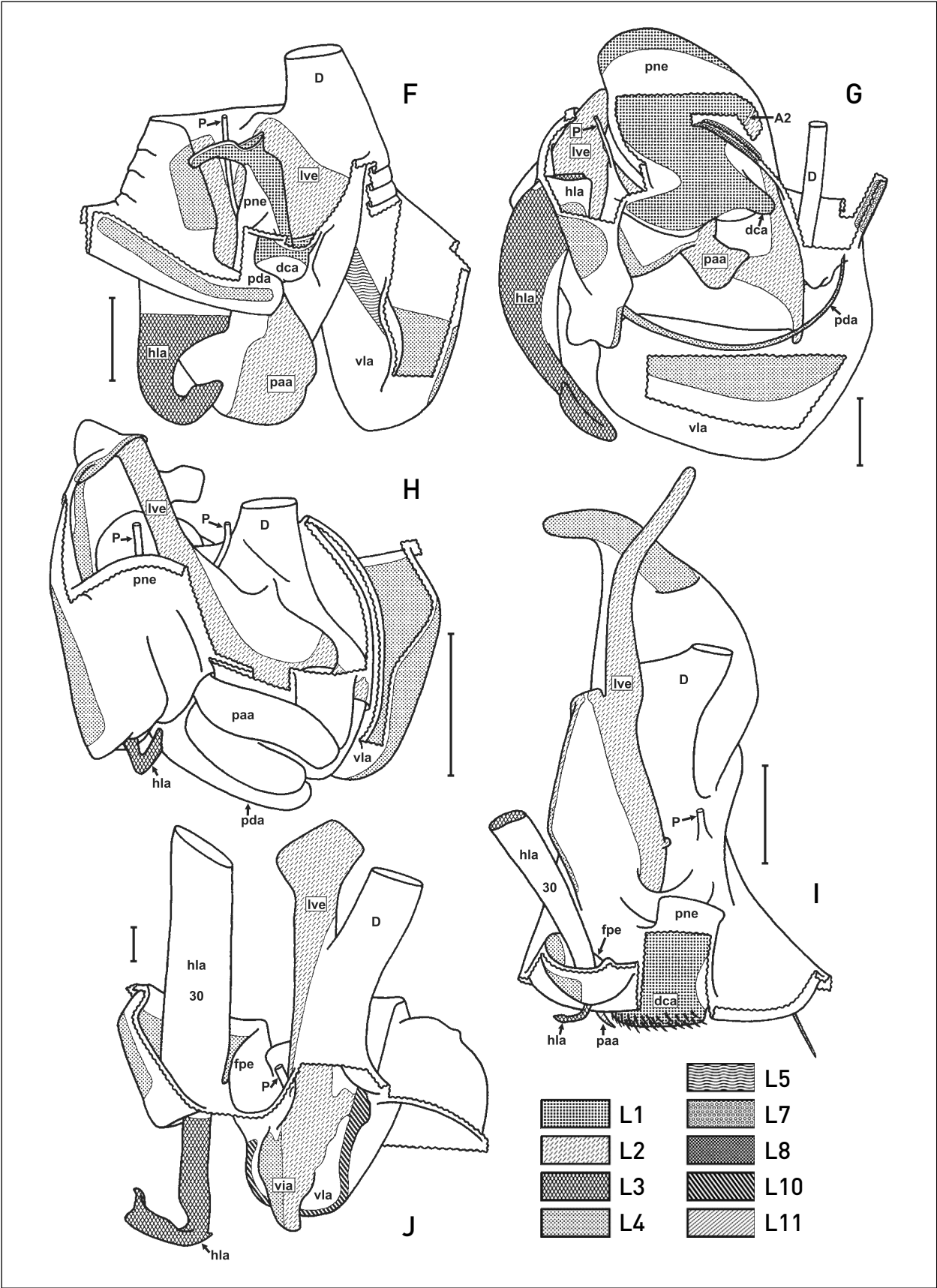
2. Material and Methods

2.1. Sampling of ingroup taxa

Our sample of Blattaria and Mantodea is identical with that in KLASS (1997; *Lauraesilpha angusta* = *Tryonicus angustus*, see Tab. 1), but *Phoetalia pallida* was added. The blattarian sample covers all 'families' and most 'subfamilies' (except those of Blaberidae) defined by MCKITTRICK (1964) and MCKITTRICK & MACKERRAS (1965). The mantodean sample includes the three genera usually considered most basal: *Mantoida*, *Chaeteessa*, and *Metallyticus* (see BEIER 1968a: 4); *Sphodromantis* is an overall strongly derived mantodean. Of the Isoptera the same three basal taxa were included as previously in THORNE & CARPENTER (1992) and DEITZ et al. (2003):



Fig. 3. Left part of male genitalia (left complex = left + ventral phallomeres) in some Mantodea and Blattaria. Dorsal view. Orientation: ← lateral, ↑ anterior. Undulate lines represent cut cuticle. Major sclerites L1, L2, L3, L4 as well as sclerites L5, L7, L8, L10, L11 (of limited occurrence) shaded differently based on topographic homology hypotheses in KLASS (1995, 1997). A1, A2 are sclerite articulations; afa, dca, hla, loa, lve, paa, pda, pne, swe, vla are formative elements; D = ejaculatory duct; P = phallomere gland. Scale 0.5 mm. **A:** *Sphodromantis* sp. (Mantidae). **B:** *Mantoida schraderi* (Mantoididae). **C:** *Archiblatta hoeveni* (Blattinae). **D:** *Polyphaga aegyptiaca* (Polyphaginae). **E:** *Tryonicus parvus* (Tryonicinae). **F:** *Cryptocercus punctulatus* (Cryptocercidae). **G:** *Lamproblatta albipalpus* (Lamproblattinae). **H:** *Anaplecta* sp. (Anaplectinae). **I:** *Nahublattella* sp. (Plectopterinae), depicted as a mirror-image. **J:** *Blaberus craniifer* (Blaberidae), depicted as a mirror-image.



Mastotermes darwiniensis, Kalotermitidae, and Termopsinae; for Kalotermitidae and Termopsinae scorings were adopted from DEITZ et al. (2003). With this sampling it is highly probable that in Blattaria, Isoptera, as well as Mantodea all basal lineages are represented. The species or taxa of higher rank that we use as terminal taxa are listed in Tab. 1; in the text generic names alone are used even if taxa were identified to species. The suprageneric classification follows MCKITTRICK (1964, 1965) and MCKITTRICK & MACKERRAS (1965) for Blattaria, BEIER (1968a) for Mantodea, and WEIDNER (1970) for Isoptera. In all but one species where KLASS (1997) studied only few selected phallomere characters, either the entire exoskeleton (*Archiblatta hoeveni*) or the exoskeleton and the musculature of the phallomeres have now been studied (*Deropeltis* sp., *Periplaneta americana*, *Ergaula capucina*, *Supella longipalpa*, *Euphyllodromia angustata*). *Ergaula capensis* and *E. capucina*, with very similar exoskeletal structure but different parts of the phallomeres studied, constitute herein a single terminal taxon; scoring of non-phallomere characters relates to *E. capucina*. In most of the blattarian and mantodean terminal taxa we scored the majority of the characters used in DEITZ et al. (2003); however, this excludes to a large extent *Archiblatta*, *Lauraesilpha*, and *Tryonicus*, which were not available for this study.

2.2. Terminologies used for the male genitalia

Phallomere characters are focal in this paper. The phallomere complex is basically composed of a small right part (Fig. 2D; right phallomere) and a large left part (Fig. 2A; left complex; left plus ventral phallomeres in MCKITTRICK 1964). There are several terminologies to address the structural components of the left and right parts. Principal sclerotizations (main sclerites or sclerite groups) have names composed of R or L + number (e.g., R1, L2; R and L stand for the right resp. left half of the phallomere complex). For subsets of these sclerotizations, two terminologies with upper- resp. lower-case letters in the third position are used. Upper-case designates discrete sclerites (e.g., sclerite L4D), i.e., continuous areas of sclerotization; different terms do not always indicate topographic non-homology but can reflect divisions or fusions of sclerites, which occur frequently. Lower-case designates particular regions of sclerotization (e.g., sclerite region L4d) according to the assumed topographic homologies – independently of sclerite borders and of the former terminology. Also the following terms are applied in accord with assumed topographic homologies. Terms like A + number are used for articulations (close contacts) between sclerites (e.g., A6). Terms composed of three lower-case letters designate formative elements (e.g., pouch 'pne', sclerotized process 'pda'). Terms lower-case letter + number are used for muscles (e.g., r2, l8, b4, s12, p1); the letter crudely specifies the location: r = right intrinsic, l = left intrinsic, b = connecting right and left parts of phallomeres, s = extrinsic to coxosternum IX, p = muscles in the periphery

of the phallomeres. Subdivisions of muscles are specified by lower-case letters in the third position (e.g., l14b, s5a). Additional information on the terminologies is found in KLASS (1997: 17ff, 23–32).

2.3. Choice and scoring of outgroup taxa

According to KRISTENSEN (1991, 1995), the Neoptera fall into 10 major lineages whose phylogenetic relationships are unresolved: the Dictyoptera, Orthoptera (= Saltatoria), Phasmatodea, Notoptera (= Grylloblattodea), Embioptera, Dermaptera, Plecoptera, Zoraptera, Acercaria (= hemipteroid orders), and Endopterygota (= Holometabola). An 11th lineage is constituted by the Mantophasmatodea (heel-walkers, gladiators; KLASS et al. 2002, 2003; see also TILGNER 2002 and KLASS 2002). Several extensive all-insect cladistic analyses have been published in recent years (WHITING et al. 1997; WHEELER et al. 2001; BEUTEL & GORB 2001; KJER 2004; TERRY & WHITING 2005); nonetheless, a solution of the relationships among these 11 lineages 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 problematic, and the significance of their phylogenetic results is thus limited; this also applies to TERRY & WHITING (2005), which used the matrix from WHEELER et al. (2001) with little modification. WHEELER et al.'s (2001: fig. 12A) molecular tree derived from 18S and 28S rDNA shows the phasmid *Timema* as the sister group of Dictyoptera, this clade being sister to Phasmatodea + Embioptera + Orthoptera + Acercaria. BEUTEL & GORB's (2001) morphological data set supports a clade ((Dictyoptera + Phasmatodea) + Notoptera) + Orthoptera. However, the phylogenetic evidence from this data set is not very strong due to the low number of characters informative on basal neopteran relationships (see DEITZ et al. 2003: 71). According to TERRY & WHITING (2005), a clade Mantophasmatodea + Notoptera is sister to Dictyoptera. Based mainly on wing characters, HAAS & KUKALOVÁ-PECK (2001) postulate a clade Blattoneoptera including Dictyoptera, Dermaptera, and Notoptera. MAEKAWA et al. (1999) obtain Notoptera as sister to Dictyoptera. Yet other relationships are obtained by KJER (2004). Eventually, the Mantophasmatodea, which are not included in most of the aforementioned hypotheses, may alone be the closest relatives of Dictyoptera (KLASS et al. 2003; DALLAI et al. 2003).

Consequently, outgroup taxa for our analysis could be quite arbitrarily recruited from among the major neopteran lineages listed above. Considering a wide range of neopteran outgroups appears thus mandatory, and outgroup evidence from palaeopteran and apterygote Insecta (= Ectognatha *sensu* HENNIG 1981) might occasionally also be relevant. On the other hand, discrete data from Mantophasmatodea, Phasmatodea, Orthoptera, Dermaptera, and Notoptera should also be included, as well as data from Plecoptera, which are widely considered to display basal neopteran conditions in many characters.

We thus applied two different procedures in outgroup comparison.

(1) We scored six discrete outgroup taxa with sufficient literature data available, selected from lower neopteran orders that are good candidates to be closely related to Dictyoptera: *Karoophasma biedouwensis* (Mantophasmatodea; data from KLASS et al. 2003; R. Dallai pers. comm.; G. Pass pers. comm.; T. Myles pers. comm.; and original examinations); *Grylloblatta campodeiformis* (Notoptera; data from WALKER 1931, 1933, 1938, 1943, 1949; BEIER 1972; VISSCHER et al. 1982; NESBITT 1956; and original examinations); *Locusta migratoria* (Orthoptera-Caelifera; data from ALBRECHT 1953; RAGGE 1955; BEIER 1972; and original examinations; literature data compared with data for the closely related *Dissosteira carolina* in SNODGRASS 1929, 1935; RAGGE 1955; and NESBITT 1941; all available data identical for the characters here scored); *Timema cristinae* (Phasmatodea; data from TILGNER et al. 1999; BEIER 1968b; and original examinations); *Echinosoma yorkense* (Dermaptera; data from GILES 1963; POPHAM 1965; GÜNTHER & HERTER 1974; KLASS 2003b; HAAS & KUKALOVÁ-PECK 2001; and original examinations); *Dinocras cephalotes* (Plecoptera; data from ZWICK 1973, 1980; ILLIES 1955; BRINCK 1956; FAUSTO et al. 2003). Data for several taxa come from HUDSON (1945, 1947; tentorium), JAMIESON et al. (1999; sperm structure), JUDD (1948; proventriculus), NUTTING (1951; circulatory system), and WHITE (1976; karyology).

(2) We established an artificial “hypothetical ancestor” whose scorings are based on data from Zygentoma, Archaeognatha, and the various pterygotan orders (excluding Acercaria and Endopterygota) – with limitations in terms of the availability of data for and applicability of characters to these taxa. Whenever different states of a character were represented in the whole of these groups (conditions that are clearly derived within the respective groups excluded), we entered [?] for the hypothetical ancestor. Consequently, this hypothetical ancestor is only assigned a character state in cases where character polarity is unambiguous. In few characters the hypothetical ancestor was scored on a different basis (explained in the character descriptions in the Appendix). The scoring for the hypothetical ancestor largely corresponds with outgroup scorings in DEITZ et al. (2003); differences are mentioned in the character descriptions.

For many characters the outgroup taxa could not be scored because of uncertainties surrounding the homology between dictyopteran and non-dictyopteran insects. This concerns mainly the characters of the male genitalia. Most Insecta have homologues of the blattarian/mantodean phallomeres, but because the arrangement of the components differs strongly from that in Blattaria and Mantodea, topographic homologies have remained entirely unresolved. The Mantophasmatodea and Notoptera are exceptions in as far as some phallomere components and the kind of asymmetry bear similarity to Dictyoptera. Some discrete homologies between Mantophasmatodea and Dictyoptera have been proposed

by KLASS et al. (2003: 57) for the right part of the phallomeres, and the related characters are here scored for *Karoophasma biedouwensis*.

2.4. Cladistic parsimony analysis

We extensively analyzed our data in order to explore the effects of the choice of outgroup and characters on the results of the cladistic analysis. The ingroup portion of the data consisted of 27 species or taxa of higher rank (Kalotermitidae, Termopsinae) and 175 characters of which 27 were multistate characters (matrix in Tab. 2; characters explained in Appendix). This data was analyzed as follows:

(1) We generated two data sets by once adding the hypothetical ancestor and once the six exemplar outgroup taxa. Both data sets were analyzed separately.

(2) In order to explore the effect of symbiosis characters on the phylogenetic hypothesis, both of the data sets under (1) were first analyzed *in toto* (“entire data set”) and then under the exclusion of the three characters (157–159) relating to endosymbiosis (“reduced data set”).

(3) We analyzed a “phallomere data set” only containing the phallomere characters (1–107). Due to the inapplicability of phallomere characters to Isoptera and outgroup taxa, we excluded Isoptera and rooted the tree between Mantodea and Blattaria.

(4) All analyses mentioned above were once carried out with 17 of the 27 multistate characters treated as additive and once with all characters treated as non-additive,

(5) and they were carried out once with all taxa included and once with *Lauraesilpha* and *Archiblatta* excluded. The latter taxa have a large amount of missing data.

Most cladistic analyses were carried out using PAUP* (4.0b10; SWOFFORD 2004; TBR branch swapping; 100 random taxon addition searches). Branch support was assessed using bootstrap (nreps=250) and Bremer support as facilitated by TreeRot (SORENSEN 1999). The most parsimonious tree for the entire data set (6 outgroup taxa, all ingroup taxa included, additive character coding) was also confirmed using NONA (GOLOBOFF 1993; same search options as above) in conjunction with Winclada (NIXON 2002). The latter was then used to map all character changes onto the tree using Winclada’s “fast optimization” option.

In order to compare our cladograms with previously published relationship hypotheses we assessed how many extra steps are required to obtain certain critical clades (Tab. 6). Using the “entire data set” combined with the six discrete outgroup taxa but excluding *Lauraesilpha* and *Archiblatta* and applying additive coding, we carried out “constraints” analyses in T.N.T. (GOLOBOFF et al. 2003; same search options as above) and PAUP* (4.0b10; SWOFFORD 2004; same search options as above). The trees obtained in the constrained searches were assessed for statistically significant length differences to the most parsimonious tree by using the Templeton (Wilcoxon signed-rank) test as implemented in PAUP*.

[illegible][illegible]

Tab. 3. Character matrix of phallomere data set. Symbols: lacking observations in a taxon [?]; inapplicability of a character or ambiguity in assigning a state to a taxon [-]. The three upper lines read vertically represent the character numbers; aaa and bbb are two artificial characters inserted to root the tree between Blattaria and Mantodea.

[illegible]

3. Results of the Cladistic Parsimony Analyses

3.1. Results for the entire and reduced data sets

In the analyses with several outgroup taxa, Dictyoptera are always monophyletic. All analyses using the hypothetical ancestor and those using the six discrete outgroup taxa combined with additive character treatment yielded a single most-parsimonious tree with identical ingroup relationships. The analyses using the six discrete outgroup taxa combined with consistently non-additive character treatment yielded two most-parsimonious trees with differences only with regard to the relationships among outgroup taxa and with ingroup relationships identical to the aforementioned trees. The ingroup relationships are thus fully resolved and identical in all trees obtained from the analyses of these two data sets (Fig. 4A). With *Lauraesilpha* and *Archiblatta* being excluded, the same tree was found that would result from pruning these taxa from the most-parsimonious tree obtained with these taxa included. The Bremer and bootstrap support values for the various analyses as well as tree statistics are reported in Tab. 4 (see also Fig. 5). The results of the constrained analyses and their statistical significance are summarized in Tab. 6.

3.2. Results for the phallomere data set

All analyses of the phallomere data set found the same two most-parsimonious trees, which differ with regard to the relationships in the clade Blattellidae + Blaberidae above the *Euphyllodromia* branch (Fig. 4B,C). The differences

to the trees from the entire and reduced data sets (Fig. 4A) lie in the same clade, while all other dictyopteran relationships are identical. As evident from Fig. 4B,C, phallomere characters alone cannot support monophyletic Blaberidae, which is weakly supported using the entire and reduced data sets. The Bremer and bootstrap support values for the analyses of the phallomere data set as well as their tree statistics are reported in Tab. 5.

4. Discussion

Our phylogenetic result on splitting events within Blattaria and within Mantodea (Fig. 4A) generally conforms with the phylogenetic hypothesis in K_{CLASS} (1995, 1997) (Fig. 1A), and the result on the relationships among Blattaria, Mantodea, and Isoptera conforms with the results of K_{CLASS} (1995) and DEITZ et al. (2003). The most controversial relationship hypotheses (see Introduction) are well supported by moderate to strong Bremer values (Fig. 5, Tabs. 4, 5). This also applies to the placement of the Isoptera within the Blattaria, as the sister group of Cryptocercidae. In contrast, most of the branches within Blattinae + Polyzosteriinae and Blaberidae + ‘higher’ Blattellidae (Blattellinae, Ectobiinae, Nyctiborinae) are only poorly supported (as in K_{CLASS} 1995, 1997). This is probably due to our selection of characters and taxa. They were chosen to resolve the basal splits, and not to reconstruct relationships within these subordinate groups. In order to resolve these many more taxa have to be included, and additional characters have to be studied. In the discussions below we indicate the strength of branches by the Bremer support values (BS) obtained in

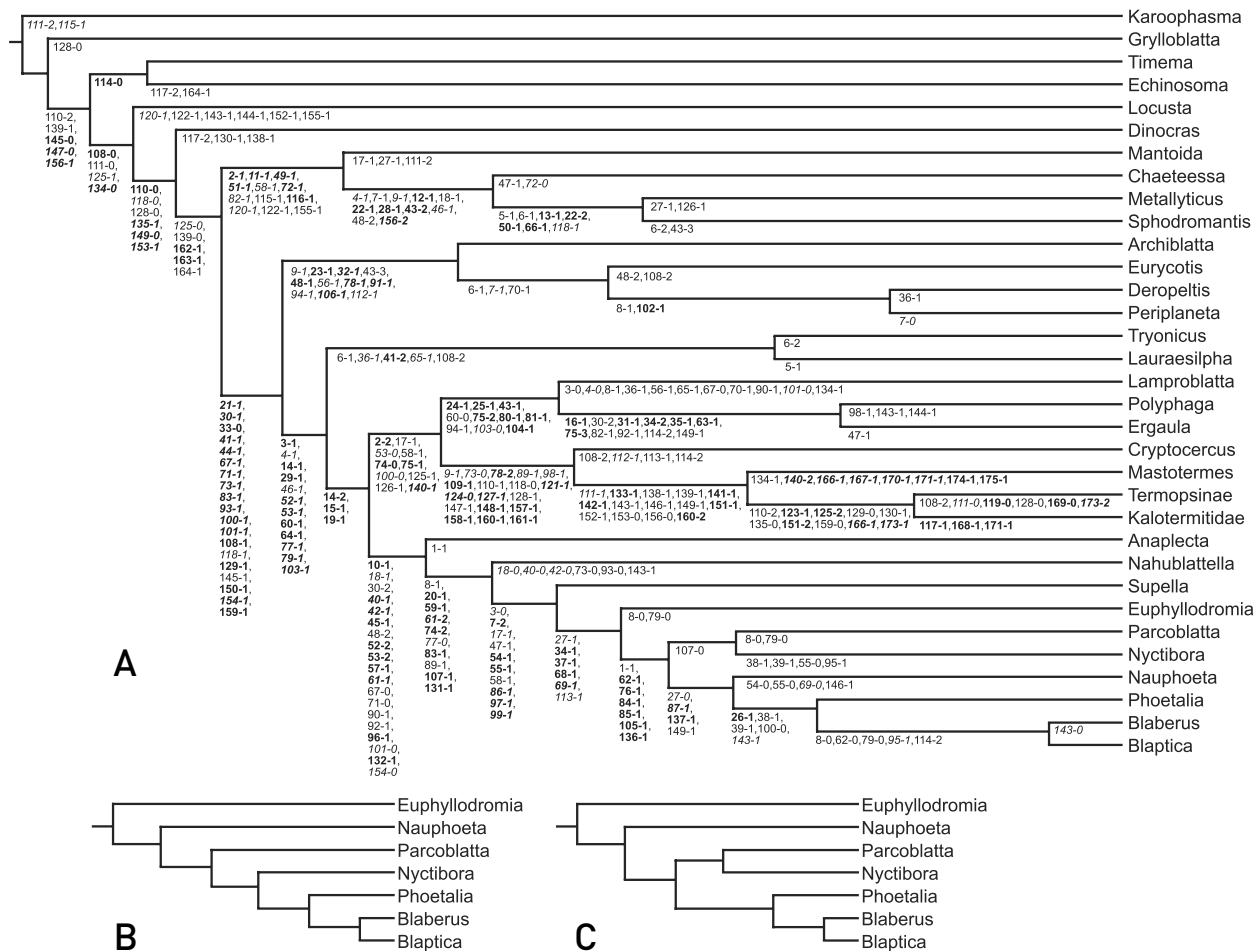


Fig. 4. Phylogenetic trees of Dictyoptera. **A:** Tree derived from analysis of entire data set with all ingroup taxa, six discrete outgroup taxa, and partly additive character treatment (see analysis AC-DO-pa-inc in Tab. 4; ingroup relationships identical in all other analyses based on entire and reduced data sets); character changes indicated below branches (number behind hyphen = character state); changes in bold type are unique, others are homoplastic; changes in normal print can only be optimized at one particular node (unambiguous changes), for those in *Italics* the placement on the tree is ambiguous ("fast optimization" was used to place them on this tree). **B, C:** The two trees resulting from all analyses of the phallomere data set; only higher Blattellidae shown, remaining ingroup parts of the tree identical with Fig. 4A.

the analysis of the entire data set using all ingroup taxa, the six discrete outgroup taxa, and partly additive coding (Tab. 4). Occasionally we point to much higher support values in analyses where taxa with many missing data were excluded (*Archiblatta* and *Lauraesilpha*; Isoptera excluded in phallomere data set).

Comparison of our results with those of other authors is difficult mainly because of different taxon sampling; in the available molecular studies several crucial taxa are lacking or under-represented (*Chaeteessa*, *Metallyticus*, Tryonicinae, *Lamproblatta*, Anaplectinae, and Plectopterinae). Only GRANDCOLAS' (1994, 1996, 1997a) morphology-based analyses include all the blattarian genera represented in our data set, though with the exception of Polyphaginae Grandcolas presented only a phylogenetic hypothesis for the relationships among the eight (sub-)families that he a priori considered monophyletic (Fig. 1B). Nevertheless, in the following discussions we present the results of analyses that we conducted upon our entire data set after having predefined certain clades hypothesized in the literature (Tab. 6); we

will give the additional costs of the most parsimonious tree including such a clade as compared to our most parsimonious tree 339 steps long (Tab. 4, column AC-DO-pa-inc).

4.1. Basal splits in Mantodea

Morphological characters strongly suggest *Mantoida* as the most basal branch (Bremer support BS4 for remaining Mantodea), and *Chaeteessa* as the following one (BS6; Figs. 4A, 5). *Mantoida* is also shown as the most basal branch of Mantodea in the tree of SVENSON & WHITING (2004), but *Chaeteessa* and *Metallyticus* are therein not included. In GRIMALDI'S (2003: fig. 26) computer-based trees the relationships among the four genera used in our analysis are unresolved, with the exception that the ordered tree shows a weakly supported clade *Mantoida* + *Metallyticus*. The tree of GRIMALDI (2003: fig. 27) that was reconstructed without the aid of a computer suggests *Chaeteessa* as sister to *Mantoida* + *Metallyticus* +

Sphodromantis, a topology contradicting our results. The monophyly of the latter clade is supported by characters 13, 20, and 21 in GRIMALDI (2003): reduced wings in the female, which, however, according to EHRMANN (2002: 217) does not apply to *Mantoida*, and two highly homoplastic characters, the lengthened 1st tarsomere of the fore leg (see GRIMALDI's matrix) and the shortened vein PCu of the forewing. The support for the clade *Mantoida* + *Metallyticus* + *Sphodromantis* is thus very weak. In our analysis this clade would cost 6 additional steps, which renders this alternative very unparsimonious.

BEIER's (1968a) family descriptions contain another character that indicates *Chaeteessa* as most basal (see also GRIMALDI 2003: character 17). In the armature of the raptorial fore legs this genus has very slender spines (seta-like) throughout and there is no tibial claw, while other extant Mantodea have usually much stouter spines (thorn-like), and the distal one of these is developed as a tibial claw/spur situated on a distal tibial lobe surpassing the base of the tarsus. However, the slender condition of the spines in *Chaeteessa* may well be a secondary adaptation (perhaps to delicate prey). The lack of the tibial claw is also plausibly considered secondary in view of the foreleg morphology in the very basal Cretaceous mantis *Jersimantis luzzii* (see GRIMALDI 1997: fig. 3, 2003: figs. 26, 27). The leg armature in this fossil appears altogether more plesiomorphic than in all extant Mantodea (including *Chaeteessa*), yet the tibial claw is much more distinctly differentiated from the other tibial spines than in *Chaeteessa* (compare KLASS & EHRMANN 2003: fig. 13.4 A and B).

In BEIER's (1968a) classification of Mantodea, besides the monogeneric Mantoididae, Chaeteessidae, and Metallyticidae, five further families are distinguished: Amorphoscelidae, Eremiaphilidae, Mantidae, Hymenopodidae, and Empusidae. In the classifications in ROY (1999) and EHRMANN (2002) several subfamilies of Mantidae *sensu* BEIER are elevated to family rank. According to the phylogenetic results of SVENSON & WHITING (2004; Eremiaphilidae not included), the 'Mantidae' of all classifications is paraphyletic with respect to Empusidae, Hymenopodidae, Amorphoscelidae, and the included taxa considered families by ROY (1999) and EHRMANN (2002). In addition at least some of the latter groups appear polyphyletic. Thus, current classifications of Mantodea appear highly artificial and require much revision. This leads to the question whether *Mantoida* and *Chaeteessa* are actually the most basal branches of Mantodea considering the entire systematic range of the order. LAGRECA (1954) illustrated the phallomeres of members of Eremiaphilidae, Amorphoscelidae, Hymenopodidae, Empusidae, and various subgroups of Mantidae (*sensu* BEIER). All species included resemble *Metallyticus* and *Sphodromantis* in phallomere structure. In particular, they have sclerite L4 divided into a dorsal and a ventral plate (L4A, L4B; character 13; in contrast to *Mantoida* and *Chaeteessa*), and L4A occupies most of the ventral wall (character 22; in contrast to *Mantoida*; the remaining characters included in our matrix cannot be assessed in LAGRECA's illustrations). The hypothesis

that *Mantoida* and, then, *Chaeteessa* are actually the most basal clades of the mantodean tree is thus quite well supported.

4.2. Basal splits in Blattaria

Our data set unambiguously supports a basal dichotomy between Blattinae + Polyzosteriinae (BS2) and all other Blattaria (BS3) (Figs. 4A, 5). This is in conflict with GRANDCOLAS (1996, 1997a), who proposed a monophyletic Blattidae, i.e., Blattinae + Polyzosteriinae + Tryonicinae + Lamproblattinae, as the sister group of the remaining Blattaria. In our analysis, 5 additional steps are required for a clade Tryonicinae + Blattinae + Polyzosteriinae, and 14 for either of the clades Lamproblattinae + Blattinae + Polyzosteriinae and Lamproblattinae + Tryonicinae + Blattinae + Polyzosteriinae. We consequently propose family status for **Lamproblattidae** (new status; type genus *Lamproblatta* Hebard, 1919) and **Tryonicidae** (new status; type genus *Tryonicus* Shaw, 1925) and their exclusion from Blattidae. We will use these names in the following (Tryonicidae including only *Tryonicus* and *Lauraesilpha*; compare GRANDCOLAS 1997a and KLASS 2001b).

The molecular studies cannot lend support to either GRANDCOLAS' or our hypothesis, because Tryonicidae and Lamproblattidae were not included. The cladogram in GRANDCOLAS et al. (2002: fig. 21), based on sequences from 12S and 16S rDNA, includes the tryonicid *Lauraesilpha*, Polyzosteriinae, and Blattinae, and the polyphagine *Therea* as the predefined outgroup. This, however, does not support GRANDCOLAS' (1994, 1996) hypothesis, because for the exemplars sampled in GRANDCOLAS et al. (2002) our results suggest the relationships (*Therea* + *Lauraesilpha*) + (Polyzosteriinae + Blattinae). Thus, we doubt that the use of *Therea* as an outgroup is appropriate, and with the root of GRANDCOLAS et al.'s (2002) tree placed differently, this tree shows the relationships we are proposing.

The close relationships between Polyzosteriinae and Blattinae are confirmed by the few molecular studies that have included members of Polyzosteriinae (KAMBHAMPATI 1995, 1996). In both studies these formed a monophyletic clade together with Blattinae. In our analysis (Fig. 4A) Polyzosteriinae (represented by *Eurycotis*) are a subgroup of Blattinae.

The molecular studies using non-dictyopteran outgroups have found different basal dichotomies within the Blattaria. Either *Cryptocercus* (KAMBHAMPATI 1995; BANDI et al. 1995) or *Cryptocercus* + Isoptera + Blattidae (LO et al. 2000, 2003) were the sister group of the remaining Blattaria. However, based on our characters these hypotheses cost 7 resp. 12 additional steps. MCKITTRICK (1964: textfig. 1) proposed a clade Blattidae + *Cryptocercus*, without Isoptera; this costs 15 additional steps.

4.3. Basal splits in non-blattid Blattaria

In our phylogenetic tree the next dichotomy separates Tryonicidae from the remaining Blattaria (Figs. 4A, 5), though the support is weak (BS2 for non-tryonicids). The remaining Blattaria fall into two well-supported clades, Cryptocercidae + Isoptera + Polyphaginae + Lamproblattidae (BS3; BS4 based on phallomere data set with Isoptera excluded) and Blattellidae + Blaberidae (BS4; BS10 based on phallomere data set).

In this context we would also like to briefly discuss the results of the molecular analyses of Blattaria that use only Isoptera as outgroup (MAEKAWA & MATSUMOTO 2000; KAMBHAMPATI 1996) although these are more likely subordinate within Blattaria (as in Fig. 4A). Once rerooted between Blattinae + Polyzosteriinae and the remaining taxa the cladograms can be compared to ours. MAEKAWA & MATSUMOTO's (2000) parsimony analysis of the COII gene obtained *Cryptocercus* + (*Polyphaga* + *Ergaula*) as the sister group of the other Blattaria. After rerooting, their result is similar to ours in indicating a monophyletic Blattellidae + Blaberidae and a clade Polyphaginae + Cryptocercidae + Isoptera. In KAMBHAMPATI's (1996) analysis of 12S rDNA (recently criticized by GRANDCOLAS & D'HAESE 2001) the rerooted tree shows the topology Cryptocercidae + (Polyphagidae + (Isoptera + (Blattellidae + Blaberidae))), hence indicating the assemblage of Cryptocercidae, Polyphagidae, and Isoptera as being paraphyletic.

4.4. Basal splits in Cryptocercidae + Isoptera + Polyphaginae + Lamproblattidae

There is strong support for *Cryptocercus* + Isoptera (BS6) being sister to *Lamproblatta* + Polyphaginae (BS4; up to BS8 based on phallomere data set). Monophyly of Isoptera (BS11) in the former clade, and of Polyphaginae (*Ergaula* + *Polyphaga*; BS4; up to BS9 based on phallomere data set) in the latter are also strongly supported (Figs. 4A, 5).

GRANDCOLAS & DELEPORTE (1992) and GRANDCOLAS (1994) placed *Cryptocercus* deeply within the Polyphaginae (see KLASS 1997: 333ff for comments). No other morphological or molecular result is congruent with such a placement, with the exception of a study of hypertrehalosaemic peptides (GÄDE et al. 1997), which yielded an altogether poor resolution of blattarian relationships (see NALEPA & BANDI 1999 and LO et al. 2000, 2003 for comments). With our taxon sample, the relationship *Polyphaga* + (*Ergaula* + *Cryptocercus*) would conform with Grandcolas' hypothesis; however, forcing it costs 23 additional steps. As a result of our study, and in contrast to GRANDCOLAS (1994 1996), we propose to retain 'Cryptocercidae' for *Cryptocercus*. We also reject GRANDCOLAS' (1997b) reconstruction of the *Cryptocercus* ancestor because it is based on the assumption that *Cryptocercus* is deeply subordinate within Polyphaginae. GRANDCOLAS (1997b) had proposed that it inhabited treeholes (or termite nests) in tropical forests of India

and Asia, was gregarious, without brood care, saprophagous, without a rich oxymonadid/hypermastigid hindgut 'fauna', and had an alarm behaviour involving the display of yellow spots on wings and pleural gland secretions.

4.5. Basal splits in Blattellidae + Blaberidae

The monophyly of the clade comprising Blattellidae and Blaberidae is almost undisputed in the literature. This clade is moderately supported in our analyses of the entire data set (BS4). The support increases with *Lauraesilpha* and *Archiblattea* being excluded (BS6), and this is the best-supported clade in our analysis of the phallomere data set (BS10). We will hereafter call this clade Blattellidae s.l. The basal dichotomy within Blattellidae s.l. is between *Anaplecta* and the remaining taxa. This is likewise undisputed among morphologists (GRANDCOLAS 1996; MCKITTRICK 1964: textfig. 3; KLASS 1995, 1997) and fairly well-supported in our analysis (BS5 for non-anaplectines; Anaplectinae were never included in molecular analyses).

In the branches above *Anaplecta*, a very interesting result is the paraphyly of the Plectopterinae (= Pseudophyllo-dromiinae) with regard to the monophyletic 'higher' Blattellidae s.l.; there is good support for *Nahublattella*, *Supella*, and *Euphyllodromia* being successive offshoots (BS5, BS3, and BS3 for the clades being sister to these offshoots).

Our analysis lends moderate support (BS3) to a monophyly of the 'higher' Blattellidae s.l., i.e., *Parcoblatta* + *Nyctibora* + Blaberidae with our taxon sample (Blattellinae + Ectobiinae + Nyctiborinae + Blaberidae; see KLASS 1995). With phallomere characters alone the support for this clade is very weak (BS1). The resolution of the phylogenetic relationships within this clade is mostly poor (Figs. 4, 5), and in the analyses of the phallomere data set the differences between our two most parsimonious trees lie within this clade (Fig. 4B,C). This is not surprising because the selection of characters and taxa was not aimed at resolving these relationships. Our tree obtained from the entire data set (Fig. 4A) maintains a monophyletic Blaberidae with *Parcoblatta* + *Nyctibora* as its sister group, but blaberid monophyly is not supported by phallomere characters alone. A monophyletic Blaberidae conforms with the view of most previous workers (including KLASS 1995, 1997 and GRANDCOLAS 1996) and is also supported by all molecular studies using decent blaberid taxon samples (KAMBHAMPATI 1995; BANDI et al. 1995).

In contrast to our results, GRANDCOLAS (1996) proposed a monophyletic Plectopterinae and a monophyletic Plectopterinae + Blaberidae (Fig. 1B). We note that GRANDCOLAS' (1996: character states 25[1], 26[1]) two plectopterine autapomorphies do not apply to many Plectopterinae (KLASS 2001b: 247f), and that otherwise the 'definition' of Plectopterinae is exclusively based on the co-occurrence of side-switched phallomeres and the plesiomorphic lack of ootheca rotation (see, e.g., ROTH 1995). Also two of GRANDCOLAS' (1996) three autapomorphies for

Characters included												
Discrete outgroups vs. hyp. ancestor												
Partly additive vs. all non-additive												
Archiblastia, Lauraesilpha												
No. MPTs ingroup (+ outgroup)												
6-96	5-97	4-95	4-96	6-99	5-98	4-97	4-98	6-97	5-97	4-97	6-99	5-99
4-92	4-86	4-88	3-88	4-96	4-89	4-88	3-87	4-92	4-90	4-89	3-84	4-91
4-91	4-91	4-91	4-92	4-98	4-97	4-97	4-98	4-94	4-92	4-93	4-98	4-98
1-64	1-72	1-68	1-79	1-64	1-76	1-57	1-79	1-67	1-64	1-63	1-73	1-65
2-83	4-99	2-73	4-100	2-85	4-99	2-64	4-100	2-85	3-98	2-70	3-99	2-87
2-88	-	2-84	-	2-87	-	2-84	-	2-91	-	2-83	-	2-91
3-86	-	1-62	-	3-91	-	1-67	-	3-82	-	1-60	-	2-91
4-95	4-96	3-95	4-96	3-97	3-99	3-94	3-98	3-93	3-93	3-94	3-89	2-95
4-85	4-86	4-86	4-81	3-93	3-93	3-83	3-85	3-79	3-78	3-76	3-68	2-88
7-99	7-97	6-96	6-92	7-98	7-99	6-97	6-97	6-98	6-96	4-87	4-86	6-98
11-100	11-100	9-100	9-100	10-100	10-99	9-100	9-100	9-99	9-100	7-100	7-99	8-99
6-82	6-83	4-74	4-69	7-97	7-97	6-91	6-96	4-61	4-62	2-52	2-48	4-89
3-59	3-66	3-54	3-52	3-89	3-89	3-75	3-78	2-44	2-40	2-35	2-35	2-81
1-39	1-45	1-43	1-41	1-38	1-39	1-45	1-41	1-43	1-42	1-41	1-38	1-42
3-81	3-77	3-80	3-82	3-80	3-81	3-84	3-82	3-82	3-81	3-81	3-77	3-81
3-85	3-85	3-87	3-84	3-84	3-80	3-85	3-81	3-87	3-85	3-82	3-86	3-85
1-44	1-47	1-48	1-38	1-40	1-39	1-44	1-43	1-48	1-44	1-42	1-43	1-44
3-85	3-79	3-84	3-82	3-76	3-81	3-81	3-81	3-82	3-81	3-79	3-81	3-82
3-94	3-95	3-92	3-94	3-94	3-95	3-94	3-96	3-93	3-95	3-91	3-92	3-94
5-97	5-97	5-97	5-97	5-96	5-97	5-97	5-99	5-96	5-96	5-97	5-98	4-98
5-91	5-90	5-92	5-85	5-88	5-91	5-91	5-89	5-89	5-89	5-90	5-90	4-87
4-98	6-100	3-99	6-100	4-99	4-99	3-99	4-99	4-98	5-97	3-99	5-99	3-99
2-34	2-36	2-44	1-36	2-53	2-49	2-51	1-46	2-28	2-21	2-27	1-27	2-51
3-40	3-45	2-38	2-45	3-67	3-60	2-52	2-66	2-35	2-28	2-26	2-32	2-62
3-61	3-68	2-60	3-61	2-88	3-94	2-88	3-95	2-44	2-41	2-39	2-41	2-78
2-54	2-59	2-54	2-60	-	-	-	-	2-49	2-45	2-43	2-39	-
339	338	331	329	303	302	299	297	335	334	327	325	298
0.807	0.801	0.805	0.801	0.834	0.829	0.828	0.825	0.805	0.799	0.803	0.799	0.833
0.602	0.604	0.616	0.620	0.660	0.662	0.669	0.673	0.600	0.602	0.615	0.618	0.659
Tree length												
RI												
CI												

Characters included	PC	PC	PC	PC
Discrete outgroups vs. hyp. ancestor	HA	HA	HA	HA
Partly additive vs. all non-additive	pa	pa	ana	ana
<i>Archiblatta</i> , <i>Lauraesilpha</i>	inc	exc	inc	exc
No. MPTs	2	2	2	2
Sph+Met	6-92	5-91	4-92	4-91
Sph+Met+Cha	6-84	5-80	5-84	3-79
Sph+Met+Cha+Man	7-78	7-74	7-81	7-81
Der+Per	1-65	1-69	1-55	1-68
Der+Per+Eur	2-81	7-96	2-69	8-96
Der+Per+Eur+Arc	2-87	-	2-79	-
Try+Lau	2-78	-	1-54	-
Pol+Erg	4-97	9-98	2-96	8-98
Pol+Erg+Lam	4-88	8-92	2-82	6-84
Pol+Erg+Lam+Cry	4-76	4-77	2-61	3-68
Blb+Blp	2-76	2-75	2-77	2-77
Blb+Blp+Pho	1-65	1-68	1-66	1-65
Blb+Blp+Pho+Nyc (tree 1 only)	0-43	0-41	0-40	0-40
Par+Nyc (tree 2 only)	0-24	0-21	0-29	0-25
Blb+Blp+Pho+Nyc+Par	1-44	1-45	1-50	1-46
Blb+Blp+Pho+Nyc+Par+Nau	1-57	1-54	1-61	1-57
Blb+Blp+Pho+Nyc+Par+Nau+Eup	3-79	3-77	3-74	3-77
Blb+Blp+Pho+Nyc+Par+Nau+Eup+Sup	3-83	4-85	2-83	4-83
Blb+Blp+Pho+Nyc+Par+Nau+Eup+Sup+Nah	3-70	4-70	2-65	4-69
Blb+Blp+Pho+Nyc+Par+Nau+Eup+Sup+Nah+Ana	2-78	10-83	1-74	8-82
Blb+Blp+Pho+Nyc+Par+Nau+Eup+Sup+Nah+Ana+Pol+Erg+Lam+Cry	2-37	2-43	1-34	1-42
Blb+Blp+Pho+Nyc+Par+Nau+Eup+Sup+Nah+Ana+Pol+Erg+Lam+Cry+Try+Lau	3-54	3-56	2-46	3-60
Blb+Blp+Pho+Nyc+Par+Nau+Eup+Sup+Nah+Ana+Pol+Erg+Lam+Cry+Try+Lau+Der+Per+Eur+Arc	7-65	7-69	7-61	7-65
Tree length	204	203	200	198
RI	0.839	0.626	0.835	0.832
CI	0.623	0.832	0.635	0.641

Tab. 5. Tree statistics and support values for analyses of the phallomere data set. The first four lines specify the analyses: PC = only phallomere characters 1–107 included; for HA, pa, ana, inc, exc see legend Tab. 4. “No. MPTs” gives the number of most-parsimonious trees obtained in the analysis, considering only relationships among in-group terminals (there are no outgroup relationships in these HA-analyses). Representation of clades and support values as in Tab. 4. The three last lines indicate tree length, retention index (RI), and consistency index (CI) for the MPTs of each analysis (identical for both MPTs of a given analysis).

Plectopterinae + Blaberidae were refuted by KLASS (2001b) on grounds of comparative morphology; the third autapomorphy listed is the side-switched phallomeres. Forcing GRANDCOLAS' (1996) clades to appear in our analysis costs 10 additional steps for Plectopterinae, and 15 additional steps for Plectopterinae + Blaberidae.

In the molecular studies, KAMBHAMPATI'S (1995) finding of a clade *Nahublattella* + (*Nyctibora* + (*Symploce* + *Parcoblatta* + *Blattella*)) as the sister group of the Blaberidae is in contrast to both Grandcolas' and our results. This would correspond to a monophyletic clade Plectopterinae + *Parcoblatta* + *Nyctibora* in our analysis, which increases tree length by 15 steps. This alternative appears thus very unparsimonious with regard to our data set. A topology that is congruent with ours but includes only few taxa is found in BELLÉS et al.'s (1999) analysis based on the nucleotide sequences of the allatostatin precursors (a neuropeptide): (*Periplaneta* + *Blatta*) + (*Supella* + (*Blattella* + Blaberidae)), with *Blatta* (Blattinae) and *Blattella* (Blattellinae) closely resembling *Periplaneta* resp. *Parcoblatta* in phallomere structure. In contrast, BELLÉS et al.'s (1999) analysis based on amino-acid sequences obtains *Supella* + ((*Periplaneta* + *Blatta*) + (*Blattella* + Blaberidae)). This is so far the only analysis proposing non-monophyly of Blattellidae s.l.

Due to the strong paraphyly of the Blattellidae with respect to the Blaberidae, a classification maintaining

Blattellidae and Blaberidae in the sense of MCKITTRICK (1964) should be abandoned. Either Blattellidae Karny, 1908 should be synonymized with Blaberidae Brunner von Wattenwyl, 1865; or Blaberidae should be retained with its present content and the Blattellidae split into several families according to the phylogenetic relationships. GRANDCOLAS (1996) favored the latter solution and erected the Anaplectidae, Pseudophyllodromiidae (= 'Plectopteridae'), and Blattellidae (= Blattellinae + Ectobiinae + Nyctiborinae). We accept the Anaplectidae; however, we would reject the remainder because the 'Pseudophyllodromiidae' are paraphyletic on our tree and the position of the Blaberidae within or beside the Blattellinae + Ectobiinae + Nyctiborinae remains unresolved. In any case, a new classification should be based on a larger taxon- and character sample of the Blattellidae s.l.

4.6. Evolution of phallomere side-switch

Side-switches of asymmetries do occasionally occur in various groups of animals. Well-known examples are gastropod Mollusca and pleuronectiform fishes, where the switches involve the entire body and occur both as anomalies within species and as clade autapomorphies. An example from the insects are the Embioptera (web-spinners), where switches were observed as anomalies

Tab. 6. Results of constrained analyses. Cost for maintaining monophyly of previously hypothesized clades (= extra steps compared to the most parsimonious tree length of 339, see Tab. 4 column AC-DO-pa-inc). The trees obtained in the constrained searches were assessed for statistically significant length differences to the most parsimonious tree by using the Templeton test as implemented in PAUP*. Templeton test: * = significance at the $p=0.05$ level; ** = significance at the $p=0.01$ level.

Clade	Steps	Templeton test	Source
(1) <i>Mantoida</i> + <i>Metallyticus</i> + <i>Sphodromantis</i>	+ 6	$p = 0.0588$	BEIER (1968)
(2) <i>Mantoida</i> + <i>Sphodromantis</i>	+ 12	$p < 0.001^{**}$	BEIER (1968)
(3) <i>Deropeltis</i> + <i>Periplaneta</i> + <i>Eurycotis</i> + <i>Tryonicus</i>	+ 5	$p = 0.102$	GRANDCOLAS (1996, 1997a)
(4) <i>Deropeltis</i> + <i>Periplaneta</i> + <i>Eurycotis</i> + <i>Lamproblatta</i>	+ 14	$p = 0.019^{*}$	GRANDCOLAS (1996)
(5) <i>Deropeltis</i> + <i>Periplaneta</i> + <i>Eurycotis</i> + <i>Lamproblatta</i> + <i>Tryonicus</i>	+ 14	$p = 0.012^{*}$	GRANDCOLAS (1996)
(6) <i>Deropeltis</i> + <i>Periplaneta</i> + <i>Eurycotis</i> + <i>Cryptocercus</i>	+ 15	$p = 0.067$	KAMBHAMPATI (1996), MCKITTRICK (1964)
(7) <i>Deropeltis</i> + <i>Periplaneta</i> + <i>Eurycotis</i> + <i>Cryptocercus</i> + <i>Mastotermitidae</i> + <i>Kalotermitidae</i> + <i>Termopsinae</i>	+ 12	$p = 0.056$	Lo et al. (2000, 2003)
(8) <i>Ergaula</i> + <i>Cryptocercus</i>	+ 23	$p = 0.001^{**}$	GRANDCOLAS (1994)
(9) <i>Ergaula</i> + <i>Cryptocercus</i> + <i>Polyphaga</i>	+ 13	$p = 0.038^{*}$	GRANDCOLAS (1994)
(10) <i>Nahublattella</i> + <i>Supella</i> + <i>Euphyllodromia</i>	+ 10	$p = 0.012^{*}$	GRANDCOLAS (1996)
(11) <i>Nahublattella</i> + <i>Supella</i> + <i>Euphyllodromia</i> + <i>Blaptica</i> + <i>Blaberus</i> + <i>Nauphoeta</i> + <i>Phoetalia</i>	+ 15	$p < 0.001^{**}$	GRANDCOLAS (1996)
(12) <i>Nahublattella</i> + <i>Supella</i> + <i>Euphyllodromia</i> + <i>Parcoblatta</i> + <i>Nyctibora</i>	+ 15	$p < 0.001^{**}$	KAMBHAMPATI (1995)
(13) all Blattaria except <i>Cryptocercus</i>	+ 7	$p < 0.002^{*}$	KAMBHAMPATI (1995), BANDI et al. (1995)

in the male terminal abdomen (Ross 2000: 46) but have apparently not become stable in any subgroup.

In Dictyoptera, few Mantodea and many Blattaria have side-switched phallomeres. In Mantodea these occur in some species of the closely related genera *Ciulfina* and *Stenomantis* (Mantidae-Liturgusinae; BALDERSON 1978), while other species of these genera have normally orientated phallomeres or are dimorphic. In Blattaria side-switches have so far been reported only for subgroups of Blattellidae s.l. For some species it has been demonstrated that side-switches only involve the male genitalic region (phallomeres, subgenital plate, paraprocts), but not the mandibles and gut curvature (BOHN 1987). In the females the weak, apparently individual asymmetries have not yet been examined sufficiently for being able to determine a side-switch, and known differences with regard to the direction into which the ootheca is rotated are likely induced by the males through mating (BROWN 1973). That the side-switch of asymmetries is largely restricted to the male genitalia should be of great interest for developmental biologists.

In Blattaria side-switched phallomeres, bearing the prominent hook 'hla' on the right side (e.g., Figs. 3I, J, which show a mirror-image of the phallomeres) rather than on the left, have so far been found in all 'Plectopterinae' and Blaberidae. Furthermore, two different lineages of the Ectobiinae have side-switched phallomeres, but this is unlikely a groundplan feature of the Ectobiinae (BOHN 1987, pers. comm.). Hence, even with a monophyletic Plectopterinae at least four independent side-switches have to be proposed. In our tree (Fig. 6), with the plectopterines *Nahublattella*, *Supella*,

and *Euphyllodromia* being three successive clades in the Blattellidae s.l., the most parsimonious assumption is that a side-switch is autapomorphic for Blattellidae s.l. excluding *Anaplecta*, and that the normal phallomere orientation of Blattellinae, Nyctiborinae, and most Ectobiinae is due to a character reversal (i.e., a second side-switch); this costs two steps, while assuming three independent side-switches in 'Plectopterinae' and one in Blaberidae costs four steps.

The side-switched conditions in different groups of Ectobiinae have probably originated independently of each other from normally orientated phallomeres; in our scenario they represent two cases of a third side-switch. According to our phylogenetic hypothesis, mirror-image phallomeres in Blaberidae result from the first side-switch and are homologous with those in 'Plectopterinae'. However, in view of the poor resolution of phylogenetic relationships within the higher Blattellidae s.l., conditions in Blaberidae may as well result from a third side-switch. In order to answer this question a larger taxon sample of the higher Blattellidae s.l. is needed. Regardless of these uncertainties, the many additional steps needed in our analysis for GRANDCOLAS' (1996) monophyletic Plectopterinae + Blaberidae (15; Tab. 6) make it likely that a side-switch is not an autapomorphy of such a clade.

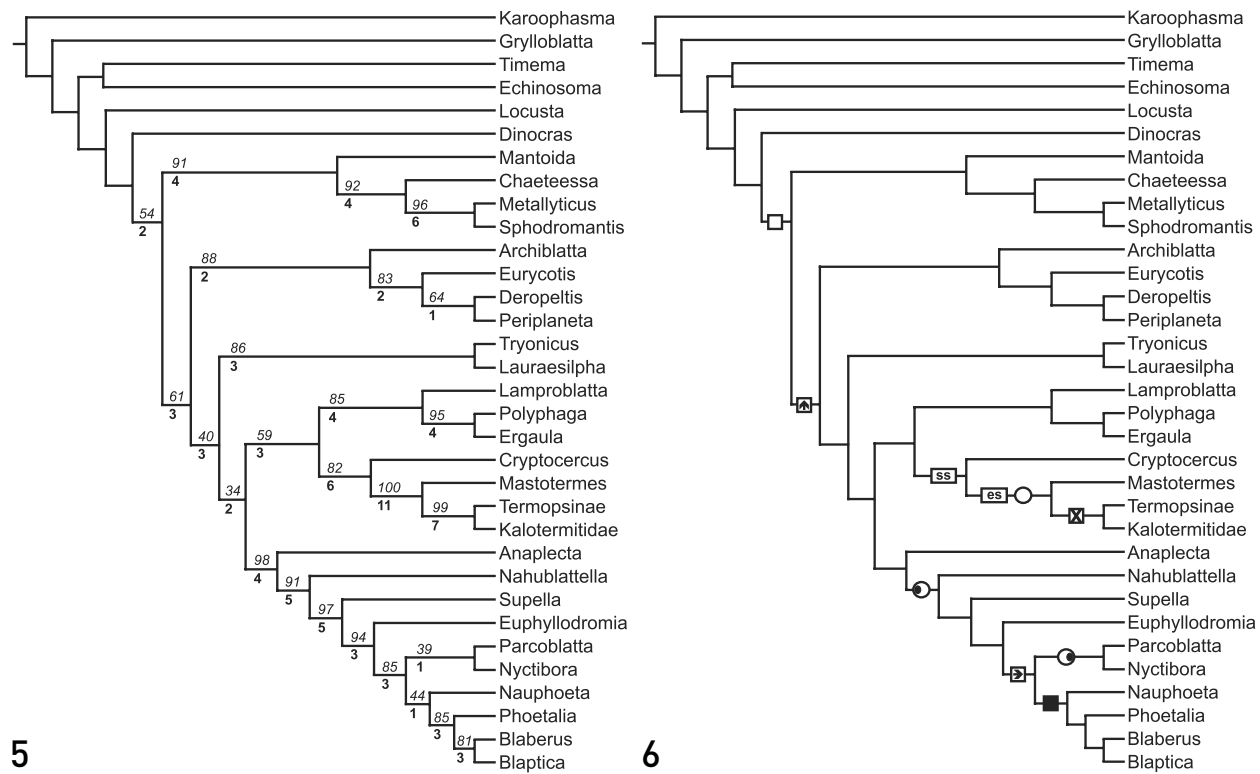


Fig. 5. Phylogenetic tree of Dictyoptera with support values of branches, derived from analysis of entire data set with all ingroup taxa, six discrete outgroup taxa, and partly additive character treatment (see analysis AC-DO-pa-inc in Tab. 4). Support values only given for ingroup relationships: number below branch, in bold type = Bremer support; number above branch, in Italics = bootstrap support.

Fig. 6. Phylogenetic tree of Dictyoptera with evolutionary events indicated, derived from same analysis as tree in Fig. 5. Squares represent events in reproductive biology: empty square = formation of ootheca by secretions from asymmetrical accessory glands; square with arrow up = formation of ootheca inside the vestibulum, originally with keel-up orientation until deposition; square with arrow to the right = rotation of ootheca inside the vestibulum, keel thus directed laterally; filled square = retraction of ootheca into brood pouch, combined with ovoviviparity; square with cross = formation of ootheca lost, eggs laid singly. Circles represent events in male genitalia: circle with dot on left side = switch from normal to mirror-image orientation; circle with dot on right side = switch from mirror-image to normal orientation; empty circle = strong reduction of male genitalia, genitalic region bilaterally symmetrical. Rectangles represent events in terms of sociality: ss = subsocial (biparental care); es = eusocial (bi- and alloparental care).

4.7. Evolution of ovoviviparity: ootheca rotation and retraction

While Mantodea build their ootheca on the substrate (BEIER 1968a), the only ootheca-forming isopteran, *Mastotermes darwiniensis*, and all Blattaria build it in the vestibulum above the outer subgenital plate (Fig. 6; NALEPA & LENZ 2000; ROTH 1970). In the Blattellidae s.l. there are two further changes in the way the ootheca is handled after its completion: rotation and retraction (Fig. 6).

All Blattellinae, Ectobiinae, Nyctiborinae, and Blaberidae, and only these, rotate the ootheca 90° from a keel-up to a keel-sideward orientation while the anterior portion of the ootheca is held within the vestibulum (advanced rotation of ROTH 1967, 1970; note that 'Plectopterinae' have partly been 'defined' by its lack). Some Polyphagidae also rotate the ootheca, but this differs substantially from rotation in the aforementioned taxa, because the ootheca is fully extruded from the vestibulum prior to rotation and held between the paraprocts thereafter (primitive rotation of ROTH 1967, 1970; absent in *Ergaula capensis* and *Polyphaga aegyptiaca*; ROTH 1967).

In few 'Plectopterinae' and Blattellinae and in all Blaberidae the ootheca is retracted into a brood pouch ('uterus'); this is always associated with ovoviviparity or, rarely, viviparity (NALEPA & BELL 1997; ROTH 1995, 1997). In the respective Blattellinae (species of *Stayella* and *Pseudanaplectina*) and in the Blaberidae retraction is preceded by rotation. Nonetheless, in few Blaberidae eggs are deposited directly and singly into the brood pouch, and since no ootheca is formed prior to this, there is neither a rotation nor a discrete retraction in these cockroaches.

The rotation is one possible solution for making the ootheca fit the proportions of the abdomen (wide and flat), hence it is an exaptation for retraction. In the respective Plectopterinae (*Sliferia*, with incomplete retraction, and *Pseudobalta*), however, ootheca retraction is not preceded by rotation; instead, oothecae are flattened dorsoventrally to fit abdominal proportions. The retracting taxa are not closely related, and retraction thus surely has evolved several times and from two different preconditions (with and without rotation). But how often has the advanced ootheca rotation evolved?

A single origin of ootheca rotation had long been uncontroversial (MCKITTRICK 1964: 119; ROTH 1967, 1970;

BOHN 1987; KLASS 1995). GRANDCOLAS (1996: fig. 25), however, proposed rotation to have originated independently in Nyctiborinae + Blattellinae + Ectobiinae and in Blaberidae. Nonetheless, in his tree the alternative that rotation ('o' in Fig. 1B) is homologous in the two clades and secondarily absent in 'Plectopterinae' (= 'Pseudophyllodromiinae') is just as parsimonious using an ACCTRAN- instead of a DELTRAN-optimization. In contrast, our topology unambiguously suggests a single origin of advanced ootheca rotation (Fig. 6), thus reviving the traditional view. In contrast to GRANDCOLAS (1996: 522), ootheca rotation has thus long preceded ootheca retraction in Blaberidae (Fig. 6).

4.8. Origin of sociality, xylophagy, and oxymonadid/hypermastigid gut 'fauna'

The occurrence of sociality with biparental care, of xylophagy, of anal trophallaxis, and of a rich diversity of oxymonadid and hypermastigid flagellates in the hind gut (e.g., HONIGBERG 1969; BOBYLEVA 1975) are the most interesting similarities between *Cryptocercus* and Isoptera. These four features are intimately correlated because xylophagy partly depends on the contribution of the flagellates to digestion (see BIGNELL 2000 and INOUE et al. 2000 for the mutual relationships between dictyopterans and flagellates), the transfer of flagellates to the next generation depends largely on anal trophallaxis, and the latter can be conducted only if some kind of (sub)sociality is present. Isoptera display biparental care only in early stages of the foundation of a new colony by alate individuals (e.g., BOHN 2003), while after the production of workers or pseudergates the colony switches to alloparental care. Few species of Oxymonadida and Hypermastigida occur in cockroaches other than *Cryptocercus* and in other insects (LORENC 1939; ROTH 1982; PARKER 1982; MÖHN 1984), but most subgroups of these flagellate taxa are restricted to *Cryptocercus* and basal Isoptera (i.e., termites excluding Termitidae, which lack these flagellates).

Our analyses consistently found, like the previous analysis of DEITZ et al. (2003) and the molecular analyses by LO et al. (2000, 2003), a monophyletic clade Cryptocercidae + Isoptera; this includes analyses from which we excluded the symbiosis characters 157–159. This is congruent with xylophagy, sociality, anal trophallaxis, and the association with rich oxymonadid and hypermastigid 'faunas' being homologous in Cryptocercidae and Isoptera.

GRANDCOLAS & DELEPORTE (1996) suggested homoplasy for these features and argued that the shared occurrence of the flagellates in *Cryptocercus* and Isoptera is due to a 'lateral' interspecific transfer (see also THORNE 1990, 1991). This hypothesis is exclusively based on considering *Cryptocercus* as being deeply subordinate within the Polyphaginae (GRANDCOLAS 1994), which is incompatible with a sistergroup relationship between *Cryptocercus* and Isoptera. However, this phylogenetic hypothesis has been refuted previously (KLASS 1997; DEITZ et al. 2003; LO et

al. 2000, 2003) and is also incompatible with the results of our present analyses.

The hypothesis of a lateral transfer and a placement of *Cryptocercus* within the Polyphaginae furthermore faces difficulties that were not considered in GRANDCOLAS & DELEPORTE (1996). Several 'genera' and 'families' of Oxymonadida and Hypermastigida are shared exclusively between *Cryptocercus* and different subgroups of Isoptera: *Cryptocercus* shares *Leptospironympha* and Spirotrichosomidae with Stolotermitinae; *Oxymonas*, Hoplonymphidae, and Staurojoeninae with Kalotermitidae; and Eucomonymphidae with Rhinotermitidae. HONIGBERG (1969) suggested that stemgroup Isoptera had a rather complete set of oxymonadid and hypermastigid subgroups, and that different losses have occurred in the various isopteran crown group clades. This view is congruent with recent intraspecific losses reported from various Isoptera (HONIGBERG 1969) and *Cryptocercus punctulatus* (see, e.g., BOBYLEVA 1975). Hence, according to the lateral-transfer hypothesis *Cryptocercus* should have obtained its gut 'fauna' either through a single lateral transfer from a stemgroup isopteran, or through several additive lateral transfers from a variety of termite taxa. The latter alternative is unparsimonious. With GRANDCOLAS' (1999a: 288) assumption that the split between *Cryptocercus* and its alleged polyphagine sister group occurred "later than Miocene" – a time long after the splitting events that produced the termite crown group 'families' – physical contact between *Cryptocercus* and stemgroup Isoptera is very unlikely and explaining the specific flagellate 'fauna' of *Cryptocercus* through lateral transfer is very difficult.

Recently PELLENS et al. (2002) reported a variety of flagellate species (Trichomonadida) to occur in the hind gut of the South American cockroach *Parasphaeria boleiriana* (Blaberidae-Zetoborinae), which is only distantly related to *Cryptocercus*. While PELLENS et al. (2002: 357) state that "among cockroaches these Protozoa are [otherwise] only known from *Cryptocercus* species" and consider this to have a bearing on the evolutionary interpretation of the similar flagellate faunas of *Cryptocercus* and Isoptera, we propose that both is not the case. BRUGEROLLE et al. (2003) further specified these trichomonadids as members of *Monocercomonas* and *Tetratrichomastix*, and they additionally reported the presence in *P. boleiriana* of two oxymonadid species of the genera *Monocercomonoides* and *Polymastix* and one diplomonadid species resembling *Hexamita*. The trichomonads *Monocercomonas* and *Tetratrichomastix* also occur in a variety of insects including cockroaches. *Monocercomonoides* and *Polymastix* are two of those basal oxymonadid genera that are widely distributed in the guts of cockroaches and other terrestrial arthropods. *Hexamita* includes many free-living sapropelic species and parasitic or commensal species in a variety of metazoan groups (for life history data on flagellates see, e.g., MÖHN 1984: 166; PARKER 1982: 500; BRUGEROLLE et al. 2003). Consequently, the gut 'fauna' of *P. boleiriana* does not include a single one of those many oxymonadid and hypermastigid subgroups that are specific to

Cryptocercus and/or termites, and the results on this cockroach underline the uniqueness of the gut fauna shared between *Cryptocercus* and Isoptera.

4.9. Evolution of symmetry in proventriculus armature

In some groups of the mandibulate Arthropoda a portion of the fore gut forms a strongly armoured proventriculus. Surprisingly, very similar structural patterns are shared between the taxa with the most complex proventriculi. These are some Dictyoptera, some Odonata (nymphs), the lepismatid *Zygentoma*, and the decapodan and mysidacean Malacostraca (KLASS 1998b,c; see also KLASS & KRISTENSEN 2001, and TILGNER et al. 1999 for Phasmatodea). To which extent the structural similarities are homologous remains unclear because proventricular structure is much simpler in most of the remaining Mandibulata.

In the Dictyoptera the wall of the proventriculus has a hexaradial symmetry created by six major longitudinal folds (primary plicae, numbered 1–6). In most subgroups each primary plica bears a large denticle placed on a heavy sclerite. Usually the single plicae are structurally different (e.g., KLASS 1998b: fig. 4). Plicae 3 and 5 are identical but mirror-imaged, and the same is true for plicae 2 and 6 (paired plicae). Each of the two remaining, opposing plicae 1 and 4 has a unique structure (unpaired plicae). Thus, there is a plane of bilateral symmetry crossing the plicae 1 and 4, which overlies the hexaradial symmetry. While each of the unpaired plicae 1 and 4 is in itself bilaterally symmetrical, each of the paired plicae 3/5 and 2/6 is in itself asymmetrical because, for instance, the tip of the denticle is inclined towards plica 4. Importantly, the degree of the differences between plicae 1, 3/5, 2/6, and 4 varies strongly within the Dictyoptera. The stronger the differences are, the stronger is the bilateral symmetry, and the weaker is the hexaradial symmetry.

Among the Dictyoptera the greatest and identical differences between the primary plicae are found in the Blattinae + Polyzoisteriinae and the Tryonicidae (McKITTRICK & MACKERRAS 1965). The Isoptera represent the other extreme: they entirely lack differences between the primary plicae, and their proventriculus is thus purely hexaradial. Most of the remaining Blattaria also have well-developed plicae, and these show moderate interplic differences of different degrees. Among these groups the Cryptocercidae approach the condition in Isoptera most closely; for instance, the paired denticles are here not laterally inclined (see KLASS 1998b, 2000: tab. 2 for further similarities). In some dictyopteran subgroups the plical armature is \pm strongly modified (partly by reductions; Polyphaginae, Ectobiinae, Blaberidae, Mantodea; see McKITTRICK 1964; MILLER & FISK 1971; KLASS 1998b), and we also note the unique symmetry in Lamproblattidae, where the tips of all six teeth are inclined counterclockwise (in an anterior view).

Based on our phylogenetic hypothesis (Figs. 4A, 5) strong interplic differences can be assumed for the ground plan of the clade Blattaria + Isoptera, because there are

the same strong differences in Blattinae + Polyzoisteriinae and Tryonicidae. Then, within the Blattaria + Isoptera the six initially fairly different primary plicae (two singles and two pairs) have become more similar, as in, e.g., Cryptocercidae and most Blattellidae. Eventually, in the Isoptera and also in few Blattellidae, all six primary plicae have become fully identical. This contrasts with the view of, for example, McKITTRICK (1964) and constitutes a quite unusual kind of anagenesis.

Conditions in the abovementioned *Zygentoma* and Malacostraca comply with this result. The proventriculus in Lepismatidae closely resembles that in Blattinae + Polyzoisteriinae, but plicae 1, 3/5, 2/6, and 4 differ even more strongly, and the hexaradial symmetry component is thus even less distinct. In Decapoda and Mysidacea 'plicae' 1, 3/5, 2/6, and 4 are so different that they hardly convey a notion of hexaradial symmetry. If proventriculi are homologous between Dictyoptera and *Zygentoma*, and perhaps even Malacostraca, strong interplic differences are confirmed as plesiomorphic for Dictyoptera, and elements of the proventriculus wall that originally were entirely different have become increasingly similar, and in the extreme case of Isoptera constitute a perfect hexaradial symmetry.

5. Conclusions

We retrieved a well-supported tree for the dictyopteran taxa we sampled (Figs. 4A, 5). Nonetheless, our hypothesis has to be elaborated and tested through a more comprehensive inclusion of characters from several useful character systems (e.g., female genitalia and their musculature, wings, proventriculus, body musculature, glands). The data for the female genitalia and the proventriculus that have been obtained from a few exemplary Dictyoptera (see KLASS 1998a,b) are essentially consistent with our topology. Comparative studies of glands (see BROSSUT 1973) and musculature (see KLASS 1999) are still at a very initial stage. Furthermore, as usual, more extensive taxon samples are needed for a better resolution of relationships within subordinate clades. Another urgent requirement is to combine morphological data with data from DNA-sequences. Unfortunately, combining data is currently impossible because of the poor taxon overlap between data sets.

Based on our phylogenetic analyses, some of the branching events in Blattaria and Mantodea appear now strongly supported. This applies to Mantoididae being the basal-most branch within the Mantodea, and Chaeteessidae being the following one. In order to further resolve mantodean relationships, there is a need for comparative studies of the male genitalia in all derived families, and the female genitalia in all families. Comparative studies on characters from other body parts throughout Mantodea could also be very helpful (such as the cervical sclerites in WIELAND 2006). In addition, sequence data are urgently required for the basal families Chaeteessidae and Metallyticidae.

In the Blattaria a basal dichotomy between the Blattidae (Blattinae + Polyzosteriinae) and the remaining Blattaria is indicated. The monophyly of the Blattidae is not very strongly supported by morphological characters but is corroborated by several molecular studies. Phallomere structure strongly suggests the exclusion of Tryonicidae and Lamproblattidae from the Blattidae, the former being a very isolated branch, and the latter appearing as the sister group of the Polyphaginae. Consequently, in order to test the morphological results we urge the inclusion of members of Tryonicidae (i.e., *Lauraesilpha* or *Tryonicus*) and Lamproblattidae into molecular studies.

The monophyly of a clade Blattellidae + Blaberidae, almost undisputed throughout all previous phylogenetic studies, is strongly confirmed in our analysis. While our proposal of Anaplectinae being most basal in this clade is also unequivocal, our strong support for paraphyletic 'Plectopterinae' (= 'Pseudophyllodromiinae') constituting at least three subsequent branches conflicts with some earlier morphology-based hypotheses. Since these two 'subfamilies' are poorly or not at all represented in molecular studies, DNA-sequence analyses including Anaplectinae and a good sample of 'Plectopterinae' are another urgent requirement for future phylogenetic research in Dictyoptera. The relationships within the very diverse 'higher' Blattellidae s.l., i.e., between Blattellinae, Nyctiborinae, Ectobiinae, and Blaberidae, remain a particularly challenging issue for future studies. Here a specialized matrix will have to be built that includes many new characters as well as a considerably larger taxon sample of this clade than in our analysis. Our results strongly indicate that phallomere side-switches as well as their reversals have occurred several times in the evolution of the Blattellidae s.l., and that ootheca rotation has evolved only once. However, detailed evolutionary scenarios for phallomere side-switches and for the origin of ovoviviparity still have to be worked out through mapping these characters on more taxon-inclusive cladograms.

The phylogenetic placement of the Cryptocercidae is surely another point of particular general interest due to the disputed close relationship of this taxon to the termites and the occurrence of sociality and unique hypermastigid and oxymonadid hindgut flagellates in these two taxa. Our analysis strongly supports a monophyletic lineage Cryptocercidae + Isoptera, which is congruent with recent molecular work, and a position of this clade as the sister group of the Lamproblattidae + Polyphaginae. Nonetheless, there are currently only few morphological characters known that have a bearing on the placement of the Isoptera. This is due to the small amount of work on the morphology of basal Isoptera. Morphological research specifically aimed at a comparison between basal termites, Cryptocercidae, and selected other cockroaches would thus be particularly desirable.

We can only conclude that thus a lot remains to be done in both morphological and molecular work on Dictyoptera phylogeny reconstruction. We hope that our results fill some major gaps in knowledge and help to identify the most urgent tasks. It should now be easier to assemble

within a relatively short time a character matrix whose analysis will yield a stable phylogenetic hypothesis for the Dictyoptera based on a diverse array of evidence.

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7. References

- ALBRECHT, F.O. 1953. The anatomy of the migratory locust. – University of London, the Athlone Press, xvi + 118 pp.
- AHMAD, M. 1950. The phylogeny of termite genera based on imago-worker mandibles. – Bulletin of the American Museum of Natural History **95**: 37–86.
- BACCETTI, B.[M.] 1987. Spermatozoa and phylogeny in orthopteroid insects. Pp. 12–112 in: BACCETTI B.M. (ed.), Evolutionary Biology of Orthopteroid Insects. – Ellis Horwood, Chichester, and John Wiley & Sons, New York.
- BALDERSON, J. 1978. Reversal of the phallic complex in the genera *Ciulfina* Giglio-Tos and *Stenomantis* Saussure (Mantodea: Mantidae: Iridopteryginae). – Journal of the Australian Entomological Society **17**: 235–239.
- BANDI, C., M. SIRONI, G. DAMIANI, L. MAGRASSI, C.A. NALEPA, U. LAUDANI & L. SACCHI 1995. The establishment of intracellular symbiosis in an ancestor of cockroaches and termites. – Proceedings of the Royal Society London B **259**: 293–299.
- BANDI, C., M. SIRONI, C.A. NALEPA, S. CORONA & L. SACCHI 1997. Phylogenetically distant intracellular symbionts in termites. – Parassitologia **39**: 71–75.
- BARNHART, C.S. 1961. The internal anatomy of the silverfish *Ctenolepisma campbelli* and *Lepisma saccharinum* (Thysanura: Lepismatidae). – Annals of the Entomological Society of America **54**: 177–196.
- BEIER, M. 1968a. 12. Ordnung Mantodea (Fangheuschrecken). Pp. 1–47 in: J.G. HELMCKE, D. STARCK & H. WERMUTH (eds.), Handbuch der Zoologie vol. 4 (2) 2/12. – De Gruyter, Berlin, New York.
- BEIER, M. 1968b. 10. Ordnung Phasmida (Stab- oder Gespenstheuschrecken). Pp. 1–56 in: J.G. HELMCKE, D. STARCK & H. WERMUTH (eds.), Handbuch der Zoologie vol. 4 (2) 2/10. – De Gruyter, Berlin, New York.
- BEIER, M. 1972. 9. Ordnung Saltatoria (Grillen und Heuschrecken). Pp. 1–217 in: J.G. HELMCKE, D. STARCK & H. WERMUTH (eds.), Handbuch der Zoologie vol. 4 (2) 2/9. – De Gruyter, Berlin, New York.
- BELLÉS, X., L.A. GRAHAM, W.G. BENDENA, Q. DING, J.P. EDWARDS, R.J. WEAVER & S.S. TOBE 1999. The molecular evolution of the allatostatin precursor in cockroaches. – Peptides **20**: 11–22.
- BEUTEL, R.G. & S.N. GORB 2001. Ultrastructure of attachment specializations of hexapods (Arthropoda): evolutionary patterns inferred from a revised ordinal phylogeny. – Journal of Zoological Systematics and Evolutionary Research **39**: 177–207.
- BIGNELL, D.E. 2000. Introduction to symbiosis. Pp. 189–208 in: T. ABE, D.E. BIGNELL & M. HIGASHI (eds.), Termites: Evolution, Sociality, Symbioses, Ecology. – Kluwer Academic Publishers, Dordrecht, Netherlands.
- BIRKET-SMITH, J. 1974. On the abdominal morphology of Thysanura (Archaeognatha and Thysanura s.str.). – Entomologica Scandinavica, Supplementum **6**: 1–67.
- BOBYLEVA, N.N. 1975. Morphology and evolution of intestinal parasitic flagellates of the far-eastern roach *Cryptocercus relictus*. – Acta Protozoologica **14**: 109–160.

- BOHN, H. 1987. Reversal of the right-left asymmetry in male genitalia of some Ectobiinae (Blattaria: Blattellidae) and its implications on sclerite homologization and classification. – *Entomologica Scandinavica* **18**: 293–303.
- BOHN, H. 2003. 15. Ordnung Isoptera, Termiten. Pp. 223–250 in: H.H. DATHE & H.-E. GRUNER (eds.), *Lehrbuch der Speziellen Zoologie, Band I: Wirbellose*, 5. Teil: Insecta, 2nd edn. – Spektrum Akademischer Verlag, Heidelberg, Berlin.
- BOHN, H. & K.-D. KLASS 2003. Dictyoptera. Pp. 181–182 in: H.H. DATHE & H.-E. GRUNER (eds.), *Lehrbuch der Speziellen Zoologie, Band I: Wirbellose Tiere*, 5. Teil: Insecta, 2nd edn. – Spektrum Akademischer Verlag, Heidelberg, Berlin.
- BREMER, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. – *Evolution* **42**: 795–803.
- BRINCK, P. 1956. Reproductive system and mating in Plecoptera I. – *Opuscula Entomologica* **21**: 57–127.
- BROSSUT, R. 1973. Evolution de système glandulaire exocrine céphalique des Blattaria et des Isoptera. – *International Journal of Insect Morphology and Embryology* **2**: 35–54.
- BROWER, A.V.Z. 2000. Homology and the inference of systematic relationships: some historical and philosophical perspectives. Pp. 10–21 in: R. SCOTLAND & R.T. PENNINGTON (eds.), *Homology and Systematics: Coding Characters for Phylogenetic Analysis*. – The Systematics Association Special Volume **58**. Taylor and Francis Inc., London and New York.
- BROWMAN, L.G. 1935. The chitinous structures in the posterior abdominal segments of certain female termites. – *Journal of Morphology (Philadelphia)* **57**: 113–129.
- BROWN, V.K. 1973. Aspects of the reproductive biology of three species of *Ectobius* (Dictyoptera: Blattidae). – *Entomologia Experimentalis et Applicata* **16**: 213–222.
- BRUGEROLLE, G., I.D. SILVA-NETO, R. PELLENS & P. GRANDCOLAS 2003. Electron microscopic identification of the intestinal protozoan flagellates of the xylophagous cockroach *Parasphaeria boeiriana* from Brazil. – *Parasitology Research* **90**: 249–256.
- CARPENTER, F.M. 1992. Superclass Hexapoda. In: R.L. KAESLER (ed.): *Treatise on Invertebrate Paleontology*, part R, Arthropoda 4, vol. 3. – The Geological Society of America Inc. (Boulder, Colorado) & The University of Kansas (Lawrence, Kansas), xxi + 277 pp.
- DALLAI, R., F. FRATI, P. LUPETTI & J. ADIS 2003. Sperm ultrastructure of *Mantophasma zephyra* (Insecta, Mantophasmatodea). – *Zoomorphology* **122**: 67–76.
- DEITZ, L.L., C.A. NALEPA & K.-D. KLASS 2003. Phylogeny of the Dictyoptera re-examined. – *Entomologische Abhandlungen* **61**: 69–91.
- DELEPORTE, P. 1993. Characters, attributes, and tests of evolutionary scenarios. – *Cladistics* **9**: 427–432.
- DESALLE, R., J. GATESY & D. GRIMALDI 1992. DNA sequences from a fossil termite in Oligo-Miocene amber and their phylogenetic implications. – *Science* **257**: 1933–1936.
- DONOVAN, S.E., D.T. JONES, W.A. SANDS & P. EGGLETON 2000. Morphological phylogenetics of termites (Isoptera). – *Biological Journal of the Linnean Society* **70**: 467–513.
- EDGERLY, J.S. 1997. Life beneath silk walls: a review of the primitively social Embiidina. Pp. 14–25 in: J.C. CHOE & B.J. CRESPI (eds.), *The Evolution of Social Behavior in Insects and Arachnids*. – Cambridge University Press.
- EGGLETON, P. 2001. Termites and trees: a review of recent advances in termites phylogenetics. – *Insectes Sociaux* **48**: 187–193.
- EHRMANN, R. 2002. Mantodea, Gottesanbeterinnen der Welt. – Natur und Tier-Verlag, Münster, Germany, 519 pp.
- FARRIS, S.M. & N.J. STRAUSFELD 2003. A unique mushroom body substructure common to basal cockroaches and to termites. – *Journal of Comparative Neurology* **456**: 305–320.
- FAUSTO, A.M., M.C. BELARDINELLI, J.M. TIerno DE FIGUEROA, R. FOCHETTI & M. MAZZINI 2003. Ultrastructural studies on Plecoptera spermatozoa: new data and comparative remarks. Pp. 431–436 in: M. GAINO (ed.), *Research Update on Ephemeroptera & Plecoptera*. – Perugia, Italy.
- GÄDE, G., P. GRANDCOLAS & R. KELLNER 1997. Structural data on hypertrehalosaemic neuropeptides from *Cryptocercus punctulatus* and *Therea petiveriana*: how do they fit into the phylogeny of cockroaches? – *Proceedings of the Royal Society London B* **264**: 763–768.
- GILES, E.T. 1963. The comparative external morphology and affinities of the Dermaptera. – *Transactions of the Royal Entomological Society London* **115**: 95–164.
- GOLOBOFF, P. 1993. Nona. Freeware available from www.zmuc.dk/public/phylogeny.
- GOLOBOFF, P.A., J. FARRIS & K. NIXON 2003. T.N.T.: Tree analysis using new technology. Program and documentation, available from the authors, and at www.zmuc.dk/public/phylogeny.
- GRANDCOLAS, P. 1994. Phylogenetic systematics of the subfamily Polyphaginae, with the assignment of *Cryptocercus* Scudder, 1862 to this taxon (Blattaria, Blaberoidea, Polyphaginae). – *Systematic Entomology* **19**: 145–158.
- GRANDCOLAS, P. 1996. The phylogeny of cockroach families: a cladistic appraisal of morpho-anatomical data. – *Canadian Journal of Zoology* **74**: 508–527.
- GRANDCOLAS, P. 1997a. Systématique phylogénétique de la sous-famille des Tryonicinae (Dictyoptera, Blattaria, Blattidae). In: J. NAIT & L. MATILE (eds.): *Zoologia Neocaledonica* vol. 4. – Mémoires du Muséum National d'Histoire Naturelle Paris **171**: 91–124.
- GRANDCOLAS, P. 1997b. What did the ancestors of the woodroach *Cryptocercus* look like? A phylogenetic study of the origin of subsociality in the subfamily Polyphaginae (Dictyoptera, Blattaria). In: P. GRANDCOLAS (ed.): *The origin of biodiversity in insects: phylogenetic tests of evolutionary scenarios*. – Mémoires du Muséum National d'Histoire Naturelle Paris **173**: 231–252.
- GRANDCOLAS, P. 1999a. Systematics, endosymbiosis, and biogeography of *Cryptocercus clevelandi* and *C. punctulatus* (Blattaria: Polyphaginae) from North America: a phylogenetic perspective. – *Annals of the Entomological Society of America* **92**: 285–291.
- GRANDCOLAS, P. 1999b. Reconstructing the past of *Cryptocercus* (Blattaria: Polyphaginae): phylogenetic histories and stories. – *Annals of the Entomological Society of America* **92**: 303–307.
- GRANDCOLAS, P. & P. DELEPORTE 1992. La position systématique de *Cryptocercus* Scudder au sein des Blattes et ses implications évolutives. – *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, serie D* **315**: 317–322.
- GRANDCOLAS, P. & P. DELEPORTE 1996. The origin of protistan symbionts in termites and cockroaches: a phylogenetic perspective. – *Cladistics* **12**: 93–98.
- GRANDCOLAS, P. & C. D'HAESE 2001. The phylogeny of cockroach families: is the current molecular hypothesis robust? – *Cladistics* **17**: 48–55.
- GRANDCOLAS, P., X. BELLÉS, M.-D. PIULACHS & C. D'HAESE 2002. Le genre *Lauraesilpha* Grandcolas 1997: Nouvelles espèces, endémisme, séquences d'ARN ribosomique et caractères d'appartenance aux Blattidae (Insectes, Dictyoptères, Blattidae, Tryonicinae). In: J. NAIT & P. GRANDCOLAS (eds.): *Zoologia Neocaledonica* vol. 5. – Mémoires du Muséum National d'Histoire Naturelle Paris **187**: 117–131.
- GRIMALDI, D. 1997. A fossil mantis (Insecta: Mantodea) in Cretaceous amber of New Jersey, with comments on the early history of the Dictyoptera. – *American Museum Novitates* No. **3204**, 11 pp.
- GRIMALDI, D. 2003. A revision of Cretaceous mantises and their relationships, including new taxa (Insecta: Dictyoptera: Mantodea). – *American Museum Novitates* No. **3412**, 47 pp.
- GÜNTHER, K. & K. HERTER 1974. 11. Ordnung Dermaptera (Ohrwürmer). Pp. 1–158 in: J.G. HELMCKE, D. STARCK & H. WERMUTH (eds.), *Handbuch der Zoologie* 4 (2) 2/11. – De Gruyter, Berlin.
- GUPTA, P.D. 1948. On the structure, development and homology of the female reproductive organs in orthopteroid insects. – *Indian Journal of Entomology* **10**: 75–123.
- GURNEY, A.B. 1938. A synopsis of the order Zoraptera, with notes on the biology of *Zorotypus hubbardi* Caudell. – *Proceedings of the Entomological Society of Washington* **40**: 57–87.
- HAAS, F. & J. KUKALOVÁ-PECK 2001. Dermaptera hindwing structure and folding: new evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). – *European Journal of Entomology* **98**: 445–509.
- HENNIG, W. 1981. *Insect phylogeny*. – Wiley Interscience Publication, John Wiley & Sons, Chichester etc.

- HONIGBERG, B.M. 1969. Protozoa associated with termites and their role in digestion. Pp. 1–36 in: K. KRISHNA & F.M. WEESNER (eds.), The biology of termites vol. 2. – Academic Press, New York.
- HUDSON, G.B. 1945. A study of the tentorium in some orthopteroid Hexapoda. – Journal of the Entomological Society of South Africa 8: 71–90.
- HUDSON, G.B. 1947. Studies in the comparative anatomy and systematic importance of the hexapod tentorium. II. Dermaptera, Embioptera, and Isoptera. – Journal of the Entomological Society of South Africa 9: 99–108.
- HURST, G.D.D., T.C. HAMMARTON, C. BANDI, T.M.O. MAJERUS, D. BERTRAND & M.E.N. MAJERUS 1997. The male-killing agent of the ladybird beetle *Coleomegilla maculata* is related to *Blattabacterium*, the beneficial symbiont of cockroaches. – Genetic Research 70: 1–6.
- ILLIES, J. 1955. 43. Teil Steinfliegen oder Plecoptera. In: M. DAHL & H. BISCHOFF (eds.), Die Tierwelt Deutschlands und der angrenzenden Meeressteile. – Gustav Fischer, Jena, 150 pp.
- IMMS, A.D. 1919. On the structure and biology of *Archotermopsis*, together with descriptions of new species of intestinal protozoa, and general observations of the Isoptera. – Philosophical Transactions of the Royal Society of London 209: 75–180.
- INOUE, T., O. KITADE, T. YOSHIMURA & I. YAMAOKA 2000. Symbiotic associations with protists. Pp. 275–288 in: T. ABE, D.E. BIGNELL & M. HIGASHI (eds.), Termites: Evolution, Eusociality, Symbioses, Ecology. – Kluwer Academic Publishers, Dordrecht, The Netherlands.
- JAMIESON, B.G.M., R. DALLAI & B.A. AFZELIUS 1999. Insects: their Spermatozoa and Phylogeny. – Science Publishers, Enfield, New Hampshire, 555 pp.
- JUDD, W.W. 1948. A comparative study of the proventriculus of orthopteroid insects with reference to its use in taxonomy. – Canadian Journal of Research (D) 26: 93–161.
- KAMBHAMPATI, S. 1995. A phylogeny of cockroaches and related insects based on DNA sequence of mitochondrial ribosomal RNA genes. – Proceedings of the National Academy of Sciences of the United States of America 92: 2017–2020.
- KAMBHAMPATI, S. 1996. Phylogenetic relationship among cockroach families inferred from mitochondrial 12S rRNA gene sequence. – Systematic Entomology 21: 89–98.
- KAMBHAMPATI, S., K.M. KJER & B.L. THORNE 1996. Phylogenetic relationship among termite families based on DNA sequence of mitochondrial 16S ribosomal RNA gene. – Insect Molecular Biology 5: 229–238.
- KEY, K.H.L. 1991. Phasmatodea (Stick-insects). Pp. 394–404 in: CSIRO (ed.), The Insects of Australia 2nd edn. – Melbourne University Press.
- KJER, K.M. 2004. Aligned 18S and insect phylogeny. – Systematic Biology 53: 506–514.
- KLASS, K.-D. 1995. Die Phylogenie der Dictyoptera. – Ph.D. Thesis, Munich University. Cuvillier, Göttingen, iii + 256 pp. + unpaginated plates.
- KLASS, K.-D. 1997. The external male genitalia and the phylogeny of Blattaria and Mantodea. – Bonner Zoologische Monographien 42: 1–341.
- KLASS, K.-D. 1998a. The ovipositor of Dictyoptera (Insecta): homology and ground-plan of the main elements. – Zoologischer Anzeiger 236: 69–101.
- KLASS, K.-D. 1998b. The proventriculus of the Dicondylia, with comments on evolution and phylogeny in Dictyoptera and Odonata (Insecta). – Zoologischer Anzeiger 237: 15–42.
- KLASS, K.-D. 1998c. Possible homologies in the proventriculi of Dicondylia (Hexapoda) and Malacostraca (Crustacea). – Zoologischer Anzeiger 237: 43–58.
- KLASS, K.-D. 1999. The pregenital abdomen of a mantid and a cockroach: musculature and nerve topography, with comparative remarks on other Neoptera (Insecta: Dictyoptera). – Deutsche Entomologische Zeitschrift 46: 3–42.
- KLASS, K.-D. 2000. The male abdomen of the relic termite *Mastotermes darwiniensis* (Insecta: Isoptera: Mastotermitidae). – Zoologischer Anzeiger 239: 231–262.
- KLASS, K.-D. 2001a. The female abdomen of the viviparous earwig *Hemimerus vosseleri* (Insecta: Dermaptera: Hemimeridae), with a discussion of the postgenital abdomen of Insecta. – Zoological Journal of the Linnean Society 131: 251–307.
- KLASS, K.-D. 2001b. Morphological evidence on blattarian phylogeny: “phylogenetic histories and stories” (Insecta, Dictyoptera). – Deutsche Entomologische Zeitschrift 48: 223–265.
- KLASS, K.-D. 2002. Mantophasmatodea: a new insect order? [Response to technical comment by Erich Tilgner] – Science 297: 731.
- KLASS, K.-D. 2003a. Relationships among the principal lineages of Dictyoptera inferred from morphological data. In: K.-D. KLASS (ed.), Proceedings of the 1st Dresden meeting on insect phylogeny: “Phylogenetic Relationships within the Insect Orders” (Dresden, September 19–21, 2003). – Entomologische Abhandlungen 61: 134–137.
- KLASS, K.-D. 2003b. The female genitalic region in basal earwigs (Insecta: Dermaptera: Pygidicranidae s.l.). – Entomologische Abhandlungen 61: 173–225.
- KLASS, K.-D. & R. EHRLMANN 2003. 13. Ordnung Mantodea, Fangschrecken, Gottesanbeterinnen. Pp. 182–197 in: H.H. DATHE & H.-E. GRUNER (eds.), Lehrbuch der Speziellen Zoologie, Band I: Wirbellose, 5. Teil: Insecta, 2nd edn. – Spektrum Akademischer Verlag, Heidelberg, Berlin.
- KLASS, K.-D. & N.P. KRISTENSEN 2001. The ground plan and affinities of hexapods: recent progress and open problems. In: T. DEUVE (ed.), Origin of the Hexapoda. – Annales de la Société d’Entomologie de France NS 37: 265–298.
- KLASS, K.-D., M.D. PICKER, J. DAMGAARD, S. VAN NOORT & K. TOJO 2003. The taxonomy, genitalic morphology, and phylogenetic relationships of southern African Mantophasmatodea. – Entomologische Abhandlungen 61: 3–67.
- KLASS, K.-D., B.L. THORNE & M. LENZ 2000. The male post-abdomen of *Stolotermes*: termites with unusually well-developed external genitalia (Dictyoptera: Isoptera: Stolotermitinae). – Acta Zoologica 81: 121–130.
- KLASS, K.-D., O. ZOMPRO, N.P. KRISTENSEN & J. ADIS 2002. Mantophasmatodea: a new insect order with extant members in the Afrotropics. – Science 296: 1456–1459.
- KRISTENSEN, N.P. 1991. Phylogeny of extant hexapods. Pp. 125–140 in: CSIRO (ed.), The Insects of Australia, 2nd edn. – Melbourne University Press.
- KRISTENSEN, N.P. 1995. Forty years’ insect phylogenetic systematics. – Zoologische Beiträge NF 36: 83–124.
- KUKALOVÁ-PECK, J. 1991. Fossil history and the evolution of hexapod structures. Pp. 141–179 in: CSIRO (ed.), The Insects of Australia, 2nd edn. – Melbourne University Press.
- KUKALOVÁ-PECK, J. & S.B. PECK 1993. Zoraptera wing structures: evidence for new genera and relationship with the blattoid orders (Insecta: Blattoneoptera). – Systematic Entomology 18: 333–350.
- KUKALOVÁ-PECK, J. & J.F. LAWRENCE 2004. Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hindwing characters. – European Journal of Entomology 101: 95–144.
- LAGRECA, M. 1954. Sulla struttura morfologica dell’apparato copulatore dei Mantodei. – Annali dell’Istituto Superiore di Scienze e Lettere di Santa Chiara, Napoli 1953/54: 1–28.
- LEBRUN, D. & A. LEQUET 1983. Etude structurale en microscopie électronique à balayage du proventricule ou gésier des espèces françaises de termites. – Bulletin de la Société des Sciences Naturelles de l’Ouest de la France N.S. 1: 1–11.
- LEBRUN, D. & A. LEQUET 1985. Relations entre le régime alimentaire et la structure du gésier des termites. – Bulletin de la Société des Sciences Naturelles de l’Ouest de la France N.S. 7: 126–139.
- LECONTE, O., J.-C. LEFEUVRE & P. RAZET 1967. Un nouveau critère taxonomique chez les blattes: l’insertion des tubes de Malpighi. – Comptes Rendus Acad. Sci. Paris Série D 265: 1397–1400.
- LO, N. 2003. Molecular phylogenetics of Dictyoptera: insights into the evolution of termite eusociality and bacterial endosymbiosis in cockroaches. In: K.-D. KLASS (ed.), Proceedings of the 1st Dresden meeting on insect phylogeny: “Phylogenetic Relationships within the Insect Orders” (Dresden, September 19–21, 2003). – Entomologische Abhandlungen 61: 137–138.
- LO, N., C. BANDI, H. WATANABE, C. NALEPA & T. BENINATI 2003. Evidence for coeladogenesis between diverse dictyopteran lineages and their intracellular endosymbionts. – Molecular Biology and Evolution 20: 907–913.

- LO, N., G. TOKUDA, H. WATANABE, H. ROSE, M. SLAYTOR, K. MAEKAWA, C. BANDI & H. NODA 2000. Evidence from multiple gene sequences indicates that termites evolved from wood-feeding cockroaches. – *Current Biology* **10**: 801–804.
- LORENC, W. 1939. Untersuchungen an Flagellaten aus dem Genus *Lophomonas*, I, II. – *Zoologica Poloniae* **3**: 225–250.
- LUCKOW, M. & A. BRUNEAU 1997. Circularity and independence in phylogenetic tests of ecological hypotheses. – *Cladistics* **13**: 145–151.
- LUYKX, P. 1983. XO:XX sex chromosomes and Robertsonian variation in the autosomes of the wood-roach *Cryptocercus punctulatus* (Dictyoptera: Blattaria: Cryptocercidae). – *Annals of the Entomological Society of America* **76**: 518–522.
- MACKERRAS, M.J. 1968. Australian Blattidae (Blattodea). IX. Revision of Polyzosteriinae tribe Methanini, Tryonicinae, and Blattinae. – *Australian Journal of Zoology* **16**: 511–575.
- MAEKAWA, K., O. KITADE & T. MATSUMOTO 1999. Molecular phylogeny of orthopteroid insects based on the mitochondrial cytochrome oxidase II gene. – *Zoological Science* **16**: 175–184.
- MAEKAWA, K. & T. MATSUMOTO 2000. Molecular phylogeny of cockroaches (Blattaria) based on mitochondrial COII gene sequences. – *Systematic Entomology* **25**: 511–519.
- MARKS, E.P. & F.A. LAWSON 1962. A comparative study of the dictyopteran ovipositor. – *Journal of Morphology* (Philadelphia) **111**: 139–171.
- MATZKE, D. & K.-D. KLASS 2005. Reproductive biology and nymphal development in the basal earwig *Tagalina papua* (Insecta: Dermaptera: Pygidicranidae), with a comparison of brood care in Dermaptera and Embioptera. – *Entomologische Abhandlungen* **62**: 99–116.
- McKITTRICK, F.A. 1964. Evolutionary studies of cockroaches. – *Memoirs of the Cornell University Agricultural Experiment Station* **389**: 1–197.
- McKITTRICK, F.A. 1965. A contribution to the understanding of cockroach-termite affinities. – *Annals of the Entomological Society of America* **58**: 18–22.
- McKITTRICK, F.A. & M.J. MACKERRAS 1965. Phyletic relationships within the Blattidae. – *Annals of the Entomological Society of America* **58**: 224–230.
- MILLER, H.K. & F.W. FISK 1971. Taxonomic implications of the comparative morphology of cockroach proventriculi. – *Annals of the Entomological Society of America* **64**: 671–687.
- MIURA, T., K. MAEKAWA, O. KITADE, T. ABE & T. MATSUMOTO 1998. Phylogenetic relationships among subfamilies in higher termites (Isoptera: Termitidae) based on mitochondrial COII gene sequences. – *Annals of the Entomological Society of America* **91**: 515–523.
- MIZUKUBO, T. & Y. HIRASHIMA 1987. Homology of male genital sclerites in cockroaches (Blattaria) by means of analysis of their association patterns. – *Journal of the Faculty of Agriculture, Kyushu University* **31**: 247–277.
- MÖHN, E. 1984. System und Phylogenie der Lebewesen vol. 1. – E. Schweizerbart'sche Verlagsbuchhandlung (Nägele & Obermiller), Stuttgart, xxxv + 834 pp.
- MORIYA, S., K. TANAKA, M. OHKUMA, S. SUGANO & T. KUDO 2001. Diversification of the microtubule system in the early stage of eukaryote evolution: elongation factor 1-alpha and alpha-tubulin protein phylogeny of termite symbiotic oxymonad and hypermastigote protists. – *Journal of Molecular Evolution* **52**: 6–16.
- MUKHA, D., B.M. WIEGMANN & C. SCHAL 2002. Evolution and phylogenetic information content of the ribosomal DNA repeat unit in the Blattodea (Insecta). – *Insect Biochemistry and Molecular Biology* **32**: 951–960.
- NALEPA, C.A. 1991. Ancestral transfer of symbionts between cockroaches and termites: an unlikely scenario. – *Proceedings of the Royal Society London B* **246**: 185–189.
- NALEPA, C.A. & C. BANDI 1999. Phylogenetic status, distribution, and biogeography of *Cryptocercus* (Dictyoptera: Cryptocercidae). – *Annals of the Entomological Society of America* **92**: 285–291.
- NALEPA, C.A. & W.J. BELL 1997. Postovulation parental investment and parental care in cockroaches. Pp. 26–51 in: J.C. CHOE (ed.), *The evolution of social behaviour in insects and arachnids*. – Cambridge University Press.
- NALEPA, C.A. & M. LENZ 2000. The ootheca of *Mastotermes darwiniensis* Froggatt (Isoptera: Mastotermitidae): homology with cockroach oothecae. – *Proceedings of the Royal Society London B* **267**: 1809–1813.
- NESBITT, H.H.J. 1941. A comparative morphological study of the nervous system of the Orthoptera and related orders. – *Annals of the Entomological Society of America* **34**: 51–81.
- NESBITT, H.H.J. 1956. Pp. 525–529 in: *Proceedings 10th International Congress of Entomology*.
- NIXON, K.C. 2002. Winclada (BETA) ver. 1.00.08. Published by the author, Ithaca, NY.
- NOIROT, C. 1995. The gut of termites (Isoptera). Comparative anatomy, systematics, phylogeny. I. Lower termites. – *Annales de la Société Entomologique de France N.S.* **31**: 197–226.
- NUTTING, W.L. 1951. A comparative anatomical study of the heart and accessory structures of the orthopteroid insects. – *Journal of Morphology* (Philadelphia) **89**: 501–597.
- PARKER, S.P. (ed.) 1982. *Synopsis and classification of living organisms* vol. 1. – McGraw-Hill, New York etc.
- PELLENS, R., P. GRANDCOLAS & I. DOMINGOS DE SILVA-NETO 2002. A new and independently evolved case of xylophagy and the presence of intestinal flagellates in the cockroach *Parasphaeria boleiriana* (Dictyoptera, Blaberidae, Zetoborinae) from the remnants of the Brazilian Atlantic forest. – *Canadian Journal of Zoology* **80**: 350–359.
- POPHAM, E.J. 1965. The functional morphology of the reproductive organs of the Common Earwig (*Forficula auricularia* L.) and other Dermaptera with reference to the natural classification of the order. – *Journal of Zoology* **146**: 1–43.
- PRADL, W.-D. 1971. Heft 14b, *Blaberus giganteus*. In: *Grosses Zoologisches Praktikum*. – Gustav Fischer Verlag, Stuttgart (Germany), 48 pp.
- PRINCIS, K. 1962–71. Blattariae. In: M. BEIER (ed.), *Orthopterorum Catalogus*, partes 3, 4, 6, 7, 8, 11, 13, 14. – Dr. W. Junk, 's-Gravenhage.
- RAGGE, D.R. 1955. The wing-venation of the Orthoptera Saltatoria with notes on dictyopteran wing-venation. – *Trustees of the British Museum*, 159 pp.
- REHN, J.W.H. 1951. Classification of the Blattaria as indicated by their wings (Orthoptera). – *Memoirs of the American Entomological Society* **14**: 1–134 + unpaginated plates.
- ROONWAL, M.L. 1955. External genitalia of termites (Isoptera). – *Journal of the Zoological Society of India* **7**: 107–114.
- ROONWAL, M.L. 1970. Isoptera. Pp. 41–46 in: S.L. TUXEN (ed.), *Taxonomist's Glossary of Genitalia in Insects*, 2nd edn. – Munksgaard, Copenhagen.
- ROONWAL, M.L. & N.S. RATHORE 1983. Wing-microsculpturing in the small house cockroach, *Supella longipalpa* (Dictyoptera, Blattidae). – *Proceedings of the Indian Academy of Sciences (Animal Sciences)* **92**: 333–342.
- ROSATI, F. 1967. Lo spermatozoo degli artropodi. II. *Blaberus craniifer* (Insecta Blattoidea). – *Bolletino di Zoologia* **34**: 167.
- ROSS, E.S. 2000. EMBIA: contributions to the biosystematics of the insect order Embiidina, part 1. – *Occasional Papers of the California Academy of Sciences* **149**: 1–53.
- ROTH, L.M. 1967. The evolutionary significance of rotation of the ootheca in the Blattaria. – *Psyche* **74**: 85–103.
- ROTH, L.M. 1968. Oöthecae of the Blattaria. – *Annals of the Entomological Society of America* **61**: 83–111.
- ROTH, L.M. 1970. Evolution and taxonomic significance of reproduction in Blattaria. – *Annual Review of Entomology* **15**: 75–96.
- ROTH, L.M. 1982. Introduction. Pp. 1–14 in: W.J. BELL & K.G. ADIYODI (eds.), *The American Cockroach*. – Chapman & Hall, London, New York.
- ROTH, L.M. 1987. The genus *Tryonicus* Shaw from Australia and New Caledonia (Dictyoptera: Blattaria: Blattidae: Tryonicinae). – *Memoirs of the Queensland Museum* **25**: 151–167.
- ROTH, L.M. 1995. *Pseudoanaplectinia yumotoi*, a new ovoviviparous myrmecophilous cockroach genus and species from Sarawak (Blattaria: Blattellidae: Blattellinae). – *Psyche* **102**: 79–87.
- ROTH, L.M. 1997. *Pseudobalta*, a new Australian ovoviviparous cockroach genus (Dictyoptera: Blattaria: Blattellidae: Pseudophyllodromiinae). – *Australian Journal of Entomology* **36**: 101–108.

- ROUSSET, A. 1973. Squelette et musculature des régions génitales et postgénitales de la femelle de *Thermobia domestica* (Packard). Comparaison avec la région génitale de *Nicoletia* sp. (Insecta: Apterygota: Lepismatida). – International Journal of Insect Morphology and Embryology 2: 55–80.
- ROY, R. 1999. Morphology and taxonomy. Pp. 19–40 in: F.R. PRETE, H. WELLS, P.H. WELLS & L.E. HURD (eds.), The Praying Mantids. – Johns Hopkins University Press, Baltimore.
- SACCHI, L., C.A. NALEPA, E. BIGLIARDI, S. CORONA, A. GRIGOLO, U. LAUDANI & C. BANDI 1998a. Ultrastructural studies of the fat body and bacterial endosymbionts of *Cryptocercus punctulatus* Scudder (Blattaria: Cryptocercidae). – Symbiosis 25: 251–269.
- SACCHI, L., C.A. NALEPA, E. BIGLIARDI, M. LENZ, C. BANDI, S. CORONA, A. GRIGOLO, S. LAMBIASE & U. LAUDANI 1998b. Some aspects of intracellular symbiosis during embryo development of *Mastotermes darwiniensis* (Isoptera: Mastotermitidae). – Parassitologia 40: 309–316.
- SACCHI, L., C.A. NALEPA, M. LENZ, C. BANDI, S. CORONA, A. GRIGOLO & E. BIGLIARDI 2000. Transovarial transmission of symbiotic bacteria in *Mastotermes darwiniensis* (Isoptera: Mastotermitidae): ultrastructural aspects and phylogenetic implications. – Annals of the Entomological Society of America 93: 1308–1313.
- SMART, J. 1952. The wing-venation of the American cockroach, *Periplaneta americana* Linn. (Insecta: Blattidae). – Proceedings of the Zoological Society of London 121: 501–509.
- SMART, J. 1956. On the wing-venation of *Chaeteessa* and other mantids (Insecta: Mantodea). – Proceedings of the Zoological Society of London 127: 545–553, plate 1.
- SNODGRASS, R.E. 1929. The thoracic mechanism of a grasshopper, and its antecedents. – Smithsonian Miscellaneous Collections 82(2): 1–111.
- SNODGRASS, R.E. 1935. The abdominal mechanisms of a grasshopper. – Smithsonian Miscellaneous Collections 94(6): 1–89.
- SORENSEN, M.D. 1999. TreeRot, version 2. Boston University, Boston, MA.
- SVENSON, G. & M. WHITING 2004. Phylogeny of Mantodea based on molecular data: evolution of a charismatic predator. – Systematic Entomology 29: 359–370.
- SWOFFORD, D.L. 2004. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.
- TERRY, M.D. & WHITING, M.F. 2005. Mantophasmatodea and the phylogeny of the lower neopterous insects. – Cladistics 21: 240–257.
- THOMPSON, G.J., L.R. MILLER, M. LENZ & R.H. CROZIER 2000. Phylogenetic analysis and trait evolution in Australian lineages of drywood termites (Isoptera, Kalotermitidae). – Molecular Phylogenetics and Evolution 17: 419–429.
- THORNE, B.L. 1990. A case for ancestral transfer of symbionts between cockroaches and termites. – Proceedings of the Royal Society London B 241: 37–41.
- THORNE, B.L. 1991. Ancestral transfer of symbionts between cockroaches and termites: an alternative hypothesis. – Proceedings of the Royal Society London B 246: 191–195.
- THORNE, B.L. & J.M. CARPENTER 1992. Phylogeny of the Dictyoptera. – Systematic Entomology 17: 253–268.
- TILGNER, E.H. 2002. Mantophasmatodea: a new insect order? [Technical comment]. – Science 297: 731.
- TILGNER, E.H., T.G. KISELYOVA & J.V. MCHUGH 1999. A morphological study of *Timema cristinae* Vickery with implications for the phylogenetics of Phasmida. – Deutsche Entomologische Zeitschrift 46: 149–162.
- VISSCHER, S.N., M. FRANCIS, P. MARTINSON & S. BARIL 1982. Laboratory studies on *Grylloblatta campodeiformis* Walker. Pp. 61–70 in: H. ANDO (ed.), Biology of the Notoptera. – Kashiyo-insatsu Co. Ltd, Nishiwada (Japan).
- VRŠANSKÝ, P. 2002. Origin and the early evolution of Mantises. – AMBA Projekt 6(1): 1–16.
- WALKER, E.M. 1931. On the anatomy of *Grylloblatta campodeiformis* Walker - 1. Exoskeleton and musculature of the head. – Annals of the Entomological Society of America 24: 519–536.
- WALKER, E.M. 1933. On the anatomy of *Grylloblatta campodeiformis* Walker - 2. Comparisons of head with those of other orthopteroid insects. – Annals of the Entomological Society of America 26: 309–344.
- WALKER, E.M. 1938. On the anatomy of *Grylloblatta campodeiformis* Walker - 3. Exoskeleton and musculature of the neck and thorax. – Annals of the Entomological Society of America 31: 588–640.
- WALKER, E.M. 1943. On the anatomy of *Grylloblatta campodeiformis* Walker - 4. Exoskeleton and musculature of the abdomen. – Annals of the Entomological Society of America 36: 681–706.
- WALKER, E.M. 1949. On the anatomy of *Grylloblatta campodeiformis* Walker - 5. The organs of digestion. – Canadian Journal of Research 27: 309–344.
- WALL, M. 1971. Zur Geschlechtsbiologie der Termite *Kalotermea flavicollis* (Fabr.) (Isoptera). – Acta Tropica 28: 17–60.
- WEESNER, F.M. 1969. External anatomy. Pp. 19–47 in: K. KRISHNA & F.M. WEESNER (eds.), Biology of Termites vol. 1. – Academic Press, New York.
- WEIDNER, H. 1970. 14. Ordnung Isoptera (Termiten). Pp. 1–147 in: J.G. HELMCKE, D. STARCK & H. WERMUTH (eds.), Handbuch der Zoologie vol. 4 (2) 2/14. – De Gruyter, Berlin, New York.
- WHEELER, W.C., M. WHITING, Q.D. WHEELER & J.M. CARPENTER 2001. The phylogeny of the extant hexapod orders. – Cladistics 17: 113–169.
- WHITE, M.[J.D.] 1976. Blattodea, Mantodea, Isoptera, Grylloblattodea, Phasmatodea, Dermaptera and Embioptera. Animal Cytogenetics 3(2). – Gebrüder Borntraeger, Berlin, v + 75 pp.
- WHITING, M., J.C. CARPENTER, Q.D. WHEELER & W.C. WHEELER 1997. The Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. – Systematic Biology 46: 1–68.
- WIELAND, F. 2006. External morphology of the mantodean prothorax and its significance for relationships within the group (Insecta: Dictyoptera). – Entomologische Abhandlungen 63: 51–76.
- WILLMANN, R. 2003. Die phylogenetischen Beziehungen der Insecta: Offene Fragen und Probleme. – Verhandlungen Westdeutscher Entomologentag 2001: 1–64.
- YUASA, H. 1920. The anatomy of the head and mouth-parts of Orthoptera and Euplexoptera. – Journal of Morphology (Philadelphia) 33: 251–307.
- ZWICK, P. 1973. Insecta: Plecoptera. Phylogenetisches System und Katalog. Das Tierreich vol. 94. – De Gruyter, Berlin, New York, 465 pp.
- ZWICK, P. 1980. 7. Ordnung Plecoptera (Steinfliegen). Pp. 1–115 in: J.G. HELMCKE, D. STARCK & H. WERMUTH (eds.), Handbuch der Zoologie 4 (2) 2/7. – De Gruyter, Berlin.

8. Appendix: Character List

8.1. Characters of the male genitalia (phallomeres)

For a complete description of structures referred to in the characters and for topographic homologies ('alignment') see KLASS (1995, 1997). 'Left' and 'right' relate to the original orientation of the male genitalia and have to be exchanged in case of taxa with side-reversed genitalia. Numbers behind character states refer to the apomorphies listed in KLASS (1997: 293ff and 308ff); '!' behind the number indicates that homoplasy was therein assumed for an apomorphy; (00) indicates autapomorphies of terminal taxa and of Blattaria that were mentioned but not numbered in KLASS (1997); FK = figures in KLASS (1995, 1997; with identical numbering) showing the differences between the character states. The term 'articulation' is used in the sense of very close contacts between sclerites, which do not necessarily include differentiations of the sclerite margins (such as ball and socket).

Sclerotizations of left side of phallomeres

1 – Presence of sclerite L1; [0] present; [1] absent (109).

– L1 is characterized by its dorsal position, the anterior part forming the walls of a pouch ('pne'; Figs. 2A, 3A–G, I), by its muscle connections l2 and l3 with left-lateral L4-sclerotizations resp. anterior L2-sclerotizations (Fig. 2H), and by its vicinity to the phallomere gland orifice. In many taxa L1 further shows a close association with projections ('dca') behind it, the formation of a sclerite ring by its posterior part, and a hood-like shape of its anterior part (see characters 2, 3). *Supella* is scored ambiguous [-] because identification of L1 is uncertain; there is a sclerite in roughly the right position, but this lacks further L1-specifics, and muscle data are not available.

2 – Shape of sclerite region L1a; [0] level (24); [1] hood-shaped, at least weakly so, but lacking anterior plateau; [2] hood-shaped and with anterior plateau (46); additive. – The anterior part of sclerite L1 (L1a) is usually included in a pouch 'pne'. It is either a level tongue (FK 54, 67, 95, 107, 243), or hood-shaped because its lateral and anterior margins are upcurved (Fig. 3B; FK 32, 34, 45); the hood can have a flattened anterior face (plateau; Figs. 3D, F; FK 105, 118, 151). *Lamproblatta* is scored ambiguous [-] because L1a is essentially level but has a broad anterior apodeme that might represent an obliquely orientated plateau (Fig. 3G; FK 177, 178). The character is not applicable to taxa lacking L1.

3 – Presence of ring-formation in posterior part of sclerite L1; [0] absent; [1] present (34). – Many Blattaria have one or more projections 'dca' at the posterior end of sclerite L1, which are of varied shape and either membranous or sclerotized by L1 (Figs. 3C–G, I). Taxa are scored [0] if the posterior part of L1 is restricted to the dorsal base or flanks of the 'dca' (or the homologous area: Mantodea) or occupies the entire 'dca' but extends independently onto each of it (FK 54, 67, 68). Taxa are scored [1] if the posterior part of L1 includes a sclerotization that entirely or with only a short gap encircles the common base of all 'dca', i.e., if L1 extends to the ventral 'dca' base where its left and right parts meet (ventral part of L1 = sclerite region L1r); also with state [1] the 'dca' can be membranous or sclerotized (FK 94, 95, 105–108, 120, 121, 153, 154, 323). The character is not applicable to taxa lacking L1.

4 – Curvature of distal part of sclerite region L1m, which bears articulation A2; [0] L1m level and not entering dorsal wall of pouch 'lve'; [1] L1m curving ventrad into dorsal wall of pouch 'lve' (6). – The right posterior part of sclerite L1 (L1m) usually forms an articulation A2 with the right end of sclerite L2 (Figs. 2A, 3D; or with the dorsal left end of L2 if the right part of L2 is upcurved: many Blattaria, Figs. 3C, E, G; see character 44). L1m can be level or bend around an edge into the pouch 'lve' (where L2 is located) to articulate with L2. State [1] is not fully identical in the Mantodea and Blattaria concerned: in the former, L1m curves ventrad to meet L2 and to terminate in this point (e.g., FK 11, 26, 34); in the latter, L1 continues beyond articulation

A2 into regions L1r and L1l to form a ring (see character 3). The character is not applicable to taxa lacking articulation A2 (due to the lack of L1 or to a reduction of the right part of L2).

5 – Presence of partial or entire division of sclerite region L1m by membrane; [0] absent; [1] present (16).

– Most taxa have the entire articulation-bearing (A2) region L1m connected with the remainder of sclerite L1 (state [0]). In *Metallyticus* and *Sphodromantis* a stripe of membrane ('2' in Fig. 3A, FK 10, 25) separates the part of L1m near A2 partially resp. entirely from the rest of L1 (state [1]). *Lauraesilpha angusta* is scored [1] because its L1m-division (FK 323h) is in a position comparable to that in the respective Mantodea. The character is not applicable to taxa lacking sclerite L1.

6 – Length of articulation A2; [0] short; [1] moderately long, somewhat hinge-like; [2] very long, distinctly hinge-like (14 modified, 41); additive. – In most taxa the contact A2 between sclerites L1 and L2 is very short (Figs. 2A, 3C, D, G). In *Eurycotis*, *Periplaneta*, and *Deropeltis* L1 and L2 also have a short area of close contact but their margins are quite approximate (though not hinged) behind it (FK 67), and in *Metallyticus* and *Lauraesilpha* A2 is a moderately long hinge (FK 26, 107); both conditions are scored [1]. In *Sphodromantis* and *Tryonicus* A2 is a very long, discrete hinge (Fig. 3E; FK 11, 94). The character is not applicable to taxa lacking the contact A2. The presence of A2 is here not defined as a character because absence is either due to a reduction of the right part of L2 (in *Cryptocercus*) or to the lack of sclerite L1 (see character 1).

7 – Shape of sclerite L2; [0] arch-shaped, at least somewhat so; [1] ribbon- or plate-shaped due to fusion of legs of arch, sclerite regions L2p and L2m (8); [2] not arch-shaped due to reduction of sclerite region L2m (94); non-additive. – For differences see FK 324, 328. L2 in *Mantoida*, *Archiblatta*, and *Polyphaga* (see Figs. 2A, D, 3B–D) is a distinctly arch-shaped ribbon extending from the left-posterior process 'paa' (region L2d) along the left (L2p), anterior (L2a), and right (L2m) inner margins of the pouch 'lve' to the right-posterior articulation A2 (tip of L2m). The arch is less distinct in *Periplaneta* (legs of arch partly fused), *Tryonicus* (right-dorsal leg L2m curved anteriad), *Cryptocercus* (right-dorsal leg L2m vestigial and anterior part L2a of arch very broad), *Anaplecta*, and *Nahublattella* (arch-shape indicated in posterior part of L2 but dominated by tube-shape of 'lve'-apodeme of anterior part L2a). All these conditions are scored [0]. In *Chaeteessa*, *Metallyticus*, *Sphodromantis*, *Deropeltis*, and *Eurycotis* L2 is a longitudinal plate or ribbon because the two legs of the arch are fused. The loss of the arch-shape in the remaining Blattellidae and Blaberidae is due to the reduction of the right leg and to the extensive development of the 'lve'-apodeme of the anterior part L2a (Fig. 3J).

8 – Presence of division between sclerite region L2d (on process 'paa') and remainder of L2; [0] absent; [1] present, resulting in sclerites L2D and L2E, or L2A and L2C (roughly 83). – For differences see FK 324, 328, 329. L2d on process 'paa' (Figs. 2B, 3A–G) is usually

connected with the remainder of L2. Its separation from L2 in some Blattaria is probably not homologous in *Lamproblatta* and *Nahublattella*, since the region L4d is connected with the main part of L2 in the former, but with L2d in the latter (divisions A10 resp. A11 in FK 329f,g). The division in some other Blattellidae/Blaberidae and that in Blattinae cannot be identified as one of the two because L4d is absent resp. separated from all parts of L2. Thus, two non-homologous conditions are likely included in state [1]. The character is not applicable to *Archiblatta*, which has 'paa' desclerotized.

9 – Presence of division between sclerite regions L4l (on process 'pda') and L2d (on process 'paa'); [0] absent; [1] present (10, 20). – The sclerotizations of the processes 'pda' (posterior part of region L4l) and 'paa' (region L2d) are in many taxa connected (Figs. 2B, 3B, D, E, G; FK 209–214, 244) but separated in others (Fig. 3F; FK 10–12, 26, 66). *Chaeteessa* lacks 'pda', but the corresponding area can be identified and has a separate sclerotization from that of 'paa' (FK 34). *Ergaula* lacks 'paa', but the corresponding area has its sclerotization connected with that of 'pda'. Most Blattellidae and Blaberidae have only one process 'via' (Fig. 3J; FK 328); it is either 'paa', or 'pda', or 'paa+pda' (see character 47), but if a process has become lost, its corresponding area is likely included within 'via'; since there is no sclerite division on 'via', the sclerotizations of 'paa' and 'pda' are best considered connected. Still, conditions in these Blattellidae and Blaberidae are scored ambiguous [-]. The character is not applicable to *Archiblatta* with its desclerotized 'paa'.

10 – Presence of a stout sclerite ring or cylinder formed by the basal part of the common sclerotization of processes 'paa' and 'pda' (sclerite regions L4l and L2d); [0] absent; [1] present. – In some of the taxa having connected 'paa'- and 'pda'-sclerotizations the basal part of this sclerotization forms a stout ring (*Anaplecta*, FK 211–214), which can be extended into a cylinder that represents the base of a process 'via' ('pda' and 'paa' then being the tips of 'via'; *Nahublattella*, FK 244, 245). Most of the remaining Blattellidae and Blaberidae likely show the latter condition ('via' in Fig. 3J and FK 328) but are scored ambiguous [-] for reasons given in character 9.

11 – Presence of sclerite L3; [0] present; [1] absent (00). – L3, the sclerite of the hook 'hla' (Figs. 2C, 3C–J) is present in all Blattaria and absent in all Mantodea.

12 – Extension of the part of sclerite region L4l anterior to process 'pda' (or the area corresponding to 'pda') within dorsal wall of left complex; [0] L4l restricted to left margin; [1] L4l reaching at least middle part (3). – In *Mantoida*, Blattinae, and Polyzosteriinae L4l is restricted to the left margin of the dorsal wall (Figs. 2A, 3B, C), and region L4d projects from L4l farther to the right. In the other Blattaria the various sclerites of region L4l are restricted to the left dorsal wall; but conditions in most Blattellidae/Blaberidae are scored ambiguous [-] because the phallomere structure differs too strongly from the aforementioned taxa. In the remaining Mantodea the dorsal L4l extends far to the right (Fig. 3A; FK 23, 31); the location of muscle

insertions (l2, l4, l7) in *Sphodromantis* in the dorsal wall instead of the left edge of the left complex demonstrates that the expanded sclerotization is here L4l rather than L4d (FK 15, 49, 50, 325a,d); the same is assumed for *Chaeteessa* and *Metallyticus* (muscles not studied).

13 – Presence of a division of sclerite region L4l by articulation A1 ('pda' ventral; L4d, l2, l4 dorsal); [0] absent; [1] present, resulting in sclerites L4A and L4B (12). – For differences see FK 325, 329. In *Mantoida*, *Chaeteessa*, Blattinae, and Polyzosteriinae the left part of L4 (regions L4l+L4d) extends continuously from the anterior ventral wall of the left complex to its posterior left edge and dorsal wall (Figs. 2A, 3B, C); a single sclerite thus includes region L4d, process 'pda', and the insertions of muscles l2 and l4 (Fig. 2H, I). In the other taxa two different divisions occur in the left phallomere edge (characters 13, 14). In *Metallyticus* and *Sphodromantis* the dorsal and ventral parts are separated by articulation A1 (resulting sclerites L4A and L4B; Fig. 3A); here 'pda' is on the ventral sclerite, and L4d and both muscle insertions (not studied in *Metallyticus*) on the dorsal one. In most Blattaria the anteroventral and the posterodorsal parts are separated by articulation A5 (resulting sclerites L4K and L4N; FK 88, 97); here 'pda' and L4d are both on the posterodorsal sclerite, and both muscles on the anteroventral one.

14 – Presence of a division of sclerite region L4l by articulation or farther separation A5 (l2, l4 ventral; 'pda', L4d dorsal); [0] absent; [1] present (resulting in sclerites L4K and L4N), separation narrow (articulation) (27); [2] present (resulting sclerites L4K and L4N), separation far (37); additive. – For basic explanations see foregoing character. Of the taxa showing a division A5, only *Tryonicus* has L4K and L4N in close contact (hinge A5, FK 88); all others show a farther separation. In taxa that lack several of the criteria distinguishing divisions A1 and A5 (l2 and l4 not studied, L4d and 'pda' lacking), or show an additional division of sclerite L4K, share other specifics of the sclerites with some taxa showing a clear A5-division (e.g., insertion of muscle l10, see character 79); this still allows identifying division A5. The character is not applicable to *Parcoblatta*, which lacks sclerite L4U (a derivative of L4K, see Fig. 3J).

15 – Presence of right-anterior part of sclerite region L4l; [0] present; [1] absent (38). – In *Mantoida*, *Chaeteessa*, Blattinae, *Eurycotis*, and *Tryonicus* region L4l in the anterior ventral wall of the left complex extends far to the right, thus passing sclerite region L4n anteriorly (L4n bears the knob 'nla' if present, see character 58; Figs. 2B, C, 3B, C; FK 325c–g). The other taxa lack this right-anterior part of L4l; this is best seen comparing sclerite L4K in *Tryonicus* and *Anaplecta* (FK 325g,l), while in most of the remaining taxa the condition is less distinct through a more extensive reduction of L4n and the anterior parts of L4l. In *Sphodromantis* and *Metallyticus* conditions are scored ambiguous [-] because of the uniform sclerotization of the ventral wall (see character 22).

16 – Location of left-anterior part of sclerite region L4l in relation to base of hook 'hla'; [0] dorsal to 'hla'-base

and/or in dorsal part of 'hla'-base; [1] in posteroventral part of 'hla'-base (57). – The character is not applicable to taxa lacking 'hla' or having the base of 'hla' at the posterior edge of the left complex (see characters 51, 52). In the assessable taxa the mentioned part of region L4l either passes the 'hla'-base left-dorsally (Figs. 2B, C, 3C; FK 53, 54, 65, 66, 97, 98), or there is a discrete sclerite L4K that comprises this part of L4l and lies (antero-) dorsal to the 'hla'-base and partly extends into it (Figs. 3F, G; FK 151, 177, 178). In *Polyphaga* sclerite L4K lies posteroventrally in the 'hla'-base, and in *Ergaula* it lies in the ventral 'hla'-base and is additionally fused with the 'hla'-sclerite L3 (L4K is here identified by the insertions of muscles l4 and l11; FK 122, 124, 132, 326, 327).

17 – Presence of sclerite region L4n (= sclerotization of and around process 'nla'); [0] present; [1] absent (42). – For the sclerotization in question see *Tryonicus*, L4n in FK 98, 325g. This sclerotization is present in most Mantodea and Blattaria but absent in *Mantoida* and several Blattaria. The character is ambiguous in the Blattellidae and Blaberidae that have a sclerite L4V within their tendon 'ate' (L4V might represent L4n; FK 289, 291). For *Polyphaga*, *Ergaula*, *Lamproblatta*, and especially *Cryptocercus*, KLASS (1997) indicated that vestiges of L4n might be included in sclerite L4K (FK 325h–k); in this case at least a strong reduction of L4n has to be assumed for these taxa.

18 – Presence and distinctness of sclerite region L4d; [0] present and distinct in outline from sclerite region L4l; [1] not distinct in outline from sclerite region L4l, and possibly absent (4, 95). – In *Mantoida* and Blattinae region L4l bears a distinct rightward-directed dorsal extension L4d; L4d is somewhat less distinct in *Eurycotis*, and distinct but more anteriad-directed in *Tryonicus* (Figs. 3B, C, E; FK 325d–g). As identified by its position relative to processes 'paa' and 'pda' and certain muscle insertions (l1, l10, l11; all confined to part of the taxa) a ribbon-shaped L4d-extension was also found in some other taxa. In most Mantodea and Blattellidae + Blaberidae, however, no such sclerotization was found (state [1]); it is either absent or integrated into sclerites of region L4l (FK 325, 328).

19 – Direction of sclerite region L4d; [0] directed rightward or right-anteriad; [1] directed leftward, left-anteriad, dorsad, or posteriad (39). – In *Mantoida*, Blattinae, *Eurycotis*, and *Tryonicus* the direction of L4d from its base on region L4l varies from rightward to (right)anteriad. In *Polyphaga*, *Ergaula*, and *Cryptocercus* L4d is directed left(anteriad) (FK 118, 150). Conditions in *Lamproblatta* (dorsad) and *Nahublattella* (posteriad) are most parsimoniously derived from that in the latter taxa and are thus assigned to the same state [1]: In *Lamproblatta* the area containing L4d has rotated 90° towards the dorsal side (FK 178), and in *Nahublattella* the entire area bearing processes 'pda' and 'paa' and L4d has become invaginated (FK 242, 244). The character is not applicable to taxa lacking a distinct L4d.

20 – Presence of sclerite region L4v; [0] present; [1] absent (85). – The ventral lobe 'vla' (= ventral phallomere) usually has an extensive ventral sclerotization all or most

of which is constituted by region L4v (FK 6, 20, 28, 41, 63, 87, 115, 148, 174, 205, 325a–l). With the exception of *Anaplecta* such a sclerotization is absent in Blattellidae and Blaberidae (with a strongly reduced lobe 'vla', see character 59; FK 239a, 266, 297a, 325m–o). It is unlikely that sclerite L10 of some Blaberidae (see character 26) is a remainder of L4v (these taxa are here scored [1]).

21 – Presence of a separation of sclerite region L4v from sclerite regions L4l and L4c; [0] absent; [1] present (resulting sclerites that include L4v: L4G, or L4M, or L4R). – In *Mantoida* and probably in *Chaeteessa* the sclerotization L4v in the right ventral wall of the left complex continues anteriorly into L4l (possibly via a short region L4c; Fig. 3B; FK 325c,d). In all Blattaria having region L4v this is separated from L4l (and from L4c when present: Blattinae and *Eurycotis*, see character 23); L4v then constitutes sclerite L4G or, if minor additional sclerotizations (regions L4a, L4x) are also present and integrated into the same plate, sclerites L4R or L4M (Fig. 3C; FK 325e–l). The character is not applicable to taxa lacking L4v, and it is scored ambiguous [-] in the Mantodea that have the entire ventral wall continuously sclerotized (see character 22).

22 – Presence and degree of sclerotization of sclerite region L4b, which occupies the ventral wall between sclerite regions L4l, L4v, L4c, and L4n; [0] absent; [1] present and weaker than surrounding L4-sclerotizations (1); [2] present and as heavy as surrounding L4-sclerotizations (13); additive. – In the ventral wall of the left complex the primary L4-regions L4l, L4n, L4c, and L4v usually form individual sclerites, with the exception of some narrow interconnections (e.g., FK 41, 63, 87, 205). However, in most Mantodea most of the ventral wall is continuously sclerotized (including the L4l-sclerotization of process 'pda'). In *Chaeteessa* the primary L4-regions are heavier than the sclerotization in between, and a sclerotization L4b filling all interspaces has thus probably been added (FK 28). Only in *Metallyticus* and *Sphodromantis* the ventral sclerotization, which likely includes parts corresponding to L4b in *Chaeteessa*, is uniformly heavy (FK 6, 20). *Polyphaga* and *Ergaula* show state [0]: the left-ventral sclerotization (regions L4v+L4a+L4x) is strongly expanded over most of the ventral wall, but is separate from the L4l-sclerotizations (of, e.g., 'pda'; FK 115, 118–123, 325k).

23 – Presence of sclerite L4F; [0] absent; [1] present, including vestigial conditions (21). – Only Blattinae and Polyzosteriinae have a peculiar sclerite L4F in the mid-posterior ventral wall of the left complex (FK 57, 63, 68; posterior part of region L4c in FK 325e,f).

24 – Presence of sclerite L7; [0] absent; [1] present (49). – Only *Lamproblatta*, *Polyphaga*, and *Ergaula* have a sclerite L7 in the leftmost part of the ventral lobe 'vla' (= ventral phallomere; Fig. 3D, G; FK 115, 174, 322k,l,m).

25 – Presence of sclerite L8; [0] absent; [1] present (48). – Only *Lamproblatta*, *Polyphaga*, and *Ergaula* have in the dorsal wall of the left complex a sclerite L8, which lies right-dorsal to the pouch 'pne' and bears or is closely adjacent to the insertions of muscles 19 (intrinsic in dorsal wall of left complex), 112 (to right part of pouch

‘lve’), and b2 (to contact area between sclerites R2 and R3 of right phallomere) (Fig. 3D, G; FK 127–129, 170, 184–186).

26 – Presence of sclerite or sclerite patches L10; [0] absent; [1] present (00). – In many Blaberidae the ventral lobe ‘vla’ bears distally small sclerite patches or a larger sclerite, which constitute L10 (Fig. 3J; FK 291, 297, 299).

Sclerotizations of right side of phallomeres

27 – Presence of a division between sclerite regions R1t and R1c; [0] absent (121); [1] present, resulting in sclerites R1D and R1E, or R1D and R1C, or R1P and R1S (the terms depend on whether the resulting sclerites are connected with surrounding sclerites or not; 114, 123). – The principal sclerite R1 has four regions, which show certain characteristics (Fig. 2D, E, J). For instance, R1c bears the right r3-insertion and articulation A3 with sclerite R3; R1t bears a toothed ridge ‘pva’ and is located on the right-dorsal flanks of the bulge ‘cbe’ and the r2-insertion; R1v is located posteroventrally (often on a ventral tooth, ‘pia’) and bears the left r3-insertion; R1d is located posterodorsally and bears the posterior r1-insertion. Due to different divisions and fusions R1 varies strongly throughout the Mantodea and Blattaria in its composition of discrete sclerites (FK 330). Region R1t is usually synsclerotic with R1c (Fig. 2E), but it is separate from it in *Mantoida*, *Metallyticus*, and some Blattellidae (FK 20, 41, 281, 319, 330b,d,o,q,r).

28 – Presence of a division within sclerite region R1c dorsal to articulation A3; [0] absent; [1] present, resulting in sclerites R1A and R1B, or R1A and R1C (11). – While region R1c is usually undivided, in most Mantodea a membranous line (called ‘4’ in FK 6, 20, 28) divides R1c into a dorsal and a ventral part, the latter bearing articulation A3.

29 – Presence of a broad connection between sclerite regions R1d and R1v posterior to membrane ‘17’ or corresponding area; [0] absent; [1] present, resulting in sclerite R1J and more derived sclerites (32). – Behind region R1c there is a membrane (labeled ‘17’ in Fig. 2D, E) that extends along the right and posterior edges of the right phallomere. The dorsal and ventral regions R1d and R1v of R1 are in Mantodea fully separated by this membrane. In Blattinae and Polyzosteriinae R1d and R1v are connected by (at most) a narrow sclerite bridge behind membrane ‘17’ (at the posterior edge of the right phallomere), while in the other Blattaria R1d and R1v are here broadly confluent (FK 330).

30 – Presence of a connection between sclerite region R1c on the one hand and R1d and R1v on the other, and presence of articulations A8 and A9 and membrane ‘17’; [0] R1c with separate connections to R1d and R1v, articulations A8 and A9 absent, membrane ‘17’ present; [1] R1c separate from R1d and R1v, articulations A8 and A9 and membrane ‘17’ present (139); [2] R1c connected along continuous line with R1d and R1v (resulting in sclerite R1M or R1N), articulations A8 and A9 and

membrane ‘17’ absent (63, 74, 128); non-additive. – In many Blattaria sclerite region R1c is fully separate from regions R1v and R1d, and it forms with region R1t a discrete sclerite R1F. The separation is narrow at the dorsal and ventral corners of R1c, where R1c is distinctly articulated upon R1d (articulation A8) resp. R1v (articulation A9). Behind the part of R1c that lies between the articulations, an extensive membrane ‘17’ occupies the right wall of the right phallomere (FK 190, 194). This configuration (state [0]) allows the posterior part of the right phallomere to rock upon the anterior part, and both parts together work as a clasper. This condition is also found in some of the taxa that have R1v and R1d fused to form a sclerite R1J (*Cryptocercus*, *Lamproblatta*, *Tryonicus*; see character 29). In the Mantodea, instead of articulating upon regions R1d and R1v, region R1c is connected with R1d dorsally and with R1v ventrally. Behind the part of R1c in between these connections a more or less extensive membrane ‘17’ occupies the right phallomere wall as in the aforementioned Blattaria (FK 17). This configuration is comprised as state [1]. In *Polyphaga*, *Ergaula*, Blattellidae, and Blaberidae the hind margin of region R1c is entirely confluent with the (fused) regions R1v and R1d – at its dorsal and ventral corners as well as in the area in between, and thus across the areas that form the articulations A8 and A9 and the membrane ‘17’ in (part of) the other taxa (FK 226, 229). This configuration, which lacks a membrane ‘17’, is comprised as state [2]. (See also FK 330 for this character; note that in Mantodea R1c itself can be subdivided, see character 28.)

31 – Extension of sclerite region R1t in ventral wall of lobe ‘fda’ to the posterior and presence of its connection with sclerite region R1v; [0] R1t restricted to anterior part of ventral wall of ‘fda’ and separate from R1v; [1] R1t extending to the far posterior ventral wall of ‘fda’ and connected with R1v (part of 63). – R1t is in most taxa confined to the anteriormost ventral wall of the dorsal lobe ‘fda’ (= right-dorsal wall of invagination ‘cbe’; Fig. 2D, E; FK 25, 99, 160, 226), though it can extend far anteriad into invagination ‘cbe’ (FK 74, 75; see character 32), and is separated from R1v or connected with it only via R1c. Only in *Polyphaga* and *Ergaula* R1t extends far backward and is fully confluent with region R1v (FK 134, 330). Conditions in some Blattellidae and Blaberidae are too aberrant for assessing this character and are scored ambiguous [-].

32 – Extension of sclerite region R1t within invagination ‘cbe’; [0] R1t confined to right-dorsal wall of ‘cbe’; [1] R1t including right-dorsal and anterior walls of ‘cbe’. – A far ventral extension of R1t over the top of ‘cbe’ is peculiar to Blattinae and Polyzosteriinae (FK 74, 75 of *Eurycotis*, more distinct in the Blattinae; compare FK 160, 226). Conditions in *Parcoblatta* (FK 281) and Mantodea are too aberrant for assessing this character and are scored ambiguous [-].

33 – Presence of sclerite R2; [0] present; [1] absent (00). – R2 (Fig. 2D) is present in all Blattaria but absent in all Mantodea (compare FK 13, 24, 31, 44 and FK 75, 100, 135, 161, 227).

34 – Extension of sclerite R2 within invagination ‘cbe’ and presence of connection of R2 with sclerite region R1t (and of articulation A6); [0] R2 confined to left-ventral base and wall of ‘cbe’, either separated from R1t (then articulation A6 distinct), or broadly connected with R1t (but not at its left-dorsal tip) due to an extension of R1t over the top of ‘cbe’ (then articulation A6 indistinct); [1] R2 confined to left-ventral base and wall of ‘cbe’, its left-dorsal tip connected with the left-dorsal tip of R1t (articulation A6 absent due to fusion), R1t not extending over top of ‘cbe’ (112); [2] R2 including left-ventral and anterior walls of ‘cbe’, broadly connected with main body of R1t (articulation A6 obliterate due to a farther separation between the left-dorsal tips of R2 and R1t) (66); non-additive. – In most Blattaria R2 is (as in Fig. 2D) confined to the area left-ventral to ‘cbe’ and is not synsclerotic with R1t, and its left-dorsal tip articulates with R1t in A6 (state [0]; this includes conditions in *Archiblatta*, where R2 is synsclerotic with R1t as a consequence of the extension of R1t over the top of ‘cbe’, see character 32). In *Polyphaga* and *Ergaula*, however, R2 extends onto the top of ‘cbe’, where it is fused with R1t (state [2]). In Blaberidae and many Blattellidae R2 is fused to R1t in the former articulation A6 (state [1], see FK 330). The character is not applicable to Mantodea because they lack R2.

35 – Presence of connection between sclerites R2 and R3 (and of articulation A7); [0] connection absent (articulation A7 or a wider separation between R2 and R3 thus present); [1] connection present, either firm or with weakly sclerotized border line (articulation A7 thus absent) (62). – While R2 and R3 are separated in most Blattaria (Fig. 2D; FK 77, 102, 163, 193, 229), they are fused in *Polyphaga* and *Ergaula* (FK 137, 330). The character is not applicable to Mantodea because they lack R2.

36 – Presence of sclerite arm R2m; [0] absent; [1] present (130). – Sclerite R2 in *Deropeltis*, *Tryonicus*, and *Lamproblatta* has a discrete mesal arm that extends into the right wall of the ventral lobe ‘vla’ (FK 91, 102, 193, 174). The character is not applicable to Mantodea because they lack R2.

37 – Shape of sclerite R3; [0] wider than long, with at least slightly convex side margins and no widened or parallel-sided, spatulate anterior tip; [1] longer than wide, with at least slightly concave side margins and a slightly widened or parallel-sided, spatulate anterior tip (00). – For the difference see FK 332. The character is considered not applicable to Mantodea because due to the lack of sclerite R2 and its articulation with R3 the orientation of R3 proper for scoring is disputable.

38 – Presence of sclerite R4; [0] absent; [1] present (119). – In the Blattellidae and Blaberidae having an accessory lobe ‘dla’ in the dorsal wall of the right phallomere (see character 69), the dorsal wall of ‘dla’ frequently has a sclerite R4. Both R4 and ‘dla’ are small in *Nyctibora* and very large in *Blaberus* (FK 308, 318, 319, 330r,s).

39 – Presence of sclerite R5; [0] absent; [1] present (118). – In some Blattellidae and Blaberidae a peculiar

sclerite R5 is present in the membrane mesoventral to the articulation between sclerites R2 and R3 (FK 309, 312, 319, 330r,s).

Formative elements of left side of phallomeres

40 – Presence of pouch ‘pne’; [0] present; [1] very indistinct or absent (111, 134). – Pouch ‘pne’ is formed in the dorsal wall of the left complex (Figs. 2A, 3A–I), around the anterior part L1a of sclerite L1 (if present); it is directed anteriorly and shows otherwise the same positional characteristics as L1 (see character 1; e.g., insertions of muscles l2, l3; Fig. 2H). The presence of ‘pne’ in *Supella* is uncertain due to the lack of muscle data.

41 – Location of membranous part of wall of pouch ‘pne’; [0] right-dorsal, on right side, or right-ventral; [1] dorsal or left-dorsal; [2] on left side or ventral (40); additive. – While parts of pouch ‘pne’ are sclerotized by L1a, the remainder is membranous (Fig. 2A, H; apart from small sclerites in *Ergaula* and *Eurycotis*). The character is not applicable to taxa lacking ‘pne’ or L1.

42 – Presence of process(es) ‘dca’; [0] present; [1] absent (110!). – The ‘dca’ are posteriad-directed projections around the posterior part of sclerite L1. Their shape varies between cushion-like, lobe-like, and sting-like, and they are membranous or sclerotized by L1 (Figs. 2A, 3C–G; FK 54, 67, 94, 105–108, 120, 153, 177). The character is scored ambiguous [-] in Mantodea because due to the different structure of the hind part of L1 the identification of projections in the corresponding area (‘loa’ in Fig. 3A, B; FK 10, 23) as ‘dca’ is unclear; these ‘loa’ could correspond to the ‘loa’ of certain Blattinae (Fig. 3C), whose interpretation as an element in addition to the ‘dca’ or as a peculiar ‘dca’ is unclear.

43 – Breadth and shape of pouch ‘lve’; [0] moderately broad, left-posterior base distinctly remote from left edge of left complex, left-anterior portion not more deeply invaginated to the left than left-posterior parts; [1] very broad, left-posterior base close to left edge of left complex, left-anterior portion not more deeply invaginated to the left than left-posterior parts (55); [2] narrow, left-posterior base distinctly remote from left edge of left complex, left-anterior portion not more deeply invaginated to the left than left-posterior parts; [3] narrow posteriorly and broad anteriorly, left-posterior base far remote from left edge of left complex, left-anterior portion much more deeply invaginated to the left than left-posterior parts (18); non-additive. – The breadth and the shape of the large pouch ‘lve’, which is partly sclerotized by L2, vary strongly among the taxa, and defining character states is difficult. In the definitions here used, states [1]–[3] represent the peculiarities of a far extension of the posterior opening of the pouch to the left [1] (FK 122, 180; watch left end of edge labeled ‘7’ therein), of a deep invagination of the anterior part to the left [3] (FK 11, 55, 68), and of a particularly narrow condition [2] (FK 26, 34). In Blattellidae and Blaberidae the strong modifications in the ‘lve’-pouch (FK 211,

242, 268) – the anterior (inner) part is shaped as a heavy, narrow apodeme and the posterior base of the pouch is strongly modified – impede with assessing the character (scored ambiguous [-]).

44 – Curvature of the right parts of pouch ‘lve’ and sclerite L2; [0] both level; [1] both bending from ventral to dorsal (00). – In Mantodea the right parts of ‘lve’ and L2 (situated in the dorsal wall of ‘lve’) are level with the left parts, and hence they lie in one horizontal plane (Fig. 2A; FK 11, 26, 34, 46). In many Blattaria the right parts of ‘lve’ and L2 curve upwards and usually somewhat towards the left (FK 54, 67, 94, 95, 118; see also FK 324). The character is not applicable to taxa having the right parts of L2 (region L2m) reduced (see character 7).

45 – Presence of ‘lve’-apodeme; [0] absent; [1] present (71). – Only in Blattellidae and Blaberidae the anterior (inner) part of pouch ‘lve’ is developed as a long, tube-like apodeme (Fig. 3H–J; FK 210, 242, 289, 291, 299; compare FK 11, 46, 67, 122).

46 – Presence of apodeme ‘swe’; [0] long and strongly developed; [1] vestigial or absent (2, 28). – *Mantoida*, *Eurycotis*, and Blattinae have an internal ridge ‘swe’ that extends along most of the anterior ventral wall and left edge of the left complex (on sclerite region L4l; Figs. 2B, 3B, C; FK 44–46, 65, 66). In *Metallyticus* and *Sphodromantis* short pieces of ‘swe’ are present (on different parts of L4l; FK 10, 23), while the remaining taxa display no traces of ‘swe’.

47 – Presence of processes ‘paa’ and ‘pda’; [0] both present and distinct from each other; [1] only one process present (93). – In the (originally) left posterior part of the left complex, where sclerites L2 and L4 are fused or in close contact, most taxa have two discrete processes with usually contiguous bases (Figs. 2A, 3B, D, G; FK 10, 23, 44, 65, 96, 117, 150, 178, 179, 208, 214, 244). In *Chaeteessa* (FK 31) and *Ergaula* the single process in this area is ‘pda’ resp. ‘paa’. Thus, two likely non-homologous conditions are included in state [1]. Identification is not possible for the single process in Blaberidae and most Blattellidae (labeled ‘via’ in Fig. 3J; FK 328), which is either the fused processes, or ‘pda’, or ‘paa’.

48 – Length of process ‘paa’; [0] very short (or absent); [1] moderately long; [2] very long (9); additive. – For conditions scored see FK 9, 24, 31, 44, 53, 66, 96, 117, 150, 177, 209, 244. The character is not applicable to those Blaberidae and Blattellidae in which the single process of the area cannot clearly be identified as ‘paa’ (see character 47).

49 – Presence of process ‘afa’; [0] absent; [1] present (00). – A process immediately to the right of the articulation A2 between L1 and L2 is present in the Mantodea; it is heavily sclerotized in *Sphodromantis* (Fig. 3A, B; FK 11, 25, 26, 34, 45, 46). Conditions in many Blattellidae and Blaberidae are scored ambiguous [-] because due to strong modifications in the area concerned the potential position of ‘afa’ cannot be determined.

50 – Sclerotization of process ‘afa’; [0] membranous; [1] sclerotized by part of sclerite region L1m (15). – For differences see Fig. 3A, B and FK 11, 25, 34, 45. The character is not applicable to taxa lacking ‘afa’.

51 – Presence of hook ‘hla’; [0] present; [1] absent (00). – All Blattaria have a prominent hook-shaped process ‘hla’ in the left part of the left complex, which is at least distally sclerotized by L3 (Figs. 2C, 3C–J; FK 54, 66, 91, 117, 150, 177, 210, 242, 269, 299). Hook ‘hla’ and L3 are absent in Mantodea (see also character 11; for possible functional explanations see KLAS 1997: 231).

52 – Location of base of hook ‘hla’ on left complex; [0] far anteriorly in left-ventral wall; [1] more posteriorly in left or left-ventral wall (36); [2] at left posterior edge of left complex (69); additive. – For differences see Fig. 3C–J and compare FK 54, 66, 117, 177, FK 88, 98, 151, and FK 210, 242, 269, 299. Conditions in *Ergaula*, *Polyphaga*, and *Lamproblatta* (Fig. 3D, G) are considered ambiguous between states [0] and [1] and scored [-]. See KLAS (1997: 303ff) for possible functional correlations. The character is not applicable to taxa lacking ‘hla’.

53 – Extension of membranous basal part ‘30’ of hook ‘hla’ and resulting retractility of ‘hla’; [0] membrane very narrow, ‘hla’ hardly retractable; [1] membrane moderately extensive, ‘hla’ moderately retractable (35); [2] membrane very extensive, ‘hla’ (almost) entirely retractable (68); additive. – For differences see Fig. 3C–J and compare FK 54, 66, 117, 122, 151, 177, FK 98, and FK 210, 242, 269, 299. The character is not applicable to taxa lacking ‘hla’.

54 – Presence of groove ‘hge’ on distal part of hook ‘hla’; [0] absent; [1] present (90). – In many Blattellidae and Blaberidae the distal, recurved part of hook ‘hla’ (Figs. 2C, 3H–J) has a groove ‘hge’ along its frontal face, and the ventral wall of the groove then usually has a notch (called ‘45’ in KLAS 1995, 1997, see character 55; FK 266, 297a). The character is not applicable to taxa lacking ‘hla’.

55 – Presence of notch ‘45’ on distal part of hook ‘hla’; [0] absent; [1] present (90). – See remarks on character 54.

56 – Presence of finger-like projection on distal part of hook ‘hla’; [0] absent; [1] present, including cases with vestigial ‘finger’ (00). – In Blattinae, Polyzosteriinae, and *Lamproblatta* the distal, recurved part of hook ‘hla’ has a small finger-like projection next to its main tip (Fig. 3C; FK 53, 60, 176). The character is not applicable to taxa lacking ‘hla’.

57 – Presence of infolding ‘fpe’; [0] absent; [1] present (70). – In the taxa that have hook ‘hla’ originating from the posterior wall of the left complex (see character 52) the left part of the left complex (bearing ‘hla’) is demarcated from the right part by a deep membranous infolding ‘fpe’ from behind (Fig. 3I, J; FK 210, 243, 269, 301).

58 – Presence of process ‘nla’; [0] present; [1] absent (43, 92). – Many Blattaria have a bulge-like sclerotized projection ‘nla’ in the left-anterior ventral wall of the left complex (Fig. 2A, C; FK 56, 63, 68, 87, 97, 206, 209); it likely serves for stabilizing the cuticle at the insertion of the strong muscle 114 of the hook ‘hla’ (Fig. 2I). *Nahublattella* is the only taxon that possesses ‘nla’ but has muscle 114 inserted on sclerite L2 (see character 83); ‘nla’ is here extended into a long thread (FK 239a, 248; see KLAS 1997: 304f for functional correlations).

59 – Size of lobe ‘vla’; [0] large; [1] small (80). – A ventral lobe ‘vla’ (= ventral phallomere) of the left complex is present in all taxa (Figs. 2A–C, 3A–H, J). It is very large in most taxa but fairly small or almost absent in all Blattellidae and Blaberidae except *Anaplecta*.

60 – Extent of separation of lobe ‘vla’ from remaining ventral wall of left complex; [0] no separation or separation only far posteriorly, ‘vla’ thus without or with a short left edge; [1] separation reaching far to the anterior, ‘vla’ thus with a long left edge (124). – For differences compare FK 41, 115, 174 and FK 87, 148, 205, 239a (with edge ‘61’, see Fig. 2C). The character is scored ambiguous [-] in *Eurycotis* because lobe ‘vla’ has a deep longitudinal cleft near its left margin (‘9’ in FK 63), and in many Blattellidae and Blaberidae because the base of ‘vla’ is strongly modified.

61 – Presence and condition of tendon ‘ate’; [0] absent; [1] present, not including sclerite region L4n; [2] present, including sclerite region L4n (sclerite L4V) or the corresponding membranous area (91); non-additive. – Tendons ‘ate’ as specified in state [2] occur in many Blattellidae and Blaberidae (FK 268, 289, 291, 302). The topographic homology between these and tendon ‘ate’ of *Anaplecta* (FK 212), which is characterized in state [1], is ambiguous due to strong structural differences in the anterior ventral wall of the left complex, which bears the tendons. Conditions in *Nahublattella* are unclear for the same reason (see KLASS 1997: 230); this taxon is scored ambiguous [-].

62 – Presence of tendon ‘tve’; [0] absent or vestigial; [1] present and distinct (116). – In some Blattellidae and Blaberidae the insertion area of muscle 10 at the base of the process ‘via’ (= ‘pda’/‘paa’, see characters 47, 79) forms a tendon ‘tve’ (FK 328e,h,i).

63 – Presence of lobe ‘lba’; [0] absent; [1] present (61). – In *Polyphaga* and *Ergaula* the right part of the lobe ‘vla’ (= ventral phallomere) is set off as a small accessory lobe ‘lba’ (Fig. 3D; FK 115, 118), which is ventrally sclerotized by L7 (see character 24). In contrast to GRANDCOLAS (1994), the musculature shows that ‘lba’ is not the homologue of the entire ‘ventral phallomere’ of the other taxa (KLASS 1997: 332). The character is scored ambiguous [-] in many Blattellidae and Blaberidae because the base of ‘vla’ is strongly modified.

Formative elements of right side of phallomeres

64 – Presence of tooth ‘pia’; [0] present; [1] absent (31). – In Mantodea, Blattinae, and Polyzosteriinae the right phallomere has a posteroventral mesad-directed projection ‘pia’, which is largely occupied by the sclerite region R1v and the posteromesal part of region R1c (FK 6, 20, 28, 41, 77, 78, 332). Projection ‘pia’ is absent in other Blattaria.

65 – Presence of apodeme ‘age’; [0] present; [1] absent (129). – The anteroventral sclerite R3 (Fig. 2D) is in all taxa invaginated to form the (left-)dorsal wall of a pouch. Along the anterior and lateral edges of the pouch, the R3-sclerotization continues in most taxa into

the (right-)ventral wall of the pouch, and R3 thus has a sclerotized groove (viewed externally) or apodeme (viewed internally) ‘age’ along parts of its margins (e.g., FK 41, 77, 137, 229, 284). This apodeme is absent in *Tryonicus* and *Lamproblatta* (FK 102, 193). *Nauphoeta* is scored ambiguous [-], because due to the small and weak condition of sclerite R3 the presence of an apodeme ‘age’ is not assessable.

66 – Depth of left part of apodeme ‘age’; [0] not deeper than right part, or only slightly deeper with depth increasing gradually from the right to the left; [1] much deeper than right part, with depth increasing abruptly from the right to the left (17). – In *Metallyticus* and especially *Sphodromantis* the left (mesal) part of apodeme ‘age’ is strongly deepened to form a plate-like apodeme (FK 6, 8, 20). In the other taxa the left part of ‘age’ is less deep or only slightly deeper than the right part (FK 28, 41, 77, 137). The character is not applicable to taxa lacking ‘age’ and – due to the anteriorly pointed shape of R3 – to many Blattellidae and Blaberidae (FK 284, 312a).

67 – Presence of tendon ‘tre’; [0] absent (73); [1] present (136). – Some Blattaria have a long membranous tendon ‘tre’ that originates from the anterodorsal wall of the right phallomere and receives muscles s8 (from coxosternum IX) and b4 (from right part of left complex) (FK 79, 99, 139, 165).

68 – Presence of cuticular swelling ‘cwe’; [0] absent; [1] present (113). – In many Blattellidae and Blaberidae the dorsomesal part of sclerite region R1t, which is articulated or fused with sclerite R2 (at A6 in Fig. 2D), shows a knob-like internal swelling ‘cwe’ (FK 282, 285, 308, 310, 318, 319, 330).

69 – Presence of lobe ‘dla’; [0] absent; [1] present (115). – In many Blattellidae and Blaberidae the anterodorsal wall of the dorsal lobe ‘fda’ of the right phallomere forms an extra lobe ‘dla’ (FK 280, 308, 318, 319), which frequently bears a dorsal sclerite R4 (see character 38). Both ‘dla’ and R4 are very large in some Blaberidae but absent in the blaberid *Nauphoeta* with its overall strongly reduced right phallomere. A small fold in the corresponding area of *Euphyllodromia*, here scored [-], cannot clearly be identified as a lobe ‘dla’.

70 – Presence of process ‘sra’; [0] absent; [1] present. – In *Lamproblatta*, *Eurycotis* and some Blattinae the dorsal lobe ‘fda’ of the right phallomere has a discrete prong ‘sra’ to the left (FK 60, 74, 171, 190); occasionally two such processes are present.

71 – Presence of groove ‘rge’; [0] absent (75); [1] present (138). – In many Blattaria a groove ‘rge’ runs along the dorsal margin of sclerite region R1c, passing the right insertion of muscle r3 dorsally in taxa where muscles were studied; ‘rge’ is a posterior continuation of the R3-groove ‘age’ if the latter is present (see character 65) (FK 74, 80, 99, 102, 134, 140, 166, 166, 190, 197). Blattellidae and Blaberidae lack ‘rge’. However, in *Nauphoeta* related sclerotizations are very weak and the presence of ‘rge’ cannot be assessed; this taxon is scored ambiguous [-].

72 – Presence of a groove on sclerite region R1c anteroventral to insertion of muscle r3; [0] absent;

[1] present (122). – Most Mantodea have such a groove, which like ‘rge’ is a posterior continuation of groove ‘age’ but targets the center of the sclerite region R1c and passes the r3-insertion anteroventrally in taxa where muscles were studied (FK 6, 14, 19, 20, 24, 41, 44, 50).

Muscles of phallomeres: intrinsics of left side

73 – Presence of muscle I1; [0] present; [1] absent (25!). – Muscle I1 (Fig. 2G), which occurs in Mantodea, *Cryptocercus*, and *Nahublattella*, connects pouch ‘pne’ with sclerite region L4d. The latter is (originally) located in the left dorsal wall of the left complex (FK 48, 155), but in the right dorsal wall in *Sphodromantis* (due to the shifts explained in character 12; FK 17), and centrally in the left complex in *Nahublattella* (due to some larger rearrangements; FK 249). I1 lies dorsal to muscle I2, which shows similar insertions on ‘pne’ and L4; in the few taxa where I1 was identified, a stout I2 is also present.

74 – Location of right insertion of muscle I2; [0] on top of pouch ‘pne’ (44); [1] in left, left-ventral, or dorsal wall of pouch ‘pne’, or in corresponding area; [2] on utmost base of hook ‘hla’ (86); additive. – In most taxa I2 (Fig. 2H) inserts on the left flank of pouch ‘pne’, with the insertion located either more dorsally or more ventrally depending on the orientation of ‘pne’ (i.e., location of membranous parts of ‘pne’-walls, see character 41; FK 15, 49, 70, 221). In *Polyphaga*, *Ergaula*, *Lamproblatta*, and *Cryptocercus* the insertion is on the anterior (inner) top of ‘pne’ (FK 128, 156, 184). In *Nahublattella*, *Parcoblatta*, *Blaberus*, and *Phoetalia* the insertion of I2 is farther posteriorly, in a position corresponding to the posterior ventral base of the ‘pne’-pouch in other taxa (‘pne’ absent in most of these taxa, see character 40), and close to or on the base of hook ‘hla’ (‘hla’-base located far posteriorly in these taxa, see character 52; FK 249, 276, 303).

75 – Location of left insertion of muscle I2; [0] In the posterior two thirds of left edge of left complex on sclerite region L4l (in some taxa on individualized sclerite L4K or L4U, or on corresponding membranous area); [1] in anterior left edge of left complex on sclerite region L4l (sclerite L4K) (45); [2] in anterior left edge of left complex, in membrane anterior to sclerite region L4l (and sclerite L4K) (54); [3] in left anterior ventral wall of left complex on sclerotization (sclerite region L4x) (60); additive. – In the taxa that have the right I2-insertion on top of ‘pne’ (see character 74) also the left I2-insertion is, to a varied extent, farther anteriorly than in the remaining taxa (usual condition in Fig. 2H and FK 49, 70, 221, 249, 303; anteriorly located insertion in FK 128, 156, 184).

76 – Presence of muscle I3; [0] present; [1] absent (99). – Muscle I3 (Fig. 2H) connects pouches ‘pne’ and ‘lve’ or the corresponding areas. It is strong in most taxa (FK 16, 50, 128, 158, 159, 187, 221, 250; divided into three bundles in *Eurycotis*, FK 71) but absent in *Parcoblatta*, *Blaberus*, and *Phoetalia*.

77 – Presence of muscle I4; [0] well developed; [1] vestigial or absent (133). – Muscle I4 (Fig. 2I) connects

pouch ‘lve’ with the left edge of the left complex, where it inserts immediately ventral to I2 (except in *Polyphaga*). It is strong in most taxa (FK 15, 50, 71, 132, 249, 276, 303) but vestigial in *Cryptocercus* (FK 155) and absent in *Lamproblatta* and *Anaplecta*.

78 – Location of ventral insertion and presence of muscle I5; [0] muscle present, insertion in anterior ventral wall of left complex on sclerite regions L4n, or L4a, or anterior L4l, or on adjacent/corresponding membranes (homology of locations not entirely clarified); [1] muscle present, insertion in posterior ventral wall of left complex on sclerite region L4c (sclerite L4F) (22); [2] muscle absent; non-additive. – The topographic homology between the muscles here considered (I5) is ambiguous. The I5 in the taxa scored [0] (Fig. 2I) take similar positions with regard to most neighboring elements (FK 15, 50, 133, 188, 223, 251, 327), and homology appears likely. The I5 in *Deropeltis*, *Periplaneta*, and *Eurycotis* may be non-homologous with the former because they have far more posteriorly located ventral insertions (FK 72); if this interpretation is correct, the step from [0] to [1] would represent the loss of one muscle plus the addition of a new one. *Cryptocercus* has no muscle corresponding to I5. Conditions in Blattellidae (except *Anaplecta* and *Nahublattella*) and Blaberidae are too modified as to allow the identification of a homologue of I5; their members are scored ambiguous [-].

79 – Presence of muscle I10; [0] absent; [1] present (29). – Muscle I10 connects sclerite L2 and pouch ‘lve’ with the sclerotization around the bases of the processes ‘paa’ and ‘pda’ (sclerite regions L4l, posterior part, and L2d; process ‘via’ in Blattellidae and Blaberidae, see character 47; FK 129, 186, 222, 250). Particularly interesting is the scattered occurrence of I10 in Blattellidae and Blaberidae (FK 328). The identification of I10 in *Cryptocercus* (FK 155) is uncertain due to its far posterior insertion on sclerite L2; this taxon is scored ambiguous [-].

80 – Presence of muscle I11; [0] absent; [1] present (50). – Muscle I11, connecting sclerite regions L4l (sclerite L4K) and L4d or the adjacent membranes, is only present in *Polyphaga*, *Ergaula*, and *Lamproblatta* (FK 128, 184, 327).

81 – Presence of muscle I12; [0] absent; [1] present (51). – Muscle I12, connecting the right parts of sclerite L2 and of pouch ‘lve’ with sclerite L8 or the corresponding area, is only present in *Polyphaga*, *Ergaula*, and *Lamproblatta* (FK 129, 186).

82 – Presence of muscle I14; [0] present; [1] absent (58). – The strong I14, which is the major extrinsic muscle of the hook ‘hla’ and sclerite L3 (Fig. 2I; see characters 11, 51), is present in most Blattaria (FK 72, 157, 184; occasionally divided into two bundles, see character 84) but is missing in *Polyphaga*, *Ergaula*, and Mantodea.

83 – Location of anterior insertion of muscle I14; [0] on sclerite region L4n or corresponding membrane, often extending to anterior L4l; [1] on sclerite region L2a (79). – See KLAAS (1997: 233, 304ff) for reasons to consider the L4-inserted muscles (FK 72, 222: on sclerotization with bulge-like projection ‘nla’; FK 157, 184: on membrane lacking bulge ‘nla’) and the L2-inserted muscles (FK

249, 276) homologous. The character is not applicable to taxa lacking l14.

84 – Presence of division of L2-inserted muscle l14 into two bundles l14a,b with closely adjacent non-‘hla’ insertions and far-separated ‘hla’-insertions; [0] absent; [1] present (98). – For differences compare FK 249 and FK 276, 303. The character is not applicable to taxa lacking a l14 inserted on L2/‘lve’.

85 – Presence of muscle l36; [0] absent; [1] present (100). – Muscle l36, extending within the membranous basis of hook ‘hla’, is present in Blaberidae and some Blattellidae (FK 276, 303). Mantodea are scored ambiguous [-] because conditions cannot be assessed.

86 – Presence of muscles l37 and l38; [0] absent; [1] present (101, 102). – l37 and l38 are diffuse groups of fibers extending along the membranous right ventral wall of the left complex (FK 277, 278, 307); a clear distinction between the two is not possible. They are found in Blaberidae and some Blattellidae.

87 – Presence of muscle l42 (or parts of other muscles with posterior insertion occupying infolding ‘fpe’ or the corresponding area); [0] absent; [1] present (00). – A muscle connecting sclerite L2 and pouch ‘lve’ with infolding ‘fpe’ is only present in Blaberidae (FK 304). The character is not applicable to Mantodea because hook ‘hla’ is absent and the area corresponding to infolding ‘fpe’ (bordering in Blattellidae and Blaberidae the ‘hla’-base to the right, see character 57) can thus not be determined.

Muscles of phallomeres: intrinsics connecting left and right side

88 – Presence of muscle b1; [0] present; [1] absent (00). – Muscle b1, connecting sclerite R3 of the right phallomere with the anterior sclerite region L4l of the left complex or the neighboring membrane, occurs only in the Mantodea (FK 16, 43).

89 – Presence of muscle b2; [0] present; [1] absent (00). – Muscle b2, connecting sclerite R3 or adjacent membrane of the right phallomere with right parts of the left complex is present in several Dictyoptera (FK 15, 49, 110, 127, 184, 198, 224, 232; see KLASS 1997: 258 for the basis of homologizing these variable muscles).

90 – Presence of muscle b4; [0] present; [1] absent (73). – Muscle b4 comprises 2 or 3 bundles (b4a, b4b in Fig. 2F) and connects the anterior dorsal margin of the right phallomere (tendon ‘tre’ if present, see character 67) with various areas in the right part of the left complex. It is present in all taxa except *Lamproblatta*, Blattellidae, and Blaberidae (FK 48, 58, 70, 109, 127, 129, 143a, 156). *Sphodromantis* is scored ambiguous [-] because the identification of b4 (FK 17) is unclear due to rearrangements in the middorsal part of the phallomere complex, which result from the shift described in character 12.

91 – Location of left insertion of muscle b4b; [0] in dorsal wall outside pouch ‘pne’; [1] on anterior top of

pouch ‘pne’ (23). – For differences compare FK 48, 127, 156 and FK 70. The character is not applicable to taxa lacking b4.

Muscles of phallomeres: intrinsics of right side

92 – Presence of muscle r3; [0] present; [1] absent (64!). – Muscle r3 (Fig. 2J), connecting sclerite regions R1c and R1v, is present in Mantodea and in the Blattaria in which these regions are separate (see character 30; FK 16, 19, 49, 50, 80, 166, 197).

93 – Presence of muscle r4; [0] present; [1] absent (00). – Muscle r4, connecting the leftmost dorsal and ventral walls of the lobe ‘fda’ of the right phallomere, is only present in Mantodea (FK 15, 49). However, *Nahublattella* is scored [0] because its muscle r10 (FK 259) has a similar position.

94 – Presence of muscle r6; [0] absent (126); [1] present (137). – Muscle r6, connecting sclerite regions R1c (groove ‘rge’) and R1d, is present in some Blattaria (FK 79, 140, 196).

95 – Presence of muscle r11; [0] absent; [1] present (120). – Muscle r11, connecting sclerite region R1c with an outfolding ‘dla’ from the dorsal wall of the right phallomere (see character 69), is present in *Nyctibora* and some Blaberidae (FK 314, with two bundles in *Blaberus*). In terms of topographic relationships, homology of r11 with r6 (see character 94) cannot be excluded.

Muscles of phallomeres: extrinsics

96 – Presence of muscle s1; [0] present; [1] absent (77). – Muscle s1 (Fig. 2F), extending from the left anterior part of coxosternum IX to the anterior part of sclerite region L4l (or to the corresponding or adjacent membrane) of the left complex, is present in all taxa except Blattellidae and Blaberidae (FK 2, 37, 59, 110, 170, 333); in *Cryptocercus* it is fused with muscle s3 (FK 144).

97 – Presence of division of muscle s3 into two bundles s3a,b; [0] absent; [1] present (105). – Muscle s3 (Fig. 2F), extending from the left anterior part of coxosternum IX to the middle part of the ventral anterior margin of the left complex, is present in all taxa. In Blaberidae and many Blattellidae it consists of two discrete bundles that insert on tendon ‘ate’ and in the area to the left of the ‘ate’-origin (FK 263, 267, 294, 298, 333).

98 – Presence of muscle s5; [0] present; [1] absent (131). – Muscle s5 (Fig. 2F), extending from the left lateral part of coxosternum IX to the membrane covering the left complex ventrolaterally, is present in all taxa except *Polyphaga* and *Cryptocercus* (FK 333; a weak s5 was found in *Ergaula capucina*, which is scored [0]).

99 – Extension of ventral insertions of muscles s5 (and s6) to the posterior; [0] confined to anterior part of subgenital plate; [1] reaching far posterior part of subgenital plate (108). – Muscles s5 and s6 (a pair; Fig. 2F), extending from the left resp. right lateral part of coxosternum IX to the membrane covering the left

complex resp. right phallomere ventrolaterally, are present in all taxa (exceptions for s5 given in character 98) and variously divided into discrete bundles. In Blaberidae and many Blattellidae the ventral insertion of the posterior bundle of s5 (s5a) is far posteriorly on coxosternum IX (FK 265, 296, 333; the same is in some taxa true for s6a).

100 – Presence of muscle s7; [0] absent (56); [1] present (135). – Muscle s7, extending from the left anterior part of coxosternum IX to the anterior (inner) part of pouch ‘lve’ of the left complex, is present in Blattinae, Polyzosteriinae, Blattellidae, and some Blaberidae (FK 58, 234, 262, 333); in *Cryptocercus* the inclusion of a s7-component within muscle s1+s3 is unclear (FK 144, 333f), and the taxon is scored ambiguous [–].

101 – Presence of muscle s8; [0] absent (73); [1] present (136). – Muscle s8, extending from the right anterior part of coxosternum IX to tendon ‘tre’ of the right phallomere, is present in all Blattaria that have a ‘tre’ (see character 67; FK 58, 109, 143a). None of the taxa lacking ‘tre’ has a muscle from coxosternum IX to the dorsal wall of the right phallomere (from where ‘tre’ originates in the other taxa).

102 – Presence of muscle s9; [0] absent; [1] present. – Muscle s9, extending from the left part of coxosternum IX to the left margin of sclerite R3 of the right phallomere, was only found in *Deropeltis* and *Periplaneta*. Since s9 is lacking in *Eurycotis*, this muscle has not been reported in KLAS (1995, 1997; but see MIZUKUBO & HIRASHIMA 1987: S4 in figs. 30, 35).

103 – Presence of muscle s10; [0] absent; [1] present (125). – Muscle s10, extending from the right anterior part of coxosternum IX to the ejaculatory duct (or to an area close to its external opening in *Anaplecta*), is only present in *Cryptocercus*, Blattellidae, and Blaberidae (FK 143a, 200, 222, 234, 262, 293, 333).

104 – Presence of muscle s12; [0] absent; [1] present (52). – Muscle s12, extending from the right anterior part of coxosternum IX to the middle part of the ventral anterior margin of the left complex (next to insertion of s3, see Fig. 2F), is only present in *Polyphaga*, *Ergaula*, and *Lamproblatta* (FK 113, 116, 173, 175, 333e,g).

105 – Presence of muscle s14; [0] absent; [1] present (106). – Muscle s14, extending from the right anterior part of coxosternum IX to the utmost right part of the ventral anterior margin of the left complex (far to the right of the s3-insertions, see character 97), is only present in Blaberidae and some Blattellidae (FK 265, 267, 296, 298, 333k,l).

106 – Spatial relationship between posteroventral insertion of left muscle p4 and leftmost base of lobe ‘fda’ of right phallomere; [0] far remote from each other; [1] close to each other (00). – Muscles p4 (a pair), extending from the lateral part of tergum IX to the membrane above and behind the phallomere complex (around sclerites Pv, see Fig. 2F), are present in all taxa and can be asymmetrical to some extent. But only in Blattinae and Polyzosteriinae the ventral insertion of the left p4 extends far to the right and thus almost reaches the mesal base of the dorsal lobe ‘fda’ and its sclerite R1H (FK 58, compare FK 37, 109, 170, 200, 234).

Further phallomere characters

107 – Orientation of phallomere asymmetry; [0] normal: left complex on left side, right phallomere on right side; [1] reversed: left complex on right side, right phallomere on left side. – For data on taxa and discussion see KLAS (1997).

8.2. Other characters applicable to non-social and social taxa

Most of these characters have been used and discussed previously by THORNE & CARPENTER (1992) and, with revisions, DEITZ et al. (2003). As compared to the latter publication, some characters are here omitted because they are evidently not informative with the taxon sample here used or include problems of various kind (explained below); some characters were split; and characters 116, 131, 132, 144, 154, and 162–164 were added. Numbers behind character definitions indicate character numbers in DEITZ et al. (2003). We studied many of these characters in the blattarian and mantodean taxa here sampled and/or searched the literature for data. In some cases where data could not be obtained in these ways, we included data from the literature that relate to species having very similar male genitalia, with shared apomorphies. This mainly refers to the adoption of data from *Mantis* for *Sphodromantis*; from *Lophoblatta* for *Nahublattella* (compare MCKITTRICK 1964: fig. 113 and KLAS 1997: fig. 236b for male genitalia); and from ‘*Anaplecta* sp. C’ for *Anaplecta* sp. (compare MCKITTRICK 1964: fig. 112 and KLAS 1997: figs. 203ff for male genitalia). Whenever an entry into the matrix relates to a different taxon than the sampled one, this will be noted.

108 – Number of ocelli (4); [0] 3 well-developed ones; [1] 2 well-developed ones; [2] 0, or 2 strongly reduced ones; additive. — See THORNE & CARPENTER (1992) and literature cited therein for Termopsinae [2] and Kalotermitidae [1]; GRANDCOLAS (1997a: 95) and ROTH (1987: 152) for *Lauraesilpha* [2] and *Tryonicus* [2]. Scoring of remaining dictyopteran taxa based on original examination (in *Eurycotis* [2] at most 2 vestigial ocelli are present). No data for *Archiblatta*. We scored the hypothetical ancestor [?] because either state occurs in the surmised ground plans of the outgroup taxa here considered (for state [1] see WILLMANN 2003: 29 on fossil Dermaptera).

109 – Shape of antenna (1); [0] filiform; [1] moniliform. – The shape of flagellomeres in Dictyoptera varies strongly along the antenna; they usually become narrower, more elongate, and more strongly constricted basally towards the distal part. For scoring this character the 10th and neighboring flagellomeres were examined. These are in *Cryptocercus* and the isopteran taxa more strongly constricted basally than in all other taxa here included, appearing ± calyx-shaped, which is the main characteristic making antennae moniliform; these taxa are scored [1]. However, the states “moniliform” and

“filiform” are difficult to define, especially because flagellomere shape varies strongly among the taxa scored [0]. See IMMS (1919: fig. 18) for Termopsinae [1]; GRANDCOLAS (1997a: fig. 27) for *Lauraesilpha* [0]. Scoring of remaining dictyopteran taxa based on original examination. No data for *Archiblatta* and *Tryonicus*. We scored the hypothetical ancestor [0] because the taxa here considered for outgroup comparison nearly all have clearly filiform antennae (with few exceptions in derived subgroups) and in Embioptera and Zoraptera antennomeres are \pm oval but not calyx-like in shape (figures in ROSS 2000; GURNEY 1938: figs. 3, 43, 48).

110 – Number of antennomeres (2); [0] ≥ 44 ; [1] 28–42; [2] ≤ 27 ; additive. – See DEITZ et al. (2003) and references therein for discussion and *Cryptocercus* [1], *Mastotermes* [1], Termopsinae [2], and Kalotermitidae [2]; GRANDCOLAS (1997a: fig. 27) for *Lauraesilpha* [0]. Scoring of remaining dictyopteran taxa [0] based on original examination. No data for *Chaeteessa*, *Archiblatta*, and *Tryonicus*. We scored the hypothetical ancestor [?] because either state occurs in the surmised ground plans of the outgroup taxa here considered.

111 – Number of marginal teeth of left mandible (5); [0] 3; [1] 2; [2] 1; non-additive. – The dentition at the mesal edge of the mandible of Blattaria consists of (1) a tooth that forms the tip of the mandible; (2) three teeth basal to the tip, placed in line, and called here (from distal to basal) the 1st (moderately sized), 2nd (large) and 3rd tooth (of varied size); basal to these three teeth there is (3) a tooth (dorsal molar tooth) that borders the molar area distally, and which continues into a \pm distinct ridge (dorsal molar ridge) that runs basally along the dorsal margin of the molar area; and (4) a tooth (ventral molar tooth) placed far anteriorly on the ventral margin of the molar area, ventral and shortly basal to the former tooth, to which it is connected by a \pm distinct ridge (ventral molar ridge). In Isoptera the molar teeth and ridges are feebly developed, and the teeth under (2) are in several subgroups reduced to two (AHMAD 1950; KLASS 1995: 183). In *Sphodromantis* a cutting edge is additionally present that likely connects the large 2nd tooth with the ventral molar tooth; the molar teeth and ridges essentially correspond with Blattaria; the 3rd tooth is still present as a small bulge on the dorsal face of the cutting edge. *Mantoida* differs strongly from *Sphodromantis*: likely, only the 1st tooth (or the 2nd?) has been retained, and a small additional tooth is present shortly basal and ventral to the mandibular tip, the two teeth and the tip being close together; the very long cutting edge runs from this distal group to a basally shifted ventral molar tooth; the 2nd tooth, dorsal molar tooth, and molar ridges are entirely absent.

This character counts the teeth under (2): 1st, 2nd, 3rd. The character states are treated as non-additive because it is unclear whether, in case of reduction, the same teeth have been lost in [1] and [2]. We scored the hypothetical ancestor [?] because according to illustrations in YUASA (1920) and our examination of discrete outgroup taxa all conditions with 1, 2, or 3 teeth and with differently formed molar areas occur in the outgroup taxa here considered.

See AHMAD (1950) for *Mastotermes* [1], Kalotermitidae [1], and Termopsinae [0]. *Mantoida* [2], *Sphodromantis* [0], and blattarian taxa [0] based on original examination. No data for *Chaeteessa*, *Metallyticus*, *Archiblatta*, *Lauraesilpha*, and *Tryonicus*.

112 – Mandibular glands (7); [0] present; [1] absent. – See DEITZ et al. (2003) for hypothetical ancestor [0], Termopsinae [?], and mantodean taxa [?]; BROSSUT (1973: 44, Tab. 1) for Kalotermitidae [0], *Mastotermes* [0], *Cryptocercus* [1], *Periplaneta* [1], *Eurycotis* [1], *Supella* [0], *Nauphoeta* [0], and *Blaberus* [0]. No data for the remaining taxa including discrete outgroup taxa.

113 – Hypopharyngeal glands (8); [0] present; [1] absent. – See DEITZ et al. (2003) for hypothetical ancestor [?], Termopsinae [?], and mantodean taxa [?]; BROSSUT (1973: 44, tab. 1) for Kalotermitidae [0], *Mastotermes* [0], *Cryptocercus* [1], *Periplaneta* [0], *Eurycotis* [0], *Supella* [0], *Nauphoeta* [1], and *Blaberus* [1]. No data for the remaining taxa including discrete outgroup taxa.

114 – Anterior duplicature of pronotum (potentially covering hind part of head) (9); [0] absent; [1] short; [2] long; additive. – We score here the relative length (as compared to the entire length of pronotum) and anterior extension of the duplicature forming the anterior marginal part of the pronotum; this duplicature is sclerotized in its dorsal and ventral walls and covers posterior parts of the head dorsally depending on its own anterior extension and the length of the cervical region. In all mantodean taxa the duplicature is present but short; in *Mantoida* [1], *Chaeteessa* [1], and *Metallyticus* [1] it covers the hind part of the head; in *Sphodromantis* [1] it does not because of the elongated cervix and because it is particularly short. In a number of Blattaria this duplicature is also very short and only the hindmost part of the head is covered dorsally; the duplicature is especially short in *Supella* [1], *Euphyllodromia* [1], *Nahublattella* [1], and *Nauphoeta* [1], but also quite short in *Periplaneta* [1], *Lamproblatta* [1], *Anaplecta* [1], *Parcoblatta* [1], and probably *Tryonicus* [1] (MACKERRAS 1968). A moderately long duplicature is present in *Deropeltis* [1], *Eurycotis* [1], *Nyctibora* [1], and *Phoetalia* [1]. A much longer duplicature and more extensive coverage of the head is found in *Polyphaga* [2], *Ergaula* [2], *Cryptocercus* [2], *Blaberus* [2], and *Blaptica* [2]. In Isoptera the duplicature is slightly shorter than in the Blattaria with the shortest one: *Mastotermes* [1] and Kalotermitidae [1] (original examination); and in contrast to Blattaria the anterior margin is not convex. No data for Termopsinae, *Lauraesilpha*, and *Archiblatta*. We scored the hypothetical ancestor [?] because all states are represented in the outgroup, see scoring of discrete outgroup taxa [0] or [1] and state [2] in (some?) members of the stem-group of Dictyoptera (or of the ‘blattoid assemblage’ in, e.g., KUKALOVÁ-PECK 1991: 166; CARPENTER 1992: fig. 80).

115 – Fore legs (14); [0] not raptorial; [1] raptorial. – See KLASS & EHRMANN (2003: fig. 13.4.) for *Mantoida* [1]; GRANDCOLAS (1997a: fig. 27) and ROTH (1987: plate 1) for *Lauraesilpha* [0] and *Tryonicus* [0]; IMMS (1919: fig. 3) for Termopsinae [0]. Scoring of all mantodean taxa [1] and remaining blattarian and isopteran taxa [0] based on

original examination. No data for *Archiblatta*. In all orders that potentially are the closest relatives of Dictyoptera fore legs are not raptorial in the ground plan – with the exception of Mantophasmatodea; specializations in the latter, however, are very different from those in Mantodea (KLASS et al. 2003). We thus scored the hypothetical ancestor [0], but note that the use of this character is preliminary. For instance, the leg spination in Blattaria, Mantodea, Mantophasmatodea, and other Pterygota requires extensive comparison for a clearer specification of raptorial apomorphies in mantodean fore legs (work in progress by A. Barton & K.-D. Klass).

116 – Presence of a distinct brush of setae on distal anterior (= mesal) face of fore femur (–); [0] absent; [1] present. – See KLASS & EHLMANN (2003: fig. 13.4.), ROY (1999: 28), and GRIMALDI (2003: fig. 25b,d) for various Mantodea. Scoring of mantodean taxa [1] and of blattarian and isopteran taxa [0] based on original examination. No data for Termopsinae, *Archiblatta*, *Tryonicus*, and *Lauraesilpha*. We scored the hypothetical ancestor [0] because for the outgroup taxa here considered no such femoral brush is apparently reported in the literature and absence was confirmed by original examination of all discrete outgroup taxa except *Dinocras*.

117 – Number of tarsomeres (15); [0] 5; [1] 4; [2] 3; additive. – See WEIDNER (1970: 14ff) for Kalotermitidae [1], Mastotermitidae [0], and Termopsinae [0]; DEITZ et al. (2003) for reduction of 2nd tarsomere in the latter group; GRANDCOLAS (1997a: fig. 27) and ROTH (1987: plate 1) for *Lauraesilpha* [0] and *Tryonicus* [0]. Scoring of all other included mantodean and blattarian taxa [0] based on original examination, but no data for *Archiblatta*. According to the data in BEUTEL & GORB (2001: character 38) we scored the hypothetical ancestor [?] ([0] in DEITZ et al. 2003). *Timema* and *Locusta* are scored [0] because on the ventral side the original composition of 5 tarsomeres is still visible in the pattern of euplantulae.

118 – Tegminization of fore wings (17); [0] absent; [1] present. – Termopsinae [0] adopted from THORNE & CARPENTER (1992). Scoring of remaining dictyopteran taxa based on original examination (for *Mantoida* [0] and *Chaeteessa* [0] see also SMART 1956). No data for *Archiblatta*; not scored in the wingless or brachypterous *Eurycotis*, *Lamproblatta*, *Cryptocercus*, *Tryonicus*, and *Lauraesilpha*. We scored the hypothetical ancestor [?], because among the outgroup taxa here considered [0] (Embioptera, Plecoptera), [1] (e.g., Dermaptera, Orthoptera), and winglessness [–] (Notoptera, Mantophasmatodea) occurs.

119 – Pimples of wings (18); [0] absent; [1] present. – See THORNE & CARPENTER (1992) as well as DEITZ et al. (2003) and references given therein for *Supella* [1] (see also ROONWAL & RATHORE 1983), *Mastotermes* [1], Kalotermitidae [1], and Termopsinae [0]. No data for the remaining taxa including discrete outgroup taxa; an investigation of wing microsculpture in further Blattaria and Mantodea would be interesting. The character is not applicable to wingless taxa.

120 – Length of forewing subcosta posterior (20); [0] less than 2/3 of wing length; [1] more than 2/3 of

wing length. – The states of this character are different from those in DEITZ et al. (2003): instead of separating very short conditions of the vein (< 1/3) from longer conditions, very long conditions (> 2/3) are separated from shorter conditions. The reason is that ScP length varies considerably in both Blattaria (even among closely related species; illustrations in REHN 1951) and Isoptera (WEIDNER 1970; unpublished data from J. Kukalová-Peck) but usually ranges from 1/5 to 1/2 of wing length. Kalotermitidae [0] and Termopsinae [0] based on unpublished data from J. Kukalová-Peck. See SMART (1956) for *Mantoida* [1] and *Chaeteessa* [1], *Metallyticus* [1], *Sphodromantis* [1], *Mastotermes* [0] (see also KUKALOVA-PECK & PECK 1993: fig. 20), and blattarian taxa [0] based on original examination. No data for *Archiblatta*; not scored in the wingless or brachypterous *Eurycotis*, *Lamproblatta*, *Cryptocercus*, *Tryonicus*, and *Lauraesilpha*. Comparison with outgroups is conflicting: see, e.g., BEIER (1972: Sc in fig. 79) and RAGGE (1955) for Orthoptera being highly variable, ZWICK (1980: fig. 32) for Plecoptera 2/3 or a bit less, ROSS (2000: figs. 27–31) for Embioptera ca. 1/3. In stemgroup representatives of Mantodea (GRIMALDI 2003: figs. 3, 6, 23; VRŠANSKÝ 2002: figs. 12–14) ScP is apparently distinctly shorter than in the extant Mantodea here scored [1], being about 2/3 of wing length (*Ambermantis*, *Cretophotina*) or even somewhat shorter (ca. 0.6 in *Baissomantis* and *Santanmantis*); this overlaps with values in Blattaria, while values in *Mantoida*, *Chaeteessa*, and *Mantis* are 0.78 or more (see illustrations in SMART 1956). We thus scored the hypothetical ancestor [0].

121 – Size of forewing clavus (23); [0] large; [1] small or absent. – This forewing area, which comprises the veins AA and AP if these are present, is in the isopteran taxa distinctly smaller (for relative size see, e.g., area behind Cu2 in WEIDNER 1970: figs. 9, 10, 13, 14, 19) than in all blattarian and mantodean taxa here scored (for relative size see, e.g., area behind Cu2 = CuP in KLASS & EHLMANN 2003: fig. 13.3, SMART 1956: figs. 1, 3, 4, and SMART 1952: fig. 1; corresponding area in REHN 1951: figs. 6–75). The character was not scored in the wingless or brachypterous *Eurycotis*, *Lamproblatta*, *Cryptocercus*, *Tryonicus*, and *Lauraesilpha*. We scored the hypothetical ancestor [0] because a size of the clavus as in [0] is found in Orthoptera (BEIER 1972: fig. 79), Plecoptera (ZWICK 1980: fig. 32), and Embioptera (ROSS 2000: figs. 24–31; though in some species approaching the small size found in Isoptera).

122 – Length of hindwing subcosta posterior (25); [0] less than 2/3 of wing length; [1] more than 2/3 of wing length. – As in character 120, in contrast to DEITZ et al. (2003) the states here defined separate very long conditions (> 2/3) from shorter conditions rather than very short conditions (< 1/3) from longer conditions. The reason is that ScP length varies considerably in both Blattaria (even among closely related species; illustrations in REHN 1951) and Isoptera (WEIDNER 1970; unpublished data from J. Kukalová-Peck) but usually ranges from 1/4 to 1/2 of wing length (though the identification of ScP in Kalotermitidae and Termopsinae is somewhat

ambiguous from the literature). Kalotermitidae [0] and Termopsinae [0] based on unpublished data from J. Kukulová-Peck. See SMART (1956) for *Mantoida* [1] and *Chaeteessa* [1], *Metallyticus* [1], *Sphodromantis* [1], *Mastotermes* [0] (see also KUKALOVÁ-PECK & PECK 1993: fig. 22), and blattarian taxa [0] (see also illustrations in REHN 1951) based on original examination. No data for *Archiblatta*; not scored in the wingless or brachypterous *Eurycotis*, *Lamproblatta*, *Cryptocercus*, *Tryonicus*, and *Lauraesilpha*. As in character 121 on the forewing ScP, comparison with potential outgroups is conflicting: see, e.g., RAGGE (1955) for Orthoptera less than 1/2 to more than 2/3, BEIER (1968b: fig. 15) and KEY (1991: fig. 25.1) for Phasmatodea ca. 2/3, ZWICK (1980: fig. 32) for Plecoptera 2/3 or a bit less, and ROSS (2000: figs. 27) for Embioptera ca. 1/3. In the abovementioned stemgroup representatives of Mantodea hind wings are less well-preserved than fore wings; only in *Baissomantis* the hindwing ScP clearly shows state [0] (GRIMALDI 2003: fig. 6; compare illustrations in SMART 1956). We thus scored the hypothetical ancestor [?].

123 – Presence of hindwing anal anterior 3+4 (26); [0] present; [1] absent. – Character 26 of DEITZ et al. (2003) has here been divided in two, one related to the presence or absence of these veins (123), and one to its terminal branching (124). State [0] includes conditions where AA3+4 joins the vein in front of it. See DEITZ et al. (2003), references therein, and HAAS & KUKALOVÁ-PECK (2001) for discussion, hypothetical ancestor [0], Termopsinae [1], and Kalotermitidae [1]; SMART (1956, “PCu”) for *Mantoida* [0] and *Chaeteessa* [0]. Scoring of other dictyopteran taxa [0] based on original examination (for *Mastotermes* [0] see also KUKALOVÁ-PECK & PECK 1993: fig. 22). No data for *Archiblatta*; not scored in the wingless or brachypterous *Eurycotis*, *Lamproblatta*, *Cryptocercus*, *Tryonicus*, and *Lauraesilpha*.

124 – Branching of hindwing anal anterior 3+4 (26); [0] ≥ 4 branches; [1] ≤ 3 branches. – See previous character, DEITZ et al. (2003), and references therein for discussion and hypothetical ancestor [?]; SMART (1956, “PCu”) for *Mantoida* [1] and *Chaeteessa* [1], *Metallyticus* [1], *Sphodromantis* [1], *Mastotermes* [0] (see also KUKALOVÁ-PECK & PECK 1993: fig. 22), and blattarian taxa [1] based on original examination. No data for *Archiblatta*; not scored in the wingless or brachypterous *Eurycotis*, *Lamproblatta*, *Cryptocercus*, *Tryonicus*, and *Lauraesilpha* as well as in Kalotermitidae and Termopsinae, which lack the vein. *Locusta* and *Dinocras* are considered inapplicable [-] because the formation of few most basal branches of AA3+4 (see interpretation in KUKALOVÁ-PECK & LAWRENCE 2004: fig. 2) is hardly comparable with the more distal branching in the taxa here scored [0].

125 – Distal extension of hindwing anojugal area (27); [0] far: reaching 0.70–1.00 of wing length; [1] not far: reaching 0.25–0.65 of wing length; [2] very short: < 0.25 of wing length (due to the generally small size of this wing area); additive. – In contrast to DEITZ et al. (2003) the distinction of three states has been adopted from THORNE & CARPENTER (1992) and the definition of

the states was refined. On the distal hind margin of the hind wing, the border between the remigium and the anojugal area is usually indicated by a notch (not true for state [2]); states [0] and [1] relate to the ratio between the distance from the wing base to this notch and the distance from the wing base to the tip of the wing (= wing length). In the dictyopteran taxa scored [0] the ratio had 0.75 as a minimum (but was usually higher) and in the dictyopteran taxa scored [1] it had 0.60 as a maximum. See illustrations in WEIDNER (1970) for Kalotermitidae [2] and Termopsinae [2]. See SMART (1956) for *Mantoida* [0] and *Chaeteessa* [0]; KLASS (1995: fig. 345a) for *Sphodromantis* [0], *Metallyticus* [0], *Mastotermes* [1] (see also KUKALOVÁ-PECK & PECK 1993: fig. 22; KLASS 1995), *Polyphaga* [1], *Ergaula* [1], and remaining blattarian taxa [0] (see also illustrations in REHN 1951) based on original examination. No data for *Archiblatta*; not scored in the wingless or brachypterous *Eurycotis*, *Lamproblatta*, *Cryptocercus*, *Tryonicus*, and *Lauraesilpha*. We scored the hypothetical ancestor [?], because most of the winged outgroup taxa here considered may have, depending on different interpretations, a large (and strongly folded, see next character) anojugal area (many Orthoptera, Phasmatodea, Plecoptera, and Dermaptera), but some have clearly not (Embioptera, Zoraptera). The scoring of the discrete outgroup taxa is based on the location of the anal fold according to KUKALOVÁ-PECK & LAWRENCE (2004) and HAAS & KUKALOVÁ-PECK (2001).

126 – Internal folding of hindwing anojugal area (–); [0] extensive: at least 4 folding lines (convex and concave alternating); [1] sparse or lacking: no discrete folding lines within the anojugal area. – In Dictyoptera, along the anal fold the anojugal area is flapped beneath the remigium (see KUKALOVÁ-PECK & PECK 1993: fig. 22). In this repose position, the anojugal area displays in most taxa a longitudinal, fan-like folding (KLASS 1995: fig. 346a,b); only in some taxa this area lacks any folding and lies flat beneath the remigium. The character is scored only in taxa having an anojugal area that can be folded beneath the remigium, and hence the character is considered not applicable to Kalotermitidae [-] and Termopsinae [-]. See BEIER (1968: 21) for *Metallyticus* [1], *Mantoida* [0] (very few folds), *Sphodromantis* [0] (see KLASS 1995: fig. 346a for *Mantis*), *Mastotermes* [1] (with two slight folds), *Polyphaga* [1], *Ergaula* [1] (both with no trace of folding), and remaining blattarian taxa [0] based on original examination. No data for *Chaeteessa* and *Archiblatta*; not scored in the wingless or brachypterous *Eurycotis*, *Lamproblatta*, *Cryptocercus*, *Tryonicus*, and *Lauraesilpha*. For scoring hypothetical ancestor [?] and for scoring of discrete outgroup taxa see foregoing character.

127 – Forewing basal suture (28); [0] absent; [1] present. – See DEITZ et al. (2003: characters 28 and 29) and references therein for all isopteran taxa [1]. State [1] has never been reported from any Blattaria or Mantodea and has neither been found in the blattarian and mantodean taxa here included, which are thus scored [0] throughout; only the wingless or brachypterous *Eurycotis*, *Lamproblatta*, *Cryptocercus*, *Tryonicus*, and *Lauraesilpha* are scored [-]

and *Archiblatta*, for which data are not available, is scored [?]. The hypothetical ancestor is scored [?], because wings are also shed in Zoraptera.

128 – Number of cercomeres (54); [0] ≥ 4 with some well-separated cercomeres; [1] ≤ 2 with at most 2 well-separated cercomeres. — As compared to DEITZ et al. (2003) we changed the cercomere numbers defining the states, because there is overlap between the number of well-separated cercomeres in various Blattaria and Termopsinae (including intraspecific variation); only the strongly fused cerci having 1 or 2 discrete cercomeres are well separated from the other conditions. Counting cercomeres is partly problematic and subjective, because cercomeres tend to fuse near the base of the cercus, may be fused laterally but not mesally, etc., and the character is generally disputable (see discussion in DEITZ et al. 2003). Due to the occasional occurrence of sexual dimorphism, all counts were made in males. See DEITZ et al. (2003) and references therein for *Cryptocercus* [1]; IMMS (1919) and WEIDNER (1970) for Termopsinae [0]; WEIDNER (1970) for Kalotermitidae [1]; KCLASS (2000) for *Mastotermes* [1]. Scoring of other dictyopteran taxa [0] based on original examination. No data for *Tryonicus*, *Lauraesilpha*, and *Archiblatta*. The hypothetical ancestor is scored [?] because both one- or two-segmented (e.g., Dermaptera, Phasmatodea, Embioptera, Orthoptera, Mantophasmatodea, Odonata) and many-segmented (e.g., Notoptera, Zygentoma) cerci occur in outgroup taxa here considered.

129 – Pair of longitudinal folds dorsally on subgenital lobe (female) (76); [0] absent; [1] present. — These are the ‘intersternal folds’ in MCKITTRICK (1964) and KCLASS (1998a) (not identical with the ‘intersternal fold’ in WEESNER 1969, which is the laterosternal shelf), which are situated on the dorsal face of the subgenital lobe sclerotized by coxosternum VII (= hind part of venter VII overlapping the venters of the following segments) and serve as a mould for ootheca formation within the vestibulum (MCKITTRICK 1964: 99). The hypothetical ancestor is scored [0], because in other insects the hind rim of venter VII overlapping (or not) venters of following segments does not bear such folds. It should be noted that apart from Dictyoptera only in Dermaptera the hind part of venter VII forms a subgenital lobe sclerotized by coxosternum VII (see KCLASS 2003b, 2001a for a variety of basal Dermaptera; compare character 164); only in this taxon such folds would make some sense but are entirely absent. See KCLASS (1998a) for *Sphodromantis* [0], *Lamproblatta* [1], and *Mastotermes* [1]; MCKITTRICK (1964) for *Deropeltis* [1] and *Anaplecta* [1] (data for *Anaplecta* sp. C); MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [1]; data in WEESNER (1969) and BROWMAN (1935) suggest Termopsinae [0]. Kalotermitidae [0] and remaining blattarian taxa [1] based on original examination. In the blaberid representatives the folds are weakly developed but distinct. No data for *Mantoida*, *Chaeteessa*, *Metallyticus*, *Archiblatta*, *Lauraesilpha*, and *Euphyllodromia*.

130 – Gonapophyses 9 and gonoplags (female) (40); [0] well developed to slightly reduced; [1] highly reduced

or absent. — All Blattaria and Mantodea here sampled as well as *Mastotermes* have these structures well developed (as in KCLASS 1998a: figs. 1–4) and are scored [0], with the exception of *Mantoida*, *Chaeteessa*, *Metallyticus*, *Archiblatta*, and *Euphyllodromia*, for which no data are available; see MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [0]; GRANDCOLAS (1997a) for *Lauraesilpha* [0]; MCKITTRICK (1964: fig. 35 of ‘*Anaplecta* sp. C’) for *Anaplecta* [0]; scoring of remaining taxa based on original examination. Only Kalotermitidae (original examination: complete lack) and Termopsinae (BROWMAN 1935) score [1]. As the presence of gonapophyses 9 and gonoplags (= coxal lobes 9) is clearly the groundplan condition in Dicondylia, we scored the hypothetical ancestor [0] though in some of the outgroup taxa here considered both processes are absent (almost) throughout (Ephemeroptera, Embioptera, Plecoptera, Zoraptera; see, e.g., KCLASS 2003b). *Echinosoma* is scored [0] though gonapophyses 9 are quite reduced (KCLASS 2003b; gonoplags huge).

131 – Presence of unpaired spermathecae on hind margin of venter 8 (female) (--); [0] present; [1] absent. — See KCLASS (1998a; 2003b: 198, 211, 213), MCKITTRICK (1964), DEITZ et al. (2003: character 45), and references therein (especially GUPTA 1948) for discussion, hypothetical ancestor [0], Termopsinae [0], and Kalotermitidae [0] (see also WALL 1971: fig. 1); KCLASS (1998a) for *Sphodromantis* [0], *Mastotermes* [0], *Lamproblatta* [0], *Periplaneta* [0], *Eurycotis* [0], and *Cryptocercus* [0]; MCKITTRICK (1964) for *Deropeltis* [0], *Anaplecta* [0] (based on ‘*Anaplecta* sp. C’), *Parcoblatta* [1], *Nyctibora* [1], *Nauphoeta* [1], *Blaberus* [1], and *Blaptica* [1]; MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [0]; GRANDCOLAS (1997a) for *Lauraesilpha* [0]. *Polyphaga* [0], *Ergaula* [0], *Nahublattella* [1], *Supella* [1], and *Phoetalia* [1] based on original examination. These plesiomorphic spermathecae are forked internally in many of the Dictyoptera here scored [0], but the external opening is single throughout (e.g., MCKITTRICK 1964: figs. 13, 15, 25B). No data for *Mantoida*, *Chaeteessa*, *Metallyticus*, *Archiblatta*, and *Euphyllodromia*.

132 – Presence of paired spermathecae (likely) on hind margin of venter 7 (female) (--); [0] absent; [1] present. — The simultaneous presence of these paired spermathecae beside the plesiomorphic unpaired spermatheca (see previous character) in some Anaplectinae (including ‘*Anaplecta* sp. C’; MCKITTRICK 1964: 58, fig. 39) shows the non-homology of the two types of spermathecae. See KCLASS (1998a; 2003b: 198, 211, 213), DEITZ et al. (2003: character 45), and references therein (especially GUPTA 1948) for discussion, hypothetical ancestor [0], Termopsinae [0], and Kalotermitidae [0] (see also WALL 1971: fig. 1); KCLASS (1998a) for *Sphodromantis* [0], *Mastotermes* [0], *Lamproblatta* [0], *Periplaneta* [0], *Eurycotis* [0], and *Cryptocercus* [0]; MCKITTRICK (1964) for *Deropeltis* [0], *Anaplecta* [1] (based on ‘*Anaplecta* sp. C’), *Supella* [1], *Parcoblatta* [1], *Nyctibora* [1], *Nauphoeta* [1], *Blaberus* [1], and *Blaptica* [1]; MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [0]; GRANDCOLAS (1997a) for *Lauraesilpha* [0]. *Polyphaga* [0], *Ergaula* [0], *Nahublattella* [1], and *Phoetalia* [1]

based on original examination. These apomorphic spermathecae are forked or multiple internally in many of the Dictyoptera here scored [1]; the external openings are mostly single on each side but occasionally they are double or multiple (e.g., MCKITTRICK 1964: figs. 43–45). No data for *Mantoida*, *Chaeteessa*, *Metallyticus*, *Archiblatta*, and *Euphyllodromia*.

133 – Antecostal ridge of paratergal extension of abdominal segment 9 (female) (46); [0] well developed; [1] absent. – See KLASS (1998a: sclerotizations tg+te and ridge ac upon them), DEITZ et al. (2003), and references therein for character definition, discussion, and hypothetical ancestor [0]; KLASS (1998a: 83–85, ac in figs. 2–4, 11–18) for *Sphodromantis* [0], *Mastotermes* [1], *Periplaneta* [0], *Eurycotis* [0], *Lamproblatta* [0], and *Cryptocercus* [0]; MCKITTRICK (1964) for *Deropeltis* [0], *Anaplecta* [0], *Parcoblatta* [0], and *Nyctibora* [0] (this scoring is based on the general statements in MCKITTRICK 1964: 47 and MCKITTRICK & MACKERRAS 1965: 19 of a ridge-like condition of these elements, which are said to be “V-shaped in cross section”; nonetheless, the single taxa should be re-investigated); MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [0]. Kalotermitidae [1], *Polyphaga* [0], *Ergaula* [0], *Nahublattella* [0], *Supella* [0], *Nauphoeta* [0], *Blaberus* [0], *Blaptica* [0], and *Phoetalia* [0] based on original examination. *Kalotermes* has sclerite ribbons corresponding in their location with tg+te of *Mastotermes* (in KLASS 1998a: fig. 4); these are separated from tergum 9 and lack a ridge; however, the interpretation as the paratergal extension 9 (tg+te) is not fully certain. No data for *Mantoida*, *Chaeteessa*, *Metallyticus*, *Archiblatta*, *Lauraesilpha*, *Euphyllodromia*, and Termopsinae (no source for their scoring of Termopsinae indicated by THORNE & CARPENTER 1992; no data in MCKITTRICK 1964). The discrete outgroup taxa have no paratergal extensions (lateral parts of tergum 9 not narrowed); but if the antecosta runs down along the anterior margin of tergum 9 to reach the articulation with genitalic sclerites (gonangulum and possibly others), they are scored [0].

134 – Connection of tergite and paratergal extensions in abdominal segment 9 (female) (47); [0] absent; [1] present. – See DEITZ et al. (2003) and KLASS (1998a) for discussion, hypothetical ancestor [?] (outgroup comparison ambiguous), and Termopsinae [?] (reliable data not available); KLASS (1998a: figs. 2–4, 11–18) for *Sphodromantis* [0], *Mastotermes* [1], *Periplaneta* [0], *Eurycotis* [0], *Lamproblatta* [1], and *Cryptocercus* [0]. Kalotermitidae [0] (see comments in foregoing character) and other blattarian taxa [0] based on original examination. No data for *Mantoida*, *Chaeteessa*, *Metallyticus*, Termopsinae, *Archiblatta*, *Deropeltis*, *Tryonicus*, *Lauraesilpha*, *Anaplecta*, and *Euphyllodromia*. The discrete outgroup taxa have no paratergal extensions, but it can be assessed whether the lateral parts of tergum 9 (articulating with the gonangulum) are separated from [0] or connected with [1] the remainder of tergum 9.

135 – Ootheca = group of eggs in mass with tanned outer coating (female) (41); [0] absent; [1] present. – See DEITZ et al. (2003) for discussion; KLASS & EHLMANN (2003:

fig. 13.71) for *Sphodromantis* [1]; NALEPA & LENZ (2000) for *Mastotermes* [1]; WEIDNER (1970: 115) for Termopsinae [0] and Kalotermitidae [0]; ROTH (1967, 1968) for *Deropeltis* [1], *Periplaneta* [1], *Eurycotis* [1], *Polyphaga* [1], *Cryptocercus* [1], *Anaplecta* [1], *Nahublattella* [1] (data for *Lophoblatta*), *Supella* [1], *Euphyllodromia* [1], *Parcoblatta* [1], *Nyctibora* [1], *Nauphoeta* [1], *Blaberus* [1]; MCKITTRICK (1964) for *Lamproblatta* [1]; ROTH (1987) for *Tryonicus* [1]. *Ergaula* [1], *Blaptica* [1], and *Phoetalia* [1] based on original observations. Egg deposition or oothecae have apparently not been described for *Lauraesilpha*, *Mantoida*, *Chaeteessa*, and *Metallyticus*, all scored [?]. We score all outgroup taxa [0], though egg pods somewhat resembling dictyopteran oothecae are produced by Caelifera and Mantophasmatodea. While in Dictyoptera the secretions come from the true accessory glands of abdominal segment IX, these glands are absent in Mantophasmatodea (KLASS et al. 2003) and most Caelifera (BEIER 1972: 140, accessory glands = “Ovipositor-drüse”), where the secretions originate from other, mesodermal glands (discussion in KLASS 1995; NALEPA & LENZ 2000). We consider production of the egg pod by secretions from asymmetrical accessory glands and the related chemical mechanisms (see NALEPA & LENZ 2000 and references therein) as one constituting criterion for an ootheca.

136 – Advanced rotation of ootheca in vestibulum (female) (--); [0] absent; [1] present. – See ROTH (1967) for discussion. Rotation is absent in *Sphodromantis* [0], which build their oothecae upon the substrate rather than in the vestibulum. The character is not applicable to those termites laying their eggs singly as well as to the outgroup taxa; hence hypothetical ancestor, Kalotermitidae, and Termopsinae are scored [-]. See MCKITTRICK (1964) for *Periplaneta* [0], *Eurycotis* [0], *Lamproblatta* [0], *Cryptocercus* [0], *Anaplecta* [0] (likely, but only observations in preserved specimens available), *Supella* [0], *Parcoblatta* [1], *Nyctibora* [1], *Nauphoeta* [1], *Blaberus* [1], and *Blaptica* [1]; ROTH (1967) for *Polyphaga* [0] and *Euphyllodromia* [0]; ROTH (1970) for *Nahublattella* [0] (data for *Lophoblatta*); NALEPA & LENZ (2000) for *Mastotermes* [0]. *Ergaula* [0], *Deropeltis* [0], and *Phoetalia* [1] based on original observation of breeding cultures. No data for *Mantoida*, *Chaeteessa*, *Metallyticus* (see foregoing character), *Archiblatta*, *Tryonicus*, and *Lauraesilpha*.

137 – Presence of brood sac posteroventrally on abdominal segment 7 and retraction of ootheca or single eggs into it (female) (--); [0] absent; [1] present.

– In all Dictyoptera the anteroventral depth of the vestibulum, beneath the laterosternal shelf, is somewhat deepened to the anterior (part ‘se’ in general scheme in KLASS 1998a: fig. 1; MCKITTRICK 1964: figs. 10, 22B, 26B, 40B). In some Blattaria this deepening is much stronger, and a brood sac is thus formed (MCKITTRICK 1964: figs. 79B, 80, 81) into which the completed ootheca (or rarely single eggs) is incubated until shortly before the nymphs hatch (ovoviviparous and viviparous taxa; see NALEPA & BELL 1997). The hypothetical ancestor and all discrete outgroup taxa are scored [0] because from no other insects

such a brood sac on the hind part of venter 7 is reported. See KLASS (1998a) for *Sphodromantis* [0], *Lamproblatta* [0] (see also MCKITTRICK 1964), and *Mastotermes* [0] (see also NALEPA & LENZ 2000); MCKITTRICK (1964) for *Periplaneta* [0], *Deropeltis* [0], *Eurycotis* [0], *Cryptocercus* [0], *Anaplecta* [0], *Parcoblatta* [0] (confirmed by recent studies of M. Olsen), and *Nyctibora* [0]; MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [0], *Polyphaga* [0], *Ergaula* [0], *Nahublattella* [0] (though with a fairly deep cavity beneath the laterosternal shelf), *Supella* [0], *Nauphoeta* [1], *Blaberus* [1], *Blaptica* [1], and *Phoetalia* [1] based on original examination of the presence of a brood sac and (in case of [1]) on the finding of a rotated ootheca located in it. No data for *Mantoida*, *Chaeteessa*, *Metallyticus*, *Archiblatta*, *Lauraesilpha*, and *Euphyllodromia*. Kalotermitidae [0] (see WALL 1971: fig. 1; original examination) and Termopsinae [0] (see WEESNER 1969 and BROWMAN 1935) are considered applicable because the absence of a brood sac can be determined and internal incubation is not dependent on ootheca formation (as shown by some blaberids incubating several single eggs).

138 – External genitalia (male) (48); [0] very complex with many sclerites, projections, and muscles; [1] very simple lobe with or without a pair of ventral sclerites, or virtually absent. — KLASS (1995, 1997) demonstrated the homology of genitalic substructures in Blattaria and Mantodea. See KLASS (1995, 1997) for all blattarian and mantodean taxa here included [0]; KLASS (2000) for *Mastotermes* [1]; ROONWAL (1955, 1970), WEESNER (1969), and KLASS et al. (2000) for statements on other isopteran taxa [1]; KLASS (2000: 249) for hypothetical ancestor [?] (though discrete genitalic similarities between Dictyoptera and most Mantophasmatodea render [0] quite likely; KLASS et al. 2003: 57). *Timema* is scored [?] because nothing is known about the complexity of its phallic structures.

139 – Symmetry of external genitalia (male) (48); [0] strongly asymmetrical; [1] (almost) bilaterally symmetrical (including virtual absence). — KLASS (1995, 1997) demonstrated the homology of asymmetry in Blattaria and Mantodea. See KLASS (1995, 1997) for all blattarian and mantodean taxa here included [0]; KLASS (2000) for *Mastotermes* [1]; ROONWAL (1955, 1970), WEESNER (1969), and KLASS et al. (2000) for other isopteran taxa [1]; no asymmetries mentioned; KLASS (2000: 249) for hypothetical ancestor [?] (though discrete genitalic similarities between Dictyoptera and most Mantophasmatodea may render [0] quite likely; KLASS et al. 2003: 57). The only slightly asymmetrical genitalia in *Echinosoma* (GILES 1963: fig. 32) are scored [1].

140 – Number of flagella per sperm cell (male) (51); [0] 1 with 9+9+2 microtubular pattern; [1] 0; [2] many with 9+0 microtubular pattern; non-additive. — See DEITZ et al. (2003) and references therein for hypothetical ancestor [0], *Mastotermes* [2], *Cryptocercus* [?], Termopsinae [1], and Kalotermitidae [1]; ROSATI (1967) for *Blaberus* [0]; JAMIESON et al. (1999) for *Periplaneta* [0]. Conditions in the remaining dictyopteran taxa here included are unknown, but some are scored based on data

given in JAMIESON et al. (1999) for likely closely related taxa: *Sphodromantis* [0] like *Iris* and *Mantis* (see also BACETTI 1987); *Parcoblatta* [0] like *Blattella*; *Nauphoeta* [0], *Blaptica* [0], and *Phoetalia* [0] like *Leucophaea*, *Blaberus*, and *Pycnoscelus* (all Blaberidae).

141 – Sperm cell acrosome (male) (52); [0] present; [1] absent. — See DEITZ et al. (2003) and references therein for hypothetical ancestor [0]; BACETTI (1987) for *Mastotermes* [1], Termopsinae [1], and Kalotermitidae [1]; JAMIESON et al. (1999) for *Periplaneta* [0] and *Blaberus* [0]; *Cryptocercus* [0] based on K.J. Mullins (pers. comm. to DEITZ et al. 2003). Conditions in the remaining dictyopteran taxa here included are unknown, but some are scored on the same basis as in the foregoing character: *Sphodromantis* [0], *Parcoblatta* [0], *Nauphoeta* [0], *Blaptica* [0], and *Phoetalia* [0].

142 – Number of mitochondrial derivatives in sperm cell (male) (74); [0] 2 (additional mitochondria absent); [1] 0 (several to many small mitochondria present). — See THORNE & CARPENTER (1992), DEITZ et al. (2003), and references therein for discussion, *Mastotermes* [1], Termopsinae [1], Kalotermitidae [1], and *Cryptocercus* [0]; JAMIESON et al. (1999) for hypothetical ancestor [0], *Periplaneta* [0], and *Blaberus* [0]. Conditions in the remaining dictyopteran taxa here included are unknown, but some are scored on the same basis as in the foregoing characters: *Sphodromantis* [0], *Parcoblatta* [0], *Nauphoeta* [0], *Blaptica* [0], and *Phoetalia* [0].

143 – Symmetry of primary sclerites and denticles of proventriculus (30); [0] with a bilateral component; [1] purely radial. — Bilateral symmetry in dictyopteran proventriculi is, if present, expressed in virtually all elements: denticles, sclerites, hairlines, pulvilli, and others (KLASS 1998b), and in all these elements the degree of bilaterality varies strongly among taxa. Weak bilaterality is difficult to detect in the membranous parts or in flat sclerites, where minor differences in relative size or proportions are concerned but hardly discrete differences in shape, but it is most pronounced in the six denticles of the primary plicae, which differ in shape according to a fairly uniform pattern. We note that the degree of bilateral symmetry is very different among the taxa here scored [0]. In contrast to DEITZ et al. (2003) we restricted the character to the armarial part of the primary plicae (sclerites and denticles). Further characters may be defined in the future for the symmetry of the other elements, but these will be difficult to handle. Based on results of KLASS (1998b) on Zygentoma-Lepismatidae and nymphs of Odonata-Corduliidae and TILGNER et al. (1999) on Phasmatodea-Timematidae the outgroup is probably best considered [0] as in DEITZ et al. (2003); nonetheless, we scored the hypothetical ancestor [?] because simply structured (simplified?) proventriculi in many insects show a purely radial symmetry. Among the discrete outgroup taxa, conditions in *Echinosoma* and *Dinocras* are unknown, and *Timema* is clearly [0]. The others are problematic to score because primary denticles are likely absent in *Karooophasma* (scored [?]) because the bilateral pattern in the sclerites differs from Dictyoptera) and *Grylloblatta* (scored [?]) because the occurrence of

bilaterality is unknown), and both primary denticles and sclerites are absent in *Locusta* (scored [1] due to the apparent lack of bilaterality in the proventricular armature).

See MCKITTRICK (1964) for *Deropeltis* [0]; MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [0]; KLASS (1998b) for *Mantoida* [0], *Sphodromantis* [0], *Mastotermes* [1], *Periplaneta* [0], *Eurycotis* [0], *Lamproblatta* [0] (but with a superimposed spiral distortion of the symmetry), and *Cryptocercus* [0]; LEBRUN & LEQUET (1983) and NOIROT (1995) for Kalotermitidae [1] and Termopsinae [1]. *Polyphaga* [1], *Ergaula* [0], *Anaplecta* [0], *Nahublattella* [1], *Supella* [0], *Euphyllodromia* [0], *Parcoblatta* [0], *Nyctibora* [0], *Nauphoeta* [0], *Blaberus* [0], *Blaptica* [1], and *Phoetalia* [1] based on original examination. No data for *Chaeteessa*, *Metallyticus*, *Archiblatta*, and *Lauraesilpha*. While bilateral symmetry is strong in the scored Blattidae, Lamproblattidae, and Tryonicidae, it is much weaker in the included members of Cryptocercidae, Polyphagidae, 'Blattellidae', and Blaberidae, and it can be completely absent in the three latter groups. In Blaberidae and Polyphagidae the structure of the armarium is fairly simple and with weak sclerotization, and only primary and secondary plicae are present but no plicae of lower rank. Especially the sclerotization of the posterior part of the primary denticles is weakened (also in *Nyctibora*). While *Nauphoeta* and *Blaberus* show a vestigial bilaterality through a sideward inclination of the paired denticles or different lengths of the (weak) primary sclerites, this is not clear in *Blaptica* and *Phoetalia*. In *Ergaula*, whose proventriculus strongly resembles that in Blaberidae, primary sclerites are of different length but denticles are (almost?) identical among the primary plicae. In *Polyphaga* plicae of both ranks have a weakly sclerotized part, somewhat elevated but not forming a denticle, and bearing many small tubercles; no clear bilateral symmetry component was detected in this pattern.

144 – Primary denticles of proventriculus (–); [0] present; [1] absent. — The primary plicae bear discrete denticles on the primary sclerites in nearly all dictyopteran taxa here studied. See MCKITTRICK (1964) for *Deropeltis* [0]; MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [0]; KLASS (1998b) for *Mantoida* [0], *Sphodromantis* [0] (both lacking the denticle on one primary plica), *Mastotermes* [0], *Periplaneta* [0], *Eurycotis* [0], *Lamproblatta* [0], and *Cryptocercus* [0]; LEBRUN & LEQUET (1983) and NOIROT (1995) for Kalotermitidae [0] and Termopsinae [0]. *Polyphaga* [1] and other scored Blattaria [0] based on original examination (see foregoing character for *Ergaula* [0]; in *Phoetalia* [0] each denticle bears several small spines). No data for *Chaeteessa*, *Metallyticus*, *Lauraesilpha*, and *Archiblatta*. For hypothetical ancestor [?] and scoring of discrete outgroup taxa see foregoing character.

145 – Secondary sclerites of proventriculus (71); [0] absent; [1] present. — In contrast to DEITZ et al. (2003) we scored the hypothetical ancestor [?], because, on the one hand, apart from Notoptera also the newly discovered Mantophasmatodea have sclerites of secondary (and tertiary) rank (KLASS et al. 2002), both taxa being good

candidates for being the closest relatives of Dictyoptera (KLASS et al. 2003). On the other hand, such sclerites are absent in Zygentoma-Lepismatidae and nymphs of Odonata-Corduliidae (KLASS 1998b), in Phasmatodea-Timematidae (TILGNER et al. 1999), and in insect taxa with simply structured proventriculi (e.g., JUDD 1948). See MCKITTRICK (1964) for *Deropeltis* [1]; MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [1]; KLASS (1998b) for *Mantoida* [0], *Sphodromantis* [0], *Mastotermes* [1], *Periplaneta* [1], *Eurycotis* [1], *Lamproblatta* [1], and *Cryptocercus* [1]; LEBRUN & LEQUET (1983) and NOIROT (1995) for Kalotermitidae [1] and Termopsinae [1]. Scoring of other blattarian taxa [1] based on original examination. No data for *Chaeteessa*, *Metallyticus*, *Lauraesilpha*, and *Archiblatta*. See notes in character 143 on Polyphagidae and Blaberidae.

146 – Secondary denticles of proventriculus (31); [0] absent; [1] present. — The sclerotized parts of the secondary plicae are in many dictyopteran taxa elevated or bulged, but only in few taxa they form discrete denticles. We scored the hypothetical ancestor [0]; this is based on results of KLASS (1998b) on Zygentoma-Lepismatidae and nymphs of Odonata-Corduliidae and TILGNER et al. (1999) on Phasmatodea-Timematidae, where such denticles are absent, and the additional absence of such denticles in insect taxa with simply structured proventriculi (e.g., JUDD 1948); tooth-like elevations on the secondary plicae of Notoptera and Mantophasmatodea are placed at the posterior end of their sclerites and are thus unlikely homologous with denticles in Dictyoptera (KLASS et al. 2002). See MCKITTRICK (1964) for *Deropeltis* [0]; MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [0]; KLASS (1998b) for *Mantoida* [0], *Sphodromantis* [0], *Mastotermes* [1], *Periplaneta* [0], *Eurycotis* [0], *Lamproblatta* [0], and *Cryptocercus* [0]; LEBRUN & LEQUET (1983) and NOIROT (1995) for Kalotermitidae [1] and Termopsinae [1]. Scoring of *Nauphoeta* [1] (denticles similar in shape to those in *Mastotermes*) and other blattarian taxa [0] based on original examination. No data for *Chaeteessa*, *Metallyticus*, *Lauraesilpha*, and *Archiblatta*. See notes in character 143 on Polyphagidae and Blaberidae.

147 – Similarity of primary and secondary sclerites of proventriculus (72); [0] secondary sclerites distinctly narrower ($< 1/2$) than primary sclerites and of different outline; [1] secondary sclerites not much narrower ($> 1/2$) than primary sclerites and of similar outline. — For hypothetical ancestor [?] see comments in character 145. For illustration of character see KLASS (1998b: fig. 4, showing state [0]). Taxa lacking secondary sclerites (see character 145) scored [–]. Regarding taxa having secondary sclerites, see LEBRUN & LEQUET (1983: plate 3; 1985: plate 1) and NOIROT (1995) for Kalotermitidae [1] and Termopsinae [1]; MCKITTRICK (1964: figs. 135, 141) for *Mastotermes* [1] and *Cryptocercus* [1]; KLASS (1998b: fig. 4) for *Periplaneta* [0]. Scoring of other blattarian taxa [0] based on original examination. No data for *Chaeteessa*, *Metallyticus*, *Deropeltis*, *Lauraesilpha*, and *Archiblatta*. While *Cryptocercus* and the isopteran taxa clearly show state [1], this state is closely approached in some of the

taxa with weak armarial sclerotizations and only two ranks of plicae (included members of Blaberidae and Polyphagidae) as well as in some Blattellidae. Blattinae, Polyzosteriinae, *Tryonicus*, and *Lamproblatta* show state [0] most clearly.

148 – Primary pulvilli of proventriculus (32); [0] hardly or moderately expanded mesally (or absent = corresponding area entirely flat); [1] strongly expanded mesally and anteriorly, partially overlapping associated sclerites. – In most Blattaria the primary pulvilli, located behind the primary denticles, are moderately expanded mesally and distinctly set off from the part of the primary plicae behind them by a notch. Only in the blaberid and polyphagid representatives here included the mesal expansion and notch are indistinct. In contrast, in *Cryptocercus* and the isopteran taxa the expansion of the primary pulvilli is particularly strong, and the pulvilli are even directed anteriorly to cover the hind parts of the primary sclerites. See LEBRUN & LEQUET (1983: plate 1 figs. 1, 4) and NOIROT (1995: figs. 20, 21, 23, 26) for illustration of state [1], Kalotermitidae [1], and Termopsinae [1]. *Mastotermes* [1], *Cryptocercus* [1], and remaining blattarian taxa [0] based on original examination and partly on KLAAS (1998b). In Mantodea the identification of the primary pulvilli is ambiguous (KLAAS 1998b), but because none of the respective elements shows state [1], *Mantoida* and *Sphodromantis* are scored [0]. No data for *Chaeteessa*, *Metallyticus*, *Deropeltis*, *Lauraesilpha*, and *Archiblatta*. The hypothetical ancestor is scored [0] since state [1] is apparently not reported for any of the taxa here considered as outgroup taxa (e.g., KLAAS 1998b; TILGNER et al. 1999; KLAAS et al. 2002; JUDD 1948). Among the discrete outgroup taxa only in *Timema* the area in question can be clearly identified (due to the clear presence of primary denticles) and scored [0], flat.

149 – Quaternary plicae of proventriculus (34); [0] present; [1] absent. – These are the elements called ‘intercalary plates’ by MCKITTRICK (1964). We scored the hypothetical ancestor [?] because – while quaternary plicae are usually clearly absent – the identification of such elements in some insects is ambiguous. See MCKITTRICK (1964) for *Deropeltis* [0]; MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [0]; KLAAS (1998b) for *Mantoida* [0], *Sphodromantis* [0] (interpretation based on number of dichotomies in proventricular grooves), *Mastotermes* [1], *Periplaneta* [0], *Eurycotis* [0], *Lamproblatta* [0], and *Cryptocercus* [0]; LEBRUN & LEQUET (1983) and NOIROT (1995) for Kalotermitidae [1] and Termopsinae [1] (see KLAAS 1998b: 27ff for interpretation of “éléments de la couronne IV”). *Polyphaga* [1], *Ergaula* [1], *Anaplecta* [0] (see below), *Nahublattella* [0] (likely), *Supella* [0], *Euphyllodromia* [0], *Parcoblatta* [0], *Nyctibora* [0], *Nauphoeta* [1], *Blaberus* [1], *Blaptica* [1], and *Phoetalia* [1] based on original examination. No data for *Chaeteessa*, *Metallyticus*, *Lauraesilpha*, and *Archiblatta*. See notes in character 143 on Polyphagidae and Blaberidae. In *Anaplecta* [0] quaternary plicae could with sufficient certainty only be identified between each tertiary and primary plica (likely the ‘sclerotized hairline ridges’ in the phragmata, MCKITTRICK 1964: 78);

between each tertiary and secondary plica there was no clear identification possible of hairline ridges either as quaternary plicae (with free posterior end) or as hairlines flanking the major plicae (joining the pulvillus of such a plica posteriorly, see KLAAS 1998b).

150 – Cardiac (stomodaeal) valve of proventriculus (77); [0] short funnel; [1] long tube. – We scored the hypothetical ancestor [0], because this state is found in Zygentoma-Lepismatidae and nymphs of Odonata-Corduliidae (KLAAS 1998b), Mantophasmatodea (KLAAS et al. 2002: fig. 2E), Dermaptera-Pygidicranidae, Notoptera (K.-D. Klass, unpublished observations), and Phasmatodea-Timematidae (TILGNER et al. 1999: figs. 39, 40); state [1] has apparently not been reported otherwise for Archaeognatha, Zygentoma, or Lower Pterygota (see, e.g., illustrations in JUDD 1948 for a variety of taxa; literature listed for discrete outgroup taxa); only derived Phasmatodea may constitute an exception (JUDD 1948: fig. 25). See NOIROT (1995), JUDD (1948: fig. 84), and IMMS (1919: text-fig. 9) for Kalotermitidae [1] and Termopsinae [1]; KLAAS (1998b) for *Mantoida* [0], *Sphodromantis* [0], *Periplaneta* [1], *Eurycotis* [1], *Lamproblatta* [1], *Cryptocercus* [1], and *Mastotermes* [1]. [1] is also very likely for *Tryonicus*, though not clearly visible in MCKITTRICK & MACKERRAS (1965: fig. 2). Scoring of remaining blattarian taxa [1] based on original examination. No data for *Chaeteessa*, *Metallyticus*, *Lauraesilpha*, *Archiblatta*, and *Deropeltis*. In the blaberid representatives and *Ergaula* the cardiac valve is very wide and not as long as in the other Blattaria and Isoptera, and thus less discretely tube-shaped, but still it projects deep into the midgut, fulfilling [1].

151 – Number of Malpighian tubules (73); [0] ≥ 17 ; [1] 12–16; [2] ≤ 10 ; additive. – See DEITZ et al. (2003) for hypothetical ancestor [?], potential paedomorphic evolution, and *Cryptocercus* [0]; NOIROT (1995: 208f) for *Mastotermes* [1], Kalotermitidae [2], and Termopsinae [2]; LECONTE et al. (1967) for *Blaberus* [0], *Periplaneta* [0], *Lamproblatta* [0], *Parcoblatta* [0], *Polyphaga* [0], *Nahublattella* [0], *Supella* [0], *Nyctibora* [0], *Nauphoeta* [0], *Blaptica* [0] based on unpublished results by H. Bohn and coworkers. *Sphodromantis* [0] and *Phoetalia* [0] based on original examination. No data for the remaining dictyopteran taxa. The arrangement of the Malpighian tubules in groups is another useful character (LECONTE et al. 1967) but needs careful examination in many taxa. Scoring of *Grylloblatta* [?] is based on its range of 14–24 Malpighian tubules.

152 – Mesothoracic alary muscles (11); [0] present; [1] absent. – See NUTTING (1951: 510f, 531) for *Mastotermes* [1], Termopsinae [1], Kalotermitidae [1], *Periplaneta* [0], *Eurycotis* [0], *Cryptocercus* [0], *Supella* [0], and *Blaberus* [0]. Although none of the mantodean taxa here considered is included in NUTTING’s sample, we tentatively score all of them [0], because the four mantodean genera studied by NUTTING (1951) consistently show this state. In other lower neopteran orders the presence of the meso- and metathoracic alary muscles varies strongly, and according to NUTTING (1951) this is correlated with the development of the wings: strong development of wings

and flight muscles goes along with these muscles lacking, while species with weakly developed wings tend to have the muscles. Possibly the muscles are present in nymphs (which have not been studied), are reduced with the flight apparatus being developed, but tend to be retained in the adult stage in taxa with a depauperate flight apparatus. Retention would thus appear as an apomorphy. On the other hand, the presence of mesothoracic alary muscles may in Dictyoptera plainly represent a plesiomorphic condition. Based on this and on comparison with other insects (NUTTING 1951) we scored the hypothetical ancestor [?].

153 – Segmental arteries in some abdominal segments (12); [0] absent; [1] present. – Such arteries are widespread in non-hexapod arthropods, but they are probably entirely absent in hexapods other than (many) Dictyoptera (KLASS 1995: 165; G. Pass, pers. comm.). We thus scored the hypothetical ancestor [0] (in contrast to DEITZ et al. 2003: outgroup [?]). Otherwise see NUTTING (1951) and DEITZ et al. (2003) for character definition and discussion. See KLASS (1999: fig. 7) for *Sphodromantis* [1]. We scored the remaining mantodean taxa [?] because none of these has been studied and NUTTING (1951: 511, 529) found both [0] and [1] in different mantodean taxa. See NUTTING (1951) for *Mastotermes* [0], Termopsinae [0], Kalotermitidae [0], *Periplaneta* [1], *Eurycotis* [1], *Cryptocercus* [1], *Supella* [1], and *Blaberus* [1].

154 – Presence of ‘lobelet’ in mushroom bodies of brain (–); [0] absent; [1] present. – See FARRIS & STRAUSFELD (2003) for discussion, Termopsinae [1], Kalotermitidae [1], *Cryptocercus* [1], *Periplaneta* [1], *Blaberus* [0] (and Mantidae: *Tenodera* [0], Blattellidae: *Blattella* [0], Blaberidae: *Diploptera* [0]). Conditions in the remaining taxa here included are unknown, but some are scored based on data given in FARRIS & STRAUSFELD (2003) for likely closely related taxa: *Sphodromantis* [0] like *Tenodera*; *Parcoblatta* [0] like *Blattella*; *Nauphoeta* [0], *Blaptica* [0], and *Phoetalia* [0] like *Diploptera* and *Blaberus* (all Blaberidae). We scored the hypothetical ancestor [?], because the condition in any other insect is not explicitly mentioned in FARRIS & STRAUSFELD (2003).

155 – Abdominal neuromeres (segmental ganglia) fused to metathoracic neuromere (13); [0] 1st only; [1] 1st + 2nd + 3rd. – See DEITZ et al. (2003) and references therein for discussion, *Periplaneta* [0], *Blaberus* [0], *Mastotermes* [0], Termopsinae [0], and Kalotermitidae [0]; KLASS (1999) for *Sphodromantis* [1]. *Mantoida* [1] based on original examination. No data for the remaining dictyopteran taxa. None of the anterior abdominal neuromeres is fused to the metathoracic one in Archaeognatha and Zygentoma (BIRKET-SMITH 1974; BARNHART 1961), and a fusion of only the first abdominal neuromere is likely the groundplan condition in all pterygote orders here considered as outgroup taxa (see, e.g., NESBITT 1941, 1956; WALKER 1943; KLASS et al. 2002) except Zoraptera; hence we scored the hypothetical ancestor [0].

156 – Chromosomal sex determination (65); [0] XX/XY; [1] XX/XO; [2] XX/X₁X₂Y; non-additive. – See DEITZ et al. (2003) and references therein for discussion,

hypothetical ancestor [?], *Mastotermes* [0], Termopsinae [?], and Kalotermitidae [0]; WHITE (1976: 15ff) for *Mantoida* [1], *Sphodromantis* [2]; WHITE (1976: 3ff) for *Deropeltis* [1], *Periplaneta* [1], *Eurycotis* [1], *Polyphaga* [1], *Lamproblatta* [1], *Cryptocercus* [1] (see also LUYKX 1983), *Nahublattella* [1], *Supella* [1], *Parcoblatta* [1], *Nyctibora* [1], *Nauphoeta* [1], *Blaberus* [1], and *Phoetalia* [1]. No data for the remaining dictyopteran taxa.

157 – Diverse ‘fauna’ of Hypermastigida in hind gut (75); [0] absent; [1] present. – We split character 75 of DEITZ et al. (2003), which refers to both Hypermastigida and Oxymonadida, into two characters, each referring to one of these groups (see also character 158). The reason is that Hypermastigida and Oxymonadida are not closely related (PARKER 1982; MÖHN 1984; MORIYA et al. 2001) and can thus be supposed to have evolved their association with *Cryptocercus* and Isoptera independently. Importantly, while a few hypermastigid and oxymonadid taxa show a wider occurrence, several family- and genus-level taxa of both groups are shared between *Cryptocercus* and various isopteran taxa but have not been found elsewhere (e.g., PARKER 1982). See DEITZ et al. (2003) and references therein for discussion, the wider occurrence of a few hypermastigid taxa, hypothetical ancestor [0], *Mastotermes* [1], Termopsinae [1], Kalotermitidae [1], and *Cryptocercus* [1]. The remaining blattarian and the mantodean taxa here considered as well as the discrete outgroup taxa are scored [0] throughout since state [1] has not been reported for any of them (only *Karoophasma* is scored [?] because the hindgut fauna was never studied in a mantophasmatodean). However, while there are many general statements of absence of a corresponding hypermastigid ‘fauna’ in Blattaria except *Cryptocercus*, explicit statements of absence in specific blattarian species/taxa as well as other insects are very limited, and it cannot be excluded that Hypermastigida of the groups presently thought to be restricted to *Cryptocercus* and Isoptera will be found in some additional Dictyoptera or non-dictyopterans.

158 – Diverse ‘fauna’ of Oxymonadida in hind gut (75); [0] absent; [1] present. – See DEITZ et al. (2003) and references therein for discussion, the wider occurrence of a few oxymonadid taxa, hypothetical ancestor [0], *Mastotermes* [1], Termopsinae [1], Kalotermitidae [1], and *Cryptocercus* [1]. The remaining blattarian and the mantodean taxa here considered as well as the discrete outgroup taxa are scored [0] throughout (only *Karoophasma* [?]), the shortcomings in the documentation being the same as in the foregoing character.

159 – *Blattabacterium* in specialized cells of fat body (55); [0] absent; [1] present. – We score presence [1] only for taxa where gene sequencing has shown that the bacterial symbionts pertain to *Blattabacterium*, while earlier reports based on cytological studies are not accepted. However, we score absence [0] also based on cytological studies that found absence of bacteriocytes in the fat body. *Blattabacterium* has not been found in insects other than Dictyoptera, with the exception of Coleoptera-Coccinellidae (HURST et al. 1997; LO et al. 2003); we thus score the hypothetical ancestor and all discrete

outgroup taxa [0], although there are shortcomings in the documentation comparable to those in the foregoing character (only *Karoophasma* is scored [?] because the fat body was never studied in a mantophasmatodean). Among Mantodea only *Mantis religiosa* has been tested for *Blattabacterium*, which was not found therein (C. Bandi and L. Sacchi pers. comm. to DEITZ et al. 2003); on this basis the closely related *Sphodromantis* is scored [0]. See SACCHI et al. (1998a,b) for Termopsinae [0]; BANDI et al. (1997) for Kalotermitidae [0] and *Mastotermes* [1]; BANDI et al. (1995) and LO et al. (2003) for *Cryptocercus* [1], *Periplaneta* [1], *Nauphoeta* [1], *Blaberus* [1], and *Polyphaga* [1].

160 – Care of juveniles (67); [0] absent (solitary or gregarious); [1] biparental (subsocal); [2] alloparental = care of young by individuals other than the mother or father (eusocial); additive. — See DEITZ et al. (2003) and references therein for discussion, *Mastotermes* [2], Termopsinae [2], Kalotermitidae [2], and *Cryptocercus* [1]. The remaining blattarian and the mantodean taxa here considered are scored [0] throughout since states [1] or [2] have not been reported for them, although explicit statements of absence of (allo)parental care are not available for many of them. A number of Blattaria here not included exhibit uni- or biparental care (NALEPA & BELL 1997: 36–38; we suggest uniparental care to be defined as a state separate from biparental care). We scored the hypothetical ancestor [0] since most insect orders do not display brood care in their ground plan; only the Dermaptera and Embioptera probably do, but they both show uniparental (maternal) brood care (e.g., EDGERLY 1997; GÜNTHER & HERTER 1974; MATZKE & KLASS 2005). Additive treatment is justified because taxa exhibiting alloparental care run through a stage of biparental care at the time a new colony is founded by a pair of (de)alates (e.g., BOHN 2003).

161 – Presence of nest (70); [0] absent; [1] present (galleries within and/or away from wood). — See DEITZ et al. (2003) and references therein for *Cryptocercus* [1]; WEIDNER (1970) for *Mastotermes* [1], Termopsinae [1], and Kalotermitidae [1]. The remaining blattarian and the mantodean taxa here considered are scored [0] throughout since nest-building has not been reported for them, although explicit statements of absence of nest-building are not available for many of them. We scored the hypothetical ancestor [?]; most insect orders do not display nest building in their ground plan, but the Dermaptera and Embioptera do (in connection with uniparental brood care, see references in foregoing character).

162 – Tentorium (--); [0] not perforated; [1] perforated. — In Dictyoptera the corpotentorium has special arms enclosing the nerve cord and fused medially, thus rendering the tentorium “perforated”. However, this character has been studied only in few species. See HUDSON (1945) for *Deropeltis* [1] and *Mastotermes* [1]; PRADL (1971) for *Blaberus*, *Sphodromantis* [1] and *Periplaneta* [1] based on original examination. We scored the hypothetical ancestor [0] because a tentorial perforation enclosing the nerve cord is not known from any non-dictyopteran insect (except some Coleoptera).

163 – Non-spiracular insertion of abdominal spiracle dilator (--); [0] on anterior corner of coxosternum; [1] on (para)tergite in front of spiracle. — In the few Dictyoptera examined the abdominal spiracle dilator inserts on the paratergite in front of the spiracle: see KLASS (1999) for *Periplaneta* [1] and *Sphodromantis* [1]; KLASS (2000) for *Mastotermes* [1]. We scored the hypothetical ancestor [?] because state [1] has also been found in abdominal segment 8 of the dermapteran *Dacnodes* (KLASS 2003b: fig. 22) and in segment 7 of the zygentoman *Thermobia* (ROUSSET 1973); state [0] is more widespread (KLASS 2000), including the dermapteran *Hemimerus* (KLASS 2001a). The character is not applicable to *Grylloblatta*, which lacks abdominal spiracle muscles (see WALKER 1943; K.-D. Klass, unpublished observations).

164 – Abdominal coxosternum 7 (female) (--); [0] not expanded posteriorly (resembling coxosternum 6); [1] strongly expanded posteriorly to form a subgenital plate (much longer and medially more produced than coxosternum 6). — We scored the hypothetical ancestor [?] because state [1] is also found in Dermaptera. For explanations see character 129. See KLASS (1998a) for *Sphodromantis* [1], *Lamproblatta* [1], and *Mastotermes* [1]; MCKITTRICK (1964) for *Deropeltis* [1] and *Anaplecta* [1] (data for *Anaplecta* sp. C); MCKITTRICK & MACKERRAS (1965) for *Tryonicus* [1]; IMMS (1919) and BROWMAN (1935) for Termopsinae [1]. Scoring of remaining dictyopteran taxa [1] based on original examination. No data for *Mantoida*, *Archiblatta*, *Lauraesilpha*, and *Euphyllodromia*.

8.3. Characters only applicable to (sub-)social taxa

These characters have also been used and discussed previously by THORNE & CARPENTER (1992) and DEITZ et al. (2003). They are applicable only to taxa that form different castes and/or build a nest, hence only to the isopteran taxa and partly to *Cryptocercus* (nest characters). All these characters have without modifications been adopted from DEITZ et al. (2003), where all scorings are explained. Numbers behind character definitions refer to character numbers in DEITZ et al. (2003).

165 – Head size and shape (soldier) (56); [0] large and elongate; [1] not large and elongate. — *Mastotermes* [1], Termopsinae [0], and Kalotermitidae [0].

166 – Ocelli (soldier) (57); [0] vestigial; [1] absent. — *Mastotermes* [0], Termopsinae [1], and Kalotermitidae [1].

167 – Bladelike forecoxa protuberance (soldier) (58); [0] absent; [1] present. — *Mastotermes* [1], Termopsinae [0], and Kalotermitidae [0].

168 – Number of cercomeres (soldier) (59); [0] 5–7; [1] 2. — *Mastotermes* [0], Termopsinae [0], and Kalotermitidae [1].

169 – Soldier neotenic (60); [0] present; [1] absent. — *Mastotermes* [1], Termopsinae [0], and Kalotermitidae [1].

170 – Chemical defense (soldier) (61); [0] absent;

[1] present. — *Mastotermes* [1], Termopsinae [0], and Kalotermitidae [0].

171 – Anterior caeca of mesenteron (worker/pseudergate) (62); [0] present; [1] absent. — *Mastotermes* [0], Termopsinae [0], and Kalotermitidae [1].

172 – Reversionary molts (worker/pseudergate) (63); [0] present; [1] absent. — *Mastotermes* [1], Termopsinae [0], and Kalotermitidae [0].

173 – Abdominal segments bearing sternal glands (worker/pseudergate) (64); [0] III+IV+V; [1] V; [2] IV; non-additive. — *Mastotermes* [0], Termopsinae [2], and Kalotermitidae [1].

174 – Foraging away from nest (69); [0] absent; [1] present. — *Mastotermes* [1], Termopsinae [0], Kalotermitidae [0], and *Cryptocercus* [0].

175 – Nest architecture (70); [0] simple galleries within wood; [1] complex galleries within and away from wood. — *Mastotermes* [1], Termopsinae [0], Kalotermitidae [0], and *Cryptocercus* [0].

8.4. Characters not used

Separation of compound eyes on vertex (3); [0] narrow; [1] broad. — Variation in this character is strong and partly concerns the generic level. Thus, while it may be helpful for phylogeny reconstruction on a lower systematic level, it does not appear useful for resolving high-rank relationships (see DEITZ et al. 2003).

Subsidiary tooth on 1st marginal tooth of right mandible (6); [0] absent; [1] present. — The subsidiary tooth is a small, low ridge basally upon the anterior margin of the first tooth of the right mandible (tooth behind tip of mandible; AHMAD 1953: fig. 6, left column). AHMAD (1953) considered it absent in Blattaria, Mastotermitidae, and Kalotermitidae but present in Termopsidae (included in Hodotermitidae therein). However, based on our studies, such a subsidiary tooth is among Blattaria distinct in, e.g., *Lamproblatta*, and recognizable in, e.g., *Deropeltis*. Even in *Cryptocercus* and *Mastotermes* the outline of the first tooth of the right mandible is a bit irregular in the respective area, suggesting a vestigial subsidiary tooth. The subsidiary tooth is thus likely a groundplan element of Blattaria and Isoptera. Since its reduction is fluent and seems to be strongly homoplastic, the character is here not used.

Wings (16); [0] fully developed or slightly reduced; [1] strongly reduced or absent. — This character is here not used because wing development often differs between the sexes of the same species and between species that are obviously closely related based on many other characters (strong variation even within genera). Thus, this character does not appear useful for resolving high-rank relationships.

Diploid chromosome number (66); [0] ≤ 93 ; [1] 98. — As previously used in THORNE & CARPENTER (1992) and DEITZ et al. (2003), the definition of states merely separates the highest number from the rest. Using pure chromosome numbers in phylogenetic reconstruction appears questionable because similar numbers might

result from different apomorphic rearrangements of chromosome parts, and very different numbers may well include the same apomorphic arrangements. We advocate that only specific differences in the topographic pattern of homologous chromosome parts be used for defining states of some character.

Presence of inquilines (68); [0] absent; [1] present. — Based on outgroup comparison polarity is from [0] to [1], and the character is not informative in our taxon sample ([1] only in Mastotermitidae).

Extension of abdominal tergum 7 (35); [0] not entirely covering more posterior parts of abdomen; [1] entirely covering more posterior parts of abdomen dorsally. — Based on outgroup comparison polarity is from [0] to [1], and the character is not informative in our taxon sample ([1] only in Cryptocercidae).

Extension of abdominal sternum 7 (male) (50); [0] not entirely covering more posterior parts of abdomen; [1] entirely covering more posterior parts of abdomen ventrally. — Based on outgroup comparison polarity is from [0] to [1], and the character is not informative in our taxon sample ([1] only in Cryptocercidae).

Presence of spine-like sensilla on gonapophyses 8 = first pair of ovipositor valves (female) (39); [0] absent; [1] present, numerous. — This refers to a dense coverage of the basal ventral walls of the gonapophyses VIII by short sensilla ('small movable spines' in MARKS & LAWSON 1962). THORNE & CARPENTER (1992) scored only *Cryptocercus* [1]. However, using a magnification of 60x, we found numerous conspicuous sensilla in the same area in *Periplaneta* and *Eurycotis*. The same is true for *Sphodromantis* and *Lamproblatta*, but here the sensilla are much less conspicuous (shorter and more delicate). In, e.g., *Polyphaga* and *Ergaula* only sparse, inconspicuous sensilla were found. We advocate that the character be used only when the equipment of the ovipositor with sensilla of different size and kind in Dictyoptera and outgroups will have been studied in some detail, best using SEM.

Laterosternal shelf of abdominal segment 7 (female) (43); [0] entire; [1] divided. — This character was excluded by DEITZ et al. (2003) because it was invariant in the chosen taxon sample. There is variation in the extended taxon sample used herein, so the character could be included again. However, a meaningful usage of this and the many other characters of the female genitalia depends on a detailed study of the female postabdomen in a large sample, which is still lacking (see KLASS 1998a).

Lateral separation between anterior arch and posterior lobes of second valvifer ring (female) (44); [0] present; [1] absent (= sclerites fused). — For discussion see DEITZ et al. (2003) and KLASS (2003b: 203ff). As the foregoing one, this character is too sporadically studied and inclusion into a character matrix must await a comprehensive study of the female genitalia.