Phylogeny of the Dictyoptera

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Abstract. Relationships among six key dictyopteran taxa (Mantodea; Blattodea (excluding Cryptocercidae); Cryptocercidae; Mastotermes darwiniensis, Termopsidae and Kalotermitidae [Isoptera]) are analysed based on seventy morphological, developmental and behavioural characters. The fossil record and the 'living fossil' genera Cryptocercus, Mastotermes and Archotermopsis are discussed in detail. Exact analysis of the character state matrix by implicit enumeration (Hennig86) resulted in one cladogram, strongly supporting Blattodea + Cryptocercidae as a sister group to Mantodea, with the Isoptera as a sister group to that complex. Arrangements within the termites are equivocal, with Termopsidae and Mastotermes darwiniensis possible as the relatively most primitive element of Isoptera.

Introduction

Historical background

The phylogeny of the dictyopteran complex (mantids, cockroaches, termites) remains unresolved. There is a general consensus that these three taxa represent a monophyletic grouping, but relationships among these 'orders', and how they fit in with other orthopteroids, are disputed. Derived characters linking these include, for example, a perforated corporo tentorium (Kristensen, 1975; see also list in Boudreaux, 1979: 277). Boudreaux (1979) considered the Blattaria and Mantodea to be sister groups, and the Isoptera to be the sister group of that complex.

Kristensen (1975) endorsed the same relationships as Hennig, but upon reevaluation Kristensen (1981) grouped all three taxa into the same order (Dictyoptera) and encouraged further work to resolve the phylogeny. In a volume edited by Rohdendorf & Rasnitsyn (1980), paleontologists at the Soviet Paleontological Institute published their consensus opinion regarding the evolution of insect orders. They felt certain enough to propose relationships among virtually all modern and extinct groups, but the Dictyoptera were left dangling amidst the orthopteroids: unrooted and with question marks.

In 1937 (and further in 1938), another Russian paleontologist, A. V. Martynov proposed a phylogeny and evolutionary time frame (1937: fig. 21) in which roaches and termites diverged in the late Devonian or early Carboniferous, and mantids radiated from roaches in the mid-Carboniferous. Martynov suggested that the solitary ancestor of the Isoptera (order 'Archisoptera') of the Devonian was the stem of all modern and extinct dictyopteroids (and also of all holometabolous orders). Martynov obviously did not structure his arguments in the context of modern systematic hypotheses, but some of his interpretations are intriguingly compelling. For example, Martynov argued that homonomous wings were very likely the ancestral condition in winged insects. The order Isoptera was named as such based upon similarity in size, shape and venation of the fore- and hindwings. Martynov emphasized the fact that termites have 'retained' extra basal branches of the radius (which he termed 'preradius', synonymous with first and second radius (Comstock, 1918; Tillyard, 1926; Emerson, 1933, 1965), radius (Smart, 1951, 1953), first radius and radial sector (Hennig, 1981) in both forewings and hindwings. The 'preradius' veins are absent in the forewings (present in the hindwings) of roaches and mantids. Martynov suggested that if termites diverged from roaches, it is difficult to envision a reversal of the wing characters back to such striking homonomy. Hennig (1981: 197) felt that Isoptera wing homomony is secondary.

Similarly, Martynov interpreted tegmina (found in roaches and mantids) as a derived character state. He argued that since termites have 'retained' membranous forewings, one must again hypothesize that termites, or solitary proto-termites, diverged from the basal stem of the modern 'roach' taxa rather than radiating from
evolved blattids with tegmina and non-homonomous wings. Tegmina have been considered an ancestral state in the Dictyoptera by Hennig (1981: 198), and interpreted as a derived character state by Holmgren (1911) and Boudreaux (1979: 220).

Martynov’s ideas have received little attention, particularly from American orthopteroid systematists. Grasse (1986: 449–459), however, discussed Martynov’s hypotheses and found them quite plausible.

The fossil record

There are four reports of fossil termites from the Cretaceous, all determined as members of the Hodotermitidae (Emerson, 1967; Jarzembowski, 1981; Lacasa-Ruiz & Martinez-Delclos, 1986; Krishna, 1990). The oldest, Meiatermes bertrani, was found in a limestone deposit in Spain dating approximately 130 million years (Lacasa-Ruiz & Martinez-Delclos, 1986).

Jarzembowski (1981) described the termite Valditermes brennæ from an early Cretaceous deposit in England (120 million years). Based on the forewing venation, Valditermes was originally described as a member of the Termopsidae (a family which was formerly considered a subfamily of the Hodotermitidae; see Grassé, 1949, but also see Emerson (1965: 16) for arguments to retain the original classification). Examination of additional specimens revealed a possible anal expansion in the hindwing (Jarzembowski, 1984), characteristic of the family Mastotermitidae. Jarzembowski felt that wing venation characters still warrant placement of Valditermes in the family Termopsidae, but shape of the hindwing is likely to stimulate a careful re-evaluation by termite taxonomists (also suggested by Krishna, 1990). Aside from these ambiguous specimens, the Mastotermitidae, which are considered by many to be the most ‘primitive’ termites, do not appear in the fossil record until the Eocene (60mya) (reviewed in Burnham, 1978).

Fossil roaches, or at least ‘roachoid’ insects, have received a reasonable amount of attention because of one rather dramatic character. Virtually every blattoid insect found in fossil strata from Paleozoic times had a long external ovipositor that looks like a functional ovipositor. Modern roaches have three pairs of internal valves that are frequently called internal ovipositors (Walker, 1919, 1922; Marks & Lawson, 1962; McKittrick, 1964, 1965). These structures manipulate the eggs and position them for the ootheca (reviewed in Marks & Lawson, 1962; McKittrick, 1964).

Many of the long blattid ovipositors are so well preserved in fossils that Vishniakova (1968) was able to determine that they are derived from the eighth and ninth abdominal sternum. This concerned her because the internal valves or ovipositors of modern roaches are associated with the seventh sternum (Walker, 1919, 1922; Roonwal, 1956; Marks & Lawson, 1962; McKittrick, 1964, 1965). (A feature common to all the Dictyoptera is that in females the seventh abdominal sternum is extended posteriorly to form a bursa or vestibulum.) Vishniakova (1968) questioned the homology of the external ovipositors of fossil roaches with the reduced internal ovipositor valves of modern cockroaches. Hennig (1981) was also worried about including the fossil ‘blattid-like’ insects with long ovipositors in the same taxon with modern roaches that all produce oothecae (excepting a few, derived groups; Roth & Willis, 1958).

The issue can be resolved based on the work of Nel (1929). He investigated the ontogeny of the genitalia in Orthoptera by examining serial sections of all developmental stages from embryos to adults. In studies of successive instars of Blatella nymphs he showed how the eighth and later the ninth sterna completely telescope within the seventh sternum which, simultaneously, gradually enlarges and becomes specialized as the subgenital plate. Further, Nel demonstrated in nymphs from the first through third instars that the lateral and inner ovipositor lobes differentiate from the ninth sternum, and that the anterior lobes (or ventral valves) are derived from the eighth sternum.

Thus, even though the three pairs of internal ovipositor valves appear to be associated with the seventh abdominal sternum in modern roaches (because that is the only one that is visible), their embryological origin is from the eighth and ninth sterna, just as was observed in fossil roaches by Vishniakova. It is therefore reasonable to interpret the external ovipositors of fossil blattids as homologous with the internal valves or ovipositors of modern forms. These internal valves are visible, albeit highly reduced, in several termite families (Browman, 1935; Geyer, 1951; Weesner, 1969). Of all termites, they remain most developed in Mastotermes darwiniensis (Crampton, 1920, 1923; Browman, 1935; Roonwal, 1956; Geyer, 1951).

‘Living fossils’: Cryptocercus and Mastotermes

Among extant forms, the three species of the cockroach family Cryptocercidae and the termite Mastotermes darwiniensis Froggatt are considered to be relicts or ‘living fossils’. Each of these groups is enshrined in the concept that as modern insects they have large numbers of uniquely primitive characters. Here we examine those interpretations, and re-evaluate selected characters.
Cryptocercus

Much of the debate on the phylogeny of the Dictyoptera involves Cryptocercus and its affinity to the termites. A common notion is that advocated by Cleveland (1934: 332), '...the evidence is overwhelming that Cryptocercus punctulatus is either the ancestor of termites or is closely related to the ancestor, which is extinct.' He based that conclusion on similarities of morphology, habitat and gut symbionts, and it has been adopted in general discussions of termite origins ever since (e.g. McKittrick, 1964; Krishna, 1970; Wilson, 1971; Burnham, 1978; Seelinger & Seelinger, 1983; Nalepa, 1984).

The key question is whether the Cryptocercidae are a sister group to the termites (reviewed in Boudreaux, 1979; Hennig, 1981), or whether they actually share more derived characters with the modern roaches (discussed in Hennig, 1981; Seelinger & Seelinger, 1983).

Many investigators have studied Cryptocercus anatomy and morphology (e.g. Judd, 1948; Nutting, 1951; Marks & Lawson, 1962; McKittrick, 1964, 1965; Brossut, 1973; Roth & Alspoh, 1978; Deleporte et al., 1988), gut symbionts (e.g. Cleveland, 1949; Cleveland et al., 1934; Nutting, 1956; Bobyleva, 1975), and social behaviour (Cleveland et al., 1934; Seelinger & Seelinger, 1983; Nalepa, 1984; 1988a, b), often comparing those characters to structures, Protozoa or behavioural patterns found in termites. There is general agreement that the family Cryptocercidae is primitive relative to other living roaches (Princis, 1960; McKittrick, 1964, 1965; Roth, 1968; Huber, 1974; Boudreaux, 1979; Hennig, 1981). However, the phylogenetic relationship between the Cryptocercidae and the Blattodea remains uncertain because the character systems have not been evaluated in light of modern systematic principles and techniques, and our analysis revealed no synapomorphies for Blattodea minus Cryptocercidae.

Protozoan gut symbionts: a homologous character shared by Isoptera and cryptocercids?

Cryptocercidae is one of two groups of roaches that feeds on wood: the other is the Panesthiinae. The Panesthiinae have bacterial gut symbionts to aid in digestion of cellulose. The Cryptocercidae have protozoan symbionts which are quite similar to those found in some termites. Presence of such similar gut fauna has frequently been cited as a character linking Cryptocercus with the termites. This contention must be reconsidered.

It appears certain that some of the intestinal Protozoa found in the lower termites and in Cryptocercus are derived from a common ancestral flagellate. The protozoa are morphologically very similar (reviewed in Bobyleva, 1975), and immunological characterizations of the Protozoa suggest that the gut fauna of the two hosts are related (Abilin, 1965; Abilin & Ritter, 1967).

It is not clear, however, that these flagellates were transferred to Cryptocercus and to modern termites by a common ancestral host, which is the general conception (also questioned by Emerson, 1935; Boudreaux, 1979). One inconsistency is that if there was a common ancestor with the symbionts, then that suggests that there was a secondary loss of the gut fauna, and coincident change in diet and habits, in all other roaches (Boudreaux, 1979). Alternatively, one could hypothesize that Cryptocercus is more closely related to the termites than to the rest of the roaches, but that is difficult to support based on any character except the gut fauna. Suggestions are occasionally made that either Cryptocercus or termites could have acquired the gut fauna from the other (Emerson, 1935; Boudreaux, 1979; Hennig, 1981), but that hypothesis has never been accepted because of differences in sexuality and physiology between Protozoa found in Cryptocercus and in termites (Honigberg, 1970; Bobyleva, 1975). Differences among Protozoa within the two hosts are unsurprising: there has probably been at least 100 million years of virtually independent evolution since both of these lineages first acquired gut symbionts, and numerous specializations or physiological adaptations could have occurred since divergence.

Successful Protozoa transfaunation between Cryptocercus and Zootermopsis (Termopsidae) has been repeatedly demonstrated under experimental conditions in which insects have been defaunated and received Protozoa from the alternate host either by feeding on recently removed hindguts (Cleveland, 1934) or by inoculation per rectum of hindgut material (Nutting, 1956). Recent work (Thorne, 1990) has demonstrated that aggression and rapid consumption behaviours exist in these two insect groups. Modern Cryptocercus and Zootermopsis live sympatrically, within the same decomposing logs in parts of California, Oregon and Washington in the United States. It is likely that their ranges, or those of their ancestors, overlapped more extensively in the past. It is thus probable that opportunities for transfer of hindgut protozoa via aggression and consumption have occurred over evolutionary time. This hypothesis for the presence of similar cellulolytic protozoa in both modern lineages (Thorne, 1990, 1991) must be considered as a valid alternative to the established theory that the symbionts were passed to Cryptocercus and to termites through a common ancestor. It seems plausible to interpret the shared habitat and nutritional physiology of Cryptocercus and the Isoptera as a result of convergence and transfaunation (but see Nalepa, 1991).

Cryptocercus characters which are derived in comparison to the Isoptera

While Cryptocercus is clearly primitive with respect to many of the other living roaches, it has many character states which are derived in comparison to the Isoptera (Table 1).

Mastotermes darwiniensis

Egg deposition: the 'ootheca'. Unlike all other termites,
Table 1.

Derived characters unique to Cryptocercus
Apterous
\(\delta\) : seventh sternum expanded
\(\delta + 9\) : seventh tergum expanded
Loss of mandibular and hypopharyngeal cephalic glands
First pair of ovipositor valves with small moveable spines

Derived characters found in Cryptocercus and other primitive cockroaches
Styli absent in \(\delta + 9\)
Presence of inferior hypostomal glands
Spermatheca opens through a pore midline of eighth sternum
Proventriculus: primary + secondary denticles conspicuously dissimilar
Proventriculus: highly modified interdental areas (intercalary plate)
Proventriculus bilateral symmetry
Paraprocts V-shaped in crosssections (flat in Isoptera)
Sex determination XX/XO

Mastotermes darwiniensis does not lay its eggs singly. Instead, eggs are deposited in an organized mass or pod (Hill, 1925). This egg pod is often called an 'ootheca', but we concur with others (Gay, 1970; Watson et al., 1977; Grassé, 1986) in thinking that that is an inappropriate term. It is certainly not an ootheca of the type produced by the mantids and roaches. The Mastotermes egg pod, which consists of two neat rows, is covered by a very thin film (Hill, 1925; McKittrick, 1964). The roach—mantid ootheca has a discrete outer shell which results from the tanning of protein and organic calcium salts secreted by the collerterial glands after deposition of the eggs (reviewed in McKittrick, 1964; Boudreaux, 1979). In roaches there is a distinct keel on the hard ootheca shell, and in mantids oothecae come in a variety of shapes. The form of the Mastotermes egg pod is really more similar to that of acridids, and may well be primitive relative to the ootheca of roaches and mantids (Boudreaux, 1979).

Mastotermes and Archotermopsis. The Mastotermitidae is defined by ancestral characters rather than by uniquely derived characters. This has led to a lot of confusion and potential misinterpretation. While the sole surviving species, Mastotermes darwiniensis, has retained a number of conspicuous characters which are probably ancestral (egg pod, enlarged pronotum, expanded hindwing jugal lobe), it also has a large number of derived features (Table 2). Another living termite with a very primitive morphology and social system is the Himalayan termite Archotermopsis wroughtoni, a member of the Termopsidae.

Space limitations prohibit a complete discussion of this topic, but conspicuous derived character states for these two taxa are listed in Table 2.

Mastotermes darwiniensis thus fits a common evolutionary pattern. It is primitive in some respects but it also has a large number of derived characters. Thus this species cannot be viewed as a clear window into the ancestry of the Isoptera.

Methods

Largely based on an extensive literature review we compiled data on six taxa key in the phylogeny of the termites and the larger dictyopteran complex. Groups included in the analysis were:

(1) Mastotermes darwiniensis — the only living member of the Mastotermitidae, which is generally regarded as a primitive family. This family is composed of at least thirteen fossil species from four genera which had a broad geographic distribution during the Tertiary (Emerson, 1965).

(2) Termopsidae and (3) Kalotermitidae — characters from both fossil and living members of these termite families were evaluated. Both of these families are thought to have originated reasonably near the stem of the Isoptera (reviewed in Emerson & Krishna, 1975).

(4) Cryptocercidae — the roach family whose sole genus is Cryptocercus. There are three living species of Cryptocercus.

(5) Blattodea (excluding Cryptocercidae) and (6) Mantodea — dictyopteran orders. We tried to determine likely character states of the ground plan in each order, basing judgements on the fossil record and present understandings of phylogenies (for roaches: Princis, 1960; McKittrick, 1964; Roth, 1968; Huber, 1974), which are basically nonexistent for the mantids (but see Beier, 1968). We could not determine whether Blattodea in this sense is monophyletic; that question is beyond the scope of this analysis.

The characters adduced in this analysis are listed below, along with the codes assigned to the character states. (Characters omitted from the analysis due to ambiguity of state, non-independence or lack of variance within the considered taxa are listed in Appendix 1.) The character state matrix for the taxa is shown in Table 3. Character state definitions and polarities largely followed prevailing theories of evolutionary change within the complex variously termed Polypeoptera (Martynov, 1925), Paurometabola
### Table 2.

#### Mastotermes darwiniensis

- **Imago characters**
  - Fused first and second teeth, left mandible
  - Forewing basal suture well defined
  - Fore- and hindwing scales long
  - Pimpule wing micro-sculpturing
  - Ninth sternum divided (?)
  - Three sternal glands
  - Sperm multiflagellate
  - Styles on δ only
  - Reduced cerci
  - Eighth sternum divided (?)
  - Ninth paratergites fused with tergum 9
  - Opening of spermatheca

#### Archotermopsis wroughtoni

- Ocelli absent
- Pronotum not expanded
- No expanded hindwing jugal lobe
- Eggs laid singly
- Bacteroids absent
- Fewer antennal segments, imago
- Fewer malpighian tubules, imago
- Reduced development of ovipositor valves

#### Non-imago characters

- Soldiers reduced no. antennal articles
- Soldier cerci 5 articles
- Bladelike protruberance front coxa, soldier
- No reproductive soldiers
- Chemical (quinone) soldier defence
- Workers (as opposed to pseudergates)
- Fully integrated termitophile
- Nest construction/covered foraging galleries
- Forage away from the nest
- Large colony population sizes (not included in character matrix)

(Hennig, 1981) or Lower Neoptera (Kristensen, 1981).

Polarity was conferred by the addition of a hypothetical ancestral taxon to the matrix, which was used to root the cladogram. This taxon had all-plesiomorph states, except for characters 41 and 49, where we could not determine the plesiomorphic condition. For these two characters the ancestor was scored as ambiguous. Multistate characters were linearly ordered, except for characters 25, 28, 34, 41, 45, 51, and 64, which were treated as nonadditive. For these characters we regard the polarity as ambiguous, based on the information at hand. Cladistic analysis (Hennig, 1966) was implemented with the Hennig86 program (Farris, 1988).

### Character state definitions

1. **ANTENNAE.** [0] long and filiform; [1] short and moniliform.

2. **NUMBER OF ANTENNAL ARTICLES (IMAGO).**

3. **POSITION OF EYES.**
   - [0] no stereoscopic vision; [1] eyes broadly separated and rounded, enabling stereoscopic vision.

4. **OCELLI (IMAGO).**
   - [0] 3 (median ocellus present); [1] 2; [2] none. Hennig (1981: 195) calls absence of the median ocellus the only undoubted derived character common to cockroaches and termites. Boudreaux (1979) says that this loss is common among insects and therefore is suspect as a synapomorphy linking termites and cockroaches.

5. **LEFT MANDIBLE.** [0] with 3 distinct marginal teeth; [1] with fused first and second marginal teeth (i.e., with 2 marginal teeth now visible). (Emerson, 1962: 22; Grassé, 1986: 506).

### Table 3. Data matrix for Dictyoptera.

A question mark indicates missing data.

<table>
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<th>Blattodea</th>
<th>Cryptocercidae</th>
<th>Mastotermitidae</th>
<th>Kalotermitidae</th>
<th>Termopsidae</th>
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</table>

(Hennig, 1981) or Lower Neoptera (Kristensen, 1981).


9. PRONOTUM. [0] not expanded; [1] expanded to cover part or all of head. Based on studies of Problattaria and Archimylacridae, Tillyard (1937) reports that fossils in which the pronotum has begun to expand forward to overlap the head capsule were unknown before the Lower Permian. Thus the typical termite pronotum (unexpanded except in Mastotermes) may represent the ancestral state. The pronotum groundplan condition in mantids is unclear. The expanded pronotum condition is apparently restricted to subordinate taxa in the higher mantid grades. Similarly, prothorax elongation is characteristic only of higher-grade mantids (Kristensen, pers. comm.).


11. AORTA/INCURRENT OSTIA/PERICARDIAL SEPTUM = ALARY MUSCLES (all related characters). [0] aorta begins at prothoracic incurrent ostia, 12 pairs incurrent ostia (3 thoracic, 9 abdominal), 12 pairs alary muscles; [1] aorta arises from mesothoracic enlargements (prothoracic lost; meso- and meta-retained), 11 pairs incurrent ostia (2 thoracic, 9 abdominal), 11 pairs alary muscles. (Nutting, 1951).

12. SEGMENTAL ARTERIES = excurrent lateral structures. [0] absent (no excurrent circulatory plan); [1] present. Segmental arteries are absent in other hexapods. (Nutting, 1951; Boudreaux, 1979: 221; Kristensen, 1981).


17. TEGMINA (forewings thickened). [0] absent; [1] present. Tegmina are known from fossil orthopteroids in the Carboniferous. Holmgren (1911) and Martynov (1937; 1938) argue that tegmina are a derived condition; Hennig (1981: 198) considers membranous forewings the derived state and hypothesizes that tegmina are probably ancestral. Concurring with Hennig, Wootton (pers. comm.) doubts if the wing homonomy of termites is plesiomorphic. He reasons that membranous wings in termites are adaptations to slow, hovering, passive wind-dispersal modes of flight.

Considering the variation of thickened forewings within the terminal taxa, possession of tegmina may not even be a groundplan trait of these groups (Kristensen, 1975: 12).


20. FOREWING SUBCOSTA. [0] short; [1] long. (Martynov, 1937: 146). Boudreaux (1979: 217–218) states that this may be the only possible credible synapomorphy between roaches and termites, and that this too may be a convergence.


23. CLAVUS (ANAL AREA) OF FOREWING. [0] large, with veins; [1] reduced or suppressed.

24. FOREWING JUGAL LOBE. [0] reduced; [1] slightly enlarged, folded under wings when at rest.


The enlarged lobe found in the hindwing of roaches, mantids and termites of the family Mastotermitidae is generally called an 'anal lobe'. This term is inaccurate or at least confusing. In 1937 Martynov published a detailed study of the basal portions of orthopteroid wings. He demonstrated that in the forewings of Mastotermes darwiniensis and cockroaches there is a broad thickened 'basal stripe' just behind the third axillary sclerite. This
stripe nearly reaches the small triangular projection of the base of the anal portion of the wings (Fig. 1). The forewing anal lobe (or clavus, Wootton, 1979) of *Mastotermes* is not well developed and shows only faint signs of tracheation. In the hindwings the same thickened stripe is seen posterior to the third axillary. Martynov recognized the chitinous jugal stripes of the fore- and hindwings as homologous. Similarly, he suggested that the broad membranous expansion behind the basal jugal stripe in the hindwing is homologous with the reduced jugal lobe in the forewing. In the hindwing the region homologous with the anal lobe or clavus of the forewing is in fact elongated and strongly narrowed. The first anal vein (A1 = PCu in Fig. 1), defining the anal region of the hindwing, is present in all primitive termites, not just *Mastotermes*.

Wootton (1979) addressed homologies and terminologies of wing areas, and recommends reference to the dictyopteran hindwing expansion as an anojugal area. Whatever the term, it should be realized that the anal lobe or region (clavus) of the forewing and the enlarged field of the hindwing are not homologous structures. All primitive termites have an anal lobe (clavus) in the forewing, but it is not usually observed or illustrated because it is anterior to the basal suture. Among termites the hindwing anojugal expansion is found only in *Mastotermes darwiniensis* and in fossil impressions of the Mastotermitidae.

28. BASAL SUTURE. [0] absent; [1] suture weak and not visible for its entire length (Emerson, 1933: 175); [2] suture well pronounced in forewing; distinct line of weakness in hindwing. Ordered nonadditively because polarity is unclear.


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Fig. 1. Basal portions of the wings of *Mastotermes darwiniensis* (redrawn from Martynov, 1937).

31. PROVENTRICULUS TEETH. [0] little differentiation in size and profile of primary and secondary plicae (= teeth); [1] primary and secondary denticles are conspicuously dissimilar. (Judd, 1948: 101–103, 123).

32. PROVENTRICULUS PUL VILLI. [0] pulvilli of primary plicae (teeth) expand anteriorly and partially overlap corresponding teeth; [1] do not. (McKittrick, 1964: 75).

33. SECONDARY PULVILLI. [0] rounded, bulbous (termites); [1] flat (roaches, including Cryptocercus). (Deleporte, 1988: 142, fig. 27).


35. TERGA. [0] all visible; [1] seventh tergum (as well as sternum) posteriorly expanded to conceal completely segments 8, 9 and 10.

36. TENTH TERGUM. [0] is true tenth tergum - mantids (Walker, 1919, 1922; Matsuda, 1976: 187); [1] a composite segment in which the supraanal lobe and the true tenth tergum are fused or undifferentiated (Matsuda, 1976: 181).


38. OVIPOSITOR BLADES. [0] protruding from body cavity; [1] internal.


41. EGG DEPOSITION. [0] eggs laid in mass, 2 rows, with secretory envelope; [1] eggs laid in ootheca with discrete outer case; [2] eggs laid singly. Ordered nonadditively because polarity is unclear.

42. EXTENSIONS OF LATEROSTERNAL SHELF (female segment 8). [0] extensions lacking; [1] postlateral extensions of shelf. (McKittrick, 1964: 100).

43. EIGHTH FEMALE STERNUM. [0] entire; [1] divided. (Imms, 1919; Crampton, 1923; Fuller, 1924: 17; Grassé, 1986: 61, fig. 53, redrawn from Crampton, 1923).

44. NINTH FEMALE STERNUM. [0] entire; [1] divided (2 plates).

45. OPENING OF FEMALE SPERMATHECA. [0] between eighth and ninth sterna; [1] on the ninth sternum; [2] through a pore midline of eighth sternum. (Imms, 1919: 121–123; Browman, 1935; Roonwal, 1956; Marks & Lawson, 1962; McKittrick, 1965; Matsuda, 1976: 186; Boudreaux, 1979: 216). Note that Matsuda (1976: 191) stated, 'In Mantis (Fernard, 1896; Ito, 1924) and Sagmomanitis (Fig. 54B) the spermatheca consists of the pyriform reservoir and the canal that opens on the 8th sternum above the gonopore. The opening lies anterior to the 9th sternum that supports the lateral valvulae.' We have not been able to determine the generality of this state in mantids.

Ordered nonadditively because polarity is unclear.


49. VASA DEFERENTIA. [0] open into ejaculatory duct from the ventral side; [1] from the dorsal side. (Weesner, 1969: 151; Matsuda, 1976: 184, fig. 53A and B).

50. MALE STERNA. [0] seventh sternum not enlarged to form genital plate, and does not cover sterna 8 and 9; [1] male sterna resemble female with enlarged seventh sternum. (Roonwal, 1956).


53. STYLI ON MATURE FEMALE. [0] present; [1] absent (lost sometime during instars from immature to imago). (Fuller, 1924: 74; Browman, 1935: 120, 121;...


60. REPRODUCTIVE SOLDIERS. [0] soldiers primitively absent; [1] yes (both sexes); [2] no − soldier gonads reduced or vestigial. (Imms, 1919; Gay & Calaby, 1970; Myles, 1986).


65. SEX DETERMINATION. [0] XX/XY; [1] XX/XO. (White, 1976; Luykx, 1983, 1990; Bedo, 1987). Bull (1983) and Luykx (1990) regard the XO male condition as derived. Luykx (1990) comments, 'The difference in their basic mechanism of chromosomal sex determination ... argues against a simple evolutionary derivation of termites (XX/XY) from cockroaches (XX/XO). It is more likely

that ... termites and cockroaches were both derived from a common ancestral stock with XX/XY sex-determination, with more rapid evolutionary loss of the Y chromosome in cockroaches.' Note: Luykx (1990) discovered one case of XX/XO sex determination in termites: Stolotermes victoriensis (Termopsidae). Luykx considers this case derived in convergence with cockroaches; not a synapomorphy.

66. CHROMOSOME NUMBER. [0] 2n = 52; [1] 2n = 98.

67. EUSOCIAL LIFE. [0] absent; [1] highly developed with caste system.


69. FORAGING AWAY FROM NEST. [0] group foraging primitively absent; [1] foraging within nest wood only; [2] foraging away from nest.

70. NEST ARCHITECTURE. [0] nest building primitively absent; [1] excavation of wood; no building of extensive gallery network; [2] nest construction away from or within host wood.

Results and Discussion

Exact analysis of the matrix in Table 3 by implicit enumeration resulted in one cladogram. It is shown in Fig. 2: the length is 109, with a consistency index (Kluge & Farris, 1969) of 0.88 and a retention index (Farris, 1989) of 0.84. This result is stable to successive weighting (Farris, 1969; Farris et al., in prep.). The cladistic diagnoses (Farris, 1979, 1980) for the cladogram are given in Table 4. The diagnoses show the distribution of all characters over the entire tree.

Fig. 2. Phylogeny of the Dictyoptera based on analysis of the matrix in Table 3. The closer relationship of Blattodea + Cryptocercidae to Mantodea is strongly supported, corroborating the hypothesis of Boudreaux (1979). Relationships of families within the Isoptera are not firmly established.
### Table 4. Cladistic diagnoses for the dictyopteran cladogram (Fig. 2). Apomorphies are listed for each component (branch point; Nelson, 1979) and terminal taxon; ambiguous optimizations, where the state could not be determined, are indicated by question marks. The numerical codes for each apomorphy in Table 4 are listed in parentheses. Blattodea is not listed separately, as it has no apomorphies.

<table>
<thead>
<tr>
<th>Component</th>
<th>Apomorphies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mantodea + (Cryptocercidae + Blattodea)</td>
<td>4. Ocelli (imago) 3 (0) or 2 (1)? 12. Segmental arteries present (1). 17. Tegmina present (1). 19. Forewing proradius absent (1). 21. Media closer to RS (1). 26. Postcubitus of hindwing simple (1). 31. Proventriculus teeth with primary and secondary denticles dissimilar (1). 33. Secondary pulvilli rounded (0) or flat (1)? 34. Proventriculus intercalaries longitudinal folds (0), intercalary plate (1) or anastomosing ridges (2)? 36. Tenth tergum present (0) or composite structure (1)? 38. Ovipositor blades protruding (0) or internal (1)? 41. Eggs laid in ootheca (1). 42. Extensions of laterosternal shelf lacking (0) or present (1)? 45. Opening of female spermatheca through a pore midline of eighth sternum (2). 46. Form of paraprocts flat (0) or V-shaped in cross-section (1)? 53. Styli on mature female present (0) or absent (1)? 55. Bacteroids in adipose tissue present (0) or absent (1)? 56. Soldiers large with flat elongated head (1). 57. Soldier ocelli present (1) or absent (2)? 58. Soldier bladelike protuberance on front coxae absent (1). 59. Soldier ceri 5–7 articles, twice length of stylus (1). 60. Reproductive soldiers (1). 61. Soldier defence mandibles only (1). 63. Worker/pseudergate developmental plasticity present (1). 64. Number of sternal glands (pseudergate/worker) 1 (1). 65. Sex determination XX/XO (1).</td>
</tr>
</tbody>
</table>
for Fig. 2. In order for Cryptocercidae to be placed as closer to Isoptera than to Mantodea, a
Cryptocercidae to Mantodea is strongly supported, cor-
of 119 is required, ten more steps than the cladogram
of Fig. 2. Thus, the closer relationship of Blattodea
length of 113 is required, four more steps than required
Isoptera. For Mastotermitidae to be placed as the relatively
most basal element of Isoptera (that is, for Termopsidae
the position of Cryptocercidae within the roach clade is
uncertain, the notion of roach paraphyly in terms of the
arrangement shown in Fig. 2 also resulted under each of
these conditions: (1) all characters were treated as nonad-
ditive, discarding all hypothesized polarities; (2) all traits
pertinent to social behaviour were deleted (i.e. characters
56–61, 63 and 66–70); and (3) the behavioural traits
were deleted and all remaining features were treated
as nonadditive. The relative disparity between the
alternative placements of Mastotermitidae is thus not great. The
arrangement shown in Fig. 2 also resulted under each of
these conditions: (1) all characters were treated as nonad-
ditive, discarding all hypothesized polarities; (2) all traits
pertinent to social behaviour were deleted (i.e. characters
56–61, 63 and 66–70); and (3) the behavioural traits
were deleted and all remaining features were treated
as nonadditive. The relative disparity between the
alternative placements of Mastotermitidae was maintained
through all these analyses (as, for that matter, was the
relative number of steps of attain roach paraphyly). Thus
on present evidence mastotermitids are evidently not
living fossils, but this should not be considered as firmly
established until a comprehensive analysis including all
termite families is performed. That analysis is currently in
progress therefore we do not make any recommendations
on classification at this time.

This data set and analysis represent a synthesis of cur-
tent information on basal groups comprising modern
Dictyoptera. We hope that the paper will function as a
provocative stimulus for future work on these taxa. Inter-
pretations and conclusions regarding the phylogeny of
this group may well be revised as new information is
compiled. Further comparative anatomical and molecular
approaches towards resolution of dictyopteran systematics
will provide an important complement to this study.

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Appendix 1. Characters omitted from analysis. The following characters were omitted due to ambiguity of state, non-independence or lack of variance within the considered taxa.

<table>
<thead>
<tr>
<th>Imago</th>
<th>Soldier</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size</td>
<td>Pilosity</td>
</tr>
<tr>
<td>Head pilosity</td>
<td>Head capsule shape</td>
</tr>
<tr>
<td>Head mobility</td>
<td>Compound eye shape</td>
</tr>
<tr>
<td>Wing pilosity</td>
<td>Compound eye pigmentation</td>
</tr>
<tr>
<td>Size third antennal article</td>
<td>No. antennal segments</td>
</tr>
<tr>
<td>Postclypeus shape</td>
<td>Frontal gland/fontanelle opening</td>
</tr>
<tr>
<td>Tibial spur number and position</td>
<td>Distinction of epicranial suture</td>
</tr>
<tr>
<td>Tarsal pulvilli</td>
<td>Ratio of third:fourth antennal segments</td>
</tr>
<tr>
<td>Front coxae shape</td>
<td>Antennal article shape</td>
</tr>
<tr>
<td>Degree of development of seminal vesicles/accessory gland complex</td>
<td>Protuberances above antennal fossae</td>
</tr>
<tr>
<td>Intersternal fold — sclerotized or membranous</td>
<td>Sex of soldiers</td>
</tr>
<tr>
<td>Forked spermatheca</td>
<td>Postclypeus longitudinal groove</td>
</tr>
<tr>
<td>No. of testicular lobes</td>
<td>Molar ridges</td>
</tr>
<tr>
<td>No. of chromosome arms (nombre fundamental)</td>
<td>Mandible serrations</td>
</tr>
<tr>
<td>Chromosome centricity (acro-, meta- or telocentric)</td>
<td>Soldier pronotum shape</td>
</tr>
<tr>
<td>Distinction of epicranial suture</td>
<td>Coxae</td>
</tr>
<tr>
<td>Secondary sclerotization of sternum 7</td>
<td>Spines on front tibiae</td>
</tr>
<tr>
<td>Archidictyon</td>
<td></td>
</tr>
<tr>
<td>Position of anal veins in forewing</td>
<td></td>
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<tr>
<td>Proportions of wing scales</td>
<td></td>
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<tr>
<td>Position of media in hindwing</td>
<td></td>
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<tr>
<td>Meta- and mesothorax morphology</td>
<td></td>
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<tr>
<td>Shape of compound eye</td>
<td></td>
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<tr>
<td>Femoral grooves, front femora</td>
<td></td>
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<tr>
<td>Independent versus joint insertion of vasa deferentia</td>
<td></td>
</tr>
<tr>
<td>Proventriculus: rigidity of dental belt</td>
<td></td>
</tr>
<tr>
<td>Proventriculus: pulvillar belt</td>
<td></td>
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<tr>
<td>Intervalvular ring = basal ring</td>
<td></td>
</tr>
<tr>
<td>No. of malpighian tubules in imago</td>
<td></td>
</tr>
<tr>
<td>No. of malpighian tubules present during first larval instar</td>
<td>Nitrogen fixation (exceedingly high in Mastotermes)</td>
</tr>
<tr>
<td>No. of insertion groups of malpighian tubules</td>
<td>Colony population size</td>
</tr>
<tr>
<td>Inferior hypostomal gland (= maxillary/accessory mandibular gland)</td>
<td></td>
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</tbody>
</table>