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Termites (Isoptera): Their Phylogeny, Classification, and Rise to Ecological Dominance

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ABSTRACT

Like ants, termites are entirely eusocial and have profound ecological significance in the tropics. Following upon recent studies reporting more than a quarter of all known fossil termites, we present the first phylogeny of termite lineages using exemplar Cretaceous, Tertiary, and Recent taxa. Relationships among Recent families were largely unaffected by the addition of extinct taxa, but the analysis revealed extensive grades of stem-group taxa and the divergence of some modern families in the Cretaceous. Rhinotermitidae, Serritermitidae, and the "higher" termites (family Termitidae), which comprise 84% of the world termite species, diverged and radiated entirely in the Tertiary, corresponding to a significant increase in termite individuals in the fossil record. Radiation of the higher termites may have affected the formation of terrestrial carbon reserves like oil and coal. The higher classification of Isoptera is slightly revised based on the phylogenetic results. The following new taxa are proposed: **Cratomastotermitidae**, new family; **Euisoptera**, new clade; **Archotermopsidae**, new family; and **Neoisoptera**, new clade. In addition, the families Stolotermitidae, Stylotermitidae, and Archeorhinotermitidae are newly recognized or resurrected, and the families Termopsidae and Hodotermitidae are significantly restricted in composition.

INTRODUCTION

"Success" of a species or group of species is typically either ecological or evolutionary. Insects, in particular, are evolutionarily very successful because of their early origins in the Devonian and subsequent radiation into millions of species. It is only certain insects, however, that account for the remarkable overall ecological dominance of insects in terrestrial ecosystems, in terms of biomass and impact on biological communities, and

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chief among them are the social insects. This report is a phylogenetic synthesis of many recent discoveries of fossil termites, which is then used to consider the origins of termite ecological success.

Advanced sociality, or eusociality, involves overlapping generations of siblings that generally share a durable domicile in which groups of individuals specialize in tasks (i.e., castes), especially reproduction, foraging, and commonly defense and brood care (Wilson, 1971). A colony's efficiency in mobilizing its foragers and soldiers fosters the superior competitive ability of major eusocial groups like ants, vespid wasps, honeybees, and termites. For example, there are approximately 19,340 modern species of bees (Apoidea: Anthophila), but it is the large, complex colonies of honey bees (genus *Apis*) that easily outcompete the native social species, even leading to the latter's localized extirpation (e.g., Roubik et al., 1986; Sugden et al., 1996). Unlike bees, all of the 12,516 living species of ants and 2,958 living species of termites are eusocial (termite species numbers valid as of 11 March 2009: Krishna et al., in press). Basal lineages of both these groups generally live in small colonies of several dozen to several hundred individuals with less caste differentiation, and the most recently derived lineages (like army ants, leaf cutter ants, and mound-building termites) form massive colonies of over one million individuals with extreme caste differentiation. Termites in tropical and subtropical ecosystems are the major consumers of the most abundant biomolecule on land, cellulose, and its more inert form, lignocellulose. It is estimated, for example, that termites ingest 50%–100% of the dead plant biomass in tropical ecosystems (Bignell and Eggleton, 2000). Their abundance, like that of ants, frequently exceeds 1,000 individuals/m^2 or 2,000 mg/m^2, and it is estimated that gas excretion from termites and their nests contributes 2%–5% of the world's atmospheric methane (Sugimoto et al., 2000). The ecological impact of termites, even apart from the commercial damage they cause, is prodigious.

There has been intensive study of the relationships and fossil record of bees (Engel, 2001, 2004; Danforth et al., 2006; Michener, 2007; Ohl and Engel, 2007) and ants (Grimaldi et al., 1997; Grimaldi and Agosti, 2001; Dlussky and Rasnitsyn, 2002; Engel and Grimaldi, 2005; Moreau et al., 2006; Brady et al., 2006). Both of these groups appear to have originated in the late Early Cretaceous, ca. 100–120 Ma, with some modern subfamilies diverging in the Late Cretaceous. Though their evolutionary history has been studied less, it is now acknowledged that termites are highly modified, eusocial roaches (Cleveland et al., 1934; McKittrick, 1964; Lo et al., 2000; Deitz et al., 2003; Grimaldi and Engel, 2005; Klass and Meier, 2006), whose earliest fossils predate those of ants and bees by approximately 35 million years (Thorne et al., 2000; Engel et al., 2007a). Recent phylogenetic work on termites involves molecular and some morphologically based analyses of living species only (e.g., Kambhampati et al., 1996; Donovan et al., 2000; Thompson et al., 2000; Bitsch and Noirot, 2002; Klass and Meier, 2006; Inward et al., 2007a, 2007b; Legendre et al., 2008). Unique for any insect order, all early fossil termites have been classified into living families, particularly the Hodotermitidae, despite the fact that such fossils may be stem groups since they lack many derived features of living families.

Here we present the first analysis of relationships among fossil and living termite lineages, along with estimates of divergence times and ecological patterns of the major lineages. Recent studies have reported 18 new termites from the Cretaceous (Krishna and Grimaldi, 2000, 2003; Engel et al., 2007a; Grimaldi et al., 2008) and 38 species from the Tertiary (Nel and Bourguet, 2006; Wappler and Engel, 2006; Engel and Krishna, 2007a, 2007b; Engel et al., 2007b; Engel, 2008; Krishna and Grimaldi, 2009), comprising about one-quarter of all described fossil species. Nearly 80% of these species are preserved in amber, from the Early Cretaceous of Lebanon, the mid-Cretaceous of Myanmar and New Jersey, the Eocene of the Baltic Region and France, and the Miocene of Mexico and the Dominican Republic (deposits are reviewed in Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005). The microscopic fidelity of preservation in amber allows uniquely detailed comparisons with living species, greatly facilitating phylogenetic analysis of extinct taxa. Insects in 110 Ma limestone from the Crato Formation of Brazil also have exceptional preservation, as mineralized replicas with cuticular microstructure and even some internal organs. As a result, Crato species preserved as series of specimens can be largely reconstructed (Grimaldi et al., 2008). Thus, now is an opportune time for deciphering nearly 140 million years of termite evolution.

MATERIALS AND METHODS

Termite specimens belonging to 38 exemplar living species of 36 genera, representing all seven traditionally recognized families and four subfamilies of the "higher" termites (family Termitidae), were dissected and directly examined; 38 extinct species in 25 genera were studied and compared to living taxa. The fossils ranged in age from Early Cretaceous (Berriasian, ca. 135 Ma, of Baissa, Siberia) to the Miocene (in amber from the Dominican Republic, ca. 17 Ma) (table 2). Species preserved as compressions or mineralized replicas were also included where bodies were preserved, not just isolated wings (we have omitted from the analysis taxa known only or largely from wings, such as *Ulmeriella* Meunier).

There were 108 morphological and biological attributes scored from imago, soldier, and worker castes where available (table 1 and appendix); outgroup taxa were other Dictyoptera, specifically the most basal mantis (*Chaeteessa* sp. Burmeister), the roaches *Periplaneta* Burmeister and *Panchlora* Burmeister, and the relict wood roaches (*Cryptocercus* spp. Scudder), the latter being the living sister group to termites. Within the matrix of 8,748 cells, 21% of the cells were coded as unknown (feature not observed in the fossils), and a further 9% as inapplicable (e.g., soldier characters in genera that lack this caste). Phylogenetic analysis employed NONA (Goloboff, 1997), using 500 replicates of the data set with random taxon addition and branch swapping on all shortest topologies. This yielded 2,088 equally most-parsimonious trees of 302 steps (C.I. 44, R.I. 86), the strict consensus of which resulted in 323 steps (unambiguous character changes mapped in figs. 1, 2, 4, 5). The relative abundance of termites through time was plotted as proportions (%) of the number of termite specimens to all insect specimens per fossil deposit (table 2); only deposits that yielded at least one termite specimen were plotted, in order to ensure the appropriate taphonomic conditions for termite preservation.

RESULTS AND DISCUSSION

PHYLOGENY

Analysis of the paleontological data resulted in a remarkably resolved topology for Isoptera (fig. 3). Structure of the consensus tree generally agrees with that from prior morphological and molecular studies (Kambhampati et al., 1996; Donovan et al., 2000; Thompson et al., 2000; Bitsch and Noirot, 2002; Inward et al., 2007a, 2007b), but depart in some respects from the recent molecular study of Legendre et al. (2008) (e.g., the relatively basal placement of Kalotermitidae). Legendre et al. (2008) had a dramatically reduced taxon sampling relative to other, more comprehensive treatments (e.g., Inward et al., 2007a).

In our analysis unequivocal relationships include *Cryptocercus* as the living sister group to the termites and *Mastotermes* Froggatt as the living sister group to all other termites—the lineage we are designating here as **Euisoptera**. *Mastotermes darwiniensis* Froggatt, from northern Australia and southern New Guinea, is the sole survivor of the formerly global Mastotermitidae (Thorne et al., 2000; Wappler and Engel, 2006), and it retains striking plesiomorphic features with roaches, such as laying its eggs in a vestigial pod or ootheca. Interestingly, the Mastotermitidae as it has historically been classified was recovered as monophyletic, despite opinion to the contrary (e.g., Jarzembowski, 1981). *Cratomastotermes* Bechly, from the Early Cretaceous Crato Formation of Brazil, was formerly placed in the Mastotermitidae (Bechly, 2007); in our analysis it is the most basal species of termite since it retains even more plesiomorphic features than Mastotermitidae (Grimaldi et al., 2008). This genus is accordingly placed in a new, extinct family, **Cratomastotermitidae**, new family (see Classification). Cretaceous fossils traditionally classified as Hodo-

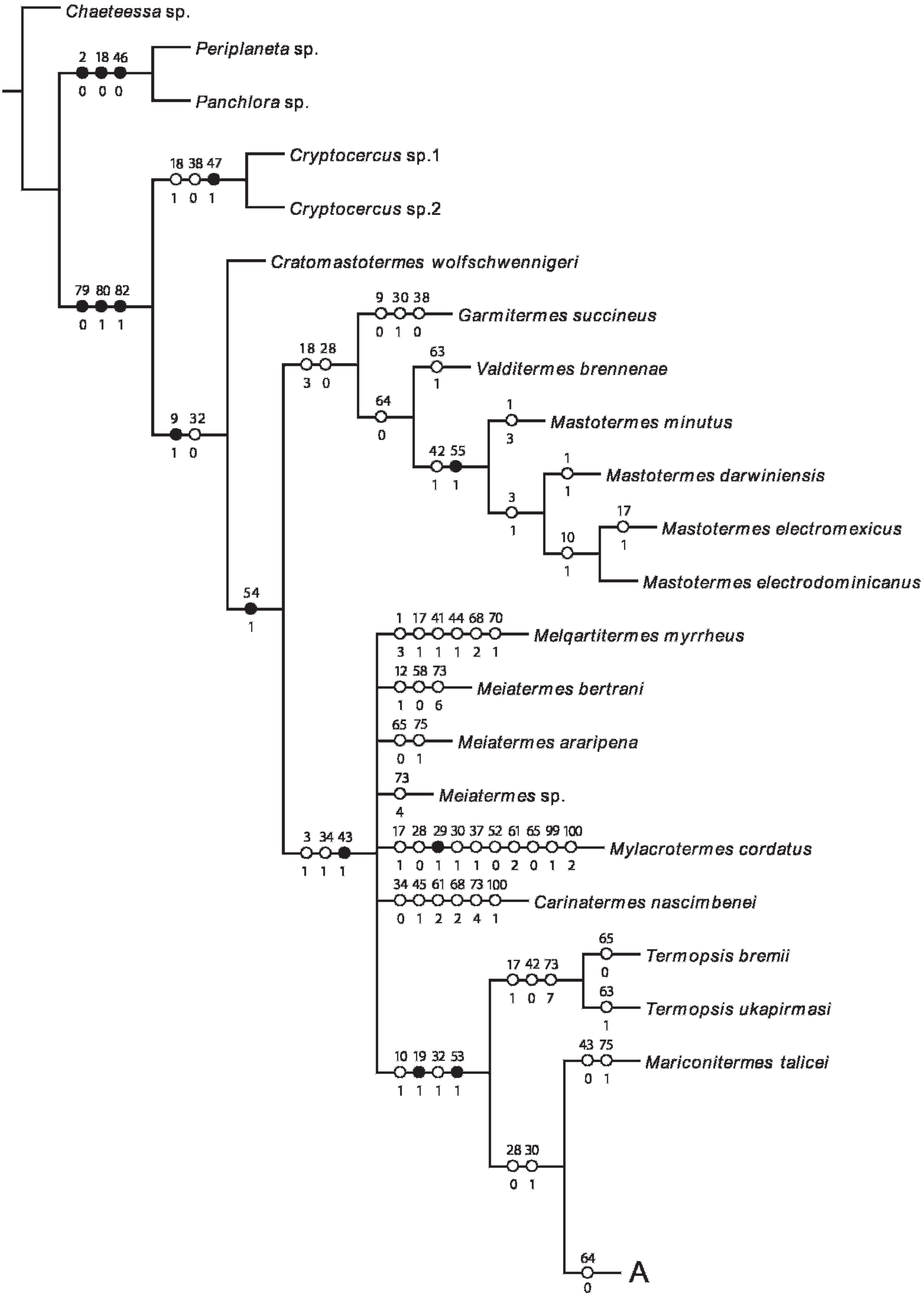


Fig. 1. Strict consensus cladogram with unambiguous character-state changes mapped. Character numbers appear above the branch, with the corresponding state beneath the branch. Branch "A" continued in figs. 2, 4, and 5. *Chaeteessa* (Mantodea), *Panchlora* (Blattaria), *Periplaneta* (Blattaria), and *Cryptocercus* (Blattaria) are the outgroup taxa.

TABLE 1

Character and Character-State Descriptions

The following list enumerates those characters and character states used in the analysis of relationships within Isoptera (refer to appendix 1 for codings). All characters were considered nonadditive and of equal weights

1. Number of alate/imago antennomeres: 50 or more antennomeres = 0; 30–40 antennomeres = 1; 23–28 antennomeres = 2; 11–22 antennomeres = 3.
2. Structure of imago flagellum: flagellomeres filiform = 0; flagellomeres moniliform = 1.
3. Apex of imago flagellum: distal 7–8 articles tapered = 0; distal 7–8 articles not tapered = 1.
4. Ocelli of alates: three present (homologous with other orders) = 0; absent = 1.
5. Ocelli of soldiers: present = 0; absent or vestigial = 1.
6. Pigmentation of soldier compound eyes: present = 0; absent = 1.
7. Soldier compound eyes: rudimentary = 0; absent = 1.
8. Frontal gland developed into distinct fontanelle: absent = 0; present = 1.
9. Position of alate head: hypo-/orthognathous = 0; prognathous = 1.
10. Ventral cervical sclerite of alate: present = 0; absent = 1.
11. Marginal teeth of left mandible of alate: greater than or equal to three = 0; two teeth = 1.
12. Subsidiary tooth of right mandible of alate: absent = 0; present = 1.
13. Lacinial teeth of maxilla: both teeth apical = 0; one tooth subapical = 1.
14. Postclypeal furrow (workers and alates): absent = 0; present as shallow longitudinal furrow = 1.
15. Clypeus (workers only) in profile: not keeled = 0; with keel = 1.
16. Shape of occipital foramen in imagos: rounded = 0; trapezoidal = 1.
17. Y-shaped coronal ecdysial cleavage line in imago: present = 0; absent or highly vestigial = 1.
18. Pair of ocelluslike structures (= ocelloids) near inner margin of compound eye: present as circular tympanalike areas = 0; vestigial as areas of weakened or pale cuticle = 1; absent = 2; present and nearly lenslike (superficially resembling ocelli and historically termed ocelli by isopterists) = 3.
19. Occipital sulcus: present = 0; absent or highly vestigial = 1.
20. Compound eye: lenticular = 0; circular = 1.
21. Notch between first and third marginal teeth: present = 0; absent = 1.
22. Mandibular excavation between apical and first marginal teeth: absent = 0; present = 1.
23. Soldier mandible: marginal teeth: distributed along length, with 1–4 teeth along middle of margin = 0; lost except small teeth/serrations at base = 1.
24. Soldier mandible: short to moderate in length, length ca 2 or less × basal width = 0; greatly elongate and narrow, length ca. 3 or more × basal width = 1; vestigial = 2.
25. Soldier mandibles: symmetrical, not clicking = 0; asymmetrical, clicking = 1.
26. Soldier head capsule: rectangular in dorsal aspect = 0; phragmotic, plug shaped = 1; nasutiform = 2.
27. Diagonal grooves between fontanelle and postclypeus: absent = 0; present = 1.
28. Pronotal posterolateral corners of imago: broadly arched = 0; acutely rounded, nearly orthogonal = 1.
29. Pronotal posterior margin of imago: straight or slightly indented = 0; rounded = 1.
30. Pronotal lateral margins of imago: subparallel = 0; converging = 1.
31. Pronotal size of imago: covering head dorsally = 0; not covering head but with width greater than or equal to head = 1; width significantly less than head width = 2.
32. Pronotal anterior margin of imago: concave = 0; relatively straight = 1; convex, with anterolateral corners developed = 2.
33. Tibial macrosetae and spurs: heavily serrate = 0; slightly pimplate = 1; smooth = 2.
34. Tibial macrosetae and spurs: asymmetrical, with one side flattened = 0; symmetrical = 1.
35. Tarsomeres: pentamerous, fully developed = 0; pentamerous, second tarsal article reduced = 1; tetramerous (second tarsal article lost) = 2; trimerous = 3.
36. Metabasitarsomere length: less than twice the width = 0; more than 3 × the width = 1.
37. Pretarsal arolium: present = 0; absent = 1.
38. Plantular pads: present = 0; absent = 1.
39. Procoxal ventral keel of alate: present = 0; absent = 1.
40. Protibial spines along length: present and extensive = 0; absent, reduced to apical spines/spurs = 1.
41. First Rs fork: in basal half = 0; near midlength or beyond = 1.
42. Length of R1: short, extending in quarter of wing length = 0; median, extending in third of wing length = 1; long, extending to or past wing midlength = 2.
43. Forewing Rs: branched basally in scale with 2–3 branches = 0; simple in scale = 1.
44. Forewing CuA: shorter, to around wing midlength = 0; long, to point within apical third of wing = 1; elongate and extensively developed, extending to apex or subapex, posteriorly along one-half wing, with 6 or more branches = 2.

TABLE 1
(Continued)

45. Multiple branches of R1: present = 0; absent = 1.
46. Forewing tegmenization: developed as tegmina = 0; not developed as complete tegmina = 1.
47. Wings: present = 0; absent = 1.
48. Forewing vein M: present = 0; absent = 1.
49. Forewing scale relative to hind wing scale: apical margin of forewing scale meeting or overlapping hind scale = 0; scales well separated = 1.
50. Wing membrane setae: absent = 0; present, microsetulose = 1.
51. Fore- and hind wings: not dehiscent = 0; dehiscent = 1.
52. Forewing basal cleavage suture: absent = 0; present = 1.
53. Hind wing basal cleavage suture: absent = 0; present but rudimentary = 1; completely developed = 2.
54. Cross veins connecting longitudinal veins: present = 0; absent = 1.
55. Sclerotization of veins: all uniformly sclerotized = 0; Sc, R, and M thick and sclerotized relative to CuA = 1; Sc and R sclerotized relative to M and CuA = 2.
56. Anal lobe of hind wing: present = 0; absent (wing homonomous) = 1.
57. Hind wing vein A1: present = 0; absent = 1.
58. Wing membrane reticulations: present, not pigmented = 0; present, pigmented = 1; absent = 2.
59. Wing membrane surface: smooth = 0; nodulose or pimplate = 1.
60. Radial fracture of forewing scale: present = 0; absent = 1.
61. Reticulations between CuA and CuP on forewing scale: veins = 0; reticulations = 1; reticulations only anterior to CuP = 2; absent = 3.
62. Distal margin of forewing scale: evenly convex = 0; straight to slightly convex = 1; straight and diagonal = 2.
63. CuP in forewing scale: convex = 0; straight or concave = 1.
64. Humeral margin of forewing scale: flat = 0; swollen beyond level of costal margin = 1.
65. Forewing CuP: terminates prior to posterior tip of basal suture = 0; terminates in basal suture = 1.
66. Position of forewing vein M: close to Rs = 0; midway between Rs and CuA or closer to latter = 1.
67. Costalization of forewing: not costalized = 0; C+Sc+R and Rs extremely close and simple and parallel = 1.
68. Branches of Rs: with dorsal and ventral branches, inferiors irregular (acute go tip) = 0; with dorsal and ventral branches, inferiors angled & parallel = 1; with short dorsal branches only or simple = 2.
69. Branches of vein M: with two or more branches = 0; with one apical branch = 1; simple (unbranched) = 2.
70. Radial field: encompassing apex or terminating at apex = 0; terminating anterior to apex = 1.
71. Development of CuP: extensive, developed as claval furrow = 0; reduced, confined to short, simple vein near wing base = 1.
72. Dichotomous branching of R and M: extensive = 0; reduced = 1.
73. Number of superior branches of Rs: none = 0; one = 1; two = 2; three = 3; four = 4; five = 5; six = 6; seven or more = 7.
74. Female styli: present = 0; absent = 1.
75. Imago cercus segmentation: four or higher = 0; three = 1; one or two = 2.
76. Castes: absent = 0; present, with workers = 1; present, without workers = 2.
77. Ootheca: present = 0; absent = 1.
78. Presence of *Blattabacterium* in fat body: present = 0; absent = 1.
79. Presence of flagellates and ciliates: present = 0; absent = 1.
80. Wood feeding: absent = 0; present = 1.
81. Social organization: absent = 0; extended parental care = 1; eusocial = 2.
82. Living in structures/nests: absent = 0; present = 1.
83. Soldiers: present = 0; lost = 1.
84. Soldier nasus: short = 0; very long, length several times width = 1.
85. Nasute fontanelle: rimmed or slitlike = 0; minute, not rimmed or slitlike = 1.
86. First proctodeal segment: expanded = 0; tubular, not dilated = 1.
87. Soldier labral apex: sclerotized = 0; hyaline = 1.
88. Soldier heads: normal = 0; flattened = 1.
89. Soldier labrum: well developed = 0; vestigial = 1.
90. Soldier pronotum: flat = 0; saddle shaped = 1.
91. Malpighian tubule number: eight or more = 0; four or fewer = 1.
92. Imago/worker fontanelle: small and round = 0; slit-, drop-, or Y-shaped = 1.
93. Anterior margin of worker/alate postclypeus: flat or concave = 0; convex = 1.
94. Imago compound eye: protruding well beyond lateral margin of head = 0; small, not protruding beyond lateral margin of head in frontal view = 1.

TABLE 1
(Continued)

95. Imago ocelloid: large, ca. 7–8x diameter of compound eye facet = 0; small, ca. 2–3x diameter of compound eye facet = 1.
96. Soldier fontanelle: normal, dorsal-facing = 0; enlarged and facing anteriad = 1.
97. Nasute head capsule: not constricted = 0; slightly constricted = 1.
98. Proventricular teeth: present = 0; highly reduced or lost = 1.
99. Protibial apical spur number: three or more = 0; two = 1.
100. Mesotibial apical spurs: four or five = 0; three = 1; two = 2.
101. Metatibial apical spurs: four = 0; three = 1; two = 2.
102. Sternal gland on third sternum: present = 0; absent = 1.
103. Sternal gland on fourth sternum: present = 0; absent = 1.
104. Sternal gland on fifth sternum: present = 0; absent = 1.
105. Soldier labral brush: absent = 0; present = 1.
106. Setulae surrounding fontanelle (directed toward fontanelle): absent = 0; present = 1.
107. Hind wing vein M: present = 0; absent = 1.
108. Soldier frontal groove: absent = 0; present (ridges anterior from fontanelle with width of fontanelle) = 1.

termitidae, such as the extinct "genus" *Meiatermes* Lacasa-Ruiz and Martínez-Delclòs, actually comprise a grade of stem-group species that fall basal to the divergence of Termopsidae, true Hodotermitidae, and all other termites. Termopsidae stat. n. (see Classification) should be restricted to the Baltic amber species of *Termposis* Heer (Engel et al., 2007b). What we are designating as the true Hodotermitidae (see Classification)

TABLE 2
Termite Abundance (% of all insect specimens) in Major Insect Deposits throughout the Cretaceous and Cenozoic

Deposit	Age	% termites	References
		CRETACEOUS	
Baissa, Siberia	137 Ma	0.1%	Rasnitsyn, 2008
Montsec, Llerida, Spain	129 Ma	0.2%	Lacasa-Ruiz and Martínez-Delclòs, 1986
Weald clay, UK	127 Ma	0.1%	Jarzembowski, 1977, 1984, 1991
Lebanese amber	120 Ma	0.2%	Azar, 2000
Crato Formation, Brazil	110 Ma	1.0%	Bechly, 2007; Grimaldi, unpubl. data
Burmese amber	100 Ma	0.2%	Grimaldi, unpubl. data
French amber (Archingeay)	100 Ma	0.03%	Perrichot et al., 2007
New Jersey amber	90 Ma	0.4%	Grimaldi et al., 2000
		CENOZOIC	
Baltic amber	45 Ma	0.2%	Sontag, 2003
Baltic amber	45 Ma	0.2%	Perkovsky et al., 2007
Baltic amber	45 Ma	0.3%	Krzemińska et al., 1992
Eckfeld Maar, Germany	45 Ma	0.5%	Wappler, 2003
Kŭclín, Czech Rep.	40 Ma	6%	Prokop, 2003
Bembridge Marls, UK	34 Ma	2.5%	Jarzembowski, 1980
Seifhennersdorf, Germany	30 Ma	6%	Prokop, 2003
Krottensee, Bohemia	18 Ma	5%	Prokop, 2003
Dominican amber	18 Ma	5.6%	Grimaldi, unpubl. data
Dominican amber	18 Ma	2.8%	Poinar and Poinar, 1999
Andance, France	15 Ma	10%	Prokop, 2003
Oeningen, Germany	15 Ma	2%	Prokop, 2003
Radoboj, Croatia	15 Ma	2%	Prokop, 2003
Zanzibar copal	1000 y.	8%	Grimaldi, unpubl. data
Colombian copal	300 y.	10%	Grimaldi, unpubl. data

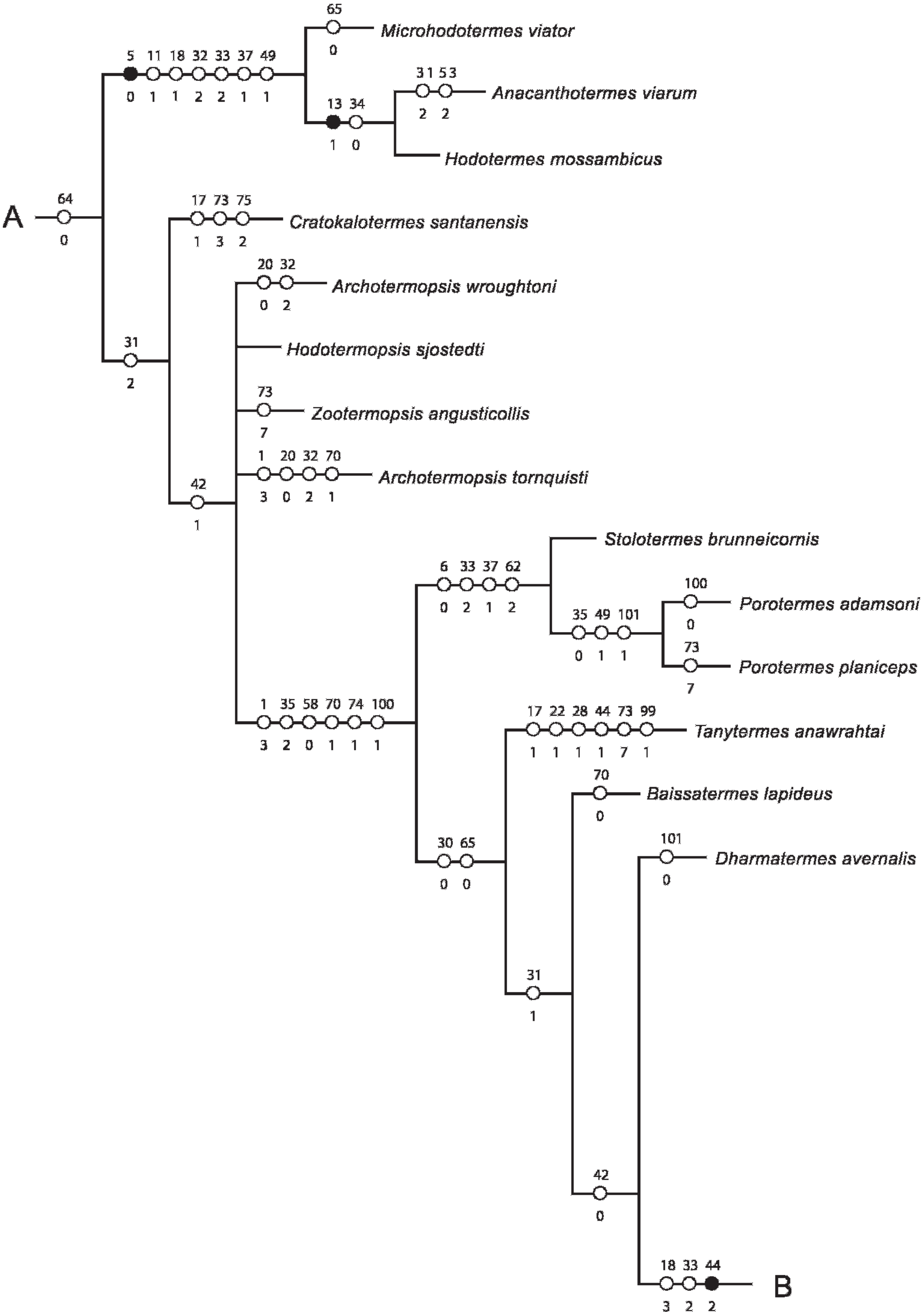


Fig. 2. Continuation of figure 1 focusing on Hodotermitidae s.s., "Termopsidae" s.s., Archotermopsidae, n. fam., Stolotermitidae, stat. n., and various stem-group lineages. Branch "B" (Kalotermitidae + Neoisoptera) is depicted in fig. 4.

is a group of three genera of the "harvesters"—*Anacanthotermes* Jacobson, *Hodotermes* Hagen, *Microhodotermes* Sjöstedt—that feed on grasses in savanna and steppe biomes of Africa and Eurasia; monophyly of this group is confirmed by other analyses (Inward et al., 2007a, 2007b; Legendre et al., 2008). Three genera of highly disjunct wood feeders that are traditionally placed in the Termopsidae s.l.—*Archotermopsis* Desneux, *Zootermopsis* Emerson, and *Hodotermopsis* Holmgren—were not found to be monophyletic, contrary to other studies. Inclusion or exclusion of the fossils made no difference to the definition of "Termopsidae s.l." except that *Archotermopsis* was sometimes found to be monophyletic. As such, the traditional concept of Termopsidae s.l. could not be supported and these genera are accordingly classified in the new family **Archotermopsidae**, new family (see Classification).

The austral disjuncts, *Stolotermes* Hagen and *Porotermes* Hagen, are sometimes placed within Termopsidae s.l. (e.g., Donovan et al., 2000; Thorne et al., 2000; Legendre et al., 2008) but should clearly be the separate family Stolotermitidae, stat. n. (= Stolotermitinae + Porotermitinae: see Classification), since they are the living sister group to Kalotermitidae plus higher termites in this study and in some molecular analyses (Inward et al., 2007a, 2007b). The divergence between Stolotermitidae and Kalotermitidae + higher termites was certainly in the Early Cretaceous, since there are three intermediate genera from the Early and mid-Cretaceous. The family Kalotermitidae, or dry-wood termites, is a cosmopolitan group of 457 living species, which has two known Cretaceous and three Tertiary stem-group taxa (only two of the latter were included in our study), with living species comprising a monophyletic group of probably Tertiary origin. Interestingly, a kalotermitid-like nest exists from the Late Cretaceous Javelina Formation of Texas (Rohr et al., 1986). Kalotermitidae is the sister group to an unequivocally monophyletic group we are calling the **Neoisoptera**, which is defined in part by the distinctive opening of the frontal gland called the fontanelle. The Neoisoptera is comprised of the Rhinotermitidae (13 living genera, 380 living species, all of which are wood feeders), the monotypic family Serritermitidae from Brazil, and the largest family, Termitidae. It also includes *Archeorhinotermes rossi* Krishna and Grimaldi in 100 Ma Burmese amber, the most derived termite from the Cretaceous, formerly placed in the Rhinotermitidae (Krishna and Grimaldi, 2003), but actually an extinct stem group to the rest of the Neoisoptera and here considered as the sole member of Archeorhinotermitidae, stat. n. (see Classification). *Parastylotermes* Snyder and Emerson and *Stylotermes* Holmgren and Holmgren (neither genus studied in prior analyses [Donovan et al., 2000; Inward et al., 2007a, 2007b; Legendre et al., 2008]) should be separated from Rhinotermitidae s. str., the latter doubtfully monophyletic (Donovan et al., 2000; Inward et al., 2007a, 2007b; Legendre et al., 2008) but clearly closely related to the Termitidae. These genera have been at times considered a separate family, as Stylotermitidae, stat. rev. (see Classification), and this status should be reinstated. The earliest rhinotermitids are *Reticulitermes antiquus* (Germar) and *Heterotermes eocenicus* Engel in Baltic amber (Engel et al., 2007b; Engel, 2008); the divergence of both families probably occurred in the Early Tertiary.

CLASSIFICATION

Several taxonomic changes are required in order to have the classification of termite families reflect our cladistic results. The revised, higher-level classification of Isoptera is outlined in table 3 (modified from Engel and Krishna, 2004a, 2004b, 2007c). The classification is that which is employed for (and will be further elaborated in) the forthcoming world catalog of Isoptera (Krishna et al., in press).

CRATOMASTOTERMITIDAE, new family

TYPE GENUS: *Cratomastotermes* Bechly.

DIAGNOSIS: Diagnosed by primitive retention of distinct cross veins, archedictyon between veins, arched humeral margin of forewing scale, large rectangular pronotum, pentamerous tarsi, and absence of ocelloids and fontanelle (refer also to Grimaldi et al., 2008).

TABLE 3

Synonymical Hierarchical Classification of Isoptera

(modified and updated from Engel and Krishna, 2004a, 2004b, 2007c)

- Order ISOPTERA Brullé
  - Family †Cratomastotermitidae Engel, Grimaldi, and Krishna, **new family**
  - Family Mastotermitidae Desneux
    - = †*Pliotermitinae Pongrácz*
    - = †*Miotermitinae Pongrácz*
  - Euisoptera Engel, Grimaldi, and Krishna, **new clade**
    - Family Incertae Sedis
      - (a grade of primitive termites whose relationships are not yet resolved)
        - = †*Cretatermitinae Emerson*
        - = †*Lutetiatermitinae Schlüter*
        - = †*Carinatermitinae Krishna and Grimaldi*
        - = †*Caatingatermitinae Martins-Neto et al.*
    - Family †Termopsidae Holmgren, sensu stricto
    - Family Hodotermitidae Desneux, sensu stricto
    - Family Archotermopsidae Engel, Grimaldi, and Krishna, **new family**
    - Family Stolotermitidae Holmgren, status novus
      - Subfamily Stolotermitinae Holmgren
      - Subfamily Porotermitinae Emerson
    - Family Kalotermitidae Froggatt
      - = *Glyptotermitinae Froggatt*
      - = †*Electrotermitinae Emerson*
    - Neoisoptera Engel, Grimaldi, and Krishna, **new clade**
      - Family †Archeorhinotermitidae Krishna and Grimaldi, status novus
      - Family Stylotermitidae Holmgren and Holmgren, status revivisco
      - Family Rhinotermitidae Froggatt
        - Subfamily Coptotermitinae Holmgren
          - = *Arrhinotermitinae Sjöstedt*
        - Subfamily Heterotermitinae Froggatt
          - = *Leucotermitinae Holmgren*
        - Subfamily Prorhinotermitinae Quennedey and Deligne
        - Subfamily Psammotermitinae Holmgren
        - Subfamily Termitogetoninae Holmgren
        - Subfamily Rhinotermitinae Froggatt
      - Family Serritermitidae Holmgren
        - = *Glossotermitinae Cancello and DeSouza, **new synonymy***
      - Family Termitidae Latreille
        - Subfamily Sphaerotermitinae Engel and Krishna
        - Subfamily Macrotermitinae Kemner
          - = *Acanthotermitinae Sjöstedt*
          - = *Odontotermitini Weidner*
        - Subfamily Foraminitermitinae Holmgren
          - = *Pseudomicrotermitinae Holmgren, **new synonymy***
        - Subfamily Syntermitinae Engel and Krishna
        - Subfamily Nasutitermitinae Hare
        - Subfamily Apicotermitinae Grassé and Noirot
          - = *Indotermitidae Roonwal and Sen Sarma*
        - Subfamily Cubitermitinae Weidner, status revivisco et novus
        - Subfamily Termitinae Latreille
          - = *Microcerotermitinae Holmgren*
          - = *Amitermitinae Kemner*
          - = *Mirocapritermitinae Kemner*
          - = *Mirotermitini Weidner*
          - = *Capritermitini Weidner*
        - Incertae Sedis †Eutermitinae Holmgren

INCLUDED GENERA: The family presently comprises a single genus, *Cratomastotermes*.

Family TERMOPSIDAE Holmgren, sensu novum

Termopsinae Holmgren, 1911: 35. Type genus: *Termopsis* Heer, 1849.

COMMENTS: Since the time of Hagen (1858), the fossil *Termopsis bremii* Heer (1849) has been intricately linked to a group of otherwise plesiomorphic modern species. Over the intervening 150 years a few additional genera and several living species have been added to the group that became known as the Termopsinae and eventually Termopsidae (e.g., Emerson, 1933). Unfortunately, no singular, specialized (i.e., apomorphic) feature has truly united these taxa and the monophyly of the group has been suspect. Our analysis reveals that those fossils of the Tertiary genus *Termopsis* are, in fact, not related to the modern members otherwise classified in the family (namely *Archotermopsis*, *Zootermopsis*, and *Hodotermopsis*, below classified into a new family). In addition, those other fossil and living genera also traditionally classified in the family (e.g., *Stolotermes* and *Porotermes* of the Stolotermitinae and Porotermitinae, respectively) were similarly found to be unrelated to *Termopsis*, as well as unrelated to the aforementioned genera of Termopsinae. Accordingly, Termopsidae is here significantly restricted and considered to comprise only the genus *Termopsis*.

ARCHOTERMOPSIDAE, new family

TYPE GENUS: *Archotermopsis* Desneux.

DIAGNOSIS: The new family can be characterized by the following combination of attributes: absence of ocelloids and fontanelle, antennae with 22–27 articles, pronotum distinctly narrower than head, tarsi pentamerous (sometimes cryptically), fourth sternite with sole sternal gland, forewing scale overlapping hind-wing scale, humeral margin of scale flat, imago-worker mandibles with three marginal teeth (left side) and subsidiary tooth between apical and first marginal teeth (right side).

INCLUDED GENERA: *Archotermopsis*, *Zootermopsis*, *Hodotermopsis*, and tentatively †*Parotermes* Scudder. The Late Miocene genus †*Gyatermes* Engel and Gross (2009) may belong herein but must await more completely preserved material.

Family HODOTERMITIDAE Desneux, sensu novum

Hodotermitini Desneux, 1904: 284. Type genus: *Hodotermes* Hagen, 1853.

COMMENTS: Numerous genera of plesiomorphic fossil termites have been historically assigned to Hodotermitidae, leaving the impression that this group was once diverse in the past but has experienced significant extinction and that the modern taxa are relicts of this former diversity. In fact, our study demonstrates that none of the fossils assigned to Hodotermitidae can be considered actual hodotermitids. Instead, this assemblage represents a grade between several families and lineages of Isoptera. Hodotermitidae was recovered as a monophyletic group but strictly for the modern genera. We have accordingly restricted the sense of Hodotermitidae to those genera (listed below) and consider the remaining groups such as Cretotermitinae, Carinatermitinae, Lutetiatermitinae, and Caatingatermitinae (the latter two ill defined on teratologies and misinterpreted characters, respectively), among numerous other genera (e.g., *Meiatermes*; *Melqartitermes* Engel, Grimaldi, and Krishna; *Mylacrotermes* Engel, Grimaldi, and Krishna; *Mariconitermes* Fontes and Vulcano; *Cratokalotermes* Bechly) as incertae sedis among basal Euisoptera (fig. 3).

INCLUDED GENERA: *Hodotermes*, *Anacanthotermes*, and *Microhodotermes*.

Family STOLOTERMITIDAE Holmgren, status novus

Stolotermitinae Holmgren, 1910: 285. Type genus: *Stolotermes* Hagen, 1858.

COMMENTS: The Stolotermitidae is here recognized to encompass the former subfamilies Stolotermitinae and Porotermitinae of Termopsidae s.l. For the moment the two subfamilies are retained despite each being monogeneric.

INCLUDED GENERA: *Stolotermes* (in Stolotermitinae) and *Porotermes* (in Porotermitinae).

Family ARCHEORHINOTERMITIDAE Krishna and Grimaldi, status novus

Archeorhinotermitinae Krishna and Grimaldi, 2003: 2. Type genus: *Archeorhinotermes* Krishna and Grimaldi, 2003.

COMMENTS: Although previously classified as a primitive lineage in the Rhinotermitidae, affinities with this group are entirely plesiomorphic. As our analysis reveals, *Archeorhinotermes* is actually a stem group, basal to all Euisoptera. Accordingly we have removed the genus from Rhinotermitidae and elevated Archeorhinotermitinae to familial rank.

INCLUDED GENERA: The family includes only *Archeorhinotermes* at present.

Family STYLOTERMITIDAE Holmgren and Holmgren, status revivisco

Stylotermitinae Holmgren and Holmgren, 1917: 141. Type genus: *Stylotermes* Holmgren and Holmgren, 1917.

COMMENTS: *Stylotermes* and the Tertiary genus *Parastylotermes* have historically been classified in the Rhinotermitidae. These genera are particularly distinctive in their possession of trimerous tarsi, a feature otherwise known only in *Indotermes* of the Termitidae. The significance of this tarsal reduction was used by some authors in the past to accord Stylotermitinae familial rank, in the same fashion that *Indotermes* was placed in a monogeneric family of its own (e.g., Roonwal, 1958). Herein we resurrect the familial status of the former. Although the trimerous condition of the tarsi is truly a distinctive synapomorphy for the group, the classificatory alteration is based on the fact that Stylotermitinae comprises a grade, along with Archeorhinotermitinae leading to Rhinotermitidae + Serritermitidae + Termitidae (fig. 3). As such, its inclusion within Rhinotermitidae renders the assemblage demonstrably paraphyletic.

INCLUDED GENERA: *Stylotermes* and *Parastylotermes*.

ECOLOGY AND EVOLUTION

The circumtropical family Termitidae, or "higher termites," comprises approximately 70% of all termite species and appears to be one of the most recent radiations of all insect groups that are ecologically significant. Monophyly of the Termitidae is well established; the family includes such familiar groups as the Macrotermitinae and Nasutitermitinae, some of which build huge mounds in grassland and scrub biomes; other nasute taxa build large arboreal nests of cartonlike, fecal material in tropical forests. The diets of Termitidae are extremely diverse, primitively being sound and rotting wood but also including humus, leaf litter, soil, grass, herbivore dung, and even the mycelia of a symbiotic fungus, *Termitomyces* R. Heim, that they cultivate in the nest like attine ants (e.g., Sands, 1969). The huge colonies and diverse diets of the Termitidae account for the overwhelming biomass of termites in tropical and subtropical environments. The earliest apparent termitid is an incomplete compression of an imago from the Oligocene of Brazil, ca. 30 Ma (Martins-Neto and Pesenti, 2006;, a putative termitid from the Bembridge Marls [Jarzembowski, 1980] is probably a rhinotermitid). The first diverse paleofaunas of Termitidae—more than 30 species—are in Miocene amber from the Dominican Republic (Krishna and Grimaldi, 2009) and Mexico, which are very similar to modern Neotropical faunas. This dramatic appearance is probably due to the fact that these ambers are the only major fossil insect deposits from the Neogene that were formed in the tropics. Were Termitidae abundant during the Eocene they should have been preserved in Baltic amber (Lutetian: ca. 45 Ma), since this deposit has yielded thus far most other living termite families (Engel et al., 2007b; Engel, 2008), as well as species belonging to a diversity of other tropical insect groups (Grimaldi and Engel, 2005). We estimate that Termitidae diverged from Rhinotermitidae sometime in the Early Paleogene (perhaps Late Paleocene or Early Eocene) and subsequently began its diversification in the latest Eocene (Priabonian-Bartonian: ca. 40 Ma) to Early Oligocene, continuing to radiate throughout the remainder of the Neogene and Quaternary.

Though Jurassic remains of Isoptera have not been found, Isoptera appear to have diverged from cryptocercid roaches in the

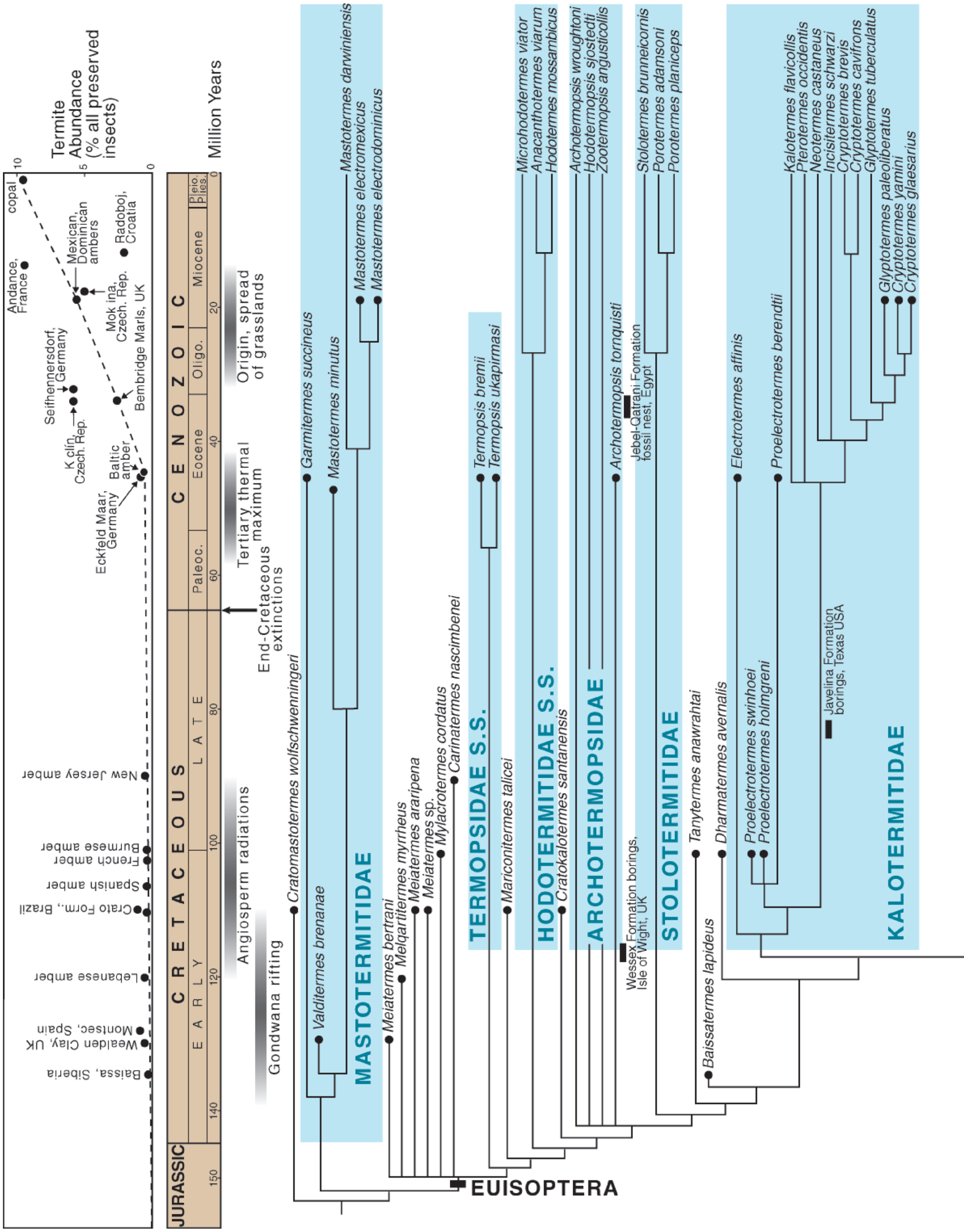
Late Jurassic. This would make termites the oldest group of eusocial animals, predating the origins of ants by some 35 million years. Major geological and biotic events in the Cretaceous probably had little effect on termites, since basal divergences appear to have preceded the drift of Gondwanan continents and the angiosperm radiations. Unfortunately, the stratigraphic sampling is too poor in the Late Cretaceous and Paleocene to determine any effects of the end-Cretaceous extinctions. The Tertiary thermal maximum of the late Paleocene and Eocene, however, probably had a profound effect on termites, specifically on the global spread of *Mastotermes* and the radiations of living Kalotermitidae and Neoisoptera. The rapid spread of C4 grasslands in the Miocene (Jacobs et al., 1999) doubtless promoted a minor diversification of the harvesters and the explosive diversification of many Termitidae, such as the Macrotermitinae. A macrotermitine nest, in fact, is known from the Miocene of Chad (Duringer et al., 2006).

Throughout the Cretaceous and early Tertiary, including the mid-Eocene, termites represented less than 1% of all insect specimens in all fossil deposits (fig. 3). Their abundance rises in the late Eocene to approximately 2%, and then spikes from 5%–10% during the Miocene as both amber and compression fossils, to the present day (in copals, or subfossil resins) (table 2, fig. 3). This spike in abundance is due to the diversification of the Termitidae. The abundance of ants rises dramatically in the Eocene (Grimaldi and Agosti, 2001; Dlussky and Rasnitsyn, 2002), and ants are generally much more abundant in Tertiary insect deposits than are termites, probably because termites feed within the wood where they nest or they travel through tunnels from nest to food sources, so foragers are rarely exposed and imagoes are exposed only during brief nuptial flights. Interestingly, many termitids will forage in the open and these are concomitantly the most abundant termites in Dominican amber and copal.

Our analysis indicates the importance of including fossils in cladistic analyses rather than mapping their putative ages onto molecular-based trees for purposes of dating. The identity of stem groups is obscured in the latter method, resulting in overestimates for divergence times. In our analyses this overestimation is highlighted by the traditional taxonomic placement of *Termopsis* and most Cretaceous fossils as Termopsidae s.l. and Hodotermitidae, respectively (fig. 3). These taxa in fact represent either a grade to more nested termite lineages or stem groups to some modern families (fig. 3). Using such fossils to calibrate the basal nodes for Hodotermitidae or Termopsidae would result in significant overestimates of the ages of these groups. A failure to distinguish stem groups in an analysis probably explains prior overestimates of the age of other insect lineages (e.g., Moreau et al., 2006; Hunt et al., 2007).

Patterns in termite diversification are very similar to those of the ants (Grimaldi and Agosti, 2001): throughout the Cretaceous both groups were rare and consisted of basal lineages. The diversity and abundance of termites and ants spiked in the Tertiary when speciose groups that form large colonies with highly specialized castes (for ants, the subfamilies Dolichoderinae, Formicinae, and Myrmecinae) eclipsed the smaller colonies of more basal taxa—the concept of “dynastic succession” (Wilson and Hölldobler, 2005). For ants, approximately 70 million years passed from origin to ecological dominance; in termites, this period was 100 million years. Thus, eusociality per se does not result in ecological success, but living in very large colonies with extreme division of labor does. Why, then, did it take so long for large colonies to evolve? We suggest that social evolution is like any other highly adaptive feature, such as the evolution of flight in feathered theropods, and thus may take tens of millions of years to refine.

Similarly, the symbiosis of termites with intestinal protozoa or bacteria which aid their break down of lignocellulose does not alone explain their ecological success as basal termite lineages exhibit the same mutualistic relationship. While their critical role as carbon recyclers is made possible by this symbiosis, this association existed for tens of millions of years before their rise in abundance and diversity (fig. 3).


Termite Abundance (% all preserved insects)
10
5
0
copal
Andance, France
Mexican, Dominican ambers
Radoboj, Croatia
Mok ina, Czech. Rep.
Seifhennersdorf, Germany
Bembridge Marls, UK
K clin, Czech. Rep.
Baltic amber
Eckfeld Maar, Germany
New Jersey amber
Burmese amber
French amber
Spanish amber
Crato Form., Brazil
Lebanese amber
Montsec, Spain
Wealden Clay, UK
Baissa, Siberia
Million Years
0
20
40
60
80
100
120
140
150
JURASSIC
CRETACEOUS
EARLY
LATE
CENOZOIC
Paleoc.
Eocene
Oligo.
Miocene
Pleis.
Plio.
Origin, spread of grasslands
Tertiary thermal maximum
End-Cretaceous extinctions
Angiosperm radiations
Gondwana rifting
Cratomastotermes wolfschwenningeri
Garmitermes succineus
Valditermes brenanae
Mastotermes minutus
Mastotermes darwiniensis
Mastotermes electromexicus
Mastotermes electrodominicus
MASTOTERMITIDAE
Meiatermes bertrani
Melqartitermes myrrheus
Meiatermes araripena
Meiatermes sp.
Mylacrotermes cordatus
Carinatermes nascimbenei
EUISOPTERA
Termopsis bremii
Termopsis ukapirmasi
TERMOPSIDAE S.S.
Mariconitermes talicei
Microhodotermes viator
Anacanthotermes viarum
Hodotermes mossambicus
Cratokalotermes santanensis
HODOTERMITIDAE S.S.
Archotermopsis wroughtoni
Hodotermopsis sjostedti
Zootermopsis angusticollis
Archotermopsis tornquisti
ARCHOTERMOPSIDAE
Wessex Formation borings, Isle of Wight, UK
Jebel-Qatrani Formation fossil nest, Egypt
Stolotermes brunneicornis
Porotermes adamsoni
Porotermes planiceps
STOLOTERMITIDAE
Tanytermes anawrahtai
Baissatermes lapideus
Dharmatermes avernalis
Electrotermes affinis
Proelectrotermes swinhoei
Proelectrotermes holmgreni
Proelectrotermes berendtii
Javelina Formation borings, Texas USA
Kalotermes flavicollis
Pterotermes occidentis
Neotermes castaneus
Incisitermes schwarzi
Cryptotermes brevis
Cryptotermes cavifrons
Glyptotermes tuberculatus
Glyptotermes paleoliberatus
Cryptotermes yamini
Cryptotermes glaesarius
KALOTERMITIDAE

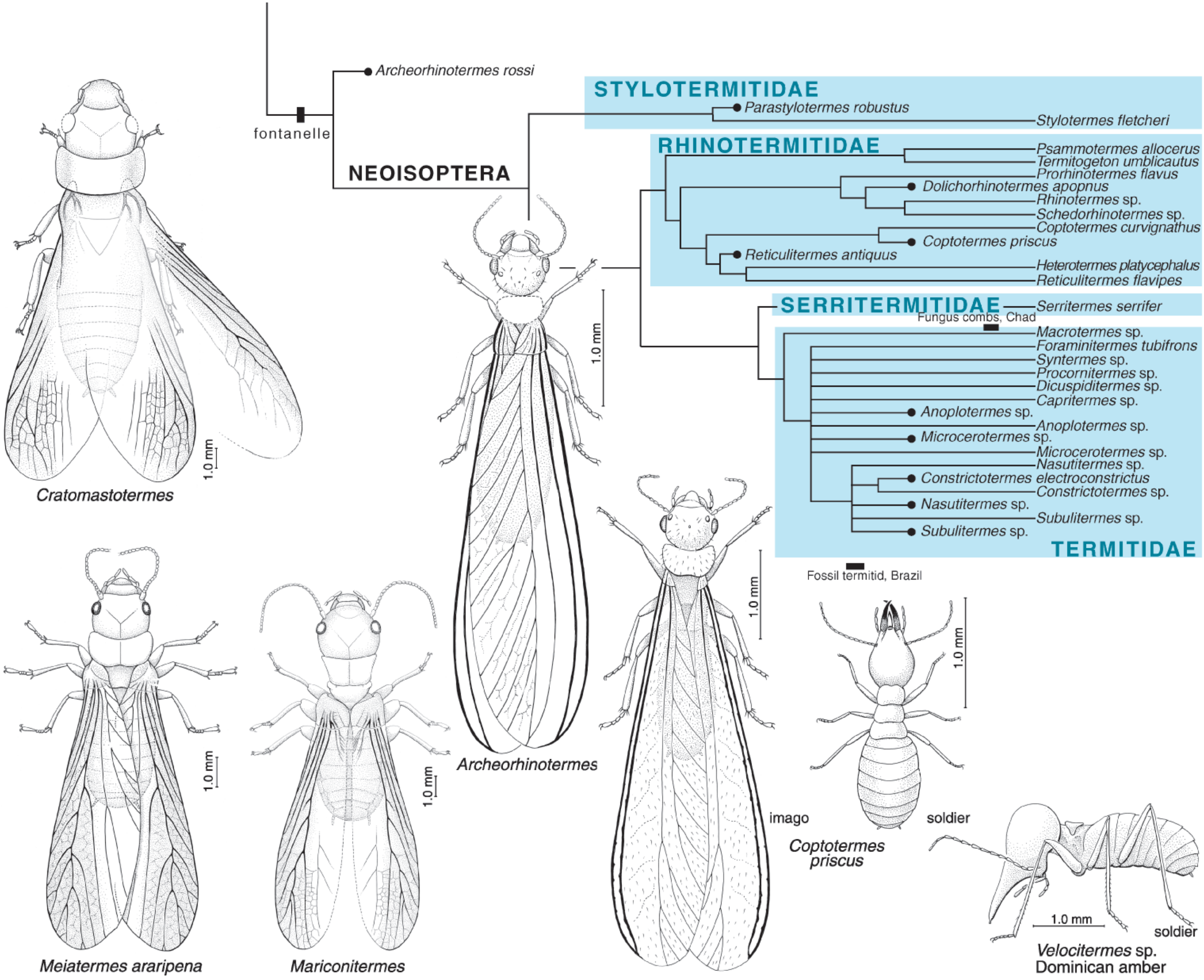


Fig. 3. Strict consensus cladogram of all termite species studied superimposed on geological time scale, with graph of termite abundance.

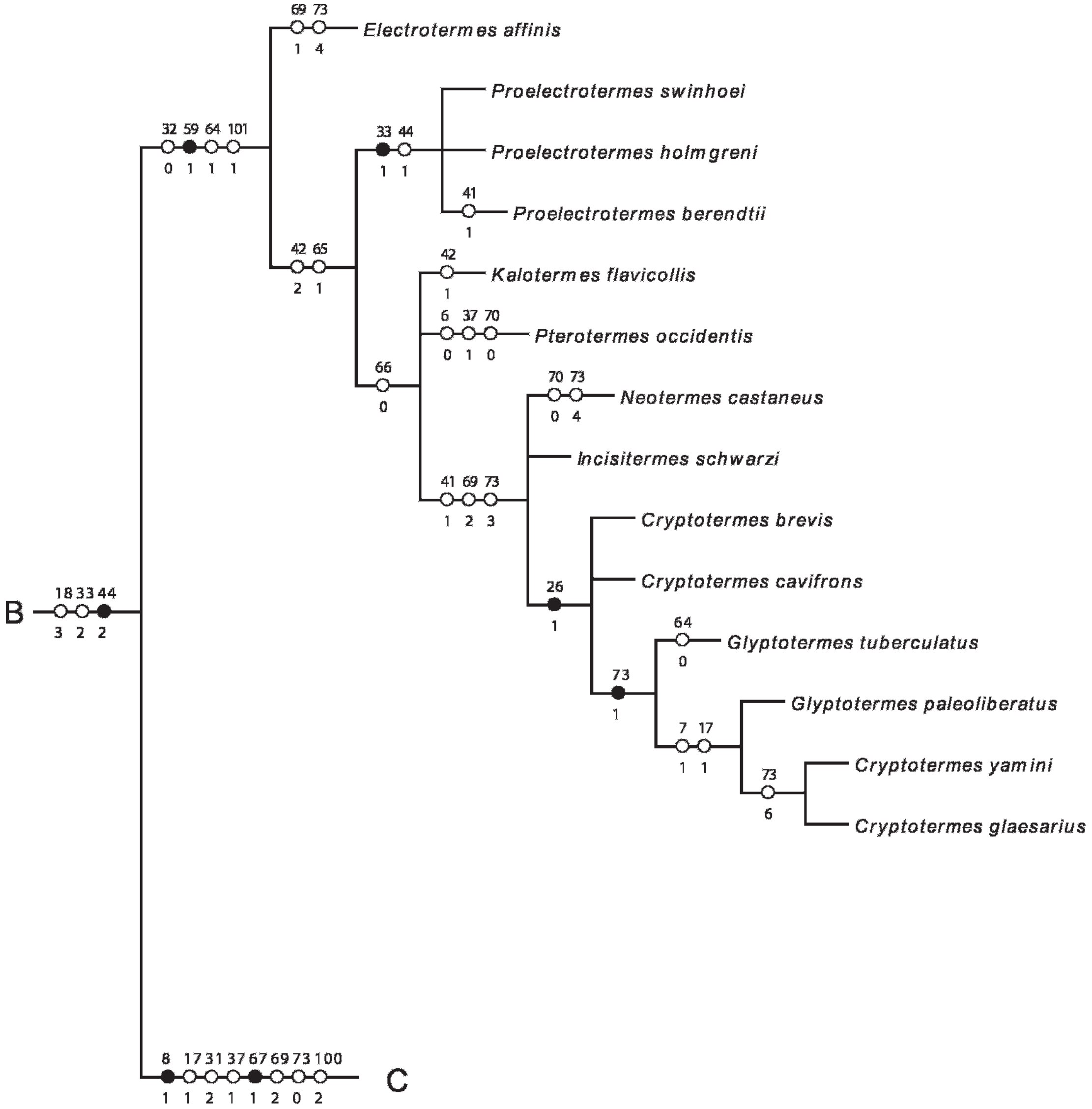


Fig. 4. Continuation of figs. 1–2 focusing on Kalotermitidae. Branch “C” (Neoisoptera) in fig. 5.

One question remains: how was wood decomposed in Mesozoic forests with few or no termites? Patterns of coal and oil deposition suggest that lignocellulose did not rapidly decompose prior to termites and the actions of fungi or other organisms at the time must have been either slow or negligible. Coal is formed from ombrotrophic, or waterlogged, peat (Scott, 1987). While there are some tropical peatlands, such as the coastal “moor” forests of western Borneo and southern Sumatra, these are dwarfed in area compared to the boreal peatlands of sphagnum and heaths that comprise some 3% of earth’s land surface. Tropical ecosystems produce more biomass, but much greater plant detritus accumulates in boreal forests and peatlands, which is traditionally explained by lower boreal evapotranspiration and because seasonality limits decomposition (Scott, 1987). Indeed, boreal peat lands lay hundreds of miles north of the most northern termites in the genus *Reticulitermes*

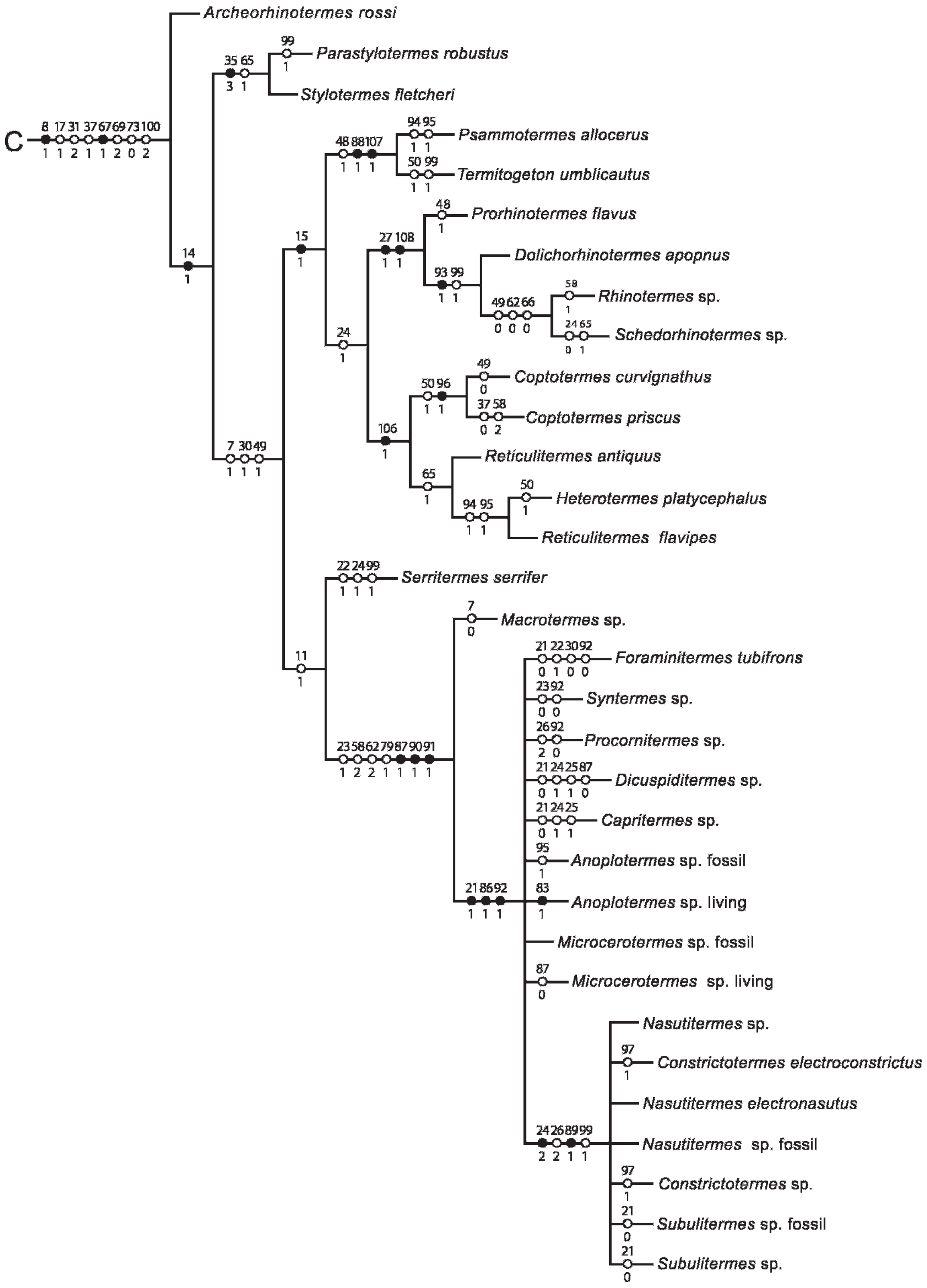


Fig. 5. Continuation of figs. 1, 2, and 4 focusing on Neoisoptera.

Holmgren (Rhinotermitidae). Maximum termite diversity is equatorial, and half of that diversity falls between 18° N and 30° S latitudes; by 48° N and S it is 1%–4% that of the diversity at the Equator (Eggleton, 2000). Tropical ecosystems where termites are most abundant and diverse have notoriously thin humus layers (Richards, 1996). This may explain why coals that were formed prior to the appearance of termites in the Paleozoic and Early Mesozoic, and in largely the same regions and habitats, decomposed less (i.e., contained significantly more vitrain) than Tertiary and modern peats (Shearer et al., 1995; Raymond et al., 2000), as well as the formation of some vast reservoirs of petroleum, like those in the Early Cretaceous Nubian sandstones of present-day Africa and the Middle East. While some Miocene coal formations are astonishingly thick (Shearer et al., 1995), these were formed in palaeoclimates that today would have very few or no termites.

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APPENDIX

Data Matrix for Characters Described in Table 1

Below is provided the suite of character-state codings for characters used in the analysis of Isoptera relationships. Within the matrix “-” indicates inapplicable codings (e.g., soldier characters for species which lack this caste); “?” indicates unknown states; “*” indicates a subset polymorphism for character 73 with states 3, 4, 5, 6, and 7; while “$” indicates a subset polymorphism for character 92 with states 0 and 1

	Character				
		1	2	3	4
Taxon	123456789	0123456789	0123456789	0123456789	01234
Chaeteessa sp.	0100---00	0--0--1020	1-0-----10	0112100010	00200
Periplaneta sp.	0001---00	0000--1000	0-0-----10	0010000010	00200
Panchlora sp.	1001---00	0--0--?-00	0-0-----10	0010000010	00200
Cryptocercus sp. 1	1101---00	0000--?010	0-0-----10	0010000000	0----
Cryptocercus sp. 2	1101---00	0000--?010	0-0-----10	0010000000	0----
Mastotermes darwiniensis	11111-101	0100000030	1000000-00	0100000010	10100
Anacanthotermes viarum	211100001	1101001011	1000000-00	1222020111	10210
Microhodotermes viator	211100001	1100001011	1000000-00	1122121111	10210
Hodotermes mossambicus	211100001	1101001011	1000000-00	1122021111	10210
Archotermopsis wroughtoni	211111001	1010001021	0000000-00	122--10011	10110
Hodotermopsis sjostedti	2111---01	1010001021	1000000---	-----10-11	10110
Zootermopsis angusticollis	211111001	1010001021	1000000-00	1210110011	10110
Porotermes adamsoni	311110001	1010001021	1000000-00	1212100111	10110
Porotermes planiceps	311110001	1010001021	1000000-00	1212100111	10110
Stolotermes brunneicornis	311110001	1010001021	1000000-00	1212120111	10110
Kalotermes flavicollis	311111001	1100001031	1000000-00	0102120011	10112
Cryptotermes brevis	311111001	1100001031	1000001-00	0102120011	11212
Cryptotermes cavifrons	311111001	1100001031	1000001-00	0102120011	11212
Neotermes castaneus	311111001	1100001031	1000000-00	0102120011	11212
Incisitermes schwarzi	311111001	1100001031	1000000-00	0102120011	11212
Pterotermes occidentis	311110001	1100001031	1000000-00	0102120111	10212
Glyptotermes tuberculatus	311111001	1100001031	1000001-00	0102120011	11012
Serritermes serrifer	31111-111	1100101131	1010100000	1212120111	1--12
Coptotermes curvignathus	31111-111	1010111131	1001100000	1212120111	1--12
Heterotermes platycephalus	31111-111	1010111131	1001100000	1212120111	1--12
Prorhinotermes flavus	31111-111	1010111131	1001100100	1212120111	1--12
Rhinotermes sp.	31111-111	1010111131	1000100100	1212120111	1--12
Psammotermes allocerus	31111-111	1010111131	1000000000	1212120111	1--12
Schedorhinotermes sp.	31111-111	1010111131	1000000100	1212120111	1--12
Reticulitermes flavipes	31111-111	1010111131	1001100000	1212120111	1--12
Termitogeton umblicautus	31111-111	1010111131	100--00000	1212120111	1--12
Foraminitermes tubifrons	31111-111	1100101131	1011000000	0212120111	1--12
Macrotermes sp.	311111011	1110101131	1001000000	1212120111	1--12
Syntermes sp.	31111-111	1100101131	1100000000	1212120111	1--12
Procornitermes sp.	31111-111	1100101131	110-002000	1212120111	1--12
Nasutitermes sp.	31111-111	1100101131	110-2-2000	1212120111	1--12
Dicuspiditermes sp.	31111-111	1100101131	10?1110000	1212120111	1--12
Capritermes sp.	31111-111	1100101131	1001110000	1212120111	1--12
Baissatermes lapideus	???????0?	???????0??	1??????-??	01????????	10110
Valditermes brennenae	?????????	??????????	??????????	????????1?	?02?0
Melqartitermes myrrheus	3111???01	0?0????1??	1??????-10	0100100011	11211
Meiatermes bertrani	?111??-01	?01????02?	100---?-10	010??000--	10210
Meiatermes araripena	2111???01	???????02?	1???????10	010??000?-	10210
Mariconitermes talicei	?1?1????1	???????02?	1??????-00	111??000?-	10200
Cratomastotermes wolfschwennigeri	???1????1	??????????	1??????-10	010??000?-	??2??
Cratokalotermes santanensis	?1?1???01	???????12?	1??????-00	121???????	?02??

APPENDIX
(Continued)

			Character		
		1	2	3	4
Taxon	123456789	0123456789	0123456789	0123456789	01234
Meiatermes sp.	?????????	??????????	???????-??	??????????	?0??0
Proelectrotermes swinhoei	3111???01	?????????3?	??????????	??????????	10?11
Proelectrotermes holmgreni	?????????	??????????	??????????	???112001?	10211
Archeorhinotermes rossi	?1?1???11	?01?0??13?	100????000	?21212011-	1--12
Mylacrotermes cordatus	?111???01	0??????120	1??????-01	110010011?	1??1?
Dharmatermes avernalis	?1?1???01	?0?0????2?	100????-00	01101?0?1?	10010
Tanytermes anawrahtai	3111???01	??0????12?	101????-10	021012001?	10111
Carinatermes nascimbenei	?111???01	????????20	1??????-10	0100000010	10210
Garmitermes succineus	2101???00	???????030	1??????-00	1100000000	1??0?
Termopsis bremii	2111???01	???????121	1??????-10	0110100011	10010
Termopsis ukapirmasi	2111???01	1??????121	1??????-10	0110100011	10010
Archotermopsis tornquisti	3111???01	???????021	0??????-00	122--10011	10110
Proelectrotermes berendtii	3111???01	???????03?	1??????-00	0101120011	11211
Electrotermes affinis	3111???01	1??????031	1??????-00	010--20011	10012
Reticulitermes antiquus	3111???11	1???1??131	1???????000	121--20111	1--12
Parastylotermes robustus	3111???11	1???1??131	1???????000	021--30111	1--12
Mastotermes electromexicus	2111???01	1??????130	1??????-00	010--00010	10100
Mastotermes electrodominicanus	21111??01	1???00?030	1??????-00	010--00010	10100
Mastotermes minutus	3101???01	???????03?	1??????-00	010??00010	10100
Stylotermes fletcheri	311111011	10101-1131	100--00000	0212130111	1--12
Constrictotermes electroconstrictus	311??????	?????????1	1????02???	??????????	1????
Nasutitermes electronasutus	311??????	?????????1	1????02???	??????????	1????
Dolichorhinotermes apopnus	3111???11	1??????1?1	1???????100	1212120111	1--12
Cryptotermes yamini	3111??101	1??????131	1??????-00	0102120011	11212
Cryptotermes glaesarius	3111??101	1??????131	1??????-00	0102120011	11212
Glyptotermes paleoliberatus	3111??101	1??????131	1??????-00	0102120011	11012
Coptotermes priscus	31111-111	1???11?131	1001???-00	1212120011	1--12
Anoplotermes sp. fossil	3111???11	11?????131	1???????000	1212120111	1--12
Anoplotermes sp. living	3111--111	1100101131	11?----000	1212120111	1--12
Microcerotermes sp. fossil	3111???11	110????131	11??????000	1212120111	1--12
Microcerotermes sp. living	31111-111	1100101131	110-000000	1212120111	1--12
Nasutitermes sp. fossil	3111??111	110????131	1?0????000	1212120111	1--12
Constrictotermes sp.	31111-111	1100101131	110-202000	1212120111	1--12
Subulitermes sp. fossil	?1111-111	1????????31	10?-202000	??2120111	1?-??
Subulitermes sp. living	31111-111	1100101131	100-202000	1212120111	1--12

			Character		
	4	5	6	7	8
Taxon	56789	0123456789	0123456789	0123456789	012345678
Chaeteessa sp.	0100-	0000000020	10----10-0	0000000011	000---00-
Periplaneta sp.	0000-	0---000010	00----10-0	0007000011	000---00-
Panchlora sp.	0000-	0000000010	00----10-0	0007000011	000---00-
Cryptocercus sp.1	--1--	----------	----------	----000000	111---00-
Cryptocercus sp.2	--1--	----------	----------	----000000	111---00-
Mastotermes darwiniensis	01000	0110110010	0100011000	0116101000	1210--000
Anacanthotermes viarum	01001	0112121010	1300011010	0115001110	1210--000
Microhodotermes viator	01001	0111121010	1300001010	0115001110	1210--000
Hodotermes mossambicus	01001	0111121010	1300011010	0115001110	1210--000
Archotermopsis wroughtoni	-100-	0111121010	130-0-10-0	011-001110	1210--000

APPENDIX
(Continued)

	Character				
Taxon	4 56789	5 0123456789	6 0123456789	7 0123456789	8 012345678
Hodotermopsis sjostedti	-100-	011-121010	130-0-10-0	011-001110	1210--000
Zootermopsis angusticollis	11000	0111121010	13000110-0	0117001110	1210--000
Porotermes adamsoni	11001	0111121100	1320011020	1115101110	1210--000
Porotermes planiceps	11001	0111121100	1320011020	1117101110	1210--000
Stolotermes brunneicornis	11000	0111121100	1320011020	1115101110	1210--000
Kalotermes flavicollis	11000	0111121001	1301110020	1115122110	1210--000
Cryptotermes brevis	11000	0111121001	1301110022	1113122110	1210--000
Cryptotermes cavifrons	11000	0111121001	1301110022	1113122110	1210--000
Neotermes castaneus	11000	0111121001	1301110022	0114122110	1210--000
Incisitermes schwarzi	11000	0111121001	1301110022	1113122110	1210--000
Pterotermes occidentis	1100-	0111121001	1301110020	0115122110	1210--000
Glyptotermes tuberculatus	11000	0111121001	1301010022	1111122110	1210--000
Serritermes serrifer	110--	0112121100	1311-0112-	1110121110	1210--?00
Coptotermes curvignathus	11000	1112121100	1311001122	1110121110	1210--?00
Heterotermes platycephalus	11001	1112121100	1311011121	1110121110	1210--?00
Prorhinotermes flavus	11011	0112121100	131100-12-	1110121110	1210--?00
Rhinotermes sp.	11000	0112121110	1301000121	1110121110	1210--?00
Psammotermes allocerus	11011	0112121100	13110?-12-	1110121110	1210--?01
Schedorhinotermes sp.	11000	0112121100	1301010120	1110121110	1210--?00
Reticulitermes flavipes	11001	0112121100	1311011120	1110121110	1210--000
Termitogeton umblicautus	11011	1112121100	131100-12-	1110121110	1210--?01
Foraminitermes tubifrons	110-1	01121211-0	132100112-	1110121111	1210--110
Macrotermes sp.	11001	0112121120	1321001122	1110121111	1210--010
Syntermes sp.	11001	0112121120	1321001122	1110121111	1210--110
Procornitermes sp.	11001	0112121120	1321001122	1110121111	121000?10
Nasutitermes sp.	11001	0112121120	1321001122	1110121111	1210111-0
Dicuspiditermes sp.	11001	0112121120	1321001122	1110121111	1210--?00
Capritermes sp.	11001	0112121120	1321001122	1110121111	1210--110
Baissatermes lapideus	1100?	011?12-??0	??0?0?1020	0115??????	????--???
Valditermes brennenae	?100?	011?1200?0	??010?1000	0116??????	????--???
Melqartitermes myrrheus	01000	011?12-?10	??001?1020	111500????	????--???
Meiatermes bertrani	0100?	01-?12-000	?10???1000	0116??1???	????--???
Meiatermes araripena	01000	01-?12-?10	?10010-000	0115?1????	????--???
Mariconitermes talicei	01000	01-?12-?10	?200111000	0115?1????	????--???
Cratomastotermes wolfschwennigeri	01000	01-?0?-?10	??????100?	011???????	????--???
Cratokalotermes santanensis	-100?	01-?12-?10	??????102?	0113?2????	????--???
Meiatermes sp.	?100?	01-?12-?10	?10???1000	011400????	????--???
Proelectrotermes swinhoei	1100?	011?121?01	130???1020	1115??????	????--???
Proelectrotermes holmgreni	1100?	011?121?01	130???1020	1115??????	????--???
Archeorhinotermes rossi	1100?	011-1?1?00	131?0?1122	1110?2????	????--???
Mylacrotermes cordatus	?1000	?100??????	12?010????	?1????????	????--???
Dharmatermes avernalis	11000	011?12-?00	1311001020	1115??????	????--???
Tanytermes anawrahtai	11000	011?12-?00	1300001020	1117??????	????--???
Carinatermes nascimbenei	11000	011?12-?10	1200111020	011400????	????--???
Garmitermes succineus	?1000	?110??????	010011????	?11???????	????--???
Termopsis bremii	01000	0111121?10	1100101000	011700????	????--???
Termopsis ukapirmasi	01000	0111121?10	11?1111000	011700????	????--???
Archotermopsis tornquisti	-100-	0111121010	130-0-1020	111-?0????	????--???
Proelectrotermes berendtii	11000	0111121001	130111102?	111*?2????	????--???
Electrotermes affinis	11000	0111121001	1301101021	1114?2????	????--???

APPENDIX
(Continued)

	Character				
	4	5	6	7	8
Taxon	56789	0123456789	0123456789	0123456789	012345678
Reticulitermes antiquus	11001	0112121100	1311011122	1110?2????	????--???
Parastylotermes robustus	11000	0112121100	1311011122	1110?2????	????--???
Mastotermes electromexicus	01000	0110110010	0100011000	011??0????	????--???
Mastotermes electrodominicanus	01000	0110110010	0100011000	0117?0????	????--?00
Mastotermes minutus	0100?	0110110010	?10???1000	011*?0????	????--???
Stylotermes fletcheri	11000	0112121100	131101112-	1110121110	1210--?00
Constrictotermes electroconstrictus	?????	??????????	??????????	??????????	???011?-0
Nasutitermes electronasutus	?????	??????????	??????????	??????????	???011?-0
Dolichorhinotermes apopnus	11001	0112121100	131100112-	1110?2????	????--???
Cryptotermes yamini	11000	0111121001	130111002-	1116?2????	????--???
Cryptotermes glaesarius	11000	0111121001	130111002-	1116?2????	????--???
Glyptotermes paleoliberatus	11000	0111121001	130111002-	1111?2????	????--???
Coptotermes priscus	11001	1112121120	131100112-	110121???	???0--?0?
Anoplotermes sp. fossil	11001	0112121120	1321001122	111012????	?????????
Anoplotermes sp. living	11001	0112121120	1321001122	1110121111	1211--1--
Microcerotermes sp. fossil	11001	0112121120	1321001122	111012????	?????????
Microcerotermes sp. living	11001	0112121120	1321001122	1110121111	1210--100
Nasutitermes sp. fossil	11001	0112121120	1321001122	111012????	?????????
Constrictotermes sp.	11001	0112121120	1321001122	1110121111	1210111-0
Subulitermes sp. fossil	?????	??????????	??????????	????1?1???	???11??0
Subulitermes sp.	11001	0112121120	1321001122	1110121111	1210111-0

	Character		
			1
	8	9	0
Taxon	9	0123456789	012345678
Chaeteessa sp.	-	-0-000--0-	-------0-
Periplaneta sp.	-	-0-000--00	00-----0-
Panchlora sp.	-	-0-000--00	00-----0-
Cryptocercus sp.1	-	-0-000--00	00-------
Cryptocercus sp.2	-	-0-000--00	00-------
Mastotermes darwiniensis	0	00-0000-00	000000-0-
Anacanthotermes viarum	0	00-00-0-00	001010-0-
Microhodotermes viator	0	00-00-0-00	001010-0-
Hodotermes mossambicus	0	00-00-0-00	001010-0-
Archotermopsis wroughtoni	0	00-00-0-00	021010-0-
Hodotermopsis sjostedti	0	00-00-0-00	001010-0-
Zootermopsis angusticollis	0	00-00-0-00	001010-0-
Porotermes adamsoni	0	00-00-0-00	011010-0-
Porotermes planiceps	0	00-00-0-00	111010-0-
Stolotermes brunneicornis	0	00-00-0-00	121010-0-
Kalotermes flavicollis	0	00-0000-00	111100-0-
Cryptotermes brevis	0	00-0000-00	111100-0-
Cryptotermes cavifrons	0	00-0000-00	111100-0-
Neotermes castaneus	0	00-0000-00	111100-0-
Incisitermes schwarzi	0	00-0000-00	111100-0-
Pterotermes occidentis	0	00-0000-00	111100-0-
Glyptotermes tuberculatus	0	00-0000-00	111100-0-
Serritermes serrifer	0	00-0000-01	221100000

APPENDIX
(Continued)

	Character		
Taxon	8 9	9 0123456789	1 0 012345678
Coptotermes curvignathus	0	0000001-00	221100100
Heterotermes platycephalus	0	0000110-00	221100100
Prorhinotermes flavus	0	0000000-00	221100001
Rhinotermes sp.	0	0001000-01	221101001
Psammotermes allocerus	0	0000110-00	221100010
Schedorhinotermes sp.	0	0001000-01	221101001
Reticulitermes flavipes	0	0000110-00	221100100
Termitogeton umblicautus	0	0000000-01	221100010
Foraminitermes tubifrons	0	1100000-10	221100000
Macrotermes sp.	0	1100000-00	221100000
Syntermes sp.	0	1100000-10	221100000
Procornitermes sp.	0	1100000-?0	221100000
Nasutitermes sp.	1	1110000001	221100000
Dicuspiditermes sp.	0	11$0000-00	221100000
Capritermes sp.	0	1110000-?0	221100000
Baissatermes lapideus	?	??????????	??????-0-
Valditermes brennenae	?	??????????	??????-?-
Melqartitermes myrrheus	?	???0-????0	00????-0-
Meiatermes bertrani	?	???0--????	??????-0-
Meiatermes araripena	?	????--????	??????-0-
Mariconitermes talicei	?	???0--????	??????-?-
Cratomastotermes wolfschwennigeri	?	???00?????	??????-?-
Cratokalotermes santanensis	?	???0--????	??????-?-
Meiatermes sp.	?	???0-?????	??????-?-
Proelectrotermes swinhoei	?	????-0????	??????-0-
Proelectrotermes holmgreni	?	????-?????	?1????-?-
Archeorhinotermes rossi	?	??00-0???0	22??????0
Mylacrotermes cordatus	?	??-0--???1	21????-?-
Dharmatermes avernalis	?	??-0--????	?0????-?-
Tanytermes anawrahtai	?	??-0--???1	12????-?-
Carinatermes nascimbenei	?	??-000???0	11????-?-
Garmitermes succineus	?	??-000???0	00????-?-
Termopsis bremii	?	??-00-???0	01????-0-
Termopsis ukapirmasi	?	??-00-???0	01????-0-
Archotermopsis tornquisti	?	??-00-???0	02????-0-
Proelectrotermes berendtii	?	??-000???0	11????-?-
Electrotermes affinis	?	??-000???0	11????-0-
Reticulitermes antiquus	?	??0000???0	22????100
Parastylotermes robustus	?	??0000???1	22????000
Mastotermes electromexicus	?	??-000???0	00????-0-
Mastotermes electrodominicanus	0	0?-0000-?0	00???0-0-
Mastotermes minutus	?	??-000???0	00????-0-
Stylotermes fletcheri	0	0000000?00	221100000
Constrictotermes electroconstrictus	1	1?????01?1	22???00-0
Nasutitermes electronasutus	1	1?????00?1	22???00-0
Dolichorhinotermes apopnus	?	??0100???1	22?????0?
Cryptotermes yamini	?	??--00???0	11????-0-
Cryptotermes glaesarius	?	??--00???0	11????-0-
Glyptotermes paleoliberatus	?	??--00???0	11????-0-
Coptotermes priscus	0	0?00001??0	22???0100

APPENDIX

(Continued)

	Character		
			1
	8	9	0
Taxon	9	0123456789	012345678
Anoplotermes sp. fossil	?	??1001???0	22?????0?
Anoplotermes sp. living	-	-11000--10	221100000
Microcerotermes sp. fossil	?	??1000???0	22?????0?
Microcerotermes sp. living	0	11$0000-?0	221100000
Nasutitermes sp. fossil	?	??1000???1	22?????0?
Constrictotermes sp.	1	11100001?1	221100000
Subulitermes sp. fossil	1	1?1??????1	22???00??
Subulitermes sp.	1	1110000001	221100000

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