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REVISION OF THE TERMITOPHILOUS TRIBE TERMITOHOSPITINI (Coleoptera : Staphylinidae)

I. The Genus *Hetairotermes* with a Numerical Analysis of the Relationships of Australian species¹

By David H. Kistner²

Abstract: The genus *Hetairotermes* is redescribed and illustrated. The type-species of the genus, *H. latebricola*, is redescribed and illustrated. The following new species are described: *H. occidentalis* from West Australia, *H. greavesi* from New South Wales, *H. borealis* from Queensland, *H. gayi* and *H. capitalis* from A. C. T., and *H. hirsutus* from Sarawak. New host data are presented for all the above species as well as an additional species (*H. agilis* Cameron) from Singapore. One species (*H. formicola*) is herewith transferred to the genus *Dabra* Olliff. All species appear to be host specific although it is apparent that least 3 host changes occurred during their evolutionary history; twice from *Coptotermes* to Nasutitermitinae and at least once within the genus *Coptotermes*. The relationships between the Australian species are analyzed numerically and it is shown that the species are not as closely related to one another as species of other genera (such as *Coptotermoecia*) that have been similarly analyzed. Since species are distributed on both sides of Weber's line, the genus probably originated before the Cretaceous period.

Several years of field work by F. J. Gay and A. E. Emerson have produced many new specimens of termitophilous Aleocharinae among which were many specimens of the genus *Hetairotermes*. This genus has never been satisfactorily monographed, as no one previously had seen enough type material. Through the study of the Bernhauer, Cameron, and Oke collections, I have been able to see holotypes or other authoritative specimens of all but 1 species. It is the purpose of this paper to redescribe and illustrate those species for which I have new material, to describe and illustrate the new species, to redescribe the genus *Hetairotermes*, and remove 1 species formerly considered to belong here. Some new host data will also be recorded. Surprisingly, the usual host of the genus, *Coptotermes*, has never before been recorded. The relationships

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between the Australian species are analyzed numerically and a summary of the host relationships given.

The methods of study used here have been described before many times, most recently by Kistner (1968). All measurements given in this paper are in millimeters unless indicated otherwise.

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The initials given in parentheses above are used in the text to indicate the deposition of specimens studied. Specimens retained in my collection are indicated (DK).

Particular thanks are given to James Clover, Margaret Enger, Lynette Hawver, Norris Sadler, and Karen Wells, all Shinner Assistants at Chico State College for technical assistance involved in this study.

Genus *Hetairotermes* Cameron

Termophila Lea, 1910: 136.—Fenyés, 1918: 91.

Hetairotermes Cameron, 1920: 223 (for *Termophila* Lea, junior homonym of *Termophila* Grassi, 1887); 1921: 357, 387.—Seevers, 1957: 201.

Not very closely related to any other genus, but probably closer to *Termitobra* Seevers than to any other. Distinguished from *Termitobra* by the overall shape of the body, by the shape of the mouthparts in which the lacinia and the galea are approximately equal in length, by the shape of the mandibles which are much broader in *Hetairotermes*, and the shape of abdominal segment IX which is considerably different.

Overall shape as in fig. 1A-1F. Head capsule wider than long, the widest point being slightly behind eyes, with epicranium bluntly produced between antennal fossae. Blunt process plus clypeus produces an overall shape which is subtriangular. Antennae inserted between eyes in rather deeply set fossae. These fossae are between eyes and insertion of anterior arms of tentorium which insert at lower portion of the deeply set fossae. Head capsule otherwise without distinction. Head capsule lacks a defined neck. Antennae 11-segmented, shaped as in fig. 3B. Gula wide, almost rectangular in shape with sides proceeding posteriorly in relatively straight lines. Submentum slightly expanded and fused to gula. Mentum distinct from submentum, shaped as in fig. 2C. Mandibles slightly asymmetrical, shaped as in fig. 2A and 2B. Maxillae shaped as in fig. 2D, palpi 4-segmented. Maxillary acetabulae not margined although slightly sunken into head. Labium shaped as in fig. 2C, palpi 3-segmented, 2nd segment extremely long. Labrum without distinction, shaped as in *Termitobra*.

Pronotum wider than long, somewhat variable in shape by species, shaped as in fig. 1A-1F. Lateral borders of pronotum reflexed inward on ventral side to about 1/4 total width of pronotum. Prosternum short, about 1/3 length of pronotum with relatively short anterolateral articulation processes; without a carina in midline between legs. Prothoracic coxal cavities

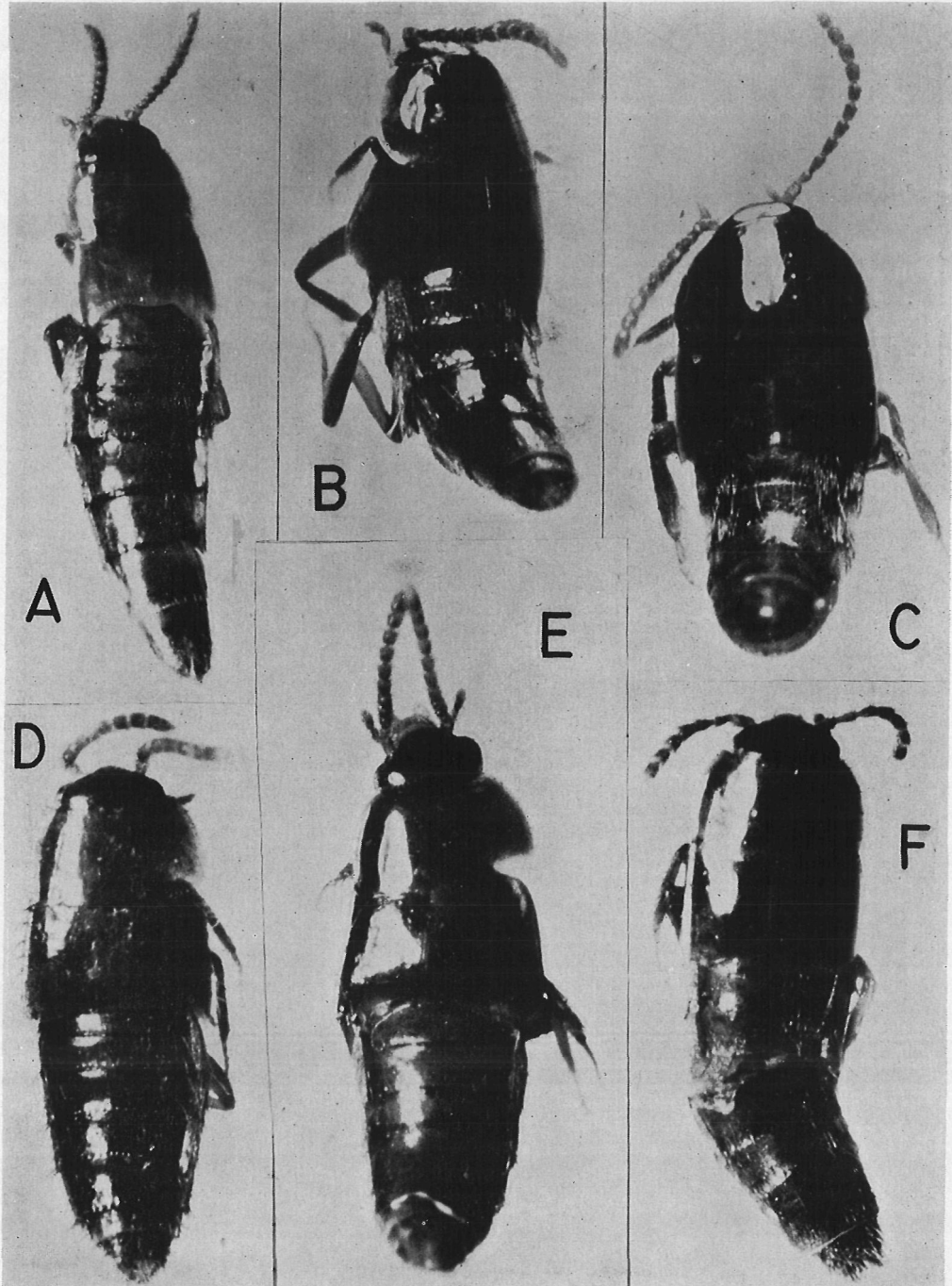


Fig. 1. Dorsal appearance of entire beetles: A, *Hetairotermes latebricola*; B, *H. greavesi*; C, *H. borealis*; D, *H. gayi*; E, *H. capitalis*; F, *H. occidentalis*.

closed behind by membrane. Mesothoracic peritremes reduced to extremely small sclerotized rings around mesothoracic spiracles. Elytra without distinction, shaped as in fig. 3A. Wings present, of normal size, and with usual staphylinid venation. Wings reduced to very small flaps in small-eyed forms of those species which have these. Mesosternum about $1/3$ length of metasternum, both relatively short, about length of pronotum. Mesosternum broadly produced between mesocoxae. Mesocoxal acetabulae completely margined. Mesosternum with a long thin sclerotized ridge between coxae, shaped as in fig. 3C. Mesosternal intercoxal process blunt, broad, and acarinate unless this broad, large flap which is produced between legs is considered to be an extreme form of a carina. Pro-, meso-, and metalegs shaped as in fig. 2E, 2F, and 2G respectively; tarsal formula, 4-4-5.

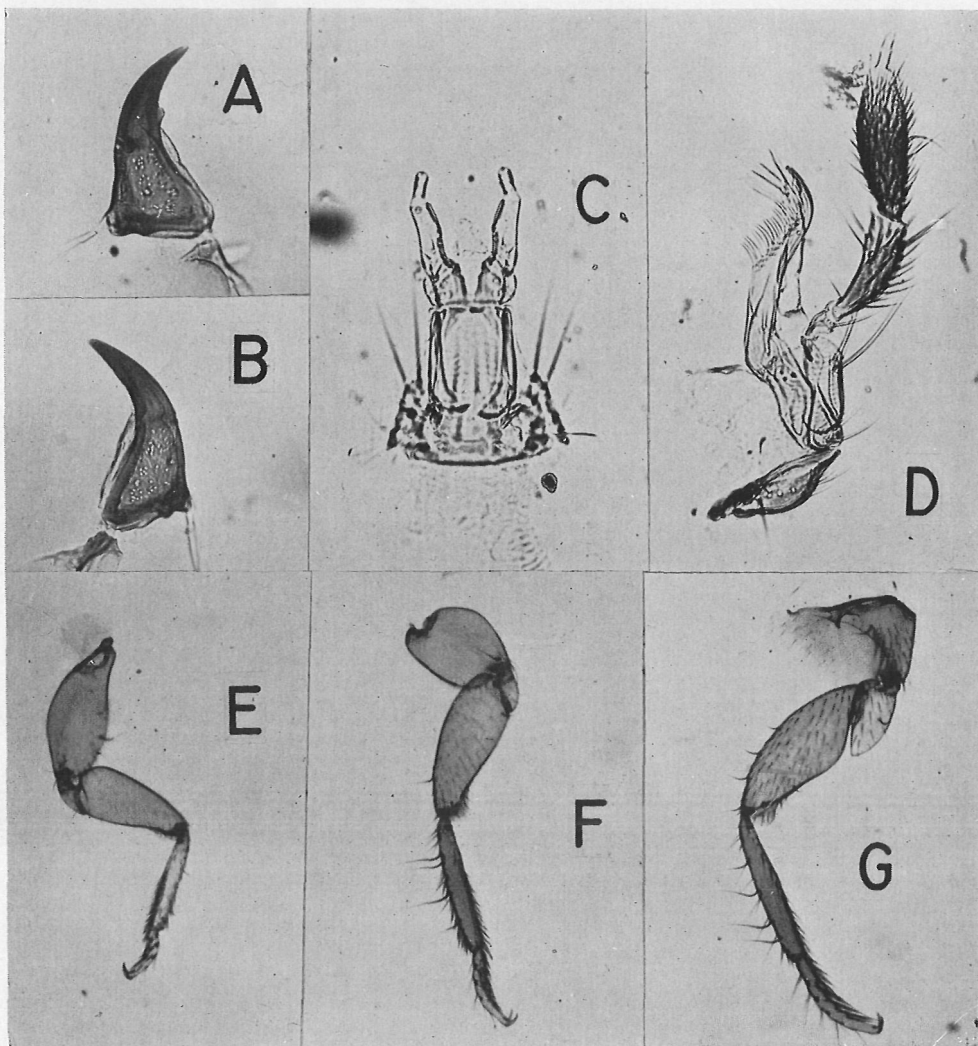


Fig. 2. *Hetairotermes latebricola*: A, left mandible; B, right mandible; C, labium; D, maxilla; E, proleg; F, mesoleg; G, metaleg.

Abdomen not physogastric, shaped as in fig. 1A-1F. Segment I represented only by the tergite fused to the metanotum. Segment II represented only by a tergite. Segments III-VII with 1 tergite, 1 sternite, and 2 pairs of paratergites each. Inner paratergites about 1.5 as wide as outer paratergites. Dorsal rim of abdomen occurs between inner and outer paratergites. Segment VI and VII shaped in fig. 3D; note extremely reduced tergal gland reservoir on segment VII, (as in fig. 7). Segment VIII represented by a tergite and a sternite only. Segment IX trilobed, shape somewhat variable by species, as in fig. 4-5; asymmetrical anterior apodemes of ♂ present and conspicuous, shaped as in fig. 5D. Male genitalia bulbous; neither median nor lateral lobes very variable by species, shaped as in fig. 6A-6B. Female spermatheca sclerotized, shape somewhat variable by species, as in fig. 4-5.

Type-species: *Hetairotermes latebricola* (Lea) (Blackwelder 1952: 184).

KEY TO AUSTRALIAN SPECIES OF HETAIROTERMES

1. Pronotal disk with 8 setae 2
 Pronotal disk with other than 8 setae 3
2. Abdominal tergite IX without anterior setae (fig. 5A) **occidentalis**
 Abdominal tergite IX with anterior setae (fig. 4D) **capitalis**
3. Pronotal disk with 6 setae **latebricola**
 Pronotal disk with more than 8 setae 4
4. Pronotal disk as well as the rest of the pronotum and elytra with too many setae to get
 an accurate count **gayi**
 Pronotal disk with 10-12 setae 5
5. Anterior border of pronotum with 12 setae; pronotum length greater than 0.50 mm
 **borealis**
 Anterior border of pronotum with 6 setae; pronotum length 0.47-0.49 mm. **greavesi**

Hetairotermes latebricola (Lea) Fig. 1A; 2; 3; 4A, B; 9.

Termophila latebricola Lea, 1910: 137 (Australia, New South Wales, Galston, ex termite nest, nest in the pipe of a large iron bark, Coll. A. M. Lea)

Hetairotermes latebricola: Cameron, 1920: 224 (changed generic name).—Seevers, 1957: 201.

Distinguished from all other species by the shape of the spermatheca, the chaetotaxy of the pronotum and elytra, and the chaetotaxy and shape of abdominal segment IX. Most closely related to *H. gayi* from which it is distinguished by all of the above characters except for the chaetotaxy of the pronotum.

Overall appearance as in fig. 1A. Color light reddish brown throughout approaching yellowish brown on small-eyed specimens and apparently somewhat darker as far as we can see on large-eyed specimens. Apices of elytra somewhat lighter than rest of the body; antennae and appendages also somewhat lighter. Dorsal surface of head with no macrochaetae. Dorsal surface of pronotum with 6 macrochaetae on anterior border, 3 more on each lateral border, 2 on posterior border, and 6 on disk. Elytra with 12 macrochaetae. Macrochaetotaxy of abdominal tergites II-VIII as follows: 2, 4, 4, 4, 4, 0, many. All sternites with apical rows of dark setae interspersed with light setae. All sternites also with an anteapical row of light setae. Sternite VIII with many dark setae. Spermatheca shaped as in fig. 4A, 4B. Abdominal segment IX shaped as in fig. 4A, 4B; note the very pointed apical portion of this segment (indicated with an arrow), as well as the absence of chaetae on the anterior end of the median portion of this segment (also indicated with an arrow). ♂ genitalia shaped exactly as in *H. greavesi*.

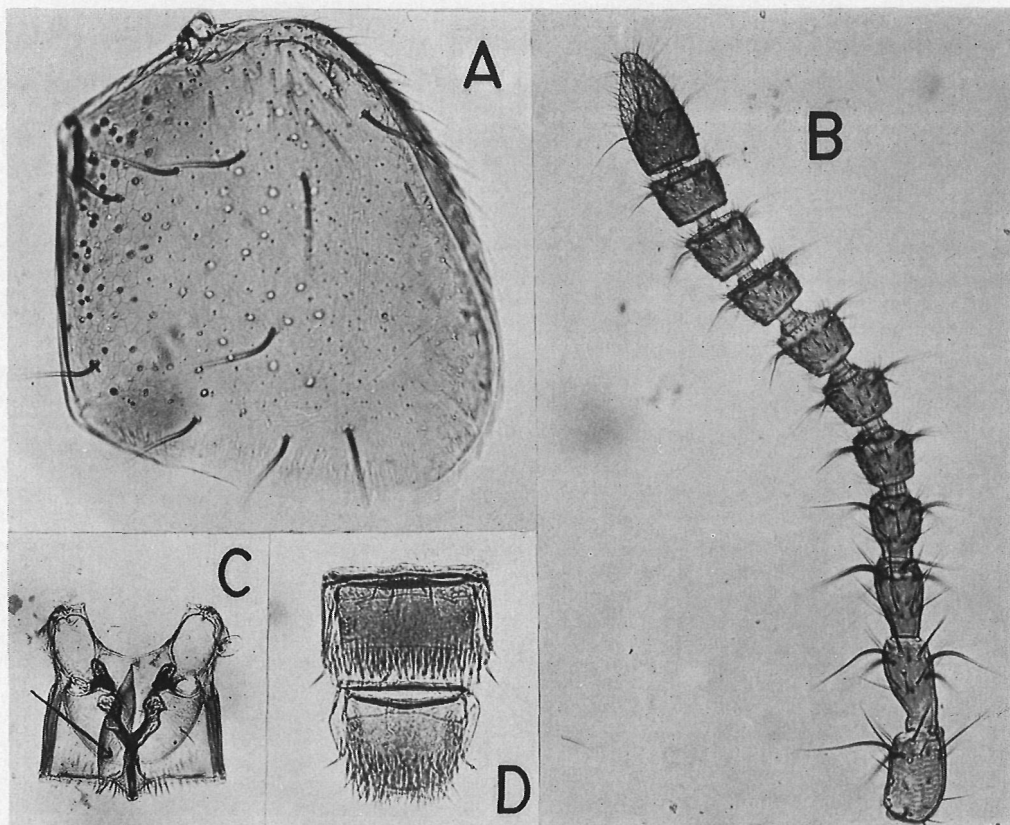


Fig. 3. *Hetairotermes latebricola*: A, right elytron; B, antenna; C, meso- and metasternum, arrow indicates the very large intercoxal ridge; D, abdominal segments VI and VII.

Measurements: Small-eyed specimens: Pronotal length, 0.39-0.41; elytral length, 0.34-0.36; eye length, 0.05-0.06; eye width, 0.01-0.02. Number measured, 10. Large-eyed specimens: Pronotal length, 0.45-0.46; elytral length, 0.35-0.37; eye length, 0.13-0.14; eye width, 0.09-0.10. Number measured, 3.

MATERIAL EXAMINED. 8, cotypes, det. A. M. Lea, Australia, N. S. Wales, Galston, Lea & Dumbrell, ex nest of termites (NMV, BMNH); 20, Australian Capital Territory, Blundell's Valley, 17.XII.1956, A. H. Wetherly (CSIRO, DK); 3, (large-eyed), same data as previous (CSIRO, DK); 4, same locality, 15.XI.1956, A. H. Wetherly (CSIRO, DK).

Notes: The hosts of all the Blundell specimens were determined to be *Coptotermes frenchi* (Hill) by A. H. Wetherly. Lea (loc. cit.) in the original description did not apparently recognize the fact that there were 2 phases of this species with respect to the eyes in his series. However, he did note that "many of the specimens are entirely pale, perhaps from immaturity." The series in the Victoria National Museum had 2 of the specimens with the small eyes whereas the other 4 had large eyes. At first it was

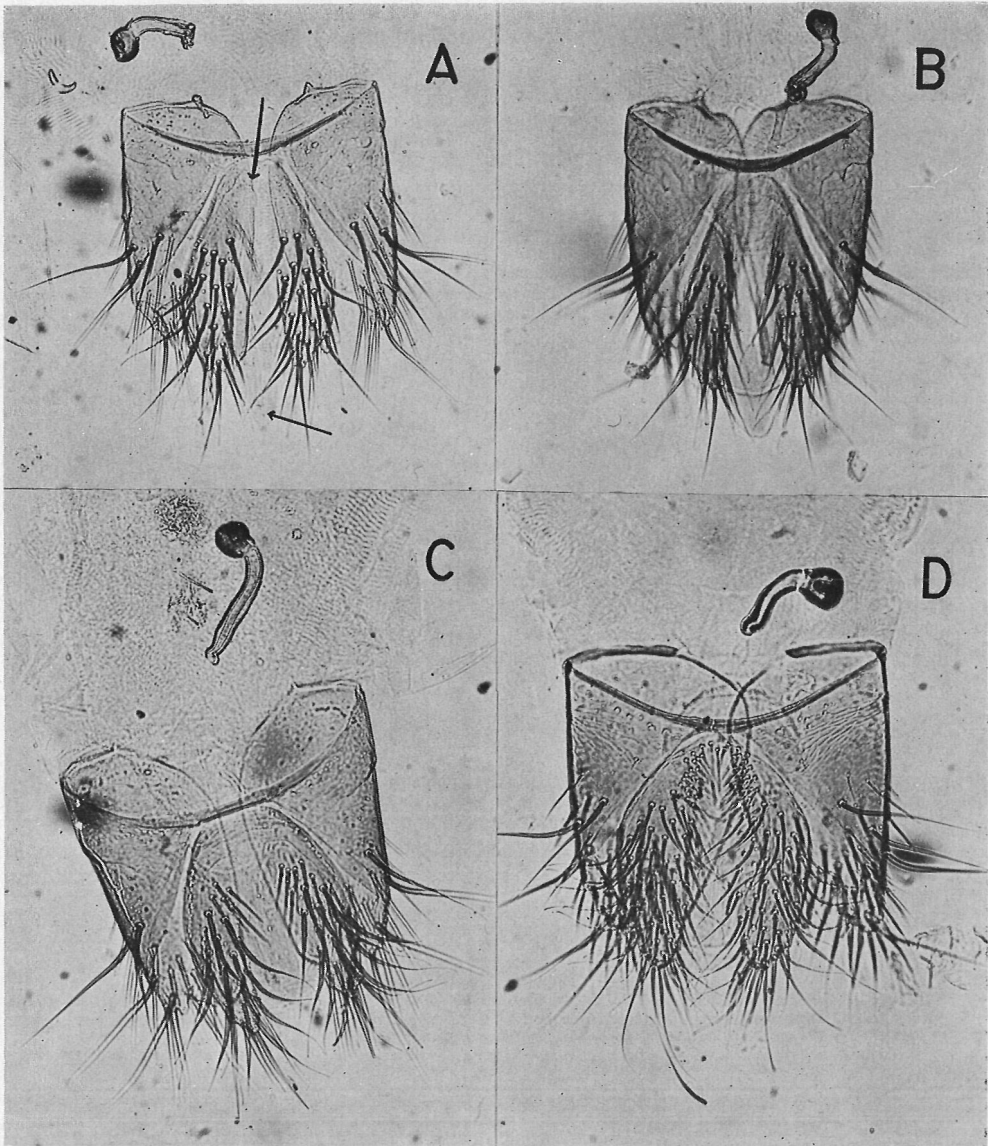


Fig. 4. Abdominal segment IX and spermatheca : A, B, *Hetairotermes latebricola*, both large-eyed and small-eyed specimens ; C, *H. gayi* ; D, *H. capitalis*. Scale arbitrary, see description for measurements. Arrows indicate the anterior portion of abdominal tergite IX and the apical portion of abdominal tergite IX.

thought that there might be 2 species involved here, but careful dissection of both large-eyed and small-eyed specimens in the series from Blundell's Valley indicated that, though the eye shape varied, the chaetotaxy, spermatheca, and shape of abdominal segment IX was exactly the same. The large-eyed species did tend to be a little darker

and a little bit larger. However, the weight of evidence is very much in favor of the interpretation that these represent the same species. The distribution of the species is shown in fig. 9.

Hetairotermes occidentalis Kistner, new species Fig. 1F; 5A; 9.

Distinguished from all other species, including *H. greavesi* to which it is most closely related, by the chaetotaxy, the chaetotaxy and the shape of abdominal segment IX, and the shape of the spermatheca.

Overall appearance as in fig. 1F. Color light reddish brown throughout, head and elytra somewhat darker than rest of body. Apices of elytra somewhat lighter than rest of body. Dorsal surface of head with no macrochaetae. Dorsal surface of pronotum with 6 macrochaetae on anterior border, 3 more on each lateral border, 2 on posterior border, and 2 rows of 4 each on disk. Elytra with 8 macrochaetae on each. Macrochaetotaxy of abdominal tergites II-VIII as follows: 2, 4, 4, 4, 4, 0, 2-4-2. All sternites with an apical row of dark setae as well as many light setae interspersed. Sternite VIII with 2 lateral long black setae and many setae between these which are long but yellow. Spermatheca shaped as in fig. 5A. Abdominal segment IX shaped as in fig. 5A; note the absence of setae on the anterior portion of the 9th tergite as well as the blunt median portion of the apex. ♂ genitalia shaped exactly as in *H. greavesi*.

Measurements: Pronotal length, 0.45-0.46; elytral length, 0.35-0.37; eye length, 0.13-0.14; eye width, 0.08-0.10. Number measured, 10.

Holotype (No. 13698), West Australia, Darling Range, Kalamunda, 12.VII.1954, H. Demarz. In the Australian National Insect Collection, CSIRO, Canberra.

Paratypes: 6, same data as holotype (CSIRO, DK); 3, same locality, 26.IX.1954, H. Demarz (CSIRO, DK).

Notes: The host termites of neither of these colonies have been located, but it is highly probable that the species was *Coptotermes acinaciformis* ssp. *raffrayi* (Wasmann) because of the distribution and prevalence of this species. The distribution of the species is shown in fig. 9.

Hetairotermes greavesi Kistner, new species Fig. 1B; 5C; 6; 9.

Most closely related to *H. borealis*, from which it is distinguished by its chaetotaxy as well as slight differences in the shape of the spermatheca.

Overall appearance as in fig. 1B. Color reddish brown throughout, apices of elytra, median border of elytra, posterior border of pronotum, side borders of pronotum somewhat lighter than rest of body; elytra somewhat darker. Dorsal surface of head with 2 macrochaetae between eyes. Dorsal surface of pronotum with 6 macrochaetae on anterior border, 4 more on each lateral border, 2 on posterior border, and 2 rows of 6 and 4 each on disk. Elytra with 11 macrochaetae on each. Macrochaetotaxy of abdominal tergites II-VIII as follows: 2, 4, 4, 4, 4, 0, 2 extra long on each side with many short (3 to 4 rows) in between. All sternites with an apical row of black macrochaetae and many long yellow setae interspersed between them. Sternite VIII with many dark setae. Spermatheca shaped as in fig. 5C. Abdominal segment IX shaped as in fig. 5C; note the presence of setae on anterior portion of tergite IX as well as blunt apical portion of tergite IX. ♂ genitalia shaped as in fig. 6.

Measurements: Pronotal length, 0.47-0.49; elytral length, 0.42-0.44; eye length, 0.16-0.17; eye width, 0.08-0.09. Number measured, 10.

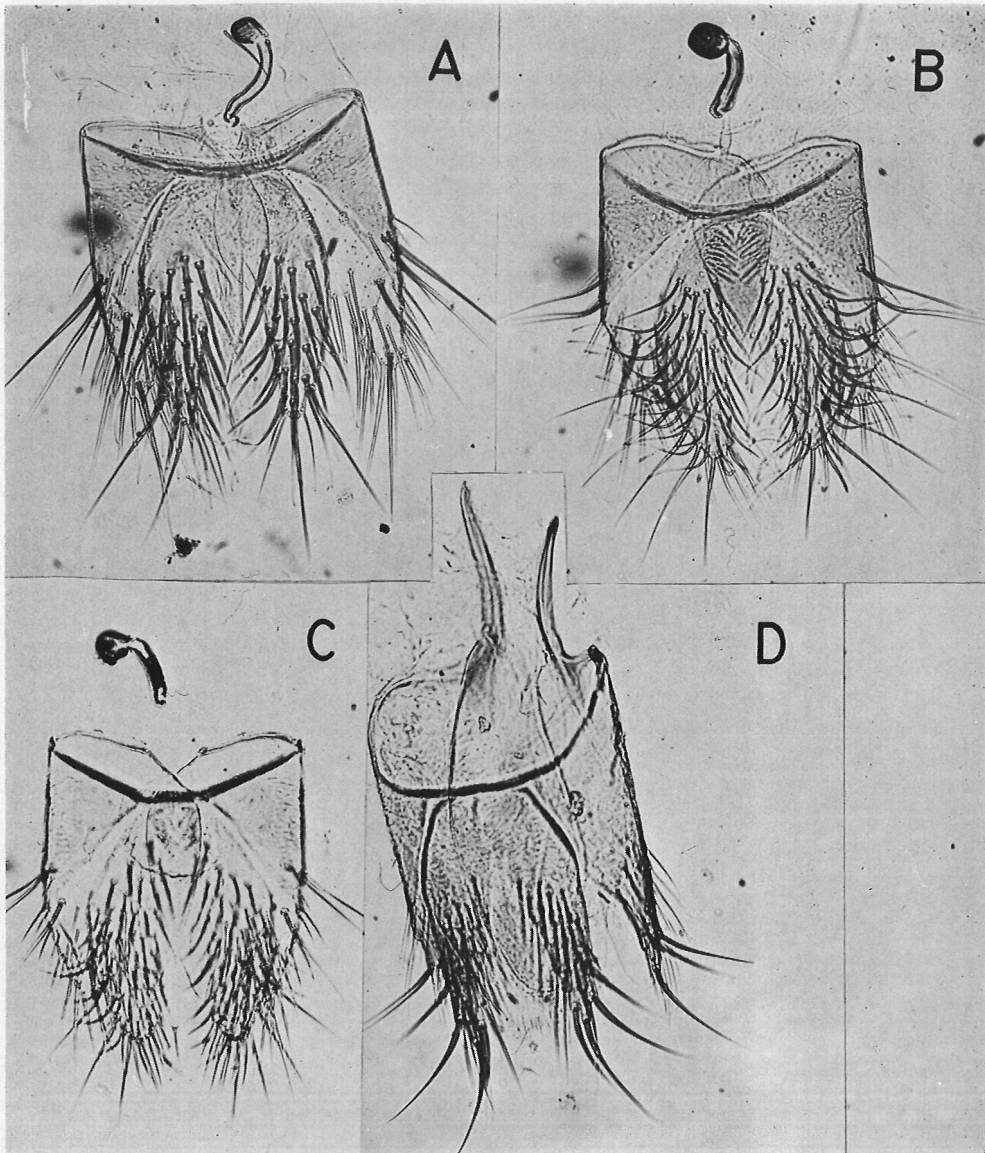


Fig. 5. Abdominal segment IX and spermatheca: A, *Hetairotermes occidentalis*; B, *H. borealis*; C, *H. greavesi*; D, *H. hirsutus*.

Holotype (No. 13699), New South Wales, Pine Creek, 11.VI.1958, Coll. T. Greaves (ANIC, CSIRO, Canberra).

Paratypes: 14, same data as holotype (CSIRO, DK).

Notes: The host termites were determined to be *Coptotermes acinaciformis* (Froggatt) by T. Greaves. Specimens of the host termites are in the Australian National Insect

Collection. The distribution of the species is shown in fig. 9. The species is named for the collector.

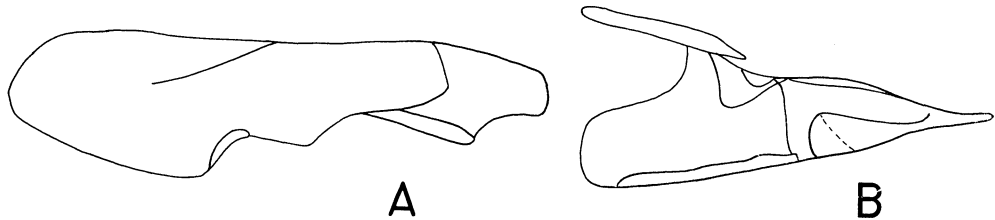


Fig. 6. *Hetairotermes greavesi*: A, lateral lobe of male genitalia; B, median lobe of male genitalia. Scale represents 0.25 mm.

Hetairotermes borealis Kistner, new species Fig. 1C; 5B; 9.

Most closely related to *H. greavesi*, from which it is distinguished by details of the chaetotaxy as well as slight differences in the shape of the spermatheca.

Overall appearance as in fig. 1C. Color light reddish brown throughout, apices of elytra and appendages somewhat lighter than rest of body, head somewhat darker. Dorsal surface of head with no macrochaetae. Dorsal surface of pronotum with 12 chaetae on anterior border, 4 more on each lateral border, 2 on posterior border, and 10-12 on disk. Elytra with 7 macrochaetae on each. Macrochaetotaxy tergites II-VIII as follows: 2, 4, 4, 4, 4, 0, many. All sternites with apical rows of black setae which are interspersed with light setae. Sternite VIII with many dark setae. Spermatheca shaped as in fig. 5B. Abdominal segment IX shaped as in fig. 5B; note the anterior setae on 9th tergite as well as blunt apex of 9th tergite. ♂ genitalia shaped exactly as in *H. greavesi*.

Measurements: Pronotal length, 0.55-0.56; elytral length, 0.45-0.46; eye length, 0.15-0.17; eye width, 0.07-0.09. Number measured, 10.

Holotype (No. 13700), Queensland, 37 km (23 mi) N of Townsville, 23.VI.1960, Coll. F. J. Gay (ANIC, CSIRO, Canberra).

Paratypes: 63, same data as holotype (CSIRO, DK).

Notes: The host termites were determined to be *Coptotermes acinaciformis* (Froggatt) by F. J. Gay. Specimens of the host are in the Australian National Insect Collection. The distribution of this species is shown in fig. 9.

Hetairotermes gayi Kistner, new species Fig. 1D; 4C; 9.

A highly distinctive species, not very closely related to any other species of the genus but probably closest to *H. latebricola*, from which it is distinguished by its chaetotaxy, the shape of the spermatheca, the shape of abdominal segment IX.

Overall appearance as in fig. 1D. Color light reddish brown, apices of elytra a little lighter than rest of body. Dorsal surface of head with no large chaetae but with about 10 very fine smaller setae scattered over surface. Dorsal surface of pronotum and elytra with far too many setae to count accurately. It is literally covered with many dark setae. Macrochaetotaxy of abdominal tergites II-VIII as follows: 2, 6, 6, 6, 6, 0, 2 long on each side with many in be-

tween. In addition to macrochaetae, there are many anteapical long yellow setae on each of tergites II-VI as well as long yellow setae between 6 black setae. Abdominal sternites each with an apical row of darker setae and many extremely long yellow setae scattered over entire surface of sternites. Sternite VIII especially with many dark setae. Spermatheca shaped as in fig. 4C. Abdominal segment IX shaped as in fig. 4C; note lack of setae on anterior portion of abdominal tergite IX as well as the blunt apical portion. ♂ genitalia shaped exactly as in *H. greavesi*.

Measurements: Pronotal length, 0.48-0.49; elytral length, 0.40-0.42; eye length, 0.11-0.12; eye width, 0.06-0.07. Number measured, 10.

Holotype (No. 13701), Australian Capital Territory, Shannon's Creek, 18.VII.1939, F. J. Gay (ANIC, CSIRO, Canberra).

Paratypes: 18, same data as holotype (CSIRO, FMNH, DK); 4, Canberra, IX.1949, F. J. Gay (CSIRO, FMNH, DK).

Notes: The host termites were determined to be *Coptotermes lacteus* (Froggatt) by F. J. Gay. Specimens of the host are in the Australian National Insect Collection. The distribution of the species is shown in fig. 9. The species is named for the collector.

Hetairotermes capitalis Kistner, new species Fig. 1E; 4D; 9.

Distinguished from *H. borealis*, to which it is most closely related, by the chaetotaxy as well as the shape of the spermatheca and abdominal segment IX.

Overall appearance as in fig. 1E. Color reddish brown throughout, apices of elytra slightly lighter than rest of body. Dorsal surface of head with no macrochaetae. Dorsal surface of pronotum with 6 macrochaetae on anterior border, 3 additional macrochaetae on each lateral border, 2 macrochaetae on posterior border, and 2 rows of 4 each on disk. Elytra with 6 macrochaetae, of which 1 is on the lateral border and 5 are on disk. Macrochaetotaxy of abdominal tergites II-VIII as follows: 2, 4, 4, 4, 4, 0, many. All sternites with an apical row of black setae which are interspersed with yellow setae. Sternite VIII with many dark setae in addition. Spermatheca shaped as in fig. 4D. Abdominal segment IX shaped as in fig. 4D; note the presence and patterning of setae on anterior portion of abdominal tergite IX as well as rounded apical portion of this tergite. ♂ genitalia shaped exactly as in *H. greavesi*.

Measurements: Pronotal length, 0.55-0.57; elytral length, 0.47-0.48; eye length, 0.15-0.16; eye width, 0.08-0.09. Number measured, 4.

Holotype (No. 13702), Australian Capital Territory, Canberra, IX.1949, Coll. F. J. Gay (ANIC, CSIRO, Canberra).

Paratypes: 3, same data as holotype (CSIRO, DK).

Notes: The host termites were determined to be *Coptotermes lacteus* (Froggatt) by F. J. Gay. Specimens of the host are in the Australian National Insect Collection. The distribution of the species is shown in fig. 9.

Hetairotermes hirsutus Kistner, new species Fig. 5D; 9.

Distinguished from all other species by the chaetotaxy of the pronotum and elytra as well as the chaetotaxy and shape of abdominal segment IX. Most closely related to *Hetairotermes agilis* Cameron from which it is distinguished by all of the above characters.

Overall shape very similar to *H. borealis* (fig. 1C). Color light reddish brown throughout

with appendages and elytra somewhat lighter than rest of body. Apices of elytra somewhat lighter than rest of body. Dorsal surface of head with no macrochaetae. Dorsal surface of pronotum with 6 black setae on anterior border, 4 more on each lateral border, and none on posterior border. Also, none on disk. Elytra with 3 long black setae on lateral border, and 4 more on each disk. In addition to black setae, the entire dorsal surfaces of head, pronotum and elytra are densely clothed with long yellow setae which tend to obscure smaller black setae which have been counted. Dorsal surface of abdominal tergites and sternites also clothed

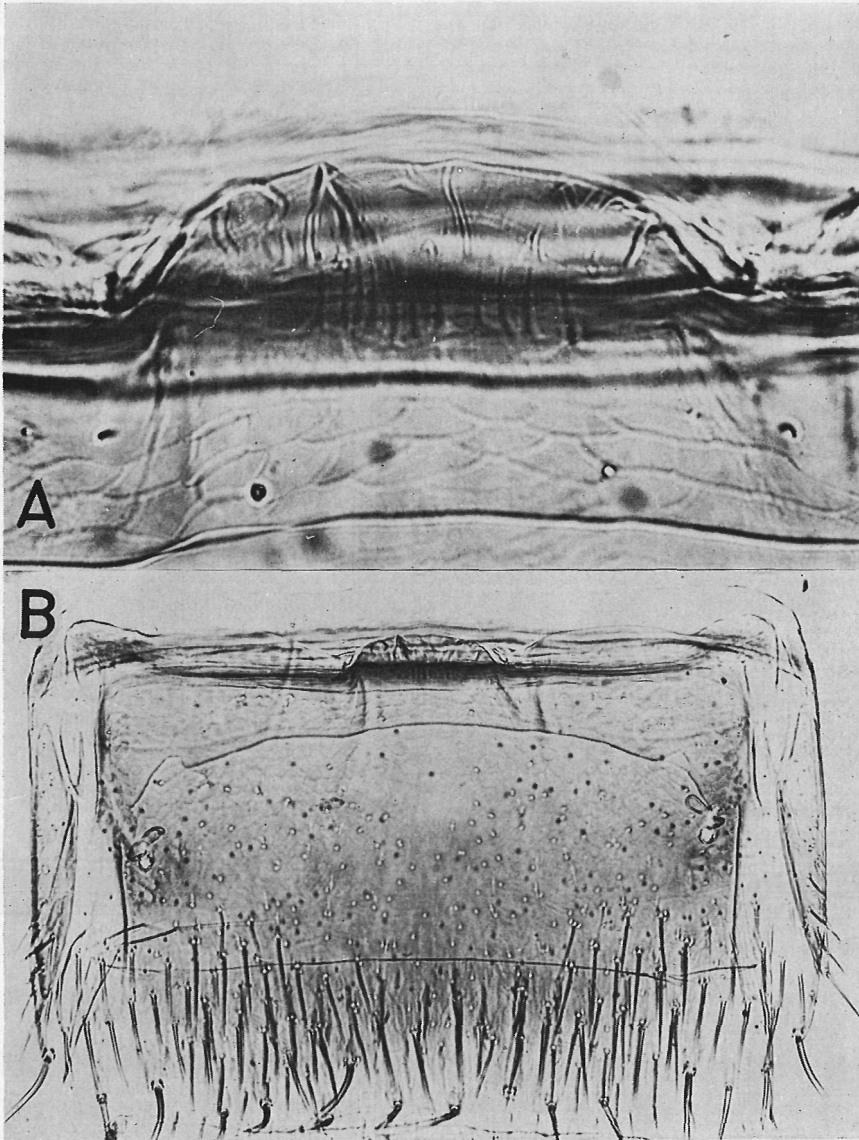


Fig. 7. *Hetairotermes greavesi*: A, details of enlarged sclerotized part of tergal gland reservoir; B, abdominal segment VII.

with a dense covering of long yellow setae. Macrochaetotaxy of abdominal tergites II-VIII as follows: 2, 4, 4, 4, 4, 4, 2-4. All sternites with apical rows of dark setae interspersed with many light setae. Sternite VIII with an antepical row of dark setae. Spermatheca unknown. Abdominal segment IX shaped as in fig. 5D. ♂ genitalia somewhat different from *H. greavesi* with longer apical tips to the lateral lobes and slightly shorter median lobes.

Measurements: Pronotal length, 0.40; elytral length, 0.30; eye length, 0.12; eye width, 0.08. Number measured, 1.

Holotype (No. 13707), Sarawak, 1°38' N, 113°34' E, 11.II.1963, Alfred & Eleanor Emerson. In large lined galleries in nests of new genus near *Termes* covering large area on buttress of tree. In the collection of the author.

Notes: The host specimens were determined to be *Hospitalitermes umbrinus* (Haviland) by A. E. Emerson. Specimens of the host termites are in the Emerson collection of the American Museum of Natural History, New York. Unless future collections show that this species is actually found with *Coptotermes* of which there are 2 species known from the above locality, this termitophile represents another host change probably from *Coptotermes* to the Nasutitermitinae. The distribution of the species is shown in fig. 9.

Hetairotermes agilis Cameron Fig. 9.

Hetairotermes agilis Cam., 1920: 223, British Museum (Nat. Hist.), Singapore, Woodlands, with a wood-dwelling termite.—Seevers, 1957: 202 (redescription).

Notes: The termite soldier pinned under a specimen from the type locality was determined to be *Coptotermes curvignathus* (Holmgren) by W. A. Sands. This is the 1st host record of this species. The type plus 1 additional specimen of the species was studied and it was found to be congeneric with *H. latebricola*. However, it will not be redescribed until additional dissection material is available. Its distribution is shown in fig. 9.

Hetairotermes bryanti Cameron Fig. 9.

Hetairotermes bryanti Cam., 1950: 98, British Museum (Nat. Hist.), Malaya, Penang, 19. X. 1913, Coll. Bryant.—Seevers, 1957: 203 (redescription).

Notes: The type was studied and found to be congeneric with *H. latebricola*. However, it will not be redescribed until additional specimens are available. Its distribution is shown in fig. 9.

Hetairotermes piceus Cameron Fig. 9.

Hetairotermes piceus Cam., 1920: 224, British Museum (Nat. Hist.), Singapore, Bukit Timah, with a wood-dwelling termite, Coll. Cameron; 1921: 387 (key).—Seevers, 1957: 202 (redescription).

Notes: The type of this species was studied and found to be congeneric with *H. latebricola*. It is closely related to *H. bryanti* and will not be redescribed until additional material is available. Its distribution is shown in fig. 9.

Hetairotermes insulanus Seevers Fig. 9.

Hetairotermes insulanus Seev., 1957: 204, U. S. National Museum, Micronesia, Palau Is., Koror I., with *Nasutitermes rufirostris* (Hill).

Notes: At the time this species was described by Seevers no termite host record had been firmly established for any of the species. It now appears that the majority of the species are found with *Coptotermes* and this host record is exceptional. However, the species does belong to the genus *Hetairotermes* and another related genus, *Termitobra* Seevers, is also found with *N. rufirostris*, so it is highly likely that a host change occurred relatively early in the evolutionary history of this species. The distribution of the species is shown in fig. 9.

Hetairotermes punctiventris (Lea) Fig. 9.

Termophila punctiventris Lea, 1910: 137, fig. 4, South Australia Museum, West Australia, Bridgetown, in a nest of white ants, Coll. A. M. Lea.

Hetairotermes punctiventris: Cameron, 1920: 223 (changed genus).—Seevers, 1957: 203 (no new data added).

Notes: The type of this species was not available for study. Characteristics given in the original description, i. e., the punctate tergite and sternite VII and the upturned and/or flattened pronotum, cast doubt upon the generic assignment. In any event, it could not be the same as the *H. occidentalis* described herein. The distribution of this is shown in fig. 9.

Dabra formicola (Oke), n. comb.

Hetairotermes formicola Oke, 1933: 135, Victoria National Museum, Australia, Victoria, Gypsum, with *Iridomyrmex nitida*, Coll. C. Oke.—Seevers, 1957: 204 (listed).

Notes: The type of this species was examined and found to be outside of reasonable generic limits of *Hetairotermes*. Insufficient material is available to properly study this species and it may be found to represent a new genus when more material is available. The whole fauna of myrmecophiles associated with *Iridomyrmex* should be revised eventually.

RELATIONSHIPS OF THE AUSTRALIAN SPECIES

The relationships between the Australian species were analyzed numerically. A list of the unit characters was developed following the general outline of Sokal & Sneath (1963). This list of 34 characters is presented in Table I. All of the Australian species except for *Hetairotermes punctiventris* which was unavailable for study were then coded for the 34 characters. If the character was present, it was coded 1. If the character was absent, it was coded 0. In this study there were no characters which could not be compared. The results of coding the 34 characters for the 6 species are given in Table II. These data were then punched onto cards and then loaded into an IBM 1620 computer with a program to produce the simple matching coefficients described by

Sokal & Michener (1958). Half of the matrix produced by this program is reproduced in Table III. This output was then reloaded into the 1620 with another program to cluster the species using the weighted-pair group method described by Sokal & Sneath (1963).

The results of these analyses are presented in fig. 8. Only those matrix values where groups join are presented in that figure. Reference to fig. 8 reveals that none of the species are very closely related to each other (as at the .900 level). The closest related species, namely *H. greavesi* and *H. borealis*, have the highest coefficient of relationship of .824. All the others have coefficients of relationships which are less than that. Thus these species differ from one another much more than species of other groups which have been analyzed in the same manner. In brief, there are no unexpected relation-

Table I. List of characters used for numerical analysis.

1. Color light reddish brown.	18. Spermatheca short and straight (as in fig. 5B).
2. Head without macrochaetae.	19. Tergite IX pointed (as in fig. 4A).
3. Anterior border of pronotum with 6 setae.	20. Tergite IX with indented posterior border (as in fig. 5A).
4. Anterior border of pronotum with 12 setae.	21. Tergite IX with setae at anterior.
5. Posterior border of pronotum with 2 setae.	22. Small-eyed form present.
6. Lateral border of pronotum with 3 more setae.	23. Pronotal length, 0.45-0.46.
7. Lateral border of pronotum with 4 more setae.	24. Pronotal length, 0.47-0.49.
8. Pronotal disk with 6 setae.	25. Elytral length, 0.35-0.37.
9. Pronotal disk with 8 setae.	26. Elytral length, 0.40-0.44.
10. Pronotal disk with 10-12 setae.	27. Eye length, (large-eyed form), 0.13-0.14.
11. Elytra with 12 setae each.	28. Eye length, 0.15-0.17.
12. Elytra with 8 setae each.	29. Elytra with 6 macrochaetae.
13. Elytra with 7 setae each.	30. Tergite III with 4 setae.
14. Tergite VIII with too many setae to count.	31. Tergite IV with 4 setae.
15. Sternite with antepical row of light setae.	32. Tergite V with 4 setae.
16. Spermatheca with multiple twists at posterior end (as in fig. 4A).	33. Tergite VI with 4 setae.
17. Spermatheca long and slender with few twists (as in fig. 4C).	34. Eye width (large-eyed form), 0.07-0.10.

Table II. Distribution of unit characters in the species of *Coptotermoeicina*. Characters are arranged sequentially from left to right following the same order given in Table I.

Species number	Species	Characters
01	<i>H. latebricola</i>	1110110100100111001001101010011111
02	<i>H. occidentalis</i>	1110110010010000100100101010011111
03	<i>H. greavesi</i>	0010101001001100010110010101011111
04	<i>H. borealis</i>	1101101001001100010110000001011111
05	<i>H. gayi</i>	11000000000010010000001010000000
06	<i>H. capitalis</i>	0110110010000100000010000001111111

Table III. Matrix of simple matching coefficients of relationship for the species of *Hetairotermes*.

	1	2	3	4	5
2	.676	1.000			
3	.382	.471	1.000		
4	.441	.529	.824	1.000	
5	.412	.500	.500	.500	1.000
6	.588	.676	.676	.676	.529

ships shown. Since species are found on both sides of Weber's Line (see fig. 9), it is apparent that the genus is of ancient origin, probably before the Cretaceous period.

HOST RELATIONSHIPS

All of the species recorded here appear to be host specific at the species level. A summary of the host relationships is given by termite host in Table IV. The host

Coptotermes acinaciformis ssp. *raffrayi* is preceded by a question mark (?) because it is not known for certain that this is the true host for the species listed for it at this time.

Table IV. Summary of host relationships by termite host.

Host Termite	Termitophile
<i>Coptotermes acinaciformis</i> (Froggatt)	<i>Hetairotermes borealis</i>
	<i>H. greavesi</i>
? <i>Coptotermes acinaciformis</i> ssp. <i>raffrayi</i> Wasmann	<i>H. occidentalis</i>
<i>Coptotermes curvignathus</i> (Holmgren)	<i>H. agilis</i>
<i>Coptotermes frenchi</i> Hill	<i>H. latebricola</i>
<i>Coptotermes lacteus</i> (Froggatt)	<i>H. capitalis</i>
	<i>H. gayi</i>
<i>Nasutitermes rufrostris</i> (Hill)	<i>H. insulanus</i>
	<i>Termitobra perinthodes</i> Seevers
<i>Hospitalitermes umbrinus</i> (Haviland)	<i>H. hirsutus</i>

Reference to the host list shows that several host changes have occurred at various times, i. e. from *Coptotermes* to *Nasutitermes* and from *Coptotermes* to *Hospitalitermes*. These 2 host changes render the idea of similar or proportionate rates of evolution of the termitophiles and their termite hosts somewhat untenable. Also, the presence of 2

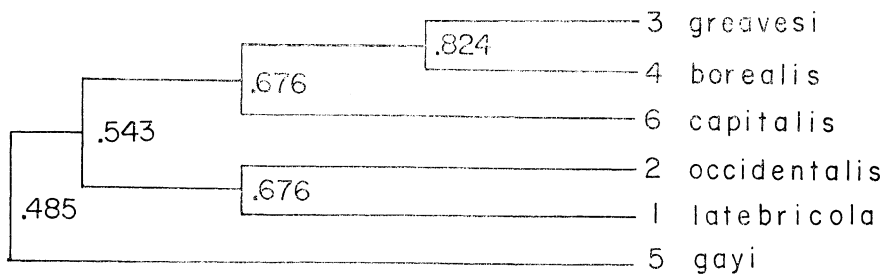


Fig. 8. Dendrogram showing relationships between most of the Australian species of *Hetairotermes*.

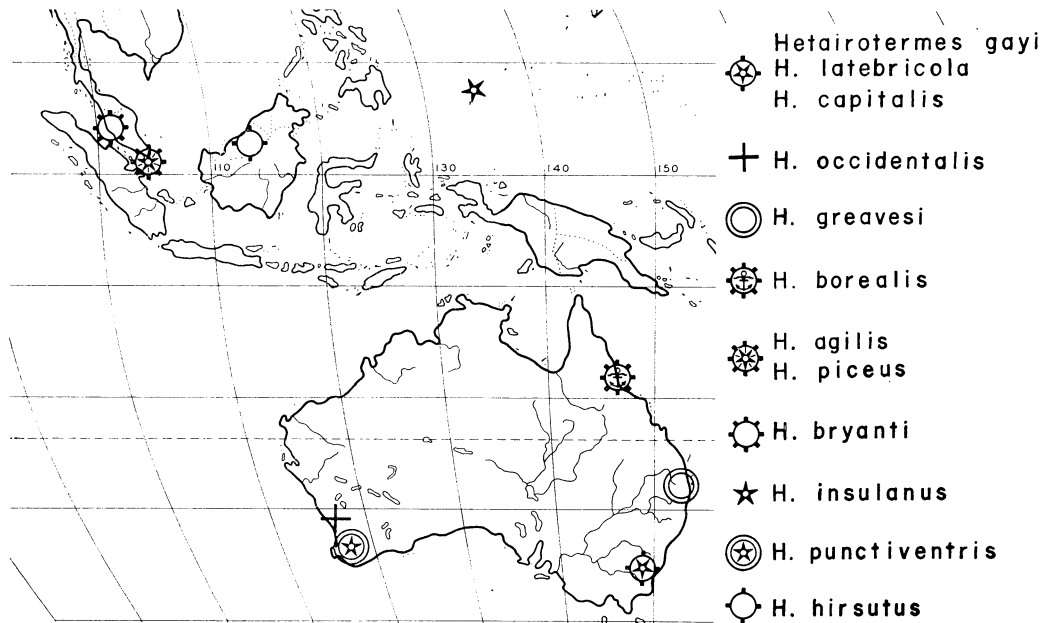


Fig. 9. Distribution of the species of *Hetairotermes*.

quite distantly related species with *Coptotermes lacteus* would seem to indicate a host change at some time or another. I think there is little doubt that the "usual" hosts of *Hetairotermes* are species of *Coptotermes*. Also it is noteworthy that the 2 most closely related species are both found with the same species of termite, i. e. *H. greavesi* and *H. borealis*, both found with *Coptotermes acinaciformis*. The relationships shown among the species of *Hetairotermes* do not show the same kind of relationship that was recently demonstrated for species of the *Coptotermocina* (see Kistner & Pasteels 1970). I attribute this lack of agreement to the fact that these species of termitophiles are not as host dependent as the *Coptotermocina* which has resulted in many more host changes during the evolutionary history of the group.

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