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TAXONOMIC REVISION OF THE TERMITOPHILOUS SUBTRIBE COPTOTERMOECIINA (Coleoptera: Staphylinidae)

with a description of some integumentary glands and a numerical analysis of their relationships[1]

By **David H. Kistner**[2] and **Jacques M. Pasteels**[3]

Abstract: The single previously known genus of the subtribe Coptotermoeciina is herein redescribed and illustrated. Three new genera are herein described, *Coptophilus, Philobrunneus,* and *Coptolimulus.* Both previously known species are herein redescribed. In addition 7 new species are described: *Coptophilus greavesi* (Australian Capital Territory); *Coptotermoecia seeversi* (Australian Capital Territory); *C. flava* (West Australia); *C. pilosa* (New South Wales); *C. robusta* (West Australia); *Philobrunneus gayi* (West Australia); and *Coptolimulus calabyi* (West Australia). Many new geographic and host data of previously described species are presented.

The integumentary glands are described for *Coptophilus* and *Coptotermoecia.* In both genera, the post-pleural glands are reduced. The tergal glands are reduced and modified but differently in each genus. Both genera possess large gland cells beneath the pronotum and additionally *Coptophilus* possesses numerous type 3 cells. Since the gland cells of the pronotum and the type 3 cells are not found in free-living species of staphylinids, they perhaps act during host-guest interactions.

The relationships between the genera and species are analyzed numerically and a dendrogram produced which matches what is thought to be the phylogeny derived by traditional means. When this phylogeny is matched to the host relationships, the relationships between the species of termitophiles match the relationships between their termite hosts as derived by F. J. Gay. All of these termitophiles are host-specific at the species level.

Acknowledgments: For providing the majority of the specimens included in this study, we are grateful to F. J. Gay, Commonwealth Scientific and Industrial Research Organization, (CSIRO), Canberra. Thanks are extended to H. S. Dybas and R. L. Wenzel, Field Museum of Natural History, (FMNH), Chicago, for providing material previously studied by Seevers. Thanks are given to A. Neboiss and his secretary for courtesies extended to Kistner while studying the Oke collection at the Victoria National Museum,

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(NMV), Melbourne. The initials given here are used in the text to indicate the deposition of specimens studied. Specimens retained in the collections of the authors are indicated (DK) or (JP).

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The first species of this group, *Coptotermoecia alutacia* Oke, was described in 1933 so that knowledge of this group is hardly ancient. In 1957, Seevers described a second species and proposed the subtribe Coptotermoeciina of the tribe Athetini to contain the 2 species. He did not attempt to diagnose the subtribe or, for that matter, the genus because of difficulties in making comparisons with the very large Athetini or Myrmedoniini complexes. These difficulties still exist today but since we have 4 genera now instead of 1, we will attempt to diagnose the subtribe.

This study is possible because of good series sent to us by F. J. Gay of the Commonwealth Scientific and Industrial Research Organization, Canberra, for which we are very grateful. It is the purpose of this paper to revise the species and genera of the subtribe Coptotermoeciina and to comment on their relationships. Since alcoholic Bouin-fixed specimens of 3 species (*Coptophilus gayi*, *Coptotermoecia seeversi*, and *C. pilosa*) were provided us, the first description of the glands of these termitophiles will be given.

The methods used in this study have been described before by Kistner (1968), Pasteels (1968a), and by Kistner & Pasteels (1969a). All measurements given in this paper are in mm unless indicated differently.

Subtribe COPTOTERMOECIINA Seevers

Species belonging to this tribe appear to have the following characteristics in common: Head wider than long. Fundamental shape of maxillae with lacinia and galea shorter than palpi. The shapes of the palpi somewhat vary. The partially margined mesocoxal acetabulae in the primitive genera. The shape of the elytra. The simple trivalved structure of the 9th abdominal segment and the simple form of the spermatheca. At least one line of setae on the inner face of the procoxa. Tarsal formula 4-5-5. Dorsal rim of the abdomen formed between the inner and the outer paratergites.

It is believed that the above characters collectively define the subtribe though this is naturally subject to revision when more tribes and subtribes are studied. The simple form of abdominal segment IX, plus the form of the maxillae serve to relate this group to the Athetini.

Key to genera

1. Antennae flattened; body form strongly limuloid .... **Coptolimulus**
   Antennae not flattened; body form usually somewhat physogastric, in any event not strongly limuloid 2
2. Second segments of antennae shorter than 3rd; large species; pronotum with posterior margin rounded and blended into lateral borders so that the distinction between posterior and lateral borders is lost .... **Philobrunneus**

Second segment of antennae equal to or slightly longer than 3rd; smaller species; pronotum with 4 distinct borders 3

3. Pronotum with large punctures; mandibles smooth on inner surface, without mandibular teeth.. **Coptotermoecia**

Pronotum smooth, with very tiny punctures or none at all; mandibles with mandibular teeth .... **Coptophilus**

Genus **Coptophilus** Kistner and Pasteels, new genus

Coptotermoecia Seevers, 1957 (in part): 249, fig. 36B; 1960 (in part): 834.

Related to *Coptotermoecia* from which it is distinguished by the smooth pronotum (except for extremely fine punctuation), 1st segment of meso- and metatarsi which are shorter than the 2nd, and inner paratergites which are about $2\times$ the width of the outers. The mandibles of *Coptophilus* are larger and possess well-developed median teeth.

Overall appearance as in fig. 1B. Head capsule wider than long with lateral borders rounded. Eyes well-developed, nearly round, placed anteriorly and laterally on head. Antennae 11-segmented, inserted between eyes, shaped as in fig. 3A, with 2nd segment approximately equal in length to the 3rd, slightly variable by species. Gula with sides subparallel. Mandibles slightly asymmetrical, shaped as in fig. 3E and 3F, with prominent mandibular teeth, slightly variable by species. Maxillae shaped as in fig. 2E; palpi 4-segmented. Lacinia with more than 1 row

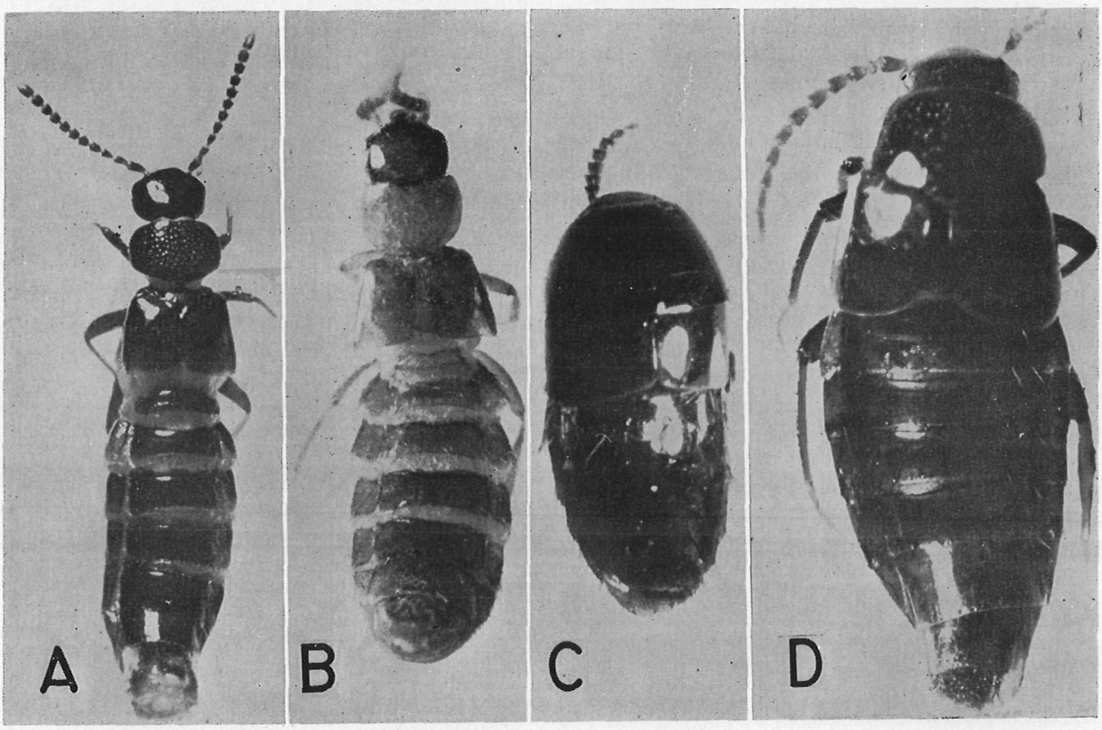


Fig. 1. Dorsal appearances of entire beetles: A, *Coptotermoecia seeversi*, paratype; B, *Coptophilus greavesi*, paratype; C, *Coptolimulus calabyi*, paratype; D, *Philobrunneus gayi*, paratype. Scale arbitrary.

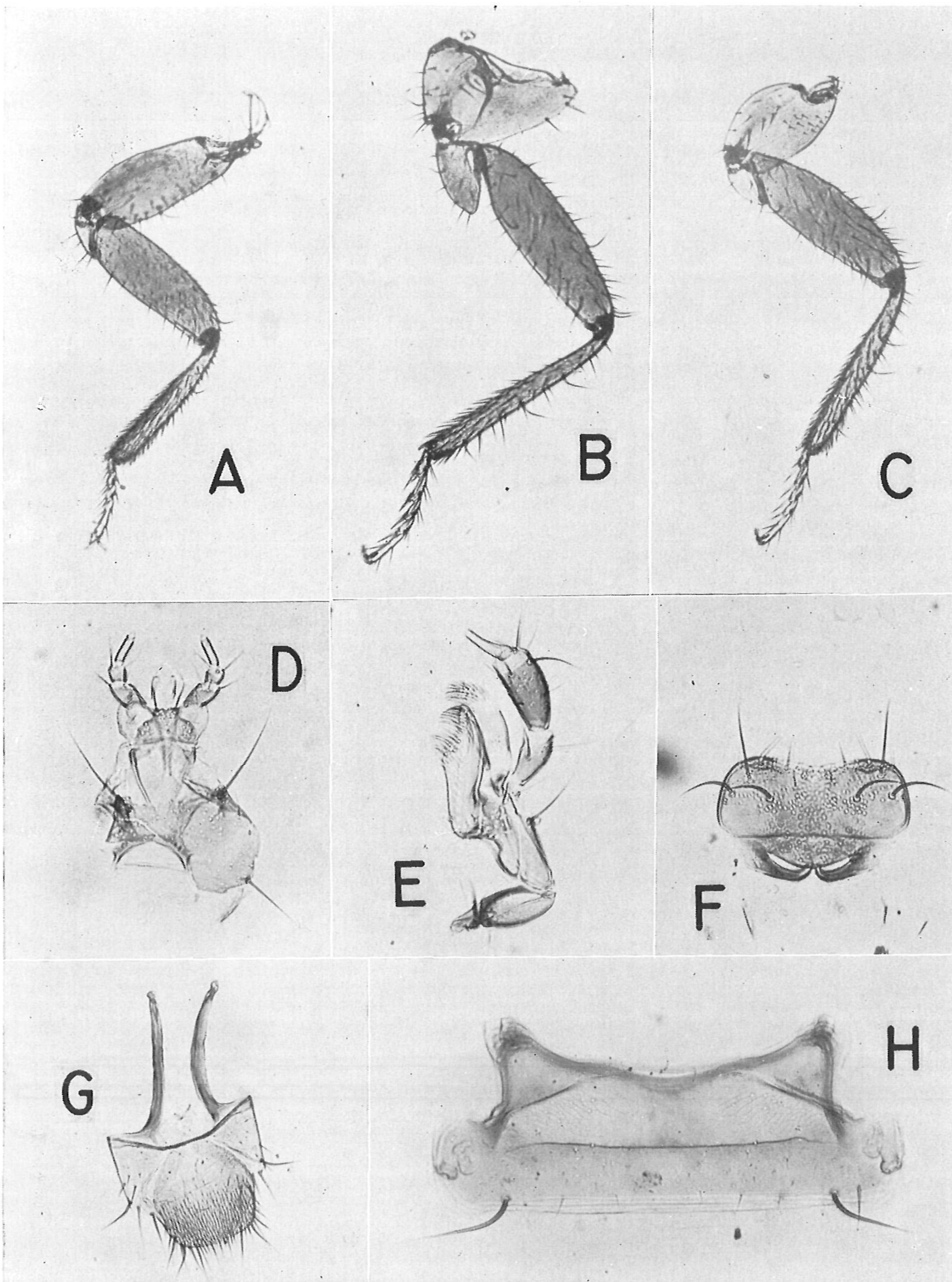


Fig. 2. *Coptophilus greavesi*: A, proleg; B, metaleg; C, mesoleg; D, labium; E, maxilla; F, labrum; G, abdominal segment IX of ♂; H, abdominal tergite I. Scale arbitrary.

of spines. Maxillary acetabula not margined. Labium shaped as in fig. 2D; palpi 3-segmented. Mentum fused to submentum. Labrum short, with anterior corners rounded, shaped as in fig. 2F.

Pronotum smooth, wider than long, anterior margin straight, posterior margin rounded. Prosternum short with a blunt carina more pronounced anteriorly between the legs and with well-developed anterolateral articulation processes. Mesothoracic peritremes membranous. Elytra without distinction, shaped as in fig. 3I, slightly variable by species. Wings absent, apparently broken off, as a small portion of the articular base is still present. Metasternum about 2× as long as mesosternum. Sternepimeron triangular, apical portion not more elongate than usual. Mesocoxal acetabula incompletely margined. Pro-, meso-, and metalegs shaped as in fig. 2A, 2C, and 2B respectively; tarsal formula, 4-5-5. First segment of meso- and metatarsi shorter than 2nd segments.

Abdomen usually moderately physogastric. Extent of physogastry somewhat variable between species as well as between mature and immature specimens of the same species. Segment I represented only by the tergite possessing short lateral processes, shaped as in fig. 2H. Segments III to VII with 1 tergite, 1 sternite, and 2 pairs of paratergites each. Inner paratergites wider than outers. Dorsal rim of abdomen between inner and outer paratergites. Segment VIII with only tergite and sternite. Tergite IX trilobed, without long anterior apodemes in ♀. Tergite IX of ♂ shaped as in fig. 2G with each valvula possessing a long, thin anterior process. Sternite IX membranous in ♀; asymmetrical in ♂, shaped as in fig. 3C and 3D, slightly variable by species. Spermatheca sclerotized, variable by species. ♂ genitalia bulbous, variable by species.

Type-species: *Coptophilus greavesi* Kistner & Pasteels, n. sp.

Key to species of Coptophilus

1. Smaller species, pronotum usually shorter than 0.43 mm, ♂ genitalia shaped as in fig. 4G .... **greavesi**
   Larger species, pronotum usually longer than 0.43 mm, ♂ genitalia shaped as in fig. 4F .... **gayi**

Coptophilus greavesi Kistner and Pasteels, new species Fig. 1B; 2, 3A, C, E, F, I, K; 4E, G; 18.

Related to *C. gayi*, from which it is distinguished by its smaller size and the shape of the ♂ genitalia.

Color yellowish brown; head and tergites reddish brown. Head smooth and shiny with 2 pairs of black setae on dorsum and a few long pale setae on ventral surface. Antennae shaped as in fig. 3A. Mandibles shaped as in fig. 3E and 3F. Pronotum shiny with about 20 black setae of which 4 are on the disc, the others on the margins. Chaetotaxy of elytra as in fig. 3I. Tergites smooth. Tergites III-VI with a subapical row of pale setae mixed with some darker setae. Posterior 1/2 of tergite VII with numerous medium-sized and a few longer setae. Tergite VIII covered with numerous medium-sized setae. Chaetotaxy of tergite IX as in fig. 2G. Sternites covered with numerous pale setae of medium size and a few darker and larger setae. Paratergites with a few dark and pale setae forming a transition between chaetotaxy of tergites and sternites. Spermatheca small, shaped as in fig. 3K. Median and lateral lobes of ♂ genitalia shaped as in fig. 4G and 4E. Tergite IX in ♂ shaped as in fig. 2G. Sternite IX of ♂ as in fig. 3C.

Measurements: Head length, 0.32–0.39; head width, 0.42–0.49; pronotal length, 0.34–0.42; pronotal width, 0.49–0.57; elytral length, 0.42–0.52. Number measured, 20.

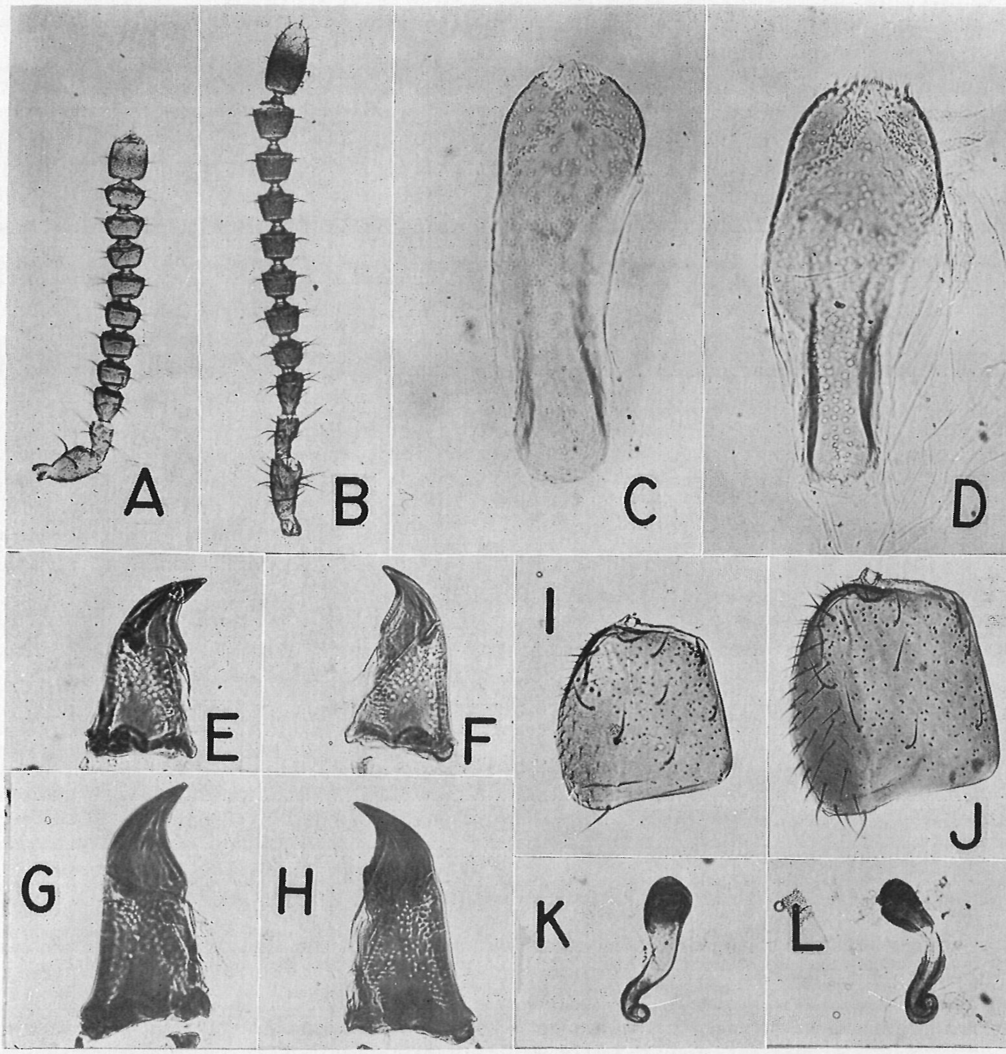


Fig. 3, *Coptophilus greavesi*: A, antenna; C, abdominal sternite IX of ♂; E, left mandible; F, right mandible; I, elytron; K, spermatheca. *Coptophilus gayi*: B, antenna; D, abdominal sternite IX of ♂; G, left mandible; H, right mandible; J, elytron; L, spermatheca. Scale arbitrary.

Holotype (No. 13555), Australia: A. C. T., Blundell's, 15. XI, 1956, A. Wetherley, ex nest of *Coptotermes frenchi* Hill. In Australian National Insect Collection, Canberra. Paratypes: Australia: 12, same data as holotype (CSIRO, DK, JP); 15, A. C. T., Blundell's, 17. XII. 1956, Wetherley, ex nest of *Coptotermes frenchi* (CSIRO, DK); 8, same data, but 17.XI.1958, Gay (CSIRO, DK).

Notes: The termite hosts were identified by the collectors, F. J. Gay and A. Wetherley and are in the Australian National Insect Collection, Canberra. The distribution is shown in fig. 18.

Coptophilus gayi (Seevers), n. comb. Fig. 3B, D, G, H, J, L; 4F; 18.

Coptotermoecia gayi Seevers, 1957: 249, fig. 36B, Australian National Insect Collection, Canberra, (Australia, A. C. T., Shannon's Creek, ex nest of *Coptotermes acinaciformis*); Seevers 1960: 834 (host correction to *C. lacteus*).

Very similar to *C. greavesi*, from which it is distinguished by its larger size, shape of the ♂ genitalia, ♂ sternite IX, and spermatheca.

Color brownish, pronotum and tergites redder than rest of body. Antennae shaped as in fig. 3B. Mandibles shaped as in fig. 3G and 3H. Chaetotaxy as in *C. greavesi*; that for the elytra as shown in fig. 3J. Median lobe of the ♂ genitalia shaped as in fig. 4F. Male sternite IX shaped as in fig. 3D. Spermatheca shaped as in fig. 3L.

Measurements: Head length, 0.39-0.44; head width, 0.47-0.52; pronotal length, 0.44-0.49; pronotal width, 0.55-0.63; elytral length, 0.53-0.63. Number measured, 10.

Material examined: AUSTRALIA: 17, Paratypes, A. C. T., Shannon's Creek, VII. 1939, F. J. Gay, with *C. lacteus* (FMNH); 2 (sectioned), A. C. T., Canberra, 17. XI. 1966, Gay, with *C. lacteus* (JP); 9 (sectioned), A. C. T., Uriarra, 16 km NW of Canberra, 26. VI. 1966, C. Mayo, with *C. lacteus* (CSIRO, JP); 12 (1 sectioned), A. C. T., Blue Range, 14. V. 1969, Gay, with *C. lacteus* (CSIRO, JP, DK); 3, A. C. T., Canberra, IX. 1949, F. J. Gay, (FMNH).

Notes: The hosts were identified by Dr. F. J. Gay. The latter nests contained additionally some *Coptotermoecia seeversi* and some others. Host specimens are in the Australian National Insect Collection, Canberra. The distribution of this species is shown in fig. 18.

Genus **Coptotermoecia** Oke

Coptotermoecia Oke, 1933: 135.—Seevers, 1957: 248; 1960: 834.

Related to *Coptophilus* from which it is distinguished by the heavily punctured pronotum, arcuate mandibles, outer paratergites which are subequal in width to the inner paratergites, and the 1st segments of meso- and metatarsi which are longer than the 2nd segments. Most closely related to *Philobrunneus*, from which it is distinguished by the relative length of the 2nd segment of the antenna, which is as long as the 3rd in *Coptotermoecia* and much shorter than the 3rd in *Philobrunneus* (fig. 8A). Also distinguished from *Philobrunneus* by the overall shape (fig. 1D) and the shape of the maxillae (fig. 8G).

Overall appearance as in fig. 1A. Head capsule wider than long, with lateral borders evenly rounded. Eyes well-developed, ovoid, placed anteriorly and laterally on head. Antennae 11-segmented, inserted between eyes, shaped as in fig. 5D, with 2nd segment subequal to or longer than 3rd. Gula with sides subparallel. Mandibles symmetrical or nearly so, strongly arcuate, with mandibular teeth greatly reduced or absent (fig. 6E and 6F), slightly variable by species.

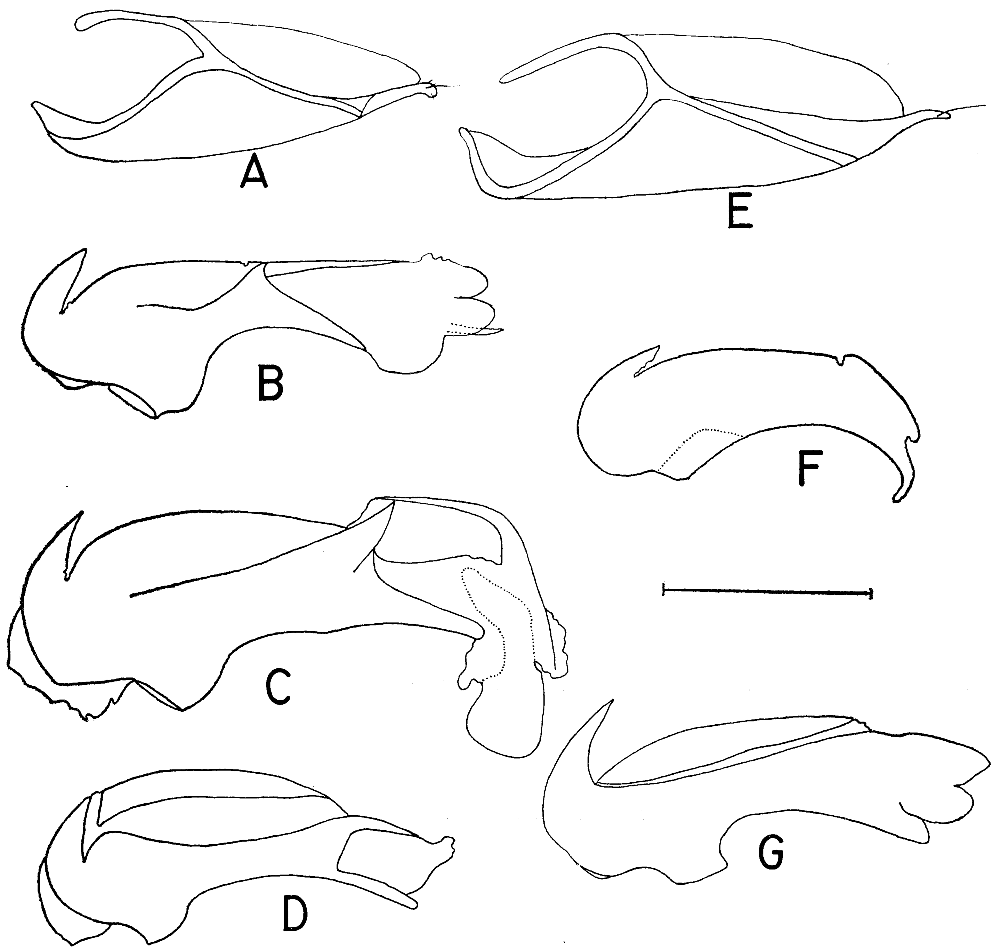


Fig. 4. Median lobes of ♂ genitalia: B, *Coptotermoecia seeversi*; C, *C. flava*; D, *C. pilosa*; F, *Coptophilus gayi*; G, *C. greavesi*. Lateral lobes of ♂ genitalia: A, *Coptotermoecia seeversi*; E, *Coptophilus greavesi*. Scale represents 0.25 mm.

Maxillae shaped as in fig. 5E; palpi 4-segmented. Lacinia with a single row of spines inserted along inner margin. Maxillary acetabula not margined. Labium shaped as in fig. 5G; palpi 3-segmented. Mentum greatly reduced in size, may be fused or not fused to the submentum. Labrum short with anterior corners angular, shape variable by species.

Pronotum densely covered with large punctures, wider than long, anterior margin straight, posterior margin rounded, as in fig. 1A. Prosternum with a blunt carina between legs more pronounced anteriorly, and with long thin anterolateral articulation processes. Wings fully developed or only a small portion of articular base present. Mesothoracic peritremes membranous. Elytra without distinction, shaped as in fig. 6A, variable by species. Metasternum about 2 × as long as mesosternum. Sternepimeron triangular with apical portion more elongate than usual in Aleocharinae. Mesocoxal acetabulae incompletely margined. Pro-, meso-, and metalegs shaped as in fig. 5A, 5B, and 5C, respectively; tarsal formula, 4-5-5. First segments of meso- and metatarsi longer than 2nd.

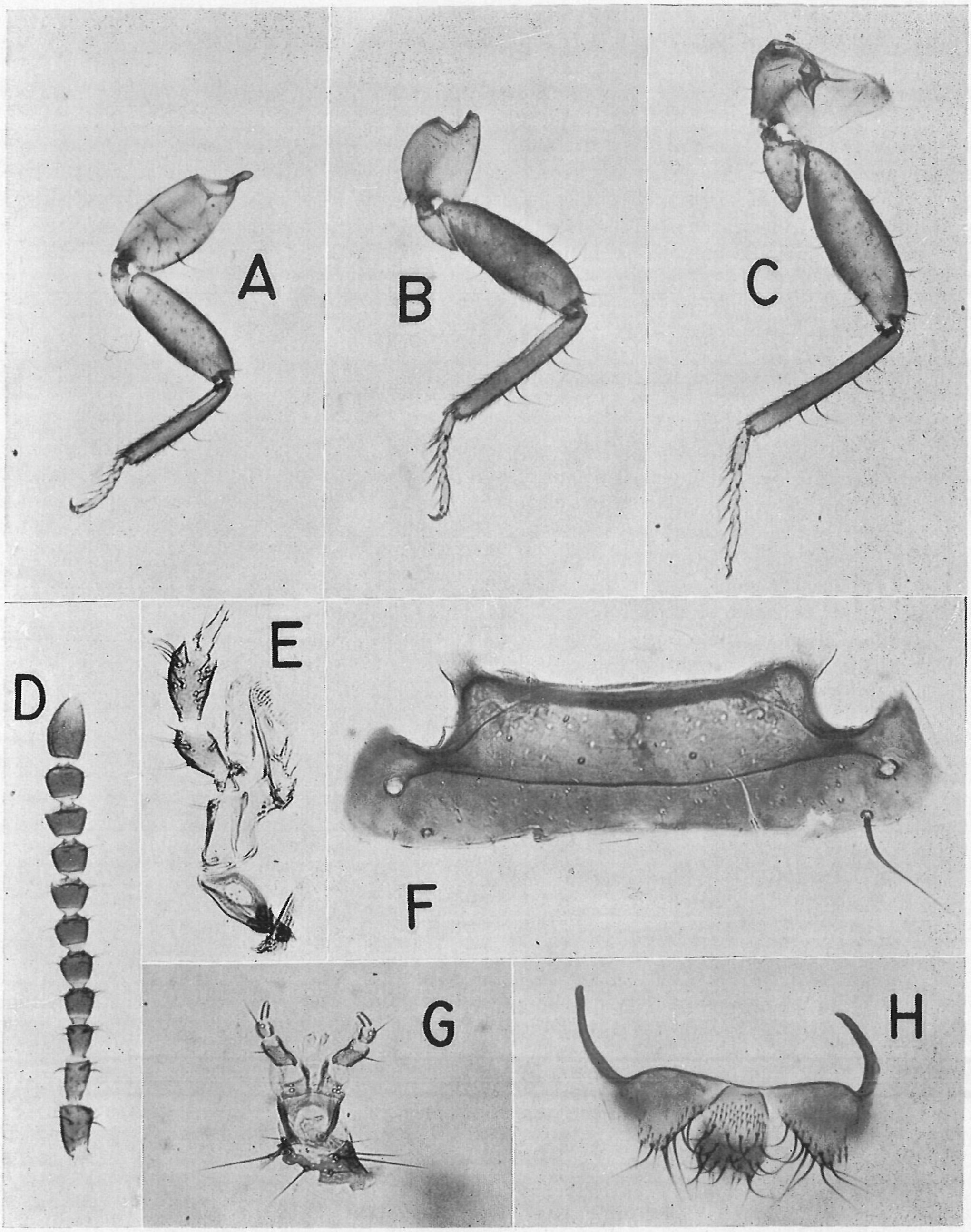


Fig. 5. *Coptotermoecia seeversi*: A, proleg; B, mesoleg; C, metaleg; D, antenna; E, maxilla; F, abdominal tergite II; G, labium; H, abdominal segment IX of ♂ spread out. Scale arbitrary.

Abdomen moderately physogastric, shaped as in fig. 1A. Segment I represented only by tergite fused to metanotum. Segment II represented only by the tergite. Tergite II with anterior corners of lateral processes somewhat anteriorly directed as in fig. 5F. Segments III-VII with 1 tergite, 1 sternite, and 2 pairs of paratergites each. Dorsal rim of abdomen between inner and outer paratergites. Outer paratergites as wide as or very slightly wider than inners. Segment VIII with a tergite and sternite only. Tergite IX trilobed, without long anteriorly directed processes. Tergite IX of ♂ shaped as in fig. 5H with valvulae symmetrical but possessing long, thin anterior asymmetrical processes. Sternite IX membranous in ♀, sclerotized and asymmetrical in ♂, shape variable by species. Spermatheca sclerotized; shape variable by species. ♂ genitalia bulbous, variable by species.

Type-species: *Coptotermoecia alutacia* Oke (Blackwelder 1952: 107, misspelled *Coprotermoecia*).

Key to species of Coptotermoecia

1. Sternites without paler setae; bearing only macrosetae .... **seeversi**
   Sternites with paler setae (usually shorter, but not always) in addition to macrosetae 2
2. Color yellowish, without a trace of reddish brown; specimens' yellowish color can be seen without microscope; posterior pronotal margin rounded .... **flava**
   Color yellowish, posterior pronotal margin straight .... **alutacia**
   Color reddish brown 3
3. Smaller species, head width less than 0.5 mm; 10-12 black macrochaetae on tergites III-VI in addition to numerous smaller and paler setae.. **pilosa**
   Larger species, head width more than 0.5 mm, 6 black macrochaetae on tergites III-VI in addition to smaller setae .... **robusta**

Coptotermoecia alutacia Oke Fig. 18.

Coptotermoecia alutacia Oke, 1933: 136, fig. 48, 84-88, National Museum of Victoria, Melbourne [Australia, Victoria, Natya, Violet Town, ex nest of *Coptotermes acinaciformis* (Froggatt)]. —Neboiss, 1964: 129 (type listing).

Distinguished from all other species except *C. flava* by its light color. Distinguished from *C. flava* by the deeper punctures of the pronotum as well as the shape of the pronotum with its straighter posterior border. When specimens of this species are available for dissection, other differences will probably be visible.

Color yellowish brown throughout; head and elytra a little dark than rest of body. Pronotum with 24 macrosetae of which 6 are on the disk and the others along the margins. Elytra with 14 macrosetae each, of which 3 are on the disk and 11 are marginal. Macrochaetotaxy of abdominal tergites II-VIII: 2, 6, 6, 6, 6, 8, 6 subapicals and 8 apicals. Outer paratergites III-V with 1 macrochaeta. Sternites not seen nor were the ♂ genitalian or the ♀ spermatheca.

Measurements: Head length, 0.34-0.39; pronotal length, 0.38-0.42. Number measured, 3.

Material examined. AUSTRALIA: 1 ♂ (No. 1315), Holotype, Victoria, Violet Town, VII. 1924, C. Oke, in nest of *C. acinaciformis*, det. G. F. Hill, (NMV); 1 ♀ allotype (No. 1316), labelled ♀ type, same data as holotype, (NMV); 2, Paratypes, (No. 1317, 1318), same data as holotype, (NMV); 2, not labelled as types, Victoria, Violet Town, Coll. C. Oke, no host data, (NMV).

Notes: The distribution of this species is shown in fig. 18.

Coptotermoecia seeversi Kistner and Pasteels, new species Fig. 1A; 4A, B; 5; 6A, E, F; 7A, D, H; 18.

Coptotermoecia alutacia Seevers, 1957: 248 (Australia, A. C. T., Shannon's Creek, VII. 1939, F. J. Gay; N. S. W., Mt. Keira, 7.X.1948, C. E. Chadwick, Host: *Coptotermes acinaciformis*); 1960: 834, [changed host to *C. lacteus* (Froggatt)].

Distinguished from all other species by the absence of sternal pubescence. Most closely related to *C. robusta*, but distinguished from it by its chaetotaxy, spermatheca, and ♂ genitalia.

Color reddish brown. Head with a few dorsal punctures and 2 pairs of macrosetae. Mandibles shaped as in fig. 6E and 6F. Labrum shaped as in fig. 7H. Pronotum with about 20 macrosetae, of which 4 are on the disk and the others along the margins. Chaetotaxy of elytra as in fig. 6A. Macrochaetotaxy of abdominal tergites II-VIII: 2, 6, 6, 6, 6, 8, 6 subapicals and 8 apicals. Outer paratergites III-V with 1 macrochaeta. Sternite III-VIII with an apical row of black setae, but only a few scattered hairs elsewhere. Sternite IX of ♂ shaped as in fig. 7A. Spermatheca shaped as in fig. 7D. Median and lateral lobes of ♂ genitalia shaped as in fig. 4B and 4A; median lobe with only a small anterior carina.

Measurements: Head length, 0.32-0.37; head width, 0.45-0.50; pronotal length, 0.36-0.41; pronotal width, 0.53-0.60; elytral length, 0.47-0.57. Number measured, 20.

Holotype (No. 13601), Australia, Shannon's Creek, 18. VII. 1939, F. J. Gay, with *Coptotermes*. In the Australian National Insect Collection, Canberra. Paratypes: 12, same data as holotype (CSIRO, FMNH, DK); 23, (3 sectioned), A. C. T., Canberra, 28. X. 1965, Gay, with *C. lacteus* (CSIRO, JP, DK); 11, A. C. T., Canberra, 27. II. 1966, Gay, with *C. lacteus* (CSIRO, JP); 17, A. C. T., Uriarra, 16 km NW of Canberra, 26. VI. 1966, C. Mayo, with *C. lacteus* (CSIRO, JP, DK); 57, A. C. T, Blue Range, 14. V. 1969, Gay, with *C. lacteus* (CSIRO, JP, DK).

Notes: The host identifications were made by F. J. Gay. Specimens of the host termites are in the Australian National Insect Collection, Canberra. The distribution of this species is shown in fig. 18.

Coptotermoecia flava Kistner and Pasteels, new species Fig. 4C; 6B, G, H; 7B, E, I; 18.

Distinguished from all other species except *C. alutacia* by its color. The median lobe of the ♂ genitalia is much larger in *C. flava* than in *C. seeversi* and *C. pilosa* and the shape of the ♂ sternite IX is even more asymmetrical. Distinguished from *C. alutacia* by the more rounded posterior border of the pronotum.

Color yellowish, the head somewhat darker. Head with 3 dorsal pairs of black setae, and 1 on each side. Dorsal surface of the head distinctly punctate and with many fine sparse yellow setae. Many long setae on ventral surface of the head. Mandibles shaped as in fig. 6G and 6H. Labrum shaped as in fig. 7I. Pronotum with many minute yellow setae and with 18 macrosetae of which 16 are along the margins and the other 2 are on the disk. Elytra with 13 macrosetae and some smaller paler setae which are chiefly lateral in distribution, as in fig. 6B. Macrochaetotaxy of abdominal tergites II-VIII as follows: 4, 6, 6, 6, 6, 10, 12. Posterior 1/2 of these tergites with many fine yellow setae. Inner paratergites with only a few small yellow setae. Outer paratergites with 1 macroseta and many fine yellow setae. Sternites III-VIII cov-

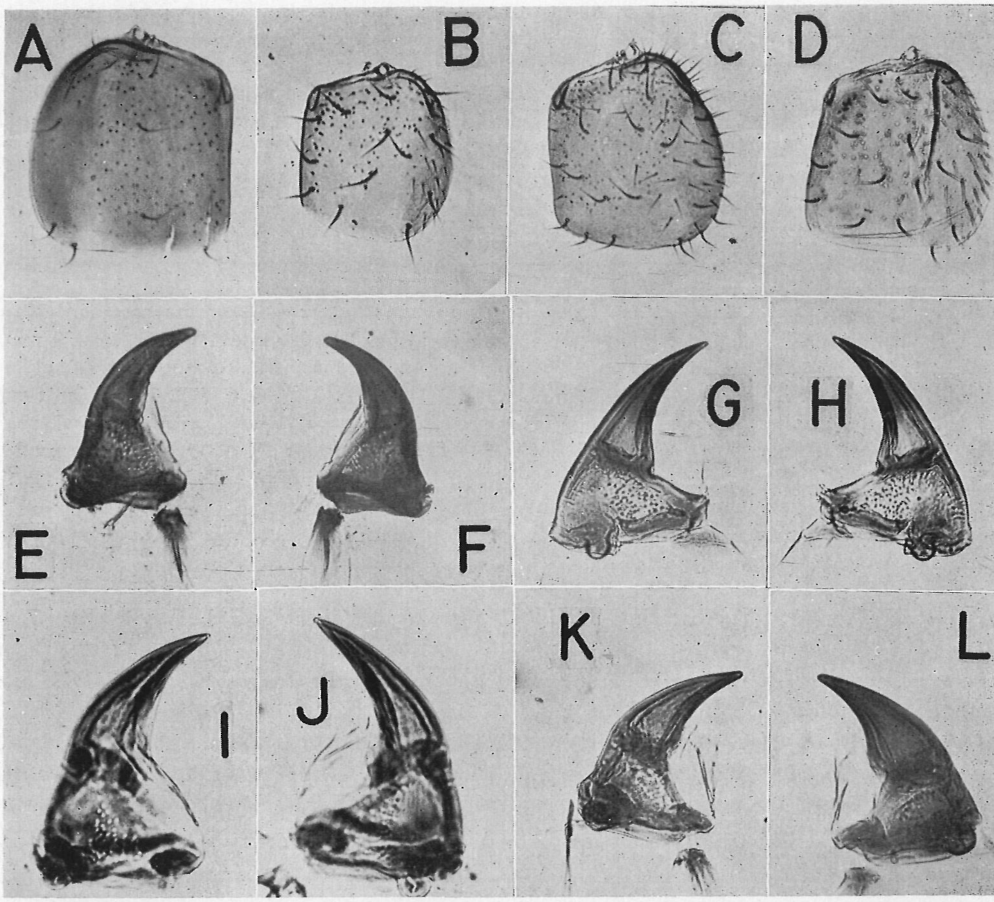


Fig. 6. *Coptotermoecia seeversi*: A, elytron; E, left mandible; F, right mandible. *C. flava*: B, elytron; G, left mandible; H, right mandible. *C. pilosa*: C, elytron; I, left mandible; J, right mandible. *C. robusta*: D, elytron; K, left mandible; L, right mandible. Scale arbitrary.

ered with fine yellow setae plus an apical row of black setae. Sternite VIII with additional black setae in median area. Spermatheca as in fig. 7E. Median lobe of ♂ genitalia as in fig. 4C, with an anterior carina sometimes somewhat indented. These indentations seem variable. ♂ sternite IX as in fig. 7B.

Measurements: Head length, 0.39–0.44; head width, 0.49–0.52; pronotal length, 0.37–0.42; pronotal width, 0.52–0.55; elytral length, 0.37–0.47. Number measured, 20.

Holotype (No. 13547), West Australia, Darling Range, Kalamunda, 12. VII. 1954, H. Demarz. In the Australian National Insect Collection, Canberra. Paratypes: 24, same data as holotype (CSIRO, DK, JP); 31, West Australia, Kalamunda, 26. IX. 1954, Demarz (FMNH, DK).

Notes: We have no host data for these specimens. The host is most likely *Coptotermes acinaciformis* ssp. *raffrayi* Wasmann according to F. J. Gay (personal communication).

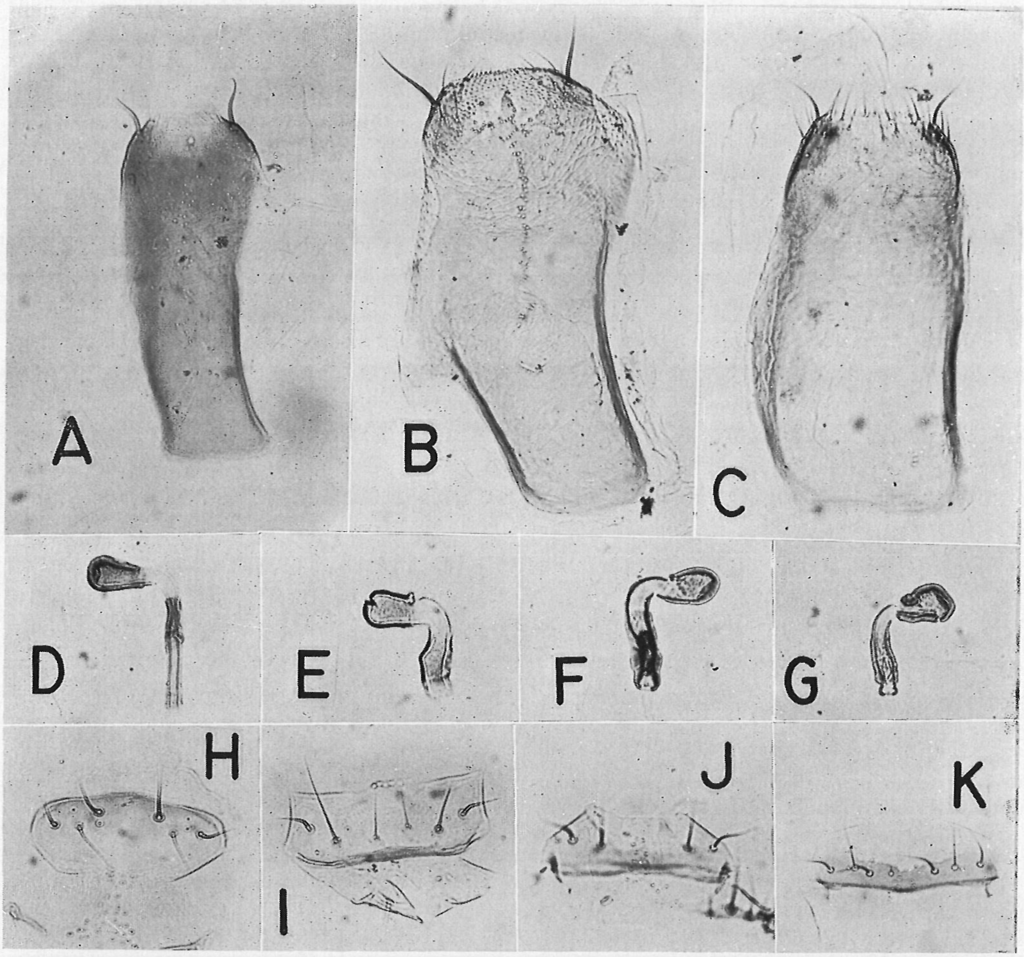


Fig. 7. *Coptotermoecia seeversi* : A, abdominal sternite IX of ♂; D, spermatheca ; H, labrum. *C. flava* : B, abdominal sternite IX of ♂ ; E, spermatheca ; I, labrum. *C. pilosa* : C, abdominal sternite IX of ♂ ; F, spermatheca ; J, labrum. *C. robusta* : G, spermatheca ; K, labrum. Scale arbitrary.

The distribution of this species is shown in fig. 18.

Coptotermoecia pilosa Kistner and Pasteels, new species Fg. 4D ; 6C, I, J ; 7C, F, J ;18.

The hairiest species of the genus. Related to *C. seeversi* by its size and color, but distinguished from this species by its chaetotaxy, the shape of the spermatheca and the shape of the ♂ genitalia. Most closely related to *C. flava* from which it is distinguished by its chaetotaxy and color.

Color reddish brown. Head, pronotum, elytra (fig. 6C), posterior margin of the tergites, paratergites, and abdominal and other sternites with numerous black setae of various sizes, some of them very long. Mandibles shaped as in fig. 6I and 6J. Labrum shaped as in fig. 7J. Macrochaetotaxy of tergites II-VII as follows: 2 lateral groups of 2 to 5 on tergite II, 8 or 10 marginals and 2 laterals on tergite III, 10 marginals and 2 laterals on tergites IV-VI, 10 marginals and 4 in a row at midlength of tergite VII. Somewhat shorter and paler setae between marginal macrosetae and numerous smaller setae in posterior 1/2 of these tergites. Spermatheca shaped as in fig. 7F. Median lobe of ♂ genitalia, with an anterior carina, shaped as in fig. 4D. Sternite IX of ♂ shaped as in fig. 7C.

Measurements: Head length, 0.31-0.39; head width, 0.41-0.50; pronotal length, 0.32-0.41; pronotal width, 0.45-0.57; elytral length, 0.39-0.52. Number measured, 20.

Holotype (No. 13548), Australia, N. S. W., Pine Creek, 11. VI. 1958, T. Greaves, in nest of *Coptotermes acinaciformis.* In the Australian National Insect Collection, Canberra. Paratypes: Australia: 4, same data as holotype (CSIRO, DK); 5, Queensland, 36.8 km N. Townsville, 23. VI. 1960, F. J. Gay, in nest of *C. acinaciformis* (CSIRO, DK); 8, Queensland, Townsville, VIII. 1965, Gay, in nest of *C. acinaciformis* (CSIRO, DK); 33 (3 sectioned) Australia, Queensland, Townsville, VIII. 1965, Gay, in nest of *C. acinaciformis* (CSIRO, JP); 7, 40 km N. of Townsville, 3. VIII. 1966, Gay, in nest of *C. acinaciformis* (CSIRO, JP).

Notes: The host identifications were made by the collectors, F. J. Gay and T. Greaves. Specimens of the hosts are located in the Australian National Insect Collection, Canberra. The distribution of this species is shown in fig. 18.

Coptotermoecia robusta Kistner and Pasteels, new species Fig. 6D, K, L; 7G, K; 18.

The largest species of the genus. Closely related to *C. pilosa* by its color, but the setae are even more abundant and longer in *C. pilosa*. Chaetotaxy similar to *C. flava*, but easily distinguished by its color.

Color reddish brown. Dorsal surface of head with few punctures, few fine yellow setae, and few macrosetae. Mandibles shaped as in fig. 6K and fig. 6L. Labrum shaped as in fig. 7K. Pronotum with 20 macrosetae inserted as in *C. seeversi* but with additional short fine yellow setae. Elytra with numerous macrosetae and with shorter setae laterally, as in fig. 6D. Macrochaetotaxy of tergites II-VII as follows: 4, 6, 6, 6, 6, 8. Posterior 1/2 of these tergites with many shorter setae. Tergite VIII with many setae of various sizes. Inner paratergites with a few pale setae. Outer paratergites with many pale setae and 1 black macroseta. Sternites with an even covering of fine yellow setae plus a marginal line of macrosetae. Sternites also with anterior and median macrosetae which increase in number from sternite III tosternite VIII. Spermatheca as in fig. 7G. ♂ unknown.

Measurements: Head length, 0.37; head width, 0.52-0.53; pronotal length, 0.39-0.41; pronotal width, 0.57-0.60; elytral length, 0.50-0.53. Number measured, 5.

Holotype (No. 13546), W. Australia, Kalamunda, 26. IX. 1954, H. Demarz. In the Australian National Insect Collection, Canberra. Paratypes: 2, same data as holotype (FMNH, DK); 2, same data, but 12. VII. 1954 (CSIRO, DK).

Notes: We have no host data for these specimens. The host is most likely *Coptotermes acinaciformis* ssp. *raffrayi* according to F. J. Gay (personal communication) based on the frequency and conspicuousness of the nest structures. The distribution of this species is shown in fig. 18.

Genus **Philobrunneus** Kistner and Pasteels, new genus

Closely related to *Coptotermoecia* from which it is distinguished by its overall shape, much larger size, the reduced 2nd segment of the antennae, the shape of the maxillae, and the shapes of the legs.

Overall appearance as in fig. 1D. Head capsule wider than long with the lateral borders rounded. Eyes well-developed, nearly round, placed anteriorly and laterally on the head. Antennae 11-segmented, inserted between the eyes, shaped as in fig. 8A with 2nd segment about 1/2 the length of 3rd. Gula with sides nearly parallel. Mandibles symmetrical or nearly so, strongly arcuate with mandibular (median) teeth greatly reduced or absent, shaped as in fig. 8F. Maxillae shaped as in fig. 8G, note stout palpi in comparison to *Coptotermoecia*; palpi 4-segmented. Lacinia with a row of spines inserted along inner margin. Maxillary acetabula not margined. Labium shaped as in fig. 8D; palpi 3-segmented. Mentum not appreciably reduced in size, fused to submentum. Labrum short, with anterior corners rounded, shaped as in fig. 8H.

Pronotum densely covered with large punctures; wider than long; anterior margin straight, posterior margin rounded so that the distinction between lateral borders and posterior border is lost, shaped as in fig. 1D. Prosternum slightly carinate at midline at anterior edge; carina blunt; with long anterolateral articulation processes. Wings absent except for a small stub at base. Mesothoracic peritremes membranous. Elytra without distinction, shaped as in fig. 1D. Metasternum about 1.5 $\times$ length of mesosternum. Mesosternal intercoxal process bluntly pointed. Sternepimeron shaped like an isosceles triangle. Mesocoxal acetabula incompletely margined. Pro-, meso-, and metalegs shaped as in fig. 8E, 8B, and 8C respectively; tarsal formula 4-5-5. First segments of meso- and metatarsi slightly longer than second.

Abdomen not physogastric; there is no extensive membrane showing between sclerites; shaped as in fig. 1D. Segment I represented only by tergite fused to metanotum. Segment II represented only by tergite. Tergite II with anterior corners of lateral processes somewhat anteriorly directed. Segments III-VII with 1 tergite, 1 sternite, and 2 pairs of paratergites each. Dorsal rim of abdomen between inner and outer paratergites. Outer paratergites narrower than inners. Segment VIII with tergite and sternite only. Tergite IX trilobed, shaped essentially as in *Coptotermoecia*, except that the setae are much longer. Sternite IX membranous in female, sclerotized and asymmetrical in ♂. Spermatheca sclerotized; shape presumed variable by species. ♂ genitalia bulbous; presumed variable by species.

Type-species: *Philobrunneus gayi* Kistner & Pasteels, n. sp.

Philobrunneus gayi Kistner and Pasteels, new species Fig. 8; 9A, B, C; 18.

Since this species is at present the only species of the genus, the characters isolated as specific are based on experience with species of *Coptotermoecia*. The species, like the genus, is immediately distinguished from all other members of the subtribe by its overall appearance.

Color reddish brown throughout. Head with some dorsal punctures and 2 pairs of macrosetae. Pronotum with a row of about 60 setae on all margins collectively; surface with many large punctures most of which contain setae. Elytra with about 42 setae on each arranged essentially in 7 rows of 6. Macrochaetotaxy of abdominal tergites II-VII: 2, 6, 6, 6, 6, 6. Tergite VIII with 3 apical rows of somewhat smaller but black setae. Sternites III-VII with an apical row of short black setae and occasional anteapical scattered setae. Sternite VIII with an apical row

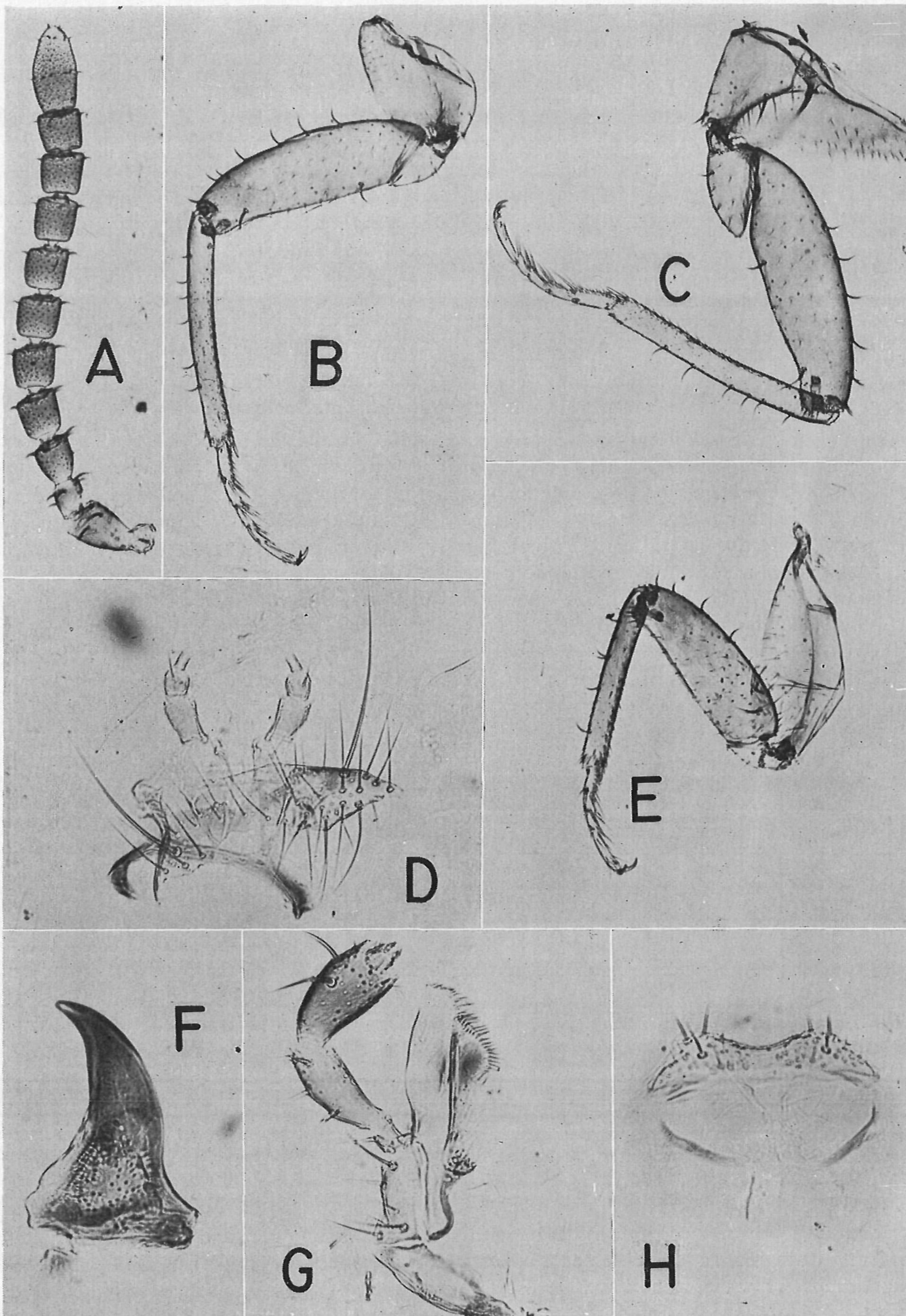


Fig. 8. *Philobrunneus gayi*: A, antenna; B, mesoleg; C, metaleg; D, labium; E, proleg; F, right mandible; G, maxilla; H, labrum. Scale arbitrary.

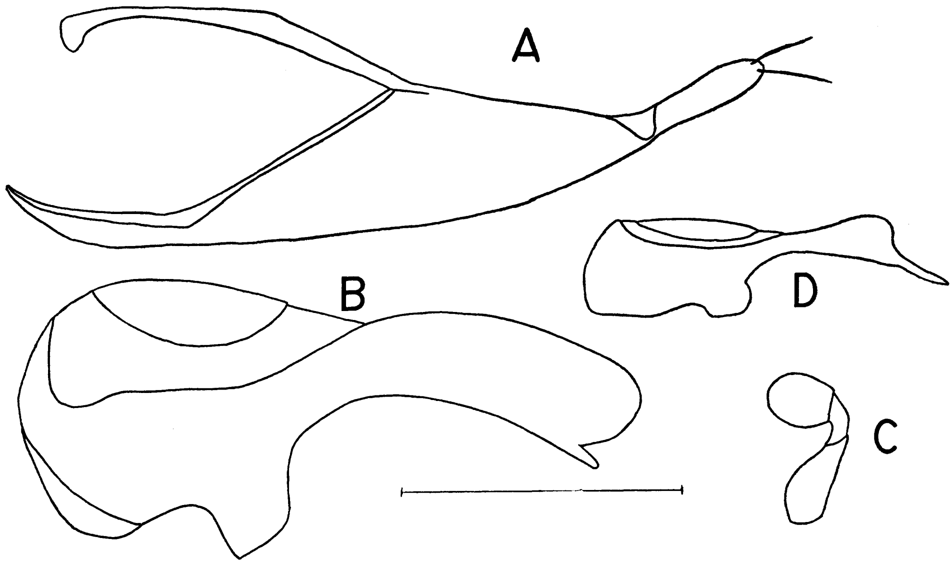


Fig. 9. *Philobrunneus gayi*: A, lateral lobe of ♂ genitalia; B, median lobe of ♂ genitalia; C, spermatheca. *Coptolimulus calabyi*: D, median lobe of ♂ genitalia. Scale represents 0.25 mm.

and a shorter anteapical row of black setae. Neither tergites nor sternites possess any but occasional short yellow setae; thus the overall impression is that they are shiny. Spermatheca shaped as in fig. 9C. Median lobe and lateral lobes of the ♂ genitalia shaped as in fig. 9B and 9A; median lobe with an anterior carina.

Measurements: Head length, 0.40–0.44; head width, 0.72–0.75; pronotal length, 0.60–0.65; pronotal width, 0.95–1.01; elytral length, 0.52–0.58. Number measured, 7.

Holotype (No. 13571), W. Australia, 69 km NNW of Galena, 23. X. 1955, F. J. Gay & J. H. Calaby, ex nest of *Coptotermes brunneus* Gay. In the Australian National Insect Collection, Canberra. Paratypes: 6, same data as holotype (CSIRO, DK).

Notes: The host was determined by F. J. Gay & J. H. Calaby and is located in the Australian National Insect Collection, Canberra. This species is named for F. J. Gay in appreciation for the privilege of studying this and other fine termitophiles. The distribution of this species is shown in fig. 18.

Genus **Coptolimulus** Kistner and Pasteels, new genus

A highly distinctive genus which is immediately recognizable by its overall form as well as the shape of its peculiarly flattened and compressed antennae. While many genera of Aleocharinae have compressed antennae, this is the only genus we know of with flattened antennae. Most closely related to *Philobrunneus* from which it is distinguished by its limuloid form, its smooth and shining pronotum, as well as the flat antennae.

Overall appearance as in fig. 1C. Head capsule wider than long; broadly semicircular in shape with the straight side along front and lateral borders rounding gently into posterior border, obliterating the distinction and presenting the curved continuous border. Eyes present and well developed, mostly directed forward on head but with a few lateral facets. Antennae 11-segmented, inserted between eyes in fairly large antennal sockets which are directed principallyforward; shaped as in fig. 10F. Note the flat, compressed structure and proportions of segments. Gula with sides diverging from anterior to posterior; shortened. Submentum is about the same length as gula. Mentum fused to submentum. Mandibles nearly symmetrical, shaped as in fig. 10E, without mandibular teeth. Maxillae shaped as in fig. 10D; palpi 4-segmented. Lacinia with more than 1 line of spines on inner edge. Maxillary acetabulum distinctly margined. Labium shaped as in fig. 10A; palpi 3-segmented. Labrum very short with rounded anterior corners, shaped as in fig. 10B, with 4 prominent macrosetae.

Pronotum much wider than long; so strongly curved that accurate width measurements cannot be taken, shaped as in fig. 1C. Pronotum surface smooth; both anterior and posterior margins rounded; overlaps the head in part. Prosternum extremely short (0.03 mm); without carinas of any kind, with long anterolateral articulation processes. Mesothoracic peritremes membranous. Elytra without distinction, shaped as in fig. 11D. Wings represented by only the smallest vestige of a basal articulation process. Metasternum slightly shorter than mesosternum. Sternepimeron triangular with apical portion more elongate than usual. Mesocoxal acetabula completely margined. Mesosternal intercoxal process acute and very slightly carinate. Pro-, meso-, and metalegs shaped as in fig. 11B, 11A, and 11C respectively; tarsal formula 4-5-5; note prominent macrosetae on legs. First segments of meso- and metatarsi longer than second.

Abdomen not physogastric; most tergites and sternites overlap so that almost no membrane is exposed. Segment I represented only by the tergite fused to metanotum. Segment II represented only by the tergite possessing only short lateral processes. Segments III-VII with 1 tergite, 1 sternite, and 2 pairs of thin paratergites. Paratergites are of approximately same width; dorsal rim of abdomen occurs between paratergites. Segment VIII with only 1 tergite and 1 sternite. Tergite IX trilobed, shaped in ♀ as in fig. 10C. Valvulae of segment IX of ♂ with the usually long asymmetrical anterior-directed apodemes. Sternite IX of ♂ asymmetrical. Spermatheca sclerotized, presumed variable by species. ♂ genitalia bulbous, presumed variable by species.

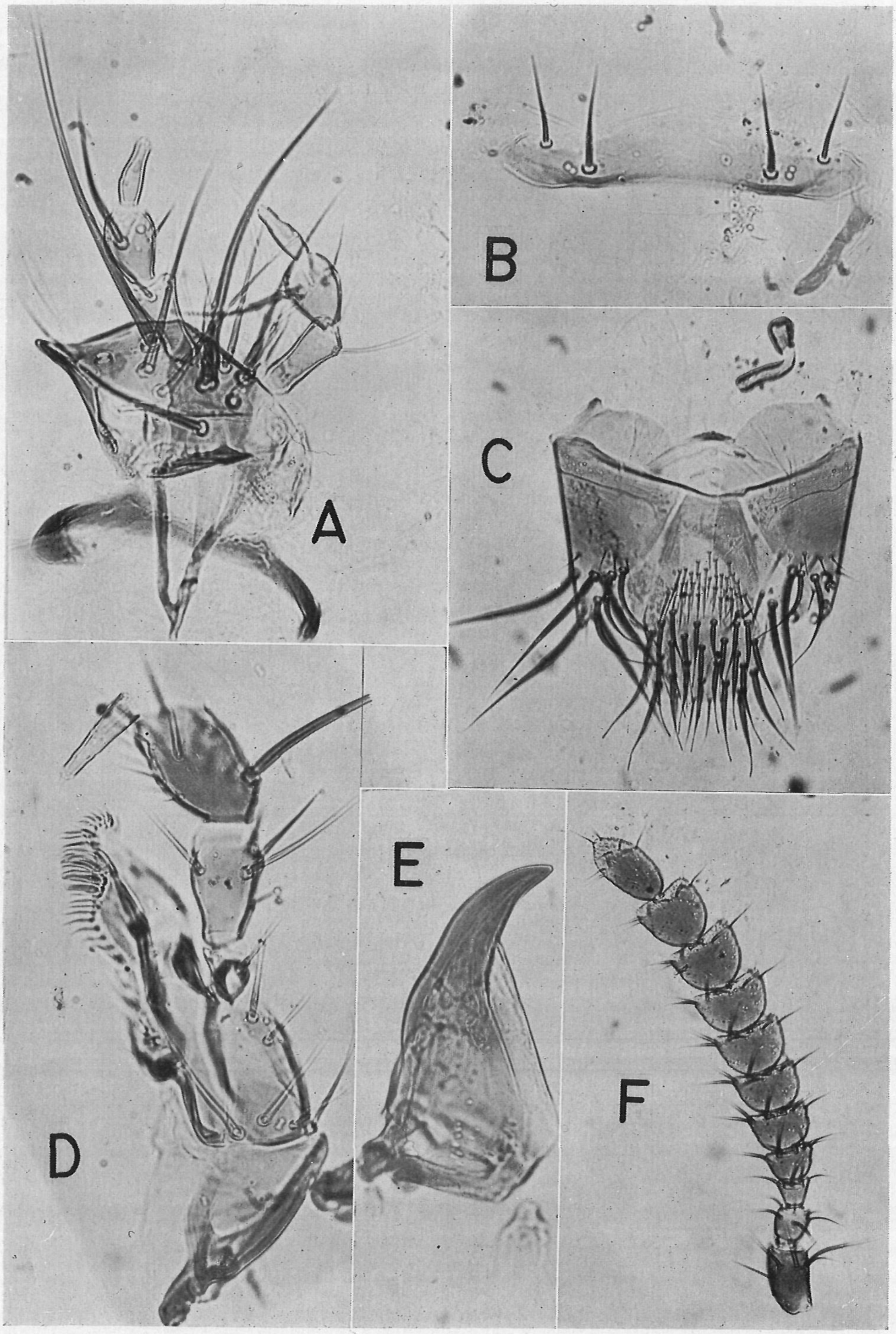
Type-species: *Coptolimulus calabyi* Kistner & Pasteels, n. sp.

Coptolimulus calabyi Kistner and Pasteels, new species Fig. 9D; 10; 11; 18.

Since this species is the only species of the genus presently known, the characters described here as specific are based on experience with *Coptotermoecia* and *Coptophilus.*

Color reddish brown throughout. Dorsal surface of entire beetle smooth and shiny with very few pale, yellow setae scattered about. Head with 8 macrosetae from anterior margin, 4 on vertex and 1 each below eyes. Also with 4-5 yellow setae on lateral margin behind eyes. Pronotum with about 20 black setae located on all margins together and about 2 on disk. Chaetotaxy of elytra as shown in fig. 11D. Macrochaetotaxy of abdominal tergites II-VIII: 2, 6, 6, 6, 6, 6 (middle 2 shorter), 8 (apical)-group of 8 (anteapical). Chaetotaxy of segment IX as in fig. 10C. Outer paratergites each with 1 macrochaeta; inners with none. Sternites III-VII each with an apical row of black macrochaetae and an anteapical curved row. Spermatheca shaped as in fig. 10C. Median lobe of ♂ genitalia shaped as in fig. 9D. Lateral lobe shaped as in *Philobrunneus gayi.*

Fig. 10. *Coptolimulus calabyi*: A, labium; B, labrum; C, abdominal segment IX of ♀ with spermatheca; D, maxilla; E, mandible; F, antenna. Scale arbitrary.


A
B
C
D
E
F

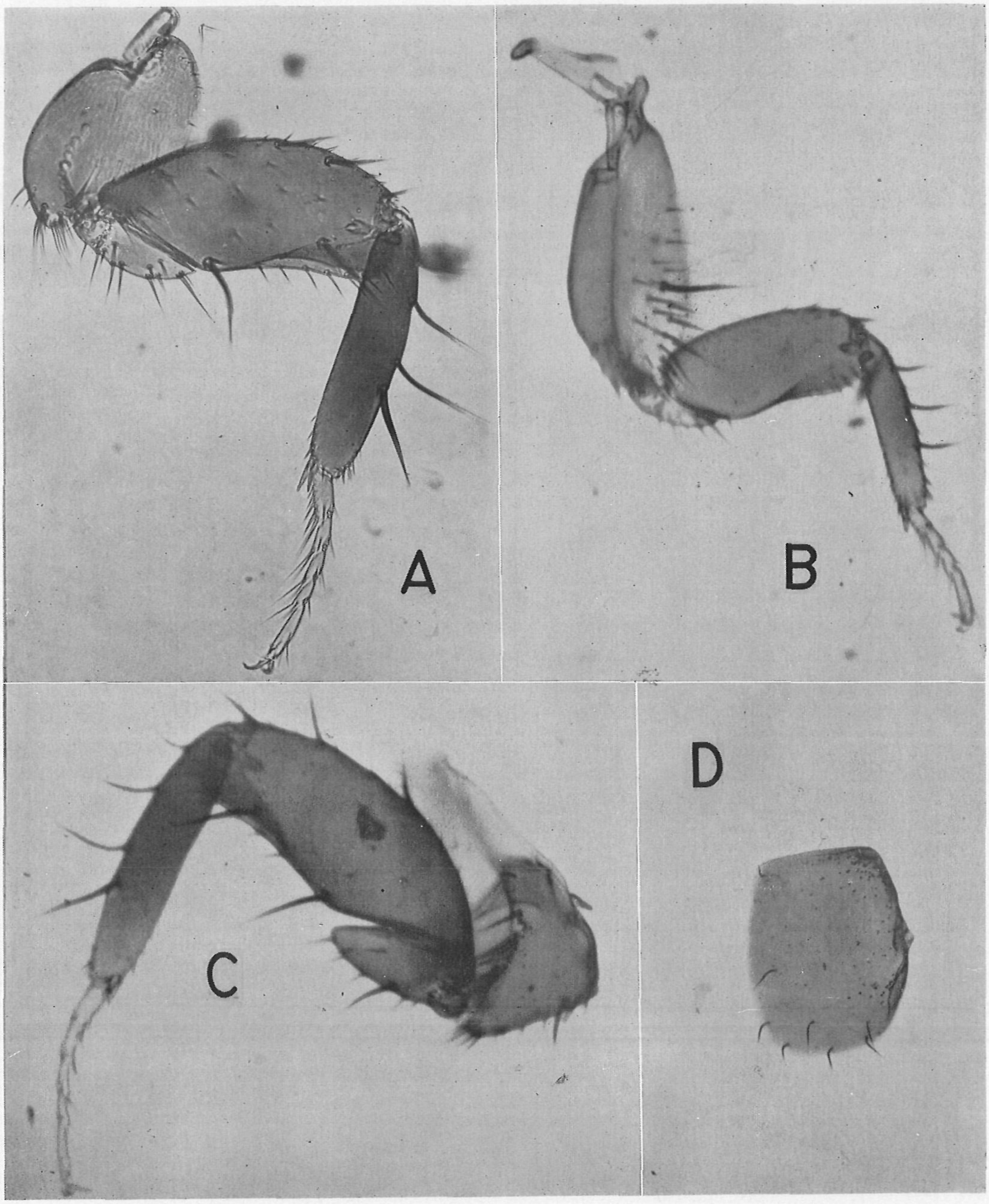


Fig. 11. *Coptolimulus calabyi*: A, mesoleg; B, proleg; C, metaleg; D, elytron. Scale arbitrary.

Measurements: Head length 0.24–0.26; head width, 0.45–0.48 pronotal length, 0.51–0.53; elytral length, 0.26–0.28 Number measured, 10.

Holotype (No. 13572), W. Australia, 69 km NNW of Galena, 23. X. 1955, J. H. Calaby & F. J. Gay, ex nest of *Coptotermes brunneus*. In the Australian National Insect Collection, Canberra. Paratypes: 38, same data as holotype (CSIRO, DK, JP).

Notes: The host was determined by Messrs. Gay and Calaby and is located in the Australian National Insect Collection, Canberra. The species is named for Mr. J. H. Calaby. The distribution of this species is shown in fig. 18.

Glandular Structures in *Coptophilus gayi*

The post-pleural glands and the tergal gland are reduced in *Coptophilus* as they are in many other termitophiles. The reduction of the post-pleural glands is moderate. Each gland possesses only about 10 to 15 cells, but the reservoir of each gland cell still has a diameter of about 11 μm (micrometer).

The usual bilobed tergal reservoir of free-living aleocharines is reduced here to 2 small reservoirs possessing a thin, non-glandular wall (fig. 16). These reservoirs are filled with a coagulate material which is not dissolved during histological preparations (fig. 12A). The gland cells themselves (about 20 cells per specimen) are not only smaller and less numerous than in free-living species, they are also somewhat atypical in that they possess an elongate secretory apparatus instead of the usual spherical one (fig. 12B).

Large and numerous gland cells form a nearly continuous subhypodermal layer under the pronotum (fig. 12C and 12D). These gland cells are believed to be derived from the type 2 cells of other aleocharines. They eliminate their secretion by a small pore in the integument, which is always located near larger sensorial pores (fig. 12E). These associations between 1 or 2 glandular pores and 1, 2, or 3 sensorial pores are responsible for the very fine punctures of the pronotum, cited in the taxonomic descriptions of this species. Some enlarged type 2 cells are also present in *Coptophilus* in the elytra. They are more abundant under tergites VII, VIII, and IX. Elsewhere they are absent or very inconspicuous.

The other elements of the primary glandular system, ie., the type 1 cells, the maxillary glands, and the articular glands, seem unmodified.

Coptophilus possesses 1 secondary glandular structure, ie., numerous type 3 cells largely distributed in the hypodermis of the entire insect. Their distribution is not uniform. They are extraordinarily abundant under the sternites (fig. 13A), the paratergites, the meso- and metasternum, and they are also numerous under the lateral valvulae of the tergite IX, and under the head capsule. On the other hand, they are rare under the tergites. They were found only laterally under the pronotum and in the elytra. Some were found also in the legs. The structure of such type 3 cells was described before for another termitophile, *Termitellodes* Seevers (Pasteels 1968b). These cells can be recognized easily by the presence of a large vacuole in each cell filled with a homogeneous secretion (fig. 13B). They do not possess a secretory apparatus like that found in types 1 and 2 cells, and their openings in the integument are of about the same size as sensorial pores. The exact structure and origin of these cells is still obscure for us. Most of them possess only a thin cytoplasm around the large vacuole, and it seems difficult to presume that important syntheses occur in such cytoplasm. We have, however, occur observed some cells (fig. 13C) with only a small amount of secretion. These cells possess cytoplasm

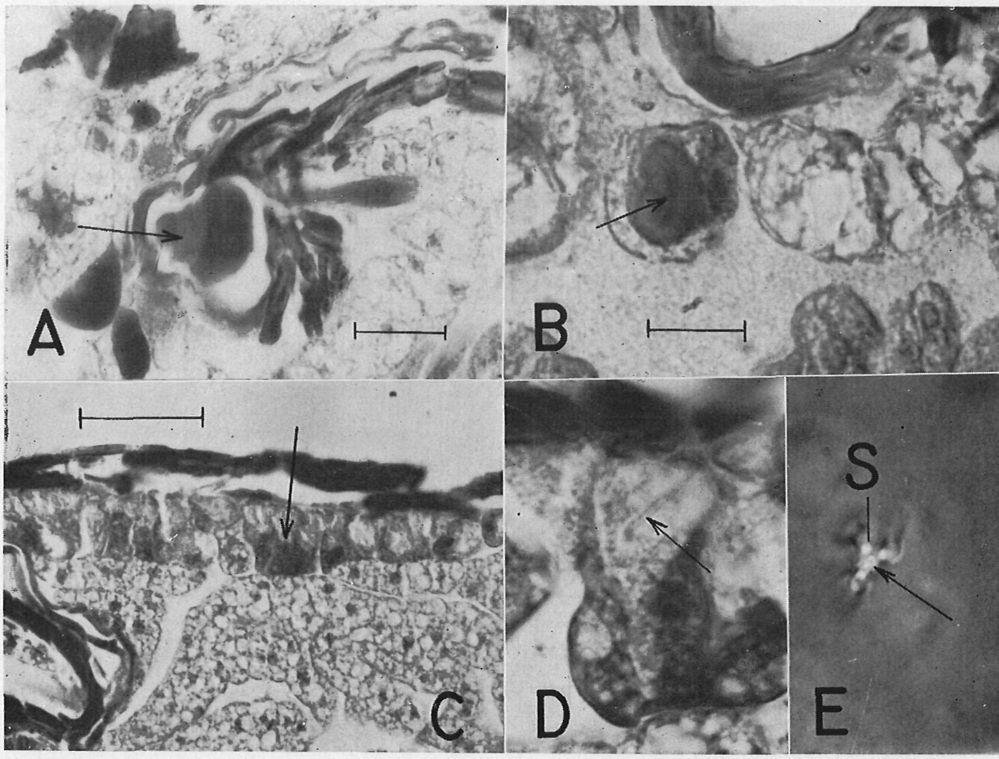


Fig. 12. *Coptophilus gayi*: Tergal gland and glandular structures associated with pronotum: A, sagittal section through reservoir of tergal gland, the arrow designates the secretion in the reservoir; B, tergal gland cell, the secretory apparatus of which is indicated by the arrow; C, large gland cells (arrow) under pronotum, sagittal section; D, detail of C, the arrow designates secretory apparatus of one of the gland cells; E, two gland pores (arrow) surround by 3 sensorial pores (S) in pronotum. All preparations were stained with azocarmin except for preparation involved in E which was cleared by KOH. Scale in A represents 20 μm. Scale in B represents 10 μm and is also valid for D and E. Scale in C represents 50 μm

which isnot distended by the secretion and it may be that synthesis occurs only at this stage. Such cells with little secretion are somewhat similar to what we believe to be trichogenic cells (fig. 13D) of campaniform sensillae, and are perhaps derived from them. It would not be the first time that trichogenic cells have evolved into exocrine glands, [ie., the paper by Grassé & Lesperon (1938)]. But this remains for the moment a guess which might be resolved through the use of an electron microscope.

Glandular Structures in *Coptotermoecia*

Two species were studied, *C. seeversi* and *C. pilosa*, with nearly similar results. The following description will be valid for both species unless otherwise specified.

The post-pleural glands of *C. pilosa* show only a moderate reduction (number of cells, about 20–25; diameter of cell reservoir, about 12 μm), but those of *C. seeversi* are much

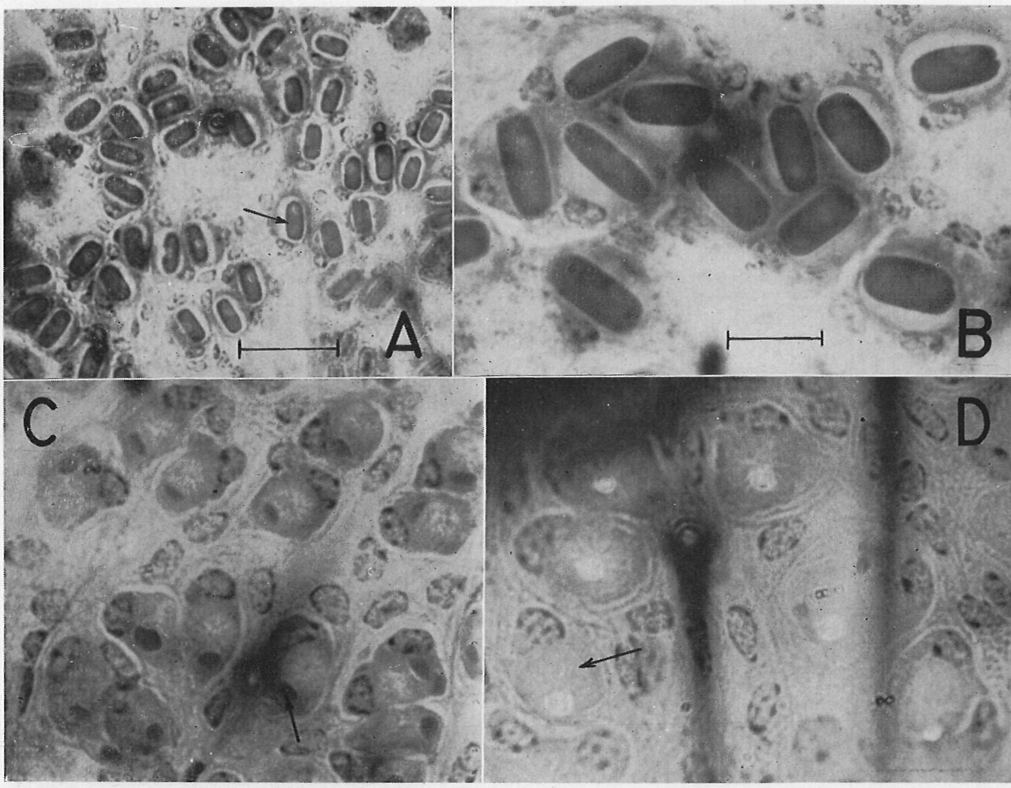


Fig. 13. *Coptophilus gayi*: Type 3 cells and possible trichogenous cells of campaniform sensillae in sternite IV: A, low magnification showing abundance of type 3 cells (arrow) in the hypodermis; B, high magnification of type 3 cells, the homogenous secretion is within the vacuole, the pores are out of focus; C, type 3 cells with a small amount of secretion (arrow) close to the vacuole, the pores are out of focus; D, possible trichogenous cells (arrow) of campaniform sensilla. "In toto" preparations stained by alcoholic hematoxylin, phloxin, light green. Scale in A represents 25 μm. Scale in B represents 10 μm and is valid also for C and D.

more reduced, possessing only a few cells close to the sternite of abdominal segment VIII.

The tergal reservoir is highly reduced in size (fig. 16), but its wall is thick and is composed of an epithelium of tall cells covered with a thin cuticle (fig. 14A and 14B). This thick epithelium is similar to the posteroventral wall of the defense reservoir of free-living species. The gland cells of the tergal gland are not reduced in this genus, but instead are highly modified. They are large and closely packed together in a thin layer located under the reservoir (fig. 14C). We have counted about 30 of those cells in *C. pilosa*. In the same species, their cytoplasm appears divided in irregular fibers and filaments (fig. 14D), but this may be due to the fixation. Each cell possesses an elongate secretory apparatus. This cell structure contrasts greatly with the usual cytology of the defense gland cells, illustrated recently for some free-living species and some termito-

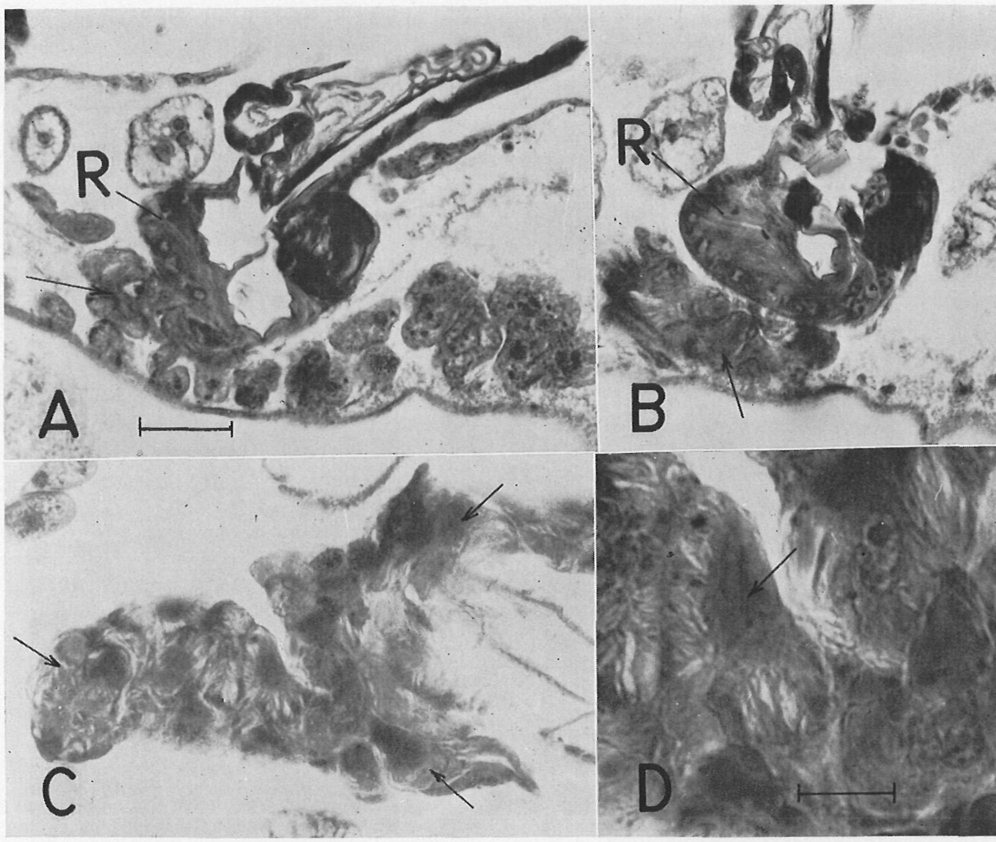


Fig. 14. *Coptotermoecia pilosa*: Tergal gland: A and B, sagittal sections, the arrow designates gland cells situated underneath reservoir, the wall of the reservoir is made of tall cells (R); C, frontal section through gland cells grouped in well-developed glandular tissue (limited by the arrows); D, high magnification of C, showing straight secretory apparatus (arrow) of 1 gland cell. Azocarmin. Scale in fig. A represents 20 μm and applies to fig. A–C. Scale in fig. D represents 10 μm.

philes by Pasteels (1968a, 1969) and by Kistner & Pasteels (1969).

Gland cells are even more abundant under the pronotum of *Coptotermoecia* than in *Coptophilus* (fig. 15A and 15B). These large cells reach the heavy punctures of the integument characteristic of this genus. The punctures of the pronotum of *C. seeversi* are the results of the grouping of 1–7 gland pores, 2–5 sensorial pores, and a very small seta (fig. 15C). In *C. pilosa*, each puncture is a little depression of the integument surrounded by 2–5 sensorial pores (fig. 15D). From 2 to 6 gland cells reach the bottom of each of these small depressions (fig. 15E), via their canaliculi.

The rest of the primary glandular system is unmodified in *Coptotermoecia*, and no secondary formations were found. The type 2 gland cells are distributed as usual and small; they do not show the modifications described for *Coptophilus*, except of course under the pronotum. Females possess vaginal glands similar to those described for *Skati-*

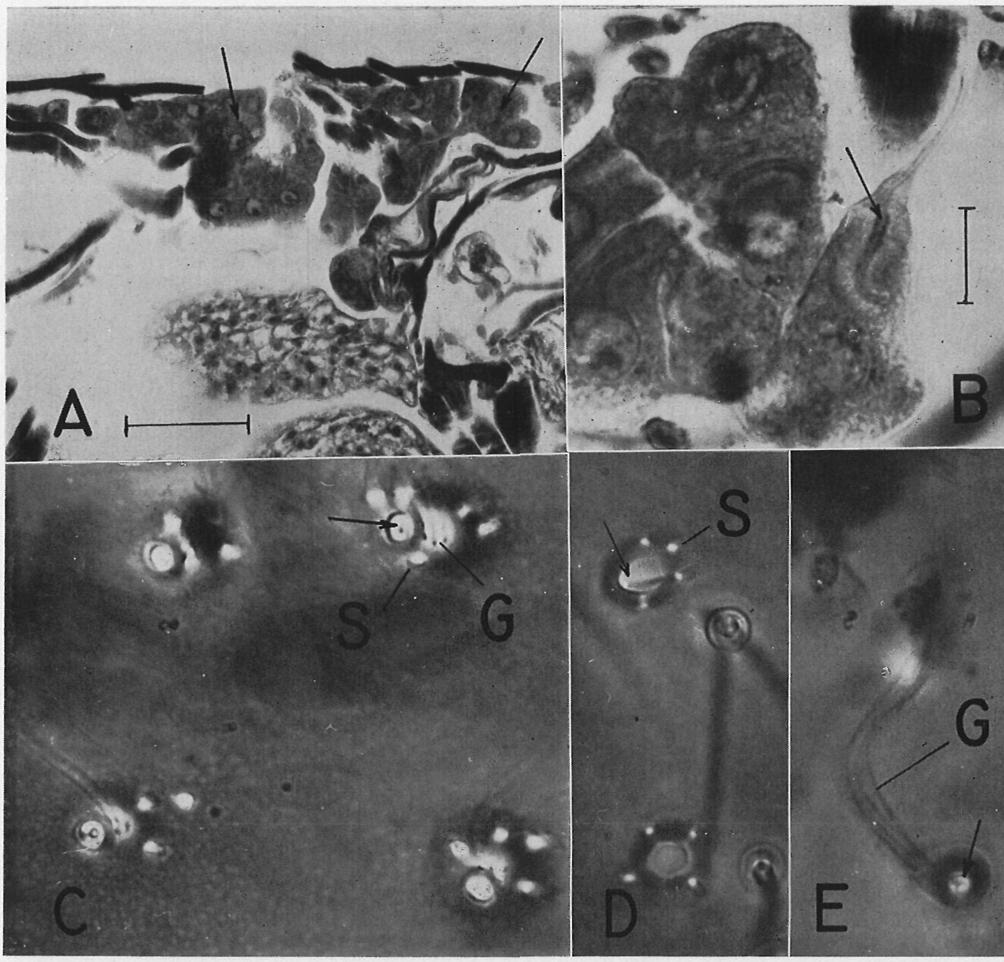


Fig. 15. *Coptotermoecia*: Glandular structures of pronotum: A, sagittal section through the pronotum of *C. pilosa*, the arrows designate the numerous gland cells; B, detail of gland cells situated underneath pronotum of *C. pilosa*, the arrow indicates the secretory apparatus; C, high magnification of 4 punctures of pronotum of *C. seeversi*, each puncture is the result of the grouping of several small gland pores (G), several large sensorial pores (S), and a small seta, the base of which is designated by the arrow; D, punctures of pronotum in *C. pilosa* which consist of a depression of the integument (arrow) surrounded by several sensorial pores (S); E, several glandular canaliculi (G) reach the bottom of the depression of a puncture in the pronotum of *C. pilosa*, the sensorial pores are out of focus. Preparations involved in fig. A and B were stained with azocarmin. Preparations involved in fig. C and D were cleared with KOH. The preparation involved in fig. E was stained with alcoholic hematoxylin. Scale in A represents 50μm. Scale in B represents 10 μm and applies to fig. B-E.

toxenus (Kistner & Pasteels 1969).

Discussion of the Histological Results

The reduction of the tergal gland and the post-pleural gland is a common feature in termitophilous aleocharines. Such a reduction was found previously in 6 independently evolved groups of termitophiles (Pasteels 1968a, 1968b, 1969; Kistner & Pasteels 1969, 1970). The reduced tergal reservoir is usually single, but double in *Skatitoxenus* (Kistner & Pasteels 1969) and in *Coptophilus*. Modification of the cytological structure of the tergal gland cells themselves is rather rare and was found previously in only *Nasutitella* Pasteels (Pasteels 1968b). Usually the modifications of the tergal glands are more or less consistent in 1 group of termitophiles, and the very different structures of the tergal glands in *Coptophilus* and in *Coptotermoecia* do not favor a very close relationship between these genera. During their evolution, the tergal glands of these termitophiles most probably lose their original defense functions. The reduced reservoirs seem too small to contain enough substances to repel an enemy with efficiency. But neither in *Coptotermoecia* nor in *Coptophilus* do these glands seem inactive and so they perhaps serve another function.

Both the type 3 cells of *Coptophilus* and the gland cells of the pronotum of *Coptophilus* and *Coptotermoecia* are very specialized structures probably related to their life in termite nests. The type 3 cells found in *Coptophilus* have evolved independently in some Termitogastrina (Pasteels 1968b), and in some Pseudoperinthini (Kistner & Pasteels 1970). However, the development of gland cells under the pronotum is an unusual feature so far found only in *Coptotermoecia* and in *Coptophilus*. This favors a close affinity between these genera. The close association of 1 gland pore and 1 or several sensorial pores is commonly found in either termitophiles or in free-living species. It is tempting to speculate that the large punctures of the pronotum of *Coptotermoecia* have evolved from

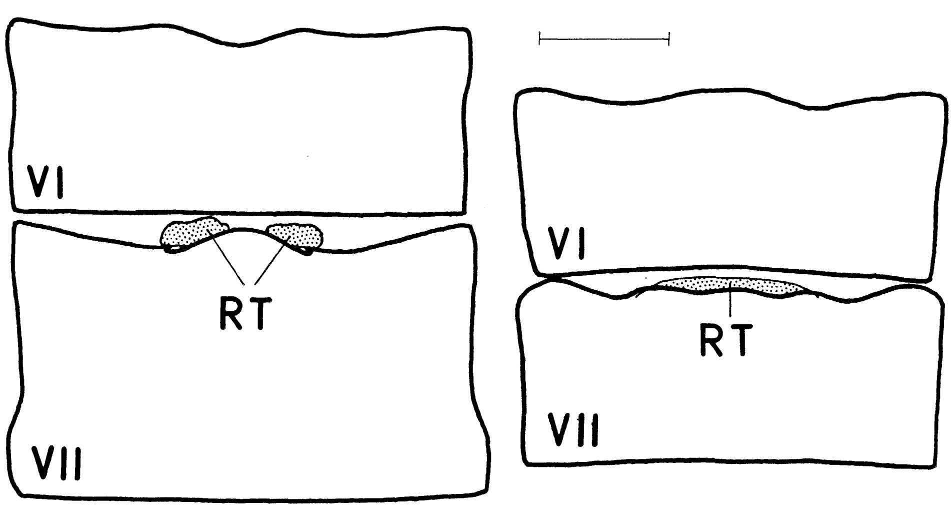


Fig. 16. Schematic representation of tergite VI, tergite VII and the tergal gland reservoir (RT) in *Coptophilus gayi* (left) and *Coptotermoecia seeversi* (right). Scale represents 0.25 mm.

such associations. *Coptophilus* would be, in this respect, at an intermediate stage between free-living species and *Coptotermoecia*.

Thus this study of the glands has given results showing relationships between *Coptophilus* and *Coptotermoecia*, which confirm relationships derived from the overall morphology of the beetles. This study strongly suggests that both genera may be well integrated into the social life of their hosts and that structures like the gland cells of the pronotum and the type 3 cells could act during their interactions with the termites. These termitophiles could prove to be excellent subjects for experimentation since they are usually found in abundance in *Coptotermes* nests (Gay, personal communication) near well-equipped laboratories.

Relationships of the genera and species

The relationships between all the species in this study were analyzed numerically. A list of unit characters was developed following the general outline of Sokal & Sneath (1963). This list of 36 characters is presented in Table I. All of the species included in this study with the exception of *Coptotermoecia alutacia* Oke were then coded for the presence or absence of these characters in Table I. If the character was present, it was coded 1. If the character was absent, it was coded 0. If there was no comparison, it was coded 3. No comparisons arose in this study if a character which was present

Table I. List of characters used for numerical analysis.

1. Antenna with 2nd segment equal in length to 3rd.
2. Gula with sides approximately parallel.
3. Mandibles asymmetrical.
4. Mandibles with mandibular teeth.
5. Lacinia with more than 1 line of spines.
6. Maxillary acetabulae margined.
7. Mentum always fused to submentum.
8. Labrum with anterior corners rounded.
9. Pronotum smooth.
10. Pronotum with anterior margin straight.
11. Pronotum with posterior margin rounded.
12. Prosternum with a blunt median longitudinal carina.
13. Length of metasternum 2 $\times$ that of mesosternum.
14. Sternepimeron with apical portion elongate.
15. 1st segment of meso- and metatarsi shorter than 2nd.
16. Abdomen moderately physogastric.
17. Abdominal tergite II with short lateral processes.
18. Inner paratergites wider than the outers.
19. Tergite IX as in fig. 2G.
20. Pronotum shorter than 0.43 mm.
21. Lateral lobe of ♂ genitalia with extra membrane medially.
22. Median lobe of ♂ genitalia with an anterior ventral carina.
23. Tergites III-VI with an anteapical row of setae.
24. Lateral setae on elytra numerous and long.
25. Mesocoxal acetabulae incompletely margined.
26. Pronotum with about 20 setae.
27. Tergites III-VI with 6 apical setae.
28. Tergite VII with 8 apical setae.
29. Color dark reddish brown.
30. maxillae with stout palpi, as in fig. 8G.
31. 1st segment of meso- and metatarsi slightly longer than 2nd.
32. Head capsule broadly semicircular in shape.
33. Antennae flat.
34. Pronotum overlaps head in part.
35. Sternepimeron shaped like an isosceles triangle.
36. Sternites with paler setae

in only 1 sex was specified and specimens of only the opposite sex were present. *C. alutacia* Oke was not coded because material that could be dissected was not available for study. (It may be placed in the resulting dendrogram very near to *C. flava*).

The results of coding the 36 characters for the 8 species are given in Table II. These data were then punched onto cards and 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).

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

Species No.	Species	Characters					
1	*Coptophilus greavesi*	111110	111111	101111	111010	110010	000001
2	*C. gayi*	111110	111111	101111	101011	110010	000001
3	*Coptotermoecia seeversi*	110000	000111	110100	011100	111110	000000
4	*C. flava*	110000	000111	110100	011100	101000	000001
5	*C. pilosa*	110000	000111	110100	011100	100010	000001
6	*C. robusta*	110000	000111	110100	013300	111110	000001
7	*Philobrunneus gayi*	010000	110101	000001	000100	101011	100010
8	*Coptolimulus calabyi*	000011	111010	010010	000000	011010	111100

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

Species No.	1	2	3	4	5	6	7
2	.944						
3	.556	.500					
4	.556	.500	.889				
5	.611	.556	.889	.944			
6	.588	.529	.971	.912	.912		
7	.417	.417	.583	.583	.583	.559	
8	.361	.361	.417	.361	.361	.412	.500

The results of these analyses are presented in fig. 17. Only the matrix values for the various clustering cycles where groups join are shown.

Reference to fig. 17, reveals first of all that species of the same genera clustered out nicely with each other and that the genus *Coptophilus* is related to the *Coptotermoecia-Philobrunneus* group rather distantly and that *Coptolimulus* is the most distantly related genus of the lot.

Coptophilus is thought to be the most primitive genus because it has a relatively elongate body with little physogastry, a body form strongly reminiscent of *Atheta* and its allies. *Philobrunneus* is a large-sized, partially limuloid genus which is clearly related through similar punctation and other structures to *Coptotermoecia*. These two genera

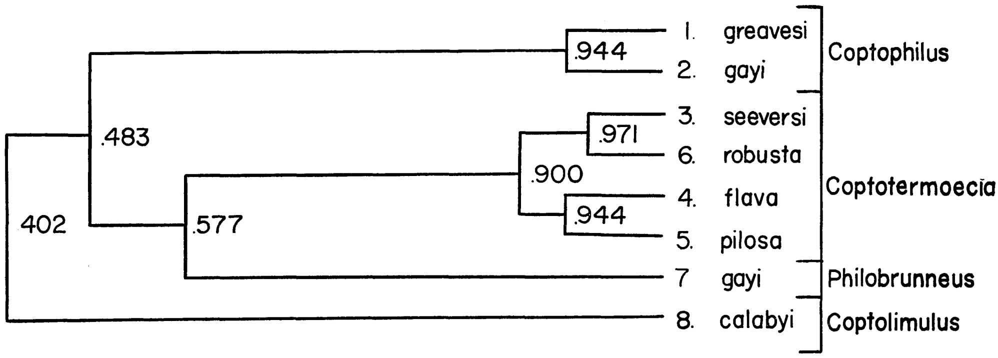


Fig. 17. Dendrogram showing relationships between all the species of the *Coptotermoeciina* except *C. alutacia.*

were probably derived from the *Coptophilus* stock at an early time in its evolutionary history. *Coptotermoecia* then developed moderate abdominal physogastry. *Coptolimulus* is a limuloid form related by the shape of abdominal segment IX to *Philobrunneus.* Also related to *Coptophilus* by the absence of specialized punctation on the pronotum. This genus is otherwise the most structurally complex genus of the group. It is also a clearly limuloid genus. Thus, in this small subtribe we have once again the derivation of a physogastric line and a limuloid line from 1 original invasion of a termite nest. This same type of adaptive radiation has developed convergently many times in the Staphylinidae.

Host relationships

All of the species reported here are host-specific at the species level. A summary of the host relationships is given by termite host in Table IV. The host *Coptotermes acinaciformis* subspecies *raffrayi* is preceded by a "?" because it is not known for certain that this is the true host for the 2 species listed for it.

If we make the assumption that the rates of evolution of the termite hosts and of the termitophiles are proportional then we should be able to predict the relationships of the

Table IV. Summary of host relationships by termite host.

Host termite	Termitophile
Coptotermes acinaciformis (Froggatt)	*Coptotermoecia alutacia*
	Coptotermoecia pilosa
?Coptotermes acinaciformis ssp. *raffrayi* Wasmann	*Coptotermoecia flava*
	Coptotermoecia robusta
Coptotermes brunneus Gay	*Philobrunneus gayi*
	Copotolimulus calabyi
Coptotermes frenchi Hill	*Coptophilus greavesi*
Coptotermes lacteus (Froggatt)	*Coptotermoecia seeversi*
	Coptophilus gayi

termites by the relationships of the termitophiles. Referring back to fig. 17 we would then predict that *Coptotermes frenchi* is more closely related to *C. lacteus* than to *C. acinaciformis* (s. lat.). We would also predict that *C. acinaciformis* subsp. *raffrayi* is closer to *C. acinaciformis* than to *C. lacteus*, because *Coptotermoecia alutacia* is closer to *Coptotermoecia flava* than to the rest of the species. (This had to be placed by hand because there was no dissection material available.) We could also predict that *C. brunneus* is a very distinctive species compared to the other Australian species of the genus. We wrote to F. J. Gay about these predictions and he stated that (personal communication), "In fact, the relationships which you have been able to deduce are a perfect match for those we have established solely on the basis of the termites themselves."

Prior to analyzing the relationships between these species numerically, we drew up a phylogenetic tree of the genera according to traditional methods, and this phylogenetic tree of the genera is exactly the same as that which was derived by numerical methods. The fact that we can get relationships between the species is an added feature of the numerical method. The ability to derive relationships between termitophiles that parallel those of the termites which are predicted by different people using different data and different methods, we think shows that biologically meaningful relationships can be derived by these computer methods.

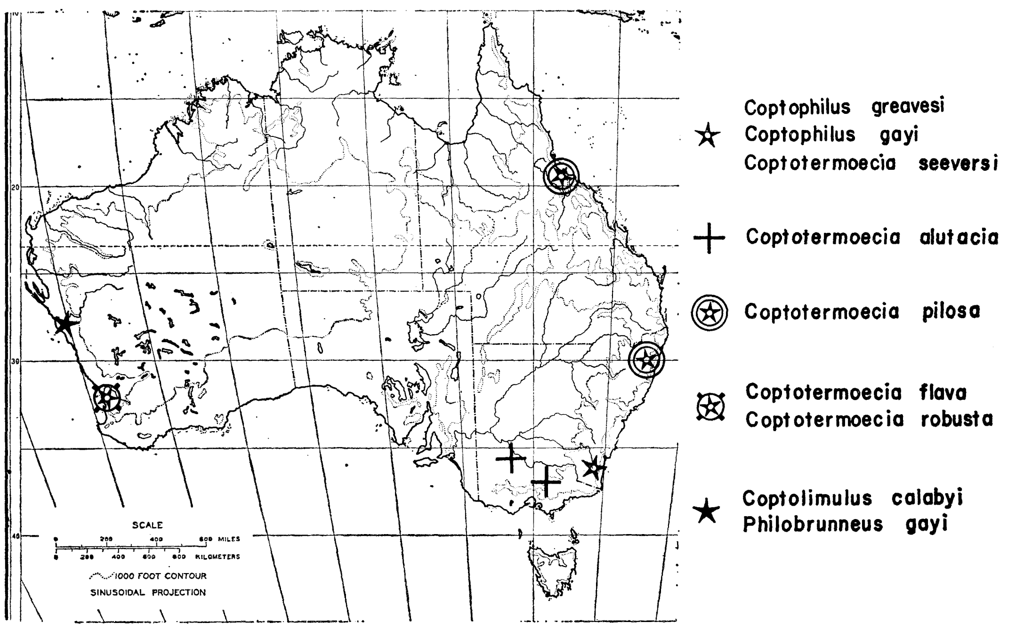


Fig. 18. Distribution of the *Coptotermoeciina*.

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