A Revision of the Termitophilous Tribe Termitodiscini (Coleoptera: Staphylinidae) Part I. The Genus *Termitodiscus* Wasmann; its Systematics, Phylogeny, and Behavior[1]

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Abstract: The genus *Termitodiscus* Wasmann is redescribed, illustrated, and a key differentiating this genus from the other two genera of the tribe is provided. All of the previously described species of the genus are redescribed and new characters illustrated. Six new species are herein described, *T.* **coatoni** from South Africa, *T.* **emersoni** from the Congo Republic, *T.* **krishnai** from Burma, *T.* **latericius** from South Africa, *T.* **sheasbyi** from Southwest Africa and *T.* **vansomereni** from Kenya. Distribution maps are presented which show the distribution of all species. Diagrams are presented showing the relationships among the species using both the phylogenetic and the phenetic approach. A summary of the host relationships is presented showing 100% host specificity to species of *Odontotermes* of the species now known. Observations on the behavior and distribution of selected species within the nests are presented which support the interpretation of the species as integrated termite guests whose principal adaptation to life within the nest is that of avoidance. The relationship of the tribe Termitodiscini with the Myrmedoniini is documented and discussed.

INTRODUCTION AND TAXONOMIC HISTORY

The termitophilous tribe Termitodiscini was reorganized as a tribe of the subfamily Aleocharinae by Seevers (1957) to contain the genera *Termitodiscus* Wasmann, *Termitogerrus* Bernhauer, and *Discoxenus* Wasmann. Prior to Seevers' revision, the group had been recognized as a separate subfamily of the Staphylinidae. I here concur with Seevers' judgment that there is no character or group of characters which could separate them absolutely as a subfamily distinct from the Aleocharinae. I shall show that the group probably arose from some free-living or loosely integrated termitophile of the aleocharine tribe Myrmedoniini. Seevers did not attempt to revise the species due to the paucity of material available. Since that time, a lot of new material has been collected due to the field efforts of Dr. William Coaton and his colleagues of the Plant Protection Research Institute, Pretoria; Dr. Alfred E. Emerson, University of Chicago; Dr. Kumar Krishna, American Museum of Natural History, New York; Dr. A. de Barros Machado and his colleagues, Museu do Dundo, and myself. Most of the new material belongs to the genus *Termitodiscus*, so that this revision is confined to that

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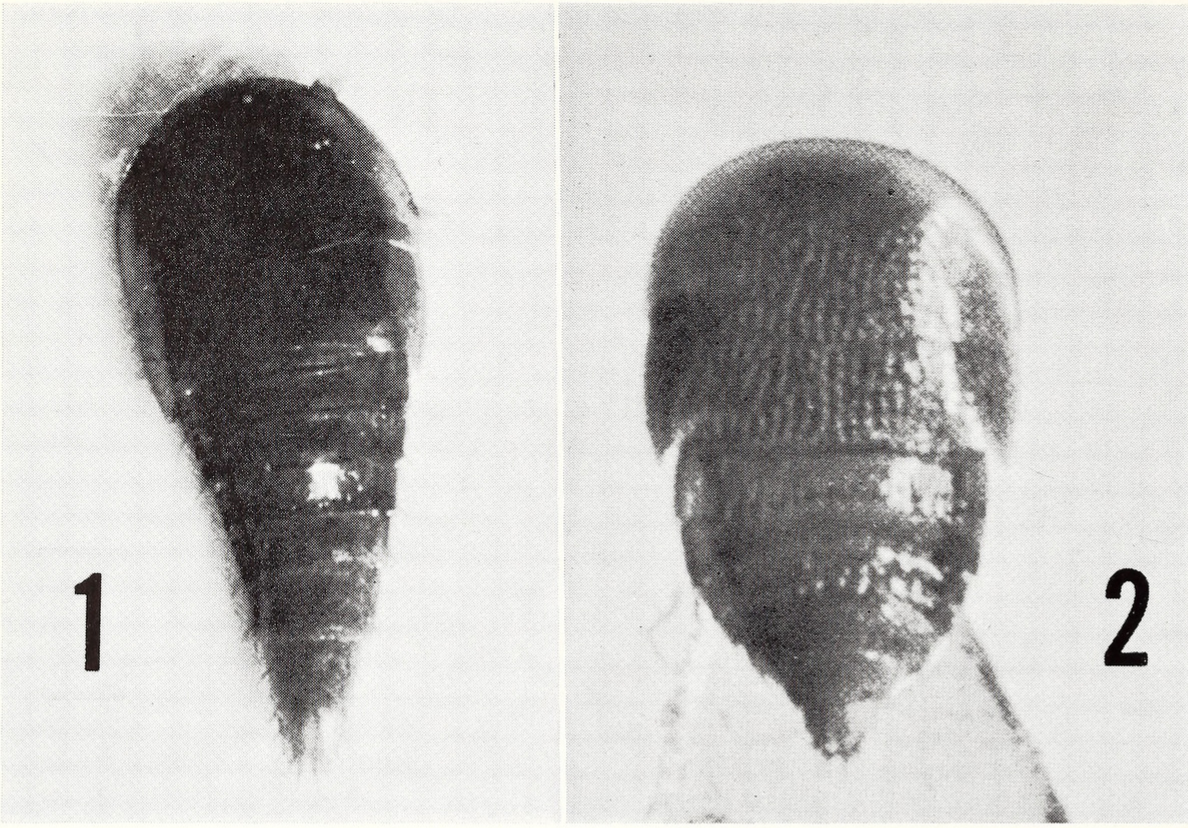
genus and revision of the other two genera will be deferred until a reasonable amount of new material becomes available. The careful study of new material has revealed characteristics which make it necessary that the key to the genera provided by Seevers be revised and this is done here. While collecting *Termitodiscus* in the field, various observations were made on their behavior, particularly in relation to their termite hosts, which bear on the integration of the termitophiles into the termite colonies. These observations and their interpretation are presented in this paper. The remainder is organized into the following sections: (1) Methods and materials; (2) Key to the genera of the tribe; (3) Redescription of the genus; (4) Key to species; (5) Descriptions of the species; (6) Relationships of the species; (7) Behavorial observations; (8) Host specificity; (9) Relationship of the tribe to the aleocharine tribe Myrmedoniini; (10) Acknowledgments; (11) Literature cited.

METHODS AND MATERIALS

Most of the routine methods used in my laboratory have been described several times, most recently by Koblick and Kistner, 1965, and Kistner, 1966. The only major change has been the substitution of a Nikon F camera with 55 mm, 50 mm, 35 mm, and 28 mm lenses plus bellows and extension tubes for the Exacta equipment used in the past. For ultra close-up photos of minute insects, this has proven superior because the corners are not chopped off the pictures and the lenses are easier to reverse to eliminate spherical aberration.

The special techniques involved in the computer analysis of the relationships between the species are discussed later. The programs themselves are not included as most laboratories have developed their own and our programs are changed just about every time we use them. Current print-outs in Fortran II will be sent to anyone requesting them.

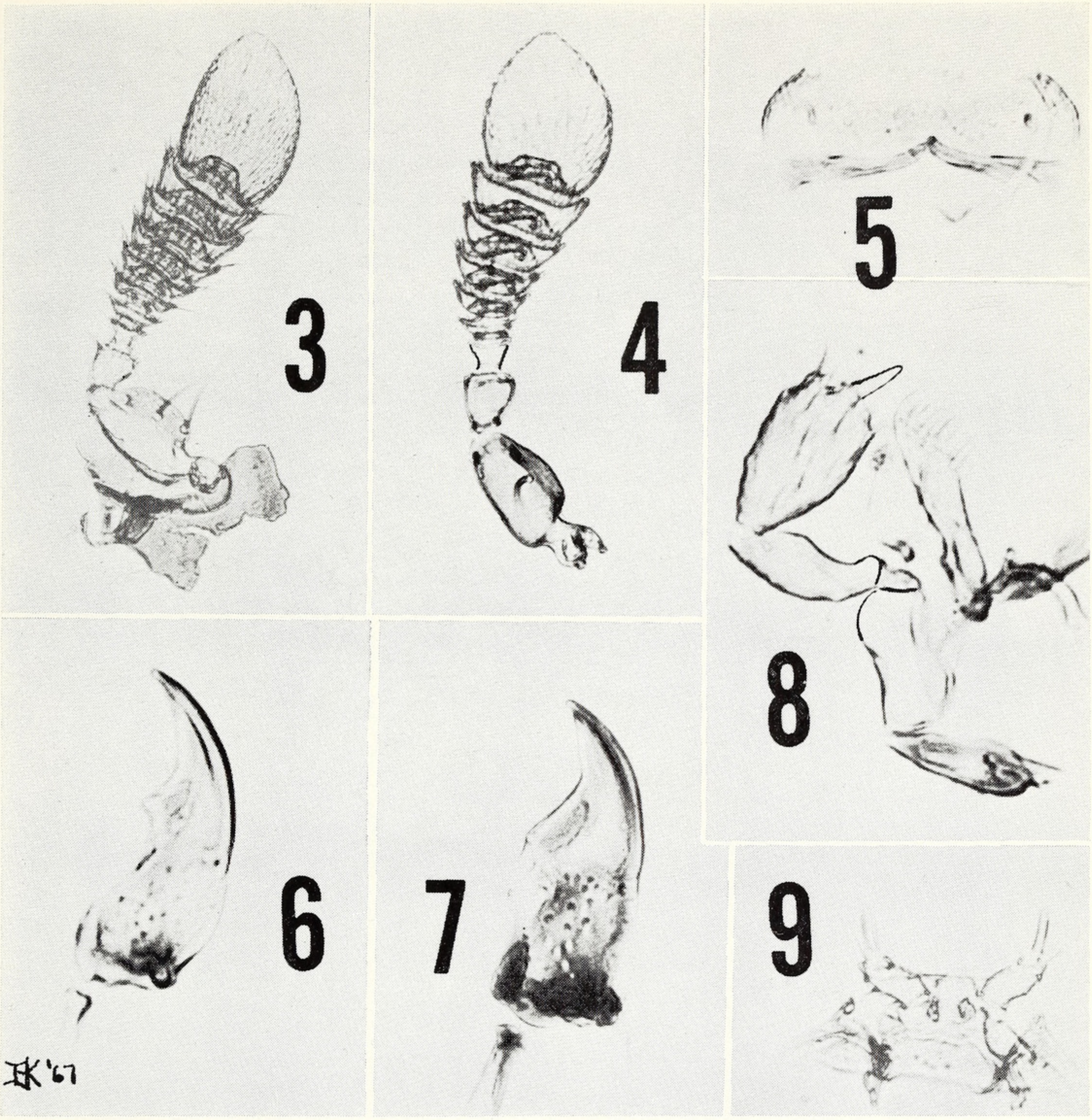
The field techniques used vary according to the way in which the *Odontotermes* hosts make their nests. Some species such as *Odontotermes taprobanes* Walker and *Odontotermes culturarum* Sjoestedt make well defined nests of which the bulk is located above the level of the surrounding ground. The queens are usually located at or near the ground level with the fungus gardens arranged in semispherical layers above the royal cell. The fungus gardens immediately above the royal cell usually yield the most specimens of *Termitodiscus*, but the other fungus combs may yield *Termitodiscus* or other species of associated insects. We try to keep the layers separate as we dig in, but individual idiosyncracies of the nests prevent absolute accuracy. The fungus gardens are removed and taken back to the laboratory or other dwelling where the fungus is carefully pulverized over a yellow plastic tray. The yellow contrasts well with the termites and the termitophiles and permits the investigator to see the termitophiles and to aspirate them up or to pick them up with a camel's hair brush. It takes about 4 to 5 times as long to sort through the fungus gardens of



Figs. 1–2. Overall appearance of dorsal surface of beetle: 1. *Termitodiscus braunsi* Wasmann; 2. *T. escherichi* Wasmann, Cotype. Scale arbitrary, see descriptions for measurements.

a productive nest than to dig it up, so it pays to at least assay the fungus in the field before taking it back. Unless collecting is extremely poor in general, I usually abandon a nest if I don't see at least a few specimens of termitophiles during the field assay.

Other species of termites such as *Odontotermes montanus* Harris or *Odontotermes transvaalensis* Sjoestedt build nests which are completely or almost completely submerged under the ground, often with little evidence on the surface of their position. Working with such nests can be extremely productive but is often extremely frustrating because a sizable investment of time and labor has to be made before one can tell if there are any termitophiles there or not, or even if the nest is there or not. The procedure we used and which is also used by Dr. Coaton and his colleagues is to dig a trench about 4 feet wide, 6 feet long and 4 feet deep to the side of where you think the nest is. Then dig in toward the nest from the side until you (hopefully) hit it. If you dig in from the top, you eventually fall into the nest which complicates the sorting process and partially destroys the ecological data. After you reach the fungus gardens, the fungus is gathered and sorted as above. I might add that I have dug until I could not throw the dirt out of the hole over my head and still not reached the nest, so I usually keep an open mind about abandoning a hole if nothing shows up quickly. A gung-ho attitude of, "I'm going to find that nest if

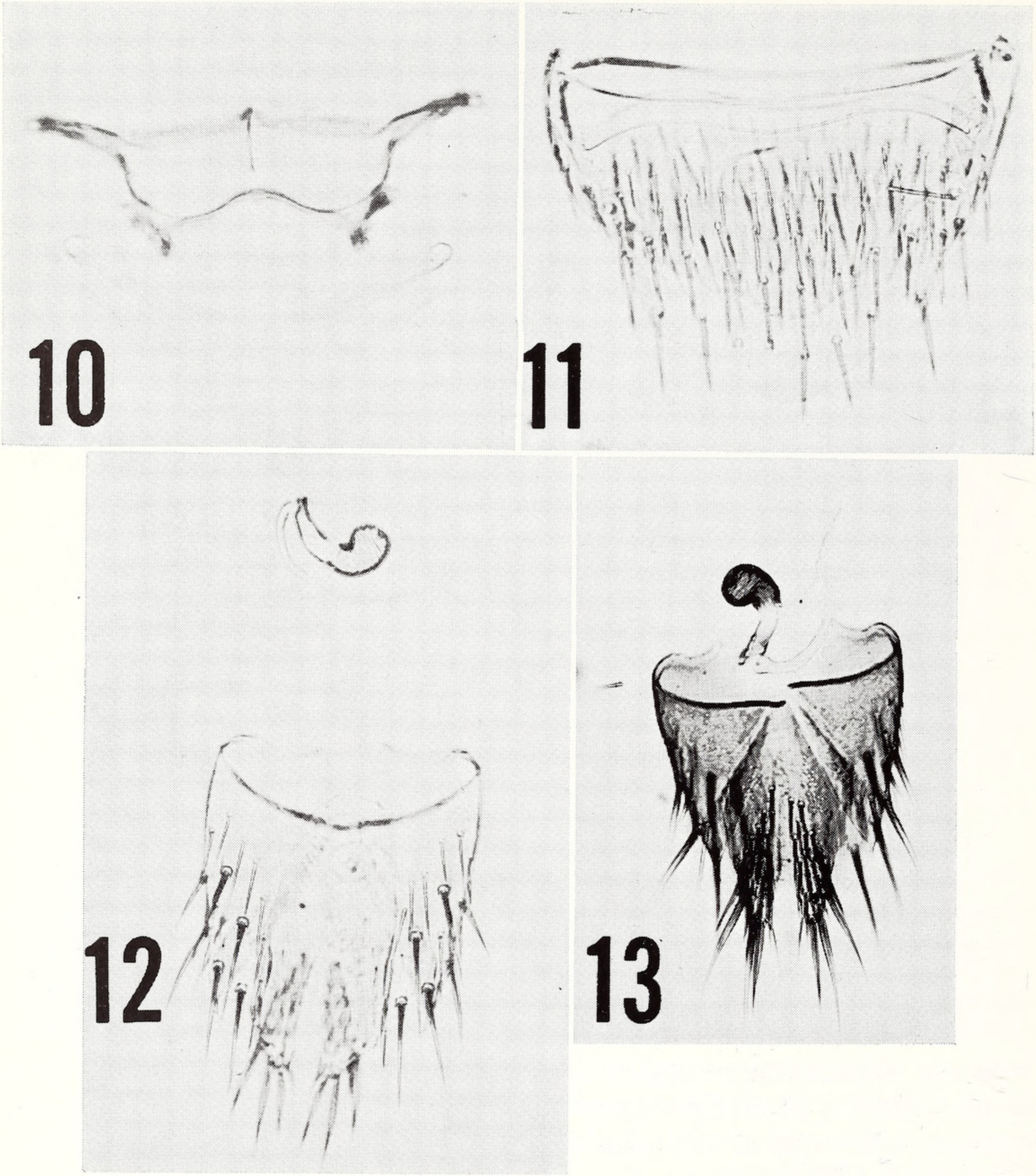


Figs. 3–9. Antennae and mouthparts: *Termitodiscus escherichi* Wasmann: 3. 10-segmented antenna; 8. Maxilla; 9. Labrum and mentum. *T. angolae* Seevers: 6. Mandible. *T. machadoi* Seevers: 4. 9-segmented antenna; 5. Labrum; 7. Mandible. Scale arbitrary, photos were taken at 100 × magnification.

it kills me," (my original attitude) just will not make economic sense in the long run. It is thus more productive to abandon a potentially dry hole while the investment in time and labor is still minimal and put that time and labor into another potential nest. The judgment necessary to make that decision came hard for us and is still based on so many subjective factors that finding the nests and then the termitophiles is still in the realm of art rather than science.

KEY TO THE GENERA OF THE TRIBE

1. Mesocoxae widely separated; antennae 9, 10, or 11 segmented, short, very slightly visible from above; antennae segments other than 1 and 2 compressed and incrassate 2

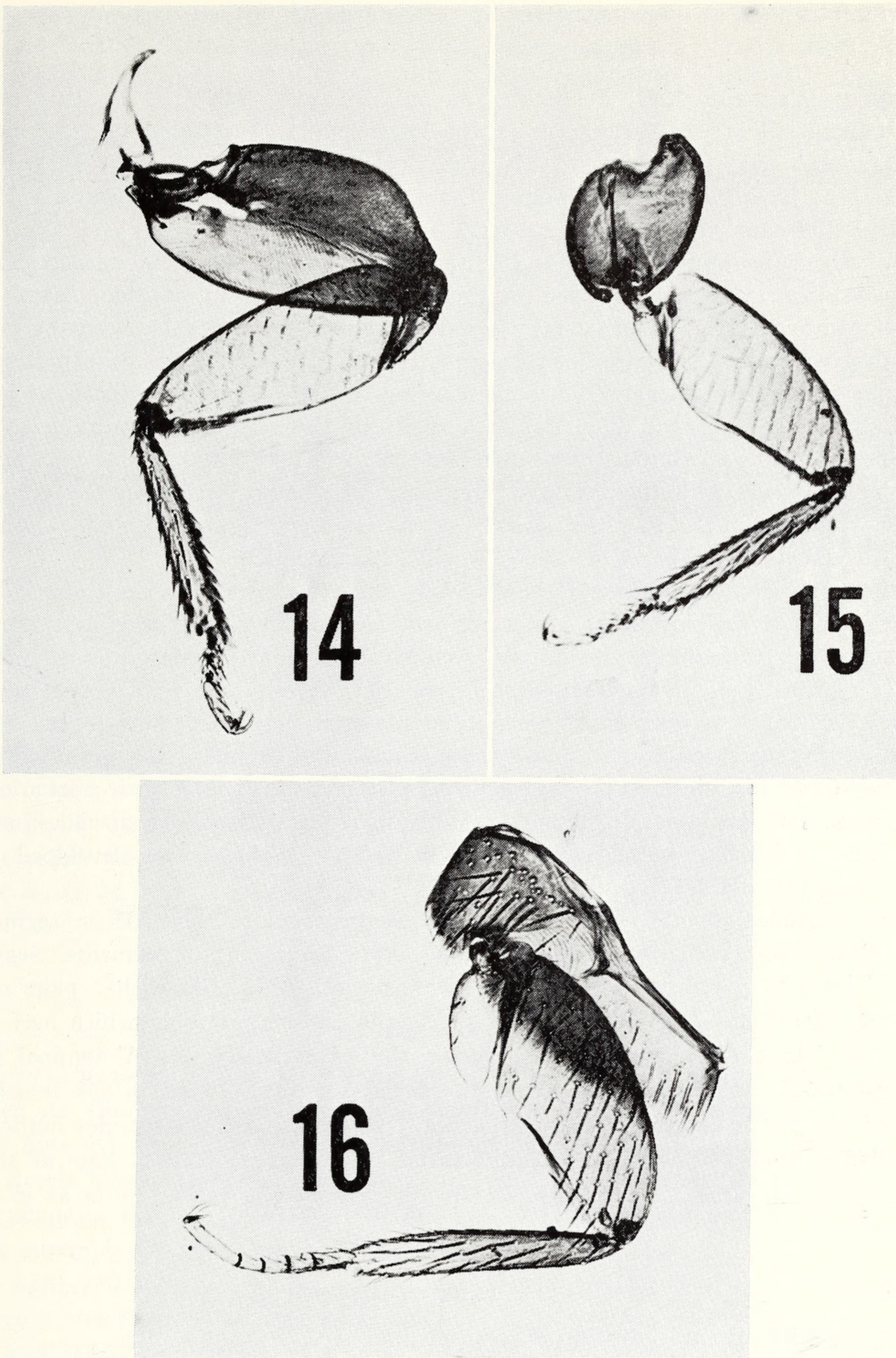


FIGS. 10–13. *Termitodiscus escherichi* Wasmann: 10. Prosternum and mesothoracic peritremes; 11. Abdominal segment VIII; 12. Abdominal segment IX and spermatheca. *T. transvaalensis* Silvestri: 13. Abdominal segment IX and spermatheca. Scale arbitrary, photos taken at 100 × magnification.

Mesocoxae narrowly separated; antennae 11-segmented, elongated, easily visible from above; antennal segments 3-11 with the sides meeting each other and covering the petiolar connections .... *Discoxenus* Wasmann

2. Antennae 9 or 10-segmented; antero-lateral margin of pronotum slightly flared; mesosternum slightly declivous in middle .... *Termitodiscus* Wasmann

Antenna 11-segmented; antero-lateral margin of pronotum not flared; mesosternum almost vertical at the middle and thus scarcely visible from below .... *Termitogerrus* Bernhauer



FIGS. 14–16. Legs of *Termitodiscus transvaalensis* Silvestri; 14. Proleg; 15. Mesoleg; 16. Metaleg. Scale arbitrary but equal for all legs; photos taken at 100 × magnification.

NOTE: *Termitogerrus* seems to be confined to Central and West Africa as careful searches of *Macrotermes* nests in South Africa and the Orient have not revealed this genus so far. *Discoxenus* has only shown up in *Odontotermes* nests from the Orient in spite of careful searches of *Odontotermes* nests in Africa. The revision of these two genera will be delayed until there are far more new specimens available for study.

REDESCRIPTION OF THE GENUS

Genus *Termitodiscus* Wasmann

Termitodiscus Wasmann 1899, Deutsch. Entomol. Zeitschr., **1899:** 147; 1912, Zeitschr. Wissensch. Zool., **101:** 92; 1916, Zool. Jahrb. System., **39:** 179; Cameron, 1932, Fauna of Brit. India, Staph., **3:** 317; Silvestri, 1947, Arch. Zool. Ital., **31:** 125; Seevers, 1957, Fieldiana Zool., **40:** 259; 1965, Publ. cult. Companh. Diam. Angola, **69:** 129. Type species: *Termitodiscus heimi* Wasmann (Blackwelder, 1952: 377).

Overall body shape limuloid, broad and flat as in figs. 1 and 2. Head broad and short, subtriangular in form with the foramen magnum totally ventral in position. Eyes present, well developed and forward and laterally directed. Antennae inserted between the eyes with grooves developed on the genae for the reception of the large basal antennal segments. Submentum and gula extremely short. Antennae 9 or 10-segmented, shaped as in fig. 3 and 4. Labrum short, shaped as in fig. 5. Mandibular shape somewhat variable by species but the form is relatively constant, two extremes shown in figs. 6 and 7, note the one central and one apical tooth with the short stubby prostheca (barely visible in the photographs below the central tooth). Maxillae shaped as in fig. 8, palpi 4-segmented. Labium and mentum extremely small, shaped as in fig. 9, palpi 3-segmented.

Pronotum semi-circular in shape (figs. 1 and 2) such that there is no distinction between anterior and lateral margins which are henceforth referred to as the anterolateral margins. Prosternum small, carinate in the middle, shaped as in fig. 10. Mesothoracic peritremes reduced in size but present and shaped as in fig. 10. Mesosternum and metasternum both short, metasternum somewhat shorter than the mesosternum. Mesothoracic coxal cavities relatively widely separated by a smooth mesothoracic and metathoracic process. Leg axis short compared to the width of the body. Proleg shaped as in fig. 14, with a large coxa but without flanges on the femur to accept the tibia in repose. Mesoleg shaped as in fig. 15, without femoral flanges. Metaleg shaped as in fig. 16, without well developed femoral flanges. Tarsal formula 4-5-5.

Abdomen flattened, overall shape tapering gradually from segment III to segment IX. Apparent differences as in figs. 1 and 2 due to relative telescoping of segments. Segment II represented by a very reduced tergite only. Segments III–VII entire with 2 pairs of paratergites each. Segment VIII represented by the tergite and sternite only which may or may not be pointed as a secondary sexual character, shaped as in fig. 11. Abdominal segment IX trilobed with 2 lateral portions and split median portion, shaped in the female as in figs. 12 and 13. The male has longer asymmetrical projections from the anterior border of the venter. Median lobe of the male genitalia variable by species. Lateral lobe of the male genitalia somewhat variable by species but always of the same general form as in figs. 17 and 18.

KEY TO SPECIES OF TERMITODISCUS

1. Pronotum with an even covering of setae 2
   Pronotum without setae or with at most a single row along the posterior border 7
2. Antennae with 9 segments 3
   Antennae with 10 segments 4
3. Male genitalia shaped as in fig. 27, with a median spine .... **sheasbyi** n. sp.
   Male genitalia shaped as in fig. 23, without a median spine .... *machadoi* Seevers
4. Size very small, pronotum length 0.33–0.38 mm 5
   Size larger, pronotum length 0.47–0.55 mm 6
5. Pronotal setae rather sparse, male genitalia shaped as in fig. 24 .... **krishnai** n. sp.
   Pronotal setae dense, male genitalia unknown .... *minutus* Cameron

6. Male genitalia shaped as in fig. 25, with a lateral ventral spine on each side .... *heimi* Wasmann
Male genitalia shaped as in fig. 22, without latral ventral spines on each side .... *escherichi* Wasmann
Male genitalis unknown but most probably unlike either *heimi* or *escherichi*, from colonies of *Odontotermes* (*Hypotermes*) *obscuriceps* Wasmann in Ceylon (see description) .... *butteli* Wasmann
7. Elytra and abdomen with setae having bifurcated tips 8
Elytra and abdomen with setae having straight tips 11
8. Size small; pronotum length, 0.36–0.41 mm 9
Size larger; pronotum length, 0.47–0.55 mm 10
9. Sternites with 2 macrochaetae at each lateral edge; male genitalia shaped as in fig. 19 .... *angolae* Seevers
Sternites without macrochaetae except for sternite VII which has 1 on each side; male genitalia shaped as in fig. 28 .... *splendidus* Wasmann
10. Spermatheca shaped as in fig. 33 .... **emersoni** n. sp.
Spermatheca shaped as in fig. 38 .... **vansomereni** n. sp.
11. Pronotum with a single row of very fine setae along posterior border .... *transvaalensis* Silvestri
Pronotum without any setae whatsoever 12
12. Abdominal tergites III–VII with no macrochaetae, male genitalia shaped as in fig. 21 .... **coatoni** n. sp.
Abdominal tergites III–VII with some macrochaetae 13
13. Macrochaetotaxy of abdominal tergites III–VII, 4, 4, 4, 4, 4; male genitalia shaped as in fig. 26 .... **latericius** n. sp.
Macrochaetotaxy of abdominal tergites III–VII, 6, 6, 6, 6, 6; male genitalia shaped as in fig. 20 .... *braunsi* Wasmann

DESCRIPTION OF THE SPECIES

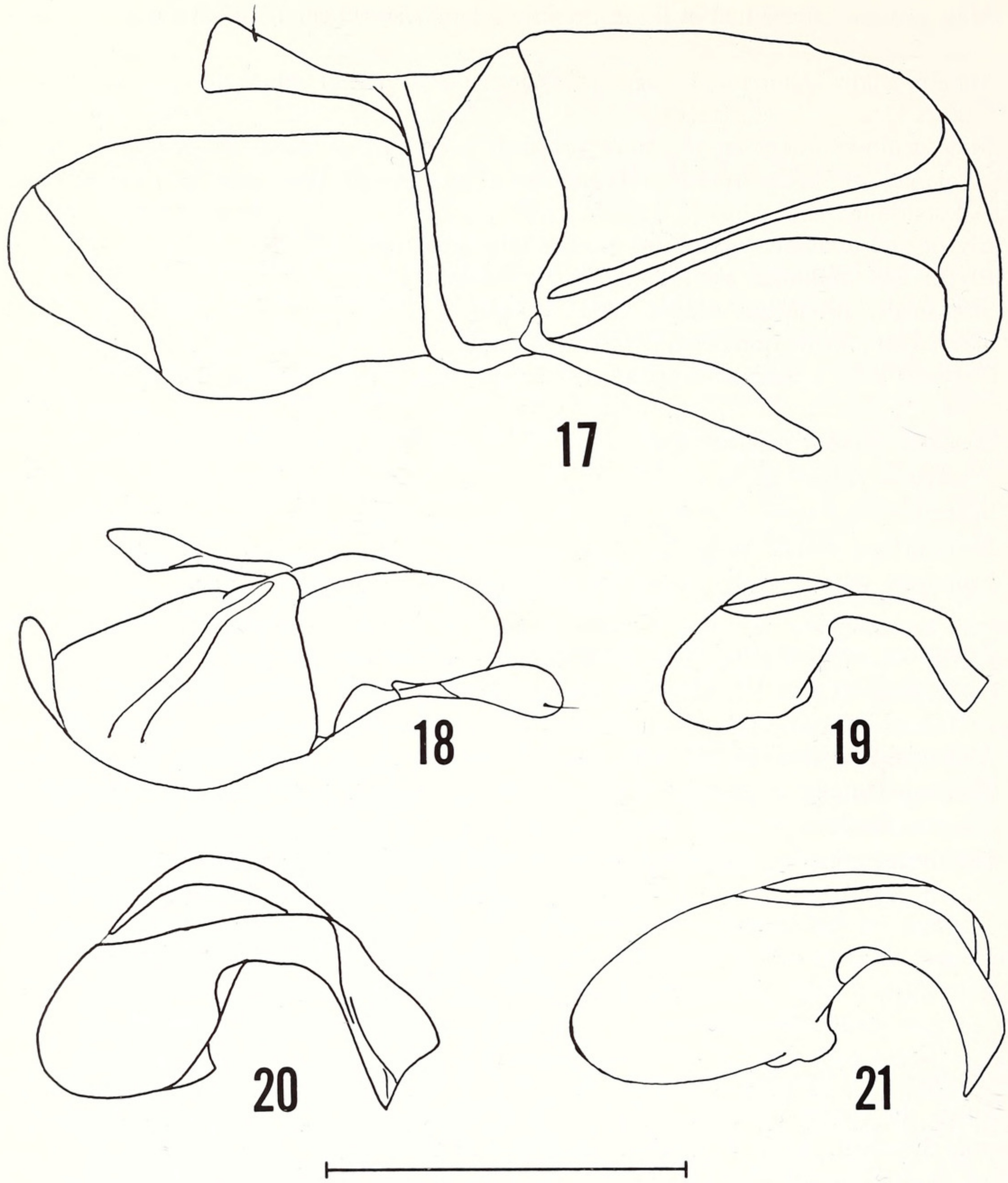
Termitodiscus angolae Seevers
Figs. 6, 19, 44

Termitodiscus angolae Seevers, 1965, Publ. cult. Comph. Diam. Angola, **69:** 134, figs. 6 and 7. Museu do Dundo (Angola: Dundo, R. Capemba, ex fungus gardens of *Odontotermes nolaensis* Sjoestedt, April, 1962, Coll. Machado and Sanjinje).

Most closely related to *T.* **emersoni** n. sp. from which it is distinguished by its smaller size and the shape of the male genitalia. Related to *T. splendidus* Wasmann through its similar size, but separable therefrom by the abdominal chaetotaxy.

Color light yellowish brown throughout with the antero-lateral edges of the pronotum and elytra a little lighter than the rest of the body. Dorsal surface of the head and pronotum smooth and shiny without setae of any kind but with fine punctures evenly but sparsely scattered about. Dorsal surface of the elytra and abdomen with an even covering of yellow, recumbent, short, stiff setae with bifurcated tips. No tergal macrochaetotaxy. Sternites III–VII with a double row of black macrochaetae on each lateral edge. Sternite VIII with the one row of black macrochaetae on each lateral edge and with the mesial row toward the middle. Apex of tergite VIII pointed in the female. Median lobe of the male genitalia shaped as in fig. 19. Antennae 9-segmented.

MEASUREMENTS: Pronotum length, 0.33 mm; elytra length, 0.18 mm; pronotum width, 0.51. Number measured, 1.



FIGS. 17–21. Male genitalia: Lateral lobes: 17. *Termitodiscus escherichi* Wasmann; 18. *T.* **vansomereni** n. sp. Median lobes: 19. *T. angolae* Seevers; 20. *T. braunsi* Wasmann; 21. *T.* **coatoni** n. sp. Scale is equal to 0.25 mm.

MATERIAL EXAMINED: 3 specimens of the type series (C.N.H.M., D.K.). Distribution shown in fig. 44.

Termitodiscus braunsi Wasmann
Figs. 1, 20, 31, 43

Termitodiscus braunsi Wasmann, 1912, Zeitschr. Wiss Zool., **101:** 94—Naturhistorisch Museum, Maastricht (Republic of South Africa: Orange Free State, Bothaville, with *Odontotermes transvaalensis* Sjoestedt); Seevers, 1957, Fieldiana Zool., **40:** 262 (key, list).

Most closely related to *T.* **latericius** n. sp. from which it is distinguished by the 9-segmented antennae, abdominal macrochaetotaxy, and the shape of the male genitalia and spermatheca.

Color light reddish brown throughout with the antero-lateral edges of the pronotum and elytra still lighter, approaching yellowish brown. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head and pronotum without setae of any kind. Dorsal surface of the elytra and abdomen with an even covering of yellow, erect setae with straight nonbifurcated tips. Macrochaetotaxy of abdominal tergites II–VII as follows: II, 0; III, 6; IV, 6; V, 6; VI, 6; VII, 6. Tergite VIII with two rows of 4 macrochaetae each. Sternites III–VII with a row of two setae on each side. Spermatheca shaped as in fig. 31. Median lobe of the male genitalia shaped as in fig. 20. Antennae 9-segmented.

MEASUREMENTS: Pronotum length, 0.47–0.52 mm; elytra length, 0.23–0.24 mm; pronotum width, 0.80–0.85 mm. Number measured, 10.

MATERIAL EXAMINED: Republic of South Africa: Orange Free State, 1, Holotype, *T. braunsi* Wasmann, det. E. Wasmann, Bothaville, Coll. Brauns, bearing label, "*Termes rubricola* Wasmann," (N.H.M.). Transvaal: 8, 36 mi. ex Pretoria-Warmbad, 18 February 1963, Coll. J. Sheasby, T-12 (N.C.I., D.K.); 1 (coll.), 34 mi. ex Pretoria-Pienaars River, 8 March 1963, Coll. J. Sheasby, T-37, (N.C.I.); 3, Rooikop, Rus de Winter, 30 June 1963, Coll. J. Sheasby, T-102 (N.C.I., D.K.); 7, 32 miles ex Pretoria-Pienaars River, 7 August 1963, Coll. J. L. Sheasby, T-132 (N.C.I., D.K.); 4, 30 mi. ex Pretoria-Pienaars River, 8 January 1964, Coll. J. L. Sheasby, T-238 (N.C.I., D.K.); 1, Rooikop, Rus de Winter, 19 March 1964, Coll. J. L. Sheasby, T-325 (N.C.I.) 2, 7 miles ex Pienaars River—Rus de Winter, 20 May 1964, Coll. J. L. Sheasby, T-345 (N.C.I., D.K.); 7, Rooikop, Rus de Winter, 10 March 1965, Coll. J. L. Sheasby, T-379 (N.C.I., D.K.); 1, 30.5 mi. ex Pretoria-Warmbad, 17 March 1966, ex fungus gardens, Coll. W. Coaton, J. L. Sheasby, and D. Kistner, No. 1438 (D.K.).

NOTES: All of the hosts of the Transvaal specimens listed above were identified as *Odontotermes transvaalensis* Sjoestedt by Dr. W. G. H. Coaton. The accession numbers of the termites, should future workers wish to check the hosts are as follows (in the same order as the data above): S-6, S-16, S-22, S-30, S-56, TM. 13360, TM. 14169, & unaccessioned, all in the National Isoptera Collection of South Africa. The last numbered 1439, nest T-160, in the collection of D. Kistner. The distribution of the species is shown in fig. 43.

Termitodiscus butteli Wasmann
Fig. 44

Termitodiscus butteli Wasmann, 1916, Zool. Jahrb. System., **39:** 181, pl. 4, fig. 10, pl. 5, fig. 10a, Naturhistorisch Museum, Maastricht (Ceylon: Peradeniya, ex fungus gardens of *Odontotermes* (*Hypotermes*) *obscuriceps* Wasmann, Coll. by von Buttel-Reepen, December 1911); Seevers 1957, Fieldiana Zool., **40:** 262 (key and list).

Closely related to *T. escherichi* Wasmann and *T. heimi* Wasmann from which it is distinguishable only by its smaller size (1.4 mm vs. 1.6–1.9 mm). See notes below.

Color yellowish brown throughout, yellower toward the antero-lateral edge of the pronotum than elsewhere. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head without setae of any kind. Dorsal surface of the pronotum, elytra, and abdomen with an even covering of fine yellow, recumbent, short, stiff setae with bifurcated tips. Macrochaetotaxy of abdominal tergites II-VII: 0, 0, 0, 0, 0, 0. Macrochaetotaxy of sternites and abdominal segment VIII unknown. Male genitalia and female spermatheca unknown. Antennae 10-segmented.

MEASUREMENTS: Pronotum length, 0.45–0.46 mm; elytra length, 0.22–0.23 mm; pronotum width, 0.85–0.92 mm. Number measured, 2.

MATERIAL EXAMINED: Type and cotype (N.H.M.); 1 cotype (B.M.N.H.). The distribution is shown in fig. 44.

NOTES: Because dissection material was not available, sufficient characters are not known to distinguish this species from either *T. heimi* or *T. escherichi.* The overall size difference was taken from the original description, but actual measurements made are all on the low side of the range for *T. escherichi.* I found and dissected one nest of *O. obscuriceps* in Kandy, Ceylon, but unfortunately did not get any specimens. No new material of this species has been collected since the original capture. The clustering program on the basis of the characters available show that it is very closely related to *heimi* and *escherichi* (1.000 correlation) and I do not believe that new material will greatly alter the association although it would undoubtedly lower the coefficient of relationship. Because *heimi* and *escherichi* are now well known, it should be easy to place this species, once material from *O. obscuriceps* colonies from reasonably close to Peradeniya is available.

Termitodiscus **coatoni** n. sp.

Figs. 21, 32, 43

Most closely related to *T. transvaalensis* Silvestri from which it is distinguished by the absence of a row of fine setae on the posterior edge of the pronotum, its 9-segmented antennae, its abdominal macrochaetotaxy, and the shape of the male genitalia and spermatheca.

Color reddish brown throughout with the antero-lateral edge of the pronotum lighter than the rest of the body, approaching yellow. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head and pronotum without any setae of any kind. Dorsal surface of the elytra and abdomen with an even covering of yellow setae with nonbifurcated straight tips. Macrochaetotaxy of abdominal tergites II–VIII as follows: 0, 0, 0, 0, 0, 0, 2. Macrochaetotaxy of abdominal sternites III–VIII as follows: III, 2; IV, 2; V, 2; VI, 4; VII, 4; VIII, 6, all lateral except for the mesial 2 on VIII. Female tergite VIII evenly rounded on posterior edge. Spermatheca shaped as in fig. 32. Median lobe of male genitalia shaped as in fig. 21. Antennae 9-segmented.

MEASUREMENTS: Pronotum length, 0.48–0.51 mm; elytra length, 0.21–0.25 mm; pronotum width, 0.80–0.85 mm. Number measured, 10.

HOLOTYPE: 1 male, No. 12515, South Africa, Transvaal, Rooikop, Rus de Winter, 19 March 1963, Coll. J. L. Sheasby No. T-47. In the National Collection of Insects, South Africa.

PARATYPES: South Africa: Transvaal: 20, same data as holotype (N.C.I., D.K.); 4, 14 mi. ex Pretoria-Pienaars River Dam, 9 August 1960, Coll. W. G. H. Coaton, TM7433 (N.C.I., D.K.); 6, Pretoria West, 14 August 1963, Coll. Rorke No. T-145 (N.C.I., D.K.).

NOTES: The hosts of all the captures were determined as *Odontotermes badius* (Haviland) by Dr. W. G. H. Coaton. The accession numbers of the termites are S-18, TM7433, and S-32 respectively and the specimens are in the National Collection of Isoptera, South Africa. The distribution of the species is shown in fig. 43.

Termitodiscus **emersoni** n. sp.
Figs. 33, 44

Most closely related to *T. angolae* Seevers from which it is distinguished by its larger size. Also related to *T.* **vansomereni** n. sp. from which it is distinguished by the shape of the female spermatheca.

Color reddish brown throughout, with the antero-lateral edges of the pronotum lighter than the rest of the body, approaching yellow. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head and pronotum without any setae of any kind. Dorsal surface of the elytra and abdomen with an even covering of fine, yellow, recumbent, stiff, short setae with bifurcated tips. No macrochaetae on abdominal tergites II–VIII. Macrochaetotaxy of abdomenal sternites III–VIII, 4, 4, 4, 4, 4, 4, all lateral in position. Spermatheca shaped as in fig. 33. Male unknown. Antennae 9-segmented.

MEASUREMENTS: Pronotum length, 0.47 mm; elytra length, 0.24–0.25 mm; pronotum width, 0.80–0.85 mm. Number measured, 2.

HOLOTYPE: 1 female, No. 12228, Congo Republic, Kivu, Keyberg, 25 April 1948, Coll. Alfred E. Emerson. In the collection of the author.

PARATYPE: 1 female, same data as the holotype (D.K.).

NOTES: The host colony was identified as *Odontotermes patruus* Sjoestedt by Dr. A. E. Emerson. Specimens of the host colony are in the Emerson collection of the American Museum of Natural History, New York. The distribution of the species is shown in fig. 44.

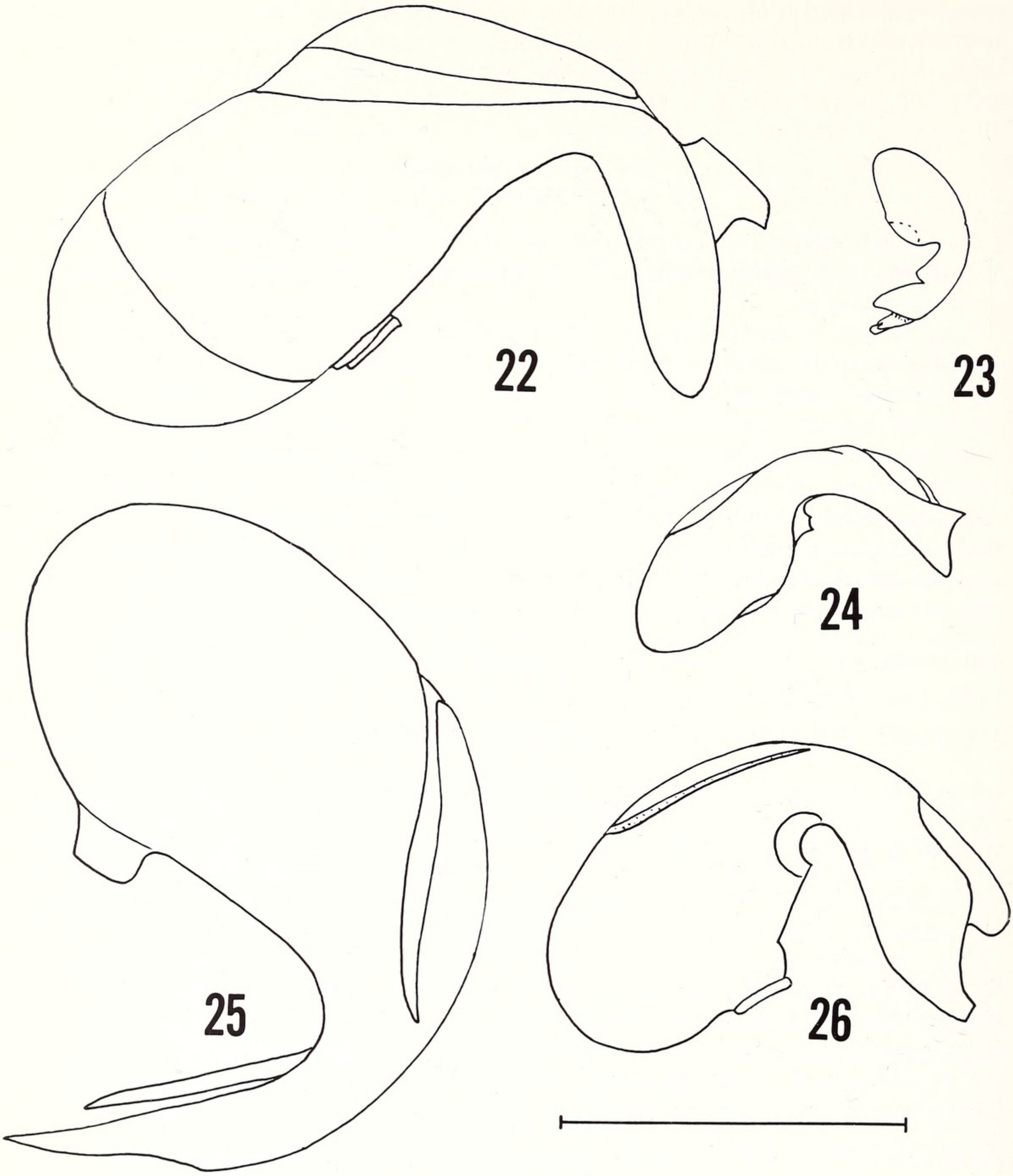
Termitodiscus escherichi Wasmann
Figs. 2, 3, 8, 9, 10, 11, 12, 17, 22, 44

Termitodiscus escherichi Wasmann, 1911, Termitenleben auf Ceylon: 231 Naturhistorisch Museum, Maastricht (Ceylon, Perandeniya, with *Odontotermes redemanni* Wasmann); 1912, Zeitschr. wissensch Zool., **101:** 94 (no additional data added); 1916, Zool. Jahrb. Syst., **39:** 181, pl. 4, fig. 9, pl. 5, fig. 9a (key); Cameron, 1932, Fauna Brit, India, Staphyl., **3:** 318 (key); Seevers, 1957, Fieldiana Zool., **40:** 260 (key).

Termitodiscus escherichi var. *picea* Wasmann, 1916, Zool. Jahrb. Syst., **39:** 181 Naturhistorisch Museum, Maastricht (Ceylon, Peradeniya, with *Odontotermes ceylonicus* Wasmann, 8 January 1912, Coll. H. von. Buttel-Reepen); Seevers, 1957, Fieldiana Zool., **40:** 260 (synonymized variety).

Most closely related to *T. heimi* Wasmann from which it is distinguished by the lack of ventral spines on the median lobe of the male genitalia and presence of 2 more macrochaetae on the sternites of each of abdominal segments VI, VII, and VIII, as well as the shape of the median lobe of the male genitalia.

Color light reddish brown throughout, with the antero-lateral edges of the pronotum lighter than the rest of the body, approaching yellow. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head without any setae of any kind. Dorsal surface of the pronotum, elytra, and abdomen with an even covering of fine, yellow, recumbent, stiff, short setae with



FIGS. 22–26. Median lobes of male genitalia: 22. *Termitodiscus escherichi* Wasmann; 23. *T. machadoi* Seevers; 24. *T.* **krishnai** n. sp.; 25. *T. heimi* Wasmann; 26. *T.* **latericius** n. sp. Scale is equal to 0.25 mm and applies to all figures except fig. 23. Fig. 23 after Seevers (1965).

bifurcated tips. Macrochaetotaxy of abdominal tergites II–VIII: 0, 0, 0, 0, 0, 0, 4. Macrochaetotaxy of abdominal sternites III–VIII: 2, 2, 4, 6, 6, 4. Median lobe of male genitalia without ventral spines, shaped as in fig. 22. Spermatheca shaped as in fig. 12. Antennae 10-segmented.

MEASUREMENTS: Pronotum length, 0.45–0.50 mm; elytra length 0.22–0.25 mm; pronotum width, 0.90–1.00 mm. Number measured, 15.

MATERIAL EXAMINED: Ceylon: Holotype and Cotype, *T. escherichi* Wasmann, det. E. Wasmann, Peradeniya, with *Odontotermes redemanni* Wasmann (N.H.M.); Holotype, *T. escherichi* var. *picea* Wasmann, det. E. Wasmann, Peradeniya, with *Odontotermes ceylonicus* Wasmann (N.H.M.); 161, Sigiriya, ex fungus gardens of nest T22, 25 August 1960, Coll. D. H. and A. C. Kistner (D.K.); 2, Sigiriya, ex fungus gardens of nest T24, 25 August 1960, Coll. D. H. and A. C. Kistner (D.K.); 2, Sigiriya, ex fungus gardens of nest T23, 24 August 1960, Coll. D. H. and A. C. Kistner (D.K.); 4, Sigiriya, ex fungus gardens of nest T21, 24 August 1960, Coll. D. H. and A. C. Kistner (D.K.). The distribution of the species is shown in fig. 44.

NOTES: The termite hosts of our Sigiriya captures were identified as *Odontotermes taprobanes* Walker by Dr. A. E. Emerson who stated that *O. redemanni* Wasmann is a synonym of that species. The specimens of the hosts are deposited in the Emerson collection of the American Museum of Natural History, New York. The royal cells of the above colonies were all located, opened, and were devoid of termitophiles.

Termitodiscus heimi Wasmann

Figs. 25, 34, 44

Termitodiscus heimi Wasmann, 1899, Deutsches Entomol. Zeitschr. **1899:** 147, pl. 1, fig. 1a–f; Naturhistorisch Museum, Maastricht (India: Ahmednagar District, Wallon, and Sangamner with *Odontotermes obesus* Rambur and *Odontotermes wallonensis* Wasmann); 1912, Zeitschr. wissensch. Zool., **101:** 93, pl. 5, fig. 4; 1916, Zool. Jahrb. Syst., **39:** 181, pl. 4, fig. 8a–b, pl. 5, fig. 8c; Cameron, 1932, Fauna Brit. India, Staphyl., **3:** 318 (key); Silvestri, 1947, Arch. Zool. Ital., **31:** 127, fig. 1 (1–7); Seevers, 1957, Fieldiana Zool., **40:** 260 (key). *Termitodiscus heimi* var. *vicinior* Silvestri, 1947, Arch. Zool. Ital., **31:** 127, fig. 2, (India: Barkuda Island, with *Odontotermes* sp.); Seevers, 1957, Fieldiana Zool., **40:** 260 (synonymized variety).

Most closely related to *T. escherichi* Wasmann from which it is distinguished by the presence of ventral spines on the median lobe of the male genitalia and the presence of 2 less macrochaetae on the sternites of each of abdominal segments VI, VII, and VIII, as well as the shape of the median lobe of the male genitalia.

Color light reddish brown throughout, with the antero-lateral edges of the pronotum lighter than the rest of the body, approaching yellow. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head without setae of any kind. Dorsal surface of the pronotum, elytra, and abdomen with an even covering of fine, yellow, recumbent, stiff, short setae with bifurcated tips. Macrochaetotaxy of abdominal tergites II–VIII, 0, 0, 0, 0, 0, 0, 2. Macrochaetotaxy of abdominal sternites III–VIII: 2, 2, 4, 4, 4, 2, all on the lateral edges. Median lobe of the male genitalia with 2 ventral spines, 1 on each side, shaped as in fig. 25. Spermatheca shaped as in fig. 34. Antennae 10-segmented.

MEASUREMENTS: Pronotum length, 0.50–0.55 mm; elytra length, 0.25–0.26 mm; pronotum width, 0.95–1.07 mm. Number measured, 10.

MATERIAL EXAMINED: India: Holotype and 1 cotype, Ahmednagar District, Wallon, with *Odontotermes obesus* Rambur (N.H.M.); 11, Bombay Province, Wallon, Coll. J. B. Heim, with *Odontotermes obesus* (D.K.); 4, Bombay

Province, Khandala, ex fungus gardens to nest T20, 21 August 1960, Coll. D. H. and A. C. Kistner (D.K.); 11, Khandala, with *Odontotermes obesus*, 1913, Coll. J. Assmuth (D.K.). The distribution is shown in fig. 44.

NOTES: Host colony T20 was determined as *Odontotermes obesus* Rambur by Dr. A. E. Emerson and the termite specimens are deposited in the Emerson Collection of the American Museum of Natural History, New York. No specimens were found in the royal cell of this nest either.

Termitodiscus **krishnai** n. sp.
Figs. 24, 35, 44

Most closely related to *T. minutus* Cameron from which it is presently distinguishable only by the more sparse setae on the pronotum, elytra, and abdomen of *T.* **krishnai**. When dissection material of *T. minutus* is available other characters will undoubtedly emerge.

Color yellowish brown throughout, with the antero-lateral edges of the pronotum lighter than the rest of the body. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head without setae of any kind. Dorsal surface of the pronotum, elytra, and abdomen with an even covering of fine, yellow, recumbent, stiff, short setae with bifurcated tips. Macrochaetotaxy of abdominal tergites II–VIII, 0, 0, 0, 0, 0, 0, 2. Macrochaetotaxy of abdominal sternites III–VIII, 0, 0, 0, 0, 0, 2. Median lobe of the male genitalia shaped as in fig. 24. Spermatheca shaped as in fig. 35. Antennae 10-segmented.

MEASUREMENTS: Pronotum length, 0.33–0.38 mm; elytra length, 0.17–0.18 mm; pronotum width, 0.63–0.64 mm. Number measured, 2.

HOLOTYPE: 1 male, No. 12518, Burma, 21 mi. ex Mandalay, 23 October 1961, Coll. K. Krishna. In the collection of the author.

PARATYPE: 1 female, same data as the holotype (D.K.).

NOTES: The host of the above specimens was identified as *Odontotermes hainanensis* (Light) by Dr. Kumar Krishna. The specimens of the host are deposited in the American Museum of Natural History, New York. The distribution of the species is shown in fig. 44.

Termitodiscus **latericius** n. sp.
Figs. 26, 36, 44

Most closely related to *T. braunsi* Wasmann from which it is distinguished by its 10-segmented antennae, the tergal macrochaetotaxy, the shape of the spermatheca, and the median lobe of the male genitalia.

Color reddish brown throughout, with the antero-lateral edges of the pronotum lighter than the rest of the body, approaching yellow. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head and pronotum without setae of any kind. Dorsal surface of the elytra and abdomen with an even covering of long yellow setae with non-bifurcated tips which are not recumbent but not erect either. Macrochaetotaxy of abdominal tergites II–VIII: 0, 4, 4, 4, 4, 4, 2. Sternites III–VII with 2 macrochaetae on each lateral edge. Sternite VIII with 1 macrochaeta on the lateral edge and 1 about half way toward the middle on each side. Tergite VIII with the posterior edge pointed. Median lobe of the male gentalia shaped as in fig. 26. Spermatheca shaped as in fig. 36. Antennae 10-segmented.

MEASUREMENTS: Pronotum length, 0.47–0.55 mm; elytra length, 0.22–0.25 mm; pronotum width, 0.70–0.85 mm. Number measured, 10.

HOLOTYPE: 1 male, No. 12506, Republic of South Africa, Transvaal, 33 mi ex Pretoria-Pienaars River, 22 February 1965, Coll. J. L. Sheasby, No. T378. In the National Collection of Insects, South Africa.

PARATYPES: Republic of South Africa, Transvaal: 10, Pretoria, Waverly, 20 February 1963, Coll. J. L. Sheasby, No. T17 (N.C.I., D.K.); 4, Pretoria, Derdepoort, 4 March 1963, Coll. J. L. Sheasby, No. T31 (N.C.I., D.K.); 5, Derdepoort, 9 July 1963, Coll. J. L. Sheasby, No. T110 (N.C.I., D.K.); 1, Derdepoort, 20 January 1964, Coll. J. L. Sheasby, No. T258 (N.C.I.); 2, 9 mi ex Pretoria-Pienaars River, 2 March 1964, Coll. J. L. Sheasby, No. T306 (N.C.I., D.K.); 1, Derdepoort, 6 March 1964, Coll. J. L. Sheasby, No. T313 (N.C.I.).

NOTES: The host colonies of all the above specimens were determined as *Odontotermes latericius* (Haviland) by Dr. W. G. H. Coaton. The host specimens are in the South African National Collection of Isoptera under the following accession numbers: S-7, S-14, S-23, S-59, S-65, S-66, unaccessioned (T378). The distribution of the species is shown in fig. 44.

Termitodiscus machadoi Seevers
Figs. 4, 5, 7, 23, 44

Termitodiscus machadoi Seevers, 1965, Publ. Cult. Comph. Diam. Angola **69:** 136, figs. 8, 9, Museu do Dundo, Angola (Angola, Dundo, R. Capemba, 23 March 1962, from nest of *Odontotermes interveniens* Sjoestedt, Coll. A. De Barros Machado).

Most closely related to *T.* **sheasbyi** n. sp. from which it is distinguished by its slightly smaller size and the absence of ventral spines from the median lobe of the male genitalia as well as by the shape of the median lobe of the genitalia.

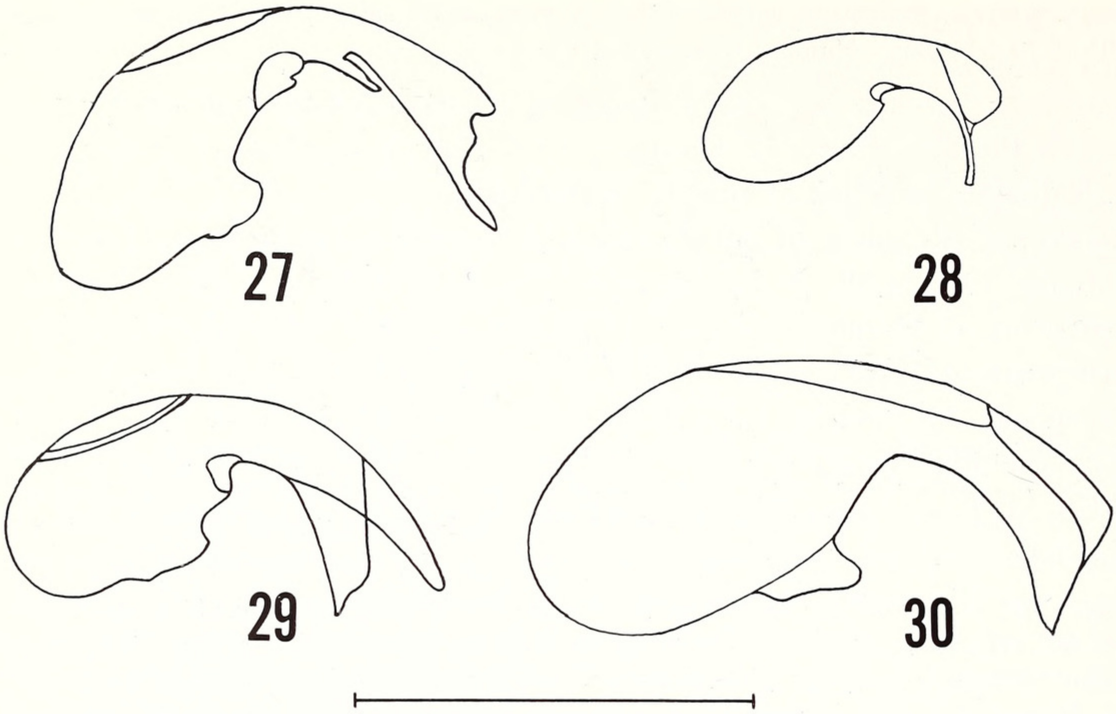
Color reddish brown throughout, with the antero-lateral edges of the pronotum lighter than the rest of the body, approaching yellow. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head without setae of any kind. Dorsal surface of the pronotum, elytra and abdomen with an even covering of fine, yellow, recumbent, stiff, short setae with bifurcated tips. No macrochaetae on either sternites or tergites. Median lobe of the male genitalia shaped as in fig. 23. Spermatheca unknown. Antennae 9-segmented.

MEASUREMENTS: Pronotum length, 0.41–0.43 mm; elytra length, 0.30–0.22 mm; pronotum width, 0.76–0.80 mm. Number measured, 3.

MATERIAL EXAMINED: 6 paratypes (F.M.N.H., D.K.). The distribution of the species is shown in fig. 44.

Termitodiscus minutus Cameron
Fig. 44

Termitodiscus minutus Cameron, 1926, Trans. Entomol. Soc. London, **74:** 171—British Museum (N.H.), London (India: Dehra Dun, in nest of termites, Coll. M. Cameron); 1932, Fauna Brit. India, Staphyl., **3:** 319 (key); Seevers, 1957, Fieldiana Zool., **40:** 262 (key, list).



FIGS. 27–30. Median lobes of male genitalia: 27. *Termitodiscus* **sheasbyi** n. sp.; 28. *T. splendidus* Wasmann; 29. *T. transvaalensis* Silvestri; 30. *T.* **vansomereni** n. sp. Scale is equal to 0.25 mm.

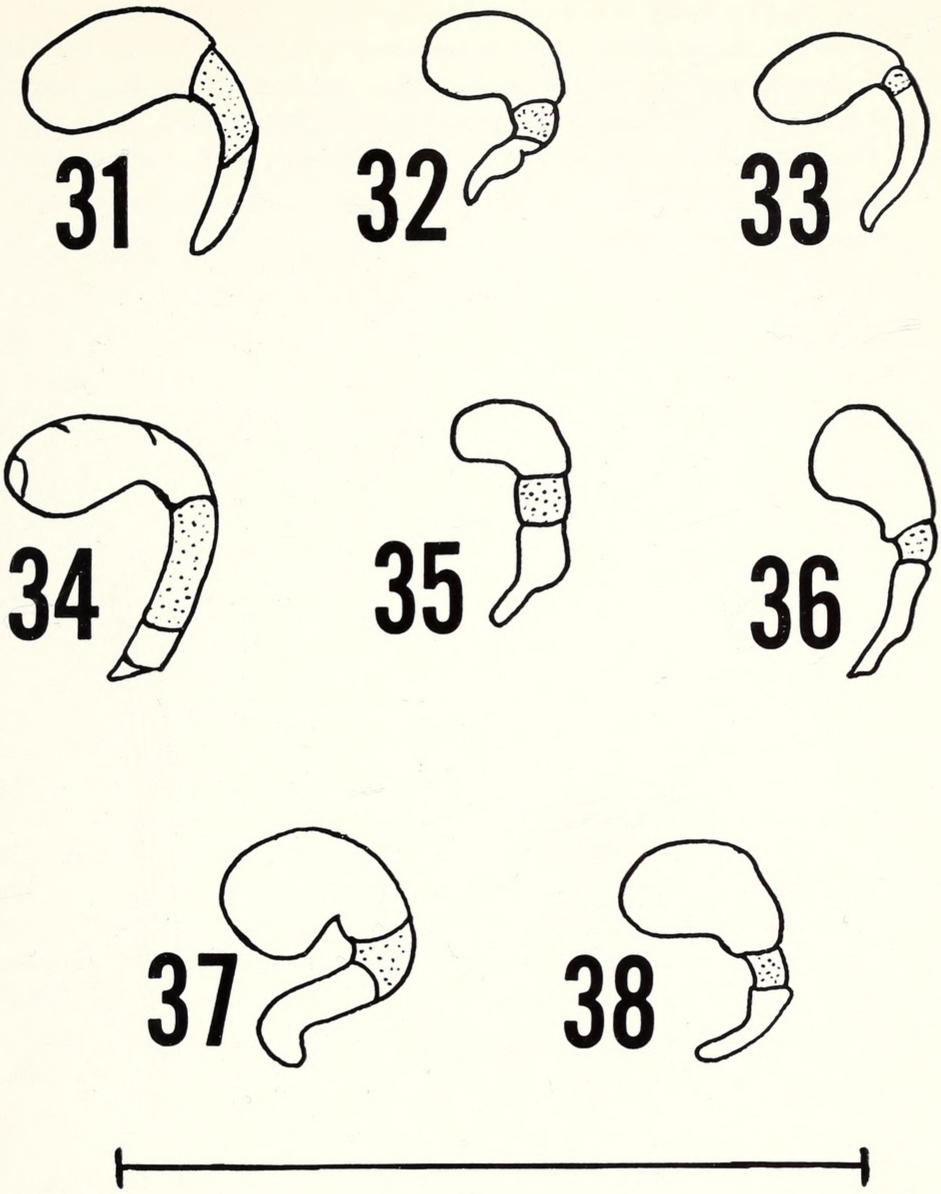
Most closely related to *T.* **krishnai** n. sp. from which it is presently distinguishable only by the presence of more setae with bifurcated tips on the pronotum, elytra, and abdomen. In this regard, it is also closely related to *T. escherichi* and *T. heimi* from which it is distinguished by its much smaller size. When dissectable material is ultimately available, more definitive characters are almost certain to be found as the range of the host of *T.* **krishnai** does not extend to Dehra Dun.

Color yellowish brown throughout, with the antero-lateral edges of the pronotum lighter than the rest of the body, approaching yellow. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head without setae of any kind. Dorsal surface of the pronotum, elytra, and abdomen with an even covering of fine, yellow, recumbent, stiff, short setae with bifurcated tips. No macrochaetae on any of the tergites. Macrochaetotaxy of the sternites unknown. Male genitalia and spermatheca unknown. Antennae 10-segmented.

MEASUREMENTS: Pronotum length, 0.33 mm; elytra length, 0.18 mm; pronotum width, 0.66–0.70 mm. Number measured, 2.

MATERIAL EXAMINED: Holotype plus 1, India, Uttar Pradesh, Dehra Dun, 19 March 1924, Coll. M. Cameron, from the nest of a termite (B.M.N.H.).

NOTES: A search of the termite collection of the British Museum (N.H.) by Mr. W. A. Sands did not yield any *Odontotermes* bearing data corresponding to the type label. If there is any sample of the termites associated with these specimens, they might be at the Forest Research Institute at Dehra Dun, but other than that possibility, only further collections are likely to yield the host data. The distribution of the species is shown in fig. 44.



Figs. 31–38. Spermathecae: 31. *Termitodiscus braunsi* Wasmann; 32. *T.* **coatoni** n. sp.; 33. *T.* **emersoni** n. sp.; 34. *T. heimi* Wasmann; 35. *T.* **krishnai** n. sp.; 36. *T.* **latericius** n. sp.; 37. *T. transvaalensis* Silvestri; 38. *T.* **vansomereni** n. sp. Scale is equal to 0.25.

Termitodiscus **sheasbyi** n. sp.

Figs. 27, 44

Most closely related to *T. machadoi* Seevers from which it is distinguished by its slightly larger size and the presence of a ventral spine from the median lobe of the male genitalia as well as by the shape of the median lobe of the male genitalia.

Color reddish brown throughout with the antero-lateral edges of the pronotum lighter than the rest of the body, approaching yellow. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head without setae of any kind. Dorsal surface of the pronotum, elytra, and abdomen with an even covering of fine, yellow, recumbent, stiff, short setae with bifurcated tips. No tergites with macrochaetae. Macrochaetotaxy of abdominal sternites III–VIII: 0, 0, 0, 0, 0, 8. Median lobe of the male genitalia with a spine on the median ventral posterior border, shaped as in fig. 27. Female unknown. Antennae 9-segmented.

MEASUREMENTS: Pronotum length, 0.45 mm; elytra length, 0.18 mm; pronotum width, 0.75–0.90 mm. Number measured, 3.

HOLOTYPE: 1 male, No. 12503, South West Africa, 30 miles ex Tsumeb-Tsinsabis (15°, 45–59′ S., 17°, 45–59′ E.), 26 September 1966, Coll. J. L. Sheasby, No. T502, ex fungus gardens. In the National Collection of Insects, South Africa.

PARATYPES: 2 males, same data as holotype (N.C.I., D.K.).

NOTES: The host of the above species was determined as *Odontotermes* (c.f.) *latericius* (Haviland) by Dr. W. G. H. Coaton. The sample bears the accession number TM.20457 and is in the National Isoptera Collection, South Africa. The distribution of the species is shown in fig. 44.

Termitodiscus splendidus Wasmann
Figs. 28, 43

Termitodiscus splendidus Wasmann, 1899, Deutsch. Entolmol. Zeitschr. 1899: 401. Naturhistorisch Museum, Maastricht (Republic of South Africa: Natal, Shivyre, with *Odontotermes vulgaris* Haviland, Coll. Haviland); 1912, Zeitschr. wissensch. Zool., **101:** 94, pl. 5, fig. 5; Seevers, 1957, Fieldiana Zool., **40:** 262 (key, list). The (c.f.) designation given in the determination was used to indicate morphological similarity to *latericius* from South Africa. The nest however was constructed differently.

Not very closely related to any other species but bears similarity to *T.* **vansomereni**, *T.* **emersoni**, and *T. angolae* by having setae with bifurcated tips on the elytra, but distinguishable by its smaller size, the abdominal macrochaetotaxy and the shape of the male genitalia. Related to the *sheasbyi-machadoi* group through its size, macrochaetotaxy of the abdomen, and the antennal segmentation but separable therefrom by the lack of setae on the pronotum as well as genitalic characters.

Color light reddish brown throughout with the antero-lateral edges of the pronotum just about the same color as the rest of the body. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head and pronotum without setae of any kind. Dorsal surface of the elytra and abdomen with an even covering of fine, yellow, recumbent, stiff, short setae with bifurcated tips. No tergites with macrochaetae. Macrochaetotaxy of abdominal sternites III–VIII: 0, 0, 0, 0, 0, 2. Median lobe of the male genitalia small, shaped as in fig. 28. Spermatheca unknown, as the female dissected lacked a spermatheca for some inexplicable reason. Antennae 9-segmented.

MEASUREMENTS: Pronotum length, 0.36–0.41 mm; elytra length, 0.17–0.19 mm; pronotum width 0.67–0.70 mm. Number measured, 2.

MATERIAL EXAMINED: Holotype and 2 cotypes on a single pin, top specimen herewith designated hololectotype, Natal (Shivyre), November 1898, Coll. G. D. Haviland, with *Odontotermes vulgaris* Haviland (N.H.M.); 2, same locality, host and collector, 16 February 1898 (D.K.).

NOTES: The distribution of the species is shown in fig. 43.

Termitodiscus transvaalensis Silvestri
Figs. 13–16, 29, 37, 43

Termitodiscus transvaalensis Silvestri, 1947, Arch. Zool. Ital., **31:** 129, fig. 3, (Transvaal, ex nest of *Odontotermes angustatus* Rambur, Coll. C. Fuller); Seevers, 1957, Fieldiana Zool., **40:** 262 (key, list).

Not very closely related to any other species. Closely related to *T.* **vansomereni** through its size and abdominal macrochaetotaxy, but separable therefrom by its straight-tipped setae and its 10-segmented antennae. Closely related to *T.* **latericius** n. sp. but separable therefrom by the macrochaetotaxy of the abdominal tergites. Separable from all species by the presence of a row of fine setae with straight tips at the posterior edge of the pronotum as well as the shape of the male genitalia.

Color reddish brown throughout, with the antero-lateral edges of the pronotum lighter than the rest of the body, approaching yellow. Dorsal surface of the head, pronotum, and elytra smooth and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head without setae of any kind. Dorsal surface of the pronotum generally without setae, but bearing one row of fine, short yellow setae at the posterior border. Dorsal surface of the elytra and abdomen with an even covering of fine yellow setae with straight, non-bifurcated tips. Macrochaetotaxy of abdominal tergites II–VIII: 0, 0, 0, 0, 0, 0, 2. Macrochaetotaxy of abdominal sternites III–VIII: 6, 6, 6, 4, 4, 4, 4. Median lobe of male genitalia shaped as in fig. 29. Spermatheca shaped as in fig. 13. One aberrent spermatheca was shaped as in fig. 37, whereas other members of the same population matched fig. 13. Antennae 10-segmented.

MEASUREMENTS: Pronotum length, 0.47–0.51 mm; elytra length, 0.24–0.26 mm; pronotum width, 0.80–0.87 mm. Number measured, 10.

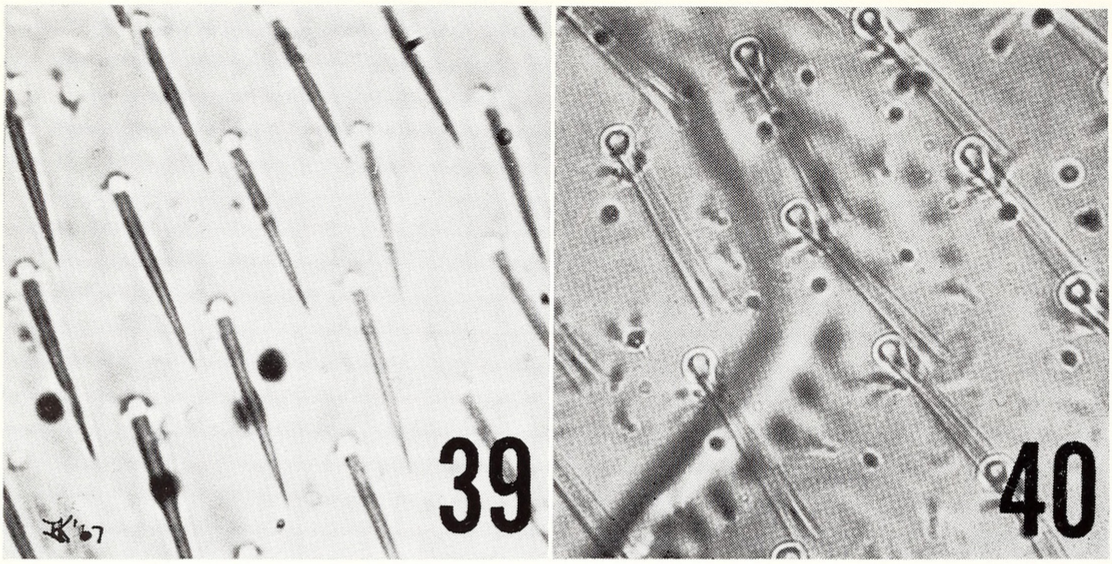
MATERIAL EXAMINED: South Africa: Transvaal: 3, 3 mi. ex Morgenson-Standerton, 10 September 1963, Coll. J. L. Sheasby, No. T160 (N.C.I., D.K.); 5, 3 mi. ex Morgenson-Standerton, 10 September 1963, Coll. J. L. Sheasby, No. T161 (N.C.I., D.K.); 1, 10 mi. ex Morgenson-Standerton, 11 September 1963, Coll. J. L. Sheasby, No. T167 (N.C.I.); 2, 13 mi. ex Morgenson-Ermelo, 12 September 1963, Coll. J. L. Sheasby, No. T168 (N.C.I., D.K.). Cape Province: 11, 6 mi. ex Sterkstroom-Tarka, 8 October 1963, Coll. J. L. Sheasby, No. T206 (N.C.I., D.K.); 13, 10 mi. ex Cala-Indwe, 7 October 1963, Coll. J. L. Sheasby, No. T202 (N.C.I., D.K.).

NOTES: The hosts of all of the above specimens were determined as *Odontotermes angustatus* (Rambur) by Dr. W. G. H. Coaton. The hosts bear the accession numbers S-37, S-40, S-41, TM 13045, TM 13059, and are in the National Collection of Isoptera, South Afirca. The distribution of the species is shown in fig. 43.

Termitodiscus **vansomereni** n. sp.
Figs. 18, 30, 38, 44

Most closely related to *T.* **emersoni** n. sp. and *T. angolae* Seevers from which it is distinguished by its larger size, the abdominal macrochaetotaxy and the shape of the male genitalia. Closely similar to *O. transvaalensis* Silvestri from which it is distinguished by the presence of setae with bifurcated tips.

Color light reddish brown throughout, with the antero-lateral edges of the pronotum lighter than the rest of the body. Dorsal surface of the head, pronotum, and elytra smooth



FIGS. 39–40. Setae on elytra: 39. Straight tipped setae, *Termitodiscus transvaalensis* Silvestri; 40. Bifurcated tipped setae, *T. escherichi* Wasmann. Scale is arbitrary, photos were taken at 440 ×.

and shiny with fine punctures evenly but sparsely scattered about. Dorsal surface of the head and pronotum without setae of any kind. Dorsal surface of the elytra and abdomen with an even covering of fine, yellow, recumbent, stiff, short setae with bifurcated tips. Tergites with no macrochaetae. Macrochaetotaxy of abdominal sternites III–VIII: 6, 6, 6, 6, 6, 6,. Median lobe of the male genitalia shaped as in fig. 30. Spermatheca shaped as in fig. 38. Antennae 9-segmented.

MEASUREMENTS: Pronotum length, 0.50–0.53 mm; elytra length, 0.26–0.30 mm; pronotum width, 0.85–0.95 mm. Number measured, 10.

HOLOTYPE: 1 male, No. 12224, Kenya, Karen, 18 June 1966, ex fungus gardens of nest T185, Coll. G. R. Cunningham-Van Someren, No. 1559. In the Collection of D. H. Kistner.

PARATYPES: 54, same data as the holotype (D.K.).

NOTES: The host of the above specimens was determined as *Odontotermes montanus* Harris by Mr. W. A. Sands. The termite sample is in the collection of the British Museum (Natural History), London. This nest was being raided by *Dorylus* (*Dorylus*) *helvolus* L. at the time of excavation. The distribution of the species is shown in fig. 44.

RELATIONSHIPS OF THE SPECIES AND HOST SPECIFICITY

In the early days of describing species, various authors made a big point about the relative size of the last joint of the antennae in relation to the length of the rest of the segments as well as the absolute length of the entire specimen. Careful slide preparations have revealed that this is an almost useless character as the size of the terminal segment is always proportionate to the rest of the antenna. Figures 3 and 4 show this well, even though the number of antennal segments vary. The length of the entire specimen is another useless character as the abdomen is able to be telescoped a great deal. Hence both of these characters were dropped.

In searching for new characteristics, microscopic examination revealed the following: Not all the species had 10-segmented antennae as was previously supposed. I first discovered this on *T. machadoi.* I then remembered that Silvestri had shown a 10-segmented antenna on both *T. transvaalensis* and *T. heimi.* This worried me as I have never known Silvestri to be wrong on a question of fact. Sure enough, both of the species studied by Silvestri had 10-segmented antennae. I then surveyed the antennae of all the species and could find no correlation of the antennal segmentation with any other character. Hence this character is here interpreted as a species specific character, and a new genus is not erected on this basis. Selection has obviously been working to compress the antennae of this beast, so a segment has been lost now and then on what appears to be a hit or miss basis. I believe that the segment has been lost between segment 3 and 5 and on one species, *T.* **vansomereni**, one can see what appears to be a fine line of fusion on the third segment.

Close study of the setae revealed that there are two types. One type is a perfectly ordinary kind with straight pointed tips as shown in fig. 39. The other type has bifurcated tips as shown in fig. 40. The difference between the setae was noted by Seevers (1957, p. 260) as being feebly notched. He interpreted this as being only in the Indian species which was not true. Among the species described at that time, *T. splendidus* also had such setae.

Using traditional phylogenetic methods, it is possible to construct a phylogeny of the species groups as shown in fig. 4. Group A consisting of *T. braunsi*, *T.* **latericius**, *T.* **coatoni**, and *T. transvaalensis* would be interpreted as the most primitive species because they have setae with straight tips which is the usual situation in the Staphylinidae and particularly true in the primitive groups. Where deviations have occurred as in *Phyllodinarda* (see Kistner 1965), the deviations are of a different nature than for *Termitodiscus* and can therefore be assumed to be of independent origin. Of the four species, *T. transvaalensis* is probably the most primitive as it still has a short row of setae on the pronotum whereas the others lack pronotal setae entirely. Again, the complete absence of setae on the pronotum of a Staphylinid is an unusual condition and is therefore interpreted as being a derivative condition. This view is reinforced by the fact that groups C, D, and E have pronotal setae, albeit modified, and modified setae had to be derived from some pre-existing setae, hence I am supposing that the common ancestor had to have setae, most likely unmodified setae on its pronotum. None of the presently known species quite fills the bill, but *T. transvaalensis* comes closest. *T.* **latericius** is more closely related to *T. transvaalensis* in that it has 10-segmented antennae whereas the other species (*T. braunsi* and *T.* **coatoni**) have 9-segmented antennae.

Groups B, C, D, and E are all related in having setae with bifurcated tips.

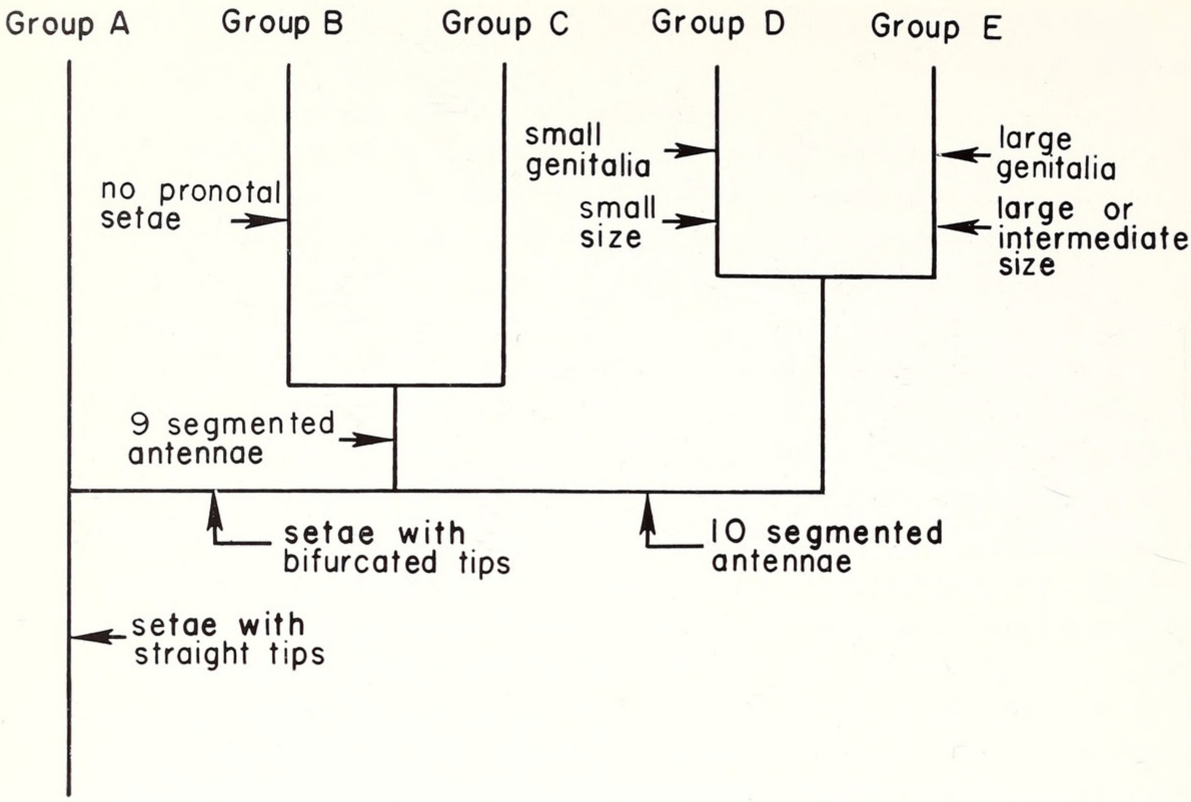


FIG. 41. Proposed phylogeny of species groups of *Termitodiscus* using traditional methods. Group A includes *T. braunsi*, *T.* **latericius**, *T.* **coatoni**, and *T. transvaalensis*. Group B includes *T. angolae*, *T.* **emersoni**, *T.* **vansomereni**, and *T. splendidus*. Group C includes *T. machadoi* and *T.* **sheasbyi**. Group D includes *T.* **krishnai** and *T. minutus*. Group E includes *T. butteli*, *T. escherichi*, and *T. heimi*.

Slide preparations of most of the species revealed that the bifurcated tips are all of the same type. *T. minutus* and *T. butteli* were not so examined but the dry preparations revealed no differences.

Group B has no pronotal setae, but the elytra and abdomen have the bifurcated setae. All the members of this group (*T. angolae*, *T.* **emersoni**, *T. splendidus*, and *T.* **vansomereni**) have 9-segmented antennae which would link them to part of group A, and also to group C.

Group C has setae with bifurcated tips on the pronotum as well as the elytra and abdomen. A careful examination of the diagram (fig. 41) will reveal that we are assuming that the common ancestor of B, C, D, and E had setae on all three regions, that this became bifurcated, and then was lost on the pronotums of group B. Thus group C would be more primitive than group B.

Groups D and E share with group C the property of having setae with bifurcated tips but differ in having 10-segmented antennae. Hence I interpret that groups D and E were split off earlier in the evolution of the groups before segment reduction. Groups D and E are very closely related to one another but differ in size and in the size of the genitalia (where known).

It is obvious from the foregoing that I did not use characters such as the macrochaetotaxy of the abdomen or the various characters of the male genitalia (other than gross size) in the construction of the phylogenetic tree. These characters, while useful for discriminating species, are presently of no use in determining phylogenies, as there is no way of determining or guessing the primitive and derivative states of such characters. Should an ancestral type be found in nature, it might be possible to judge this in the future, but this is not so at present.

Computer methods were then used to see if a more precise statement of the relationships of the species could be constructed. To do this, it was necessary to develop a list of unit characters following the general outline of Sokal and Sneath (1963). After eliminating characteristics which were redundant or invariant, the following list of 31 characters was used and coded 0 for absence, 1 for presence, and 3 for no comparison. The no comparisons arose when a male character was listed and the species was known only from a female or the material studied could not be dissected to yield the desired comparison.

LIST OF CHARACTERS USED FOR NUMERICAL ANALYSIS

1. Pronotum with setae with bifurcated tips
2. Elytra with setae with bifurcated tips
3. Abdomen with setae with bifurcated tips
4. Tergite VIII of male pointed
5. Male genitalia small
6. Pronotum with posterior edge with 1 row of straight tipped setae.
7. Ten antennal segments
8. Male genitalia with median spines
9. Tergite VIII of female pointed
10. Pronotum length, 0.47–0.55 mm
11. Pronotum length, 0.43–0.45 mm
12. Pronotum length, 0.33–0.41 mm
13. Elytra length, 0.25–0.30 mm
14. Pronotum width twice pronotum length
15. No macrochaetae on tergites II–VII
16. Tergal macrochaetotaxy (II–VII) 0, 6, 6, 6, 6, 6
17. Tergal macrochaetotaxy (II–VIII) 0, 4, 4, 4, 4, 4
18. No macrochaetae, sternite III
19. 2 macrochaetae, sternite III
20. No macrochaetae, sternite IV
21. 2 macrochaetae, sternite IV
22. No macrochaetae, sternite V
23. 2 macrochaetae, sternite V

24. 4 macrochaetae, sternite V
25. No macrochaetae, sternite VI
26. 2 macrochaetae, sternite VI
27. 4 macrochaetae, sternite VI
28. No macrochaetae, sternite VII
29. 2 macrochaetae, sternite VII
30. 4 macrochaetae, sternite VII
31. Pronotum with setae of any type

The distribution of these characteristics in the 15 species is given in Table 1. These data were then loaded into an IBM 1620 computer with a program to produce the simple matching coefficients described by Sokal and Michener (1958). The output of this program was then used to cluster the data using the weighted pair-group method described by Sokal and Sneath (1963).

The results of these analyses are presented in fig. 42. Only the matrix values where the groups join are indicated. The perfect correlation between *T. butteli* and *T. heimi* (and for that matter between *T. butteli* and *T. escherichi* also) is due to the large number of no comparisons in the original data. It is also probable that the correlation between *T.* **krishnai** and *T. minutus* will not be as high when dissection material of *T. minutus* is available.

It will be noted that there are some major discrepancies between the phylogenetic diagram and fig. 42. The most serious discrepancies are the clustering of *T.* **vansomereni** with *T. transvaalensis*, and the clustering of *T. splendidus* with the cluster *T. sheasbyi*-*T. machadoi*. Less serious but still important is the clustering of *T.* **latericius** to *T. braunsi* rather than to *T. transvaalensis*. All of these are due to a weighting of size and chaetotaxy factors as equal to kinds of setae and antennal segmentation.

TABLE 1. Distribution of unit characters in *Termitodiscus* species. Characters are arranged sequentially from left to right.

Species No.	Species name	Characters
01	*T. angolae* Seevers	0111100010010010001010100100100
02	*T. braunsi* Wasmann	0001100011001001001010100100100
03	*T. butteli* Wasmann	1113301331001110033333333333331
04	*T.* **coatoni** n. sp.	0001100001001010001010100010010
05	*T.* **emersoni** n. sp.	0113300301001010001010100100100
06	*T. escherichi* Wasmann	1111001011001110001010010000001
07	*T. heimi* Wasmann	1111001111001110001010010010011
08	*T.* **krishnai** n. sp.	1111101010010110010101000100011
09	*T.* **latericius** n. sp.	0000101011001000101010100100100
10	*T. machadoi* Seevers	1110100000100110010101001001001
11	*T. minutus* Cameron	1113301300010110033333333333331
12	*T.* **sheasbyi** n. sp.	1110100101000110010101001001001
13	*T. splendidus* Wasmann	0110100000010010010101001001000
14	*T. transvaalensis* Silvestri	0000111001001010000000000000000
15	*T.* **vansomereni** n. sp.	0111100001001010000000000000000

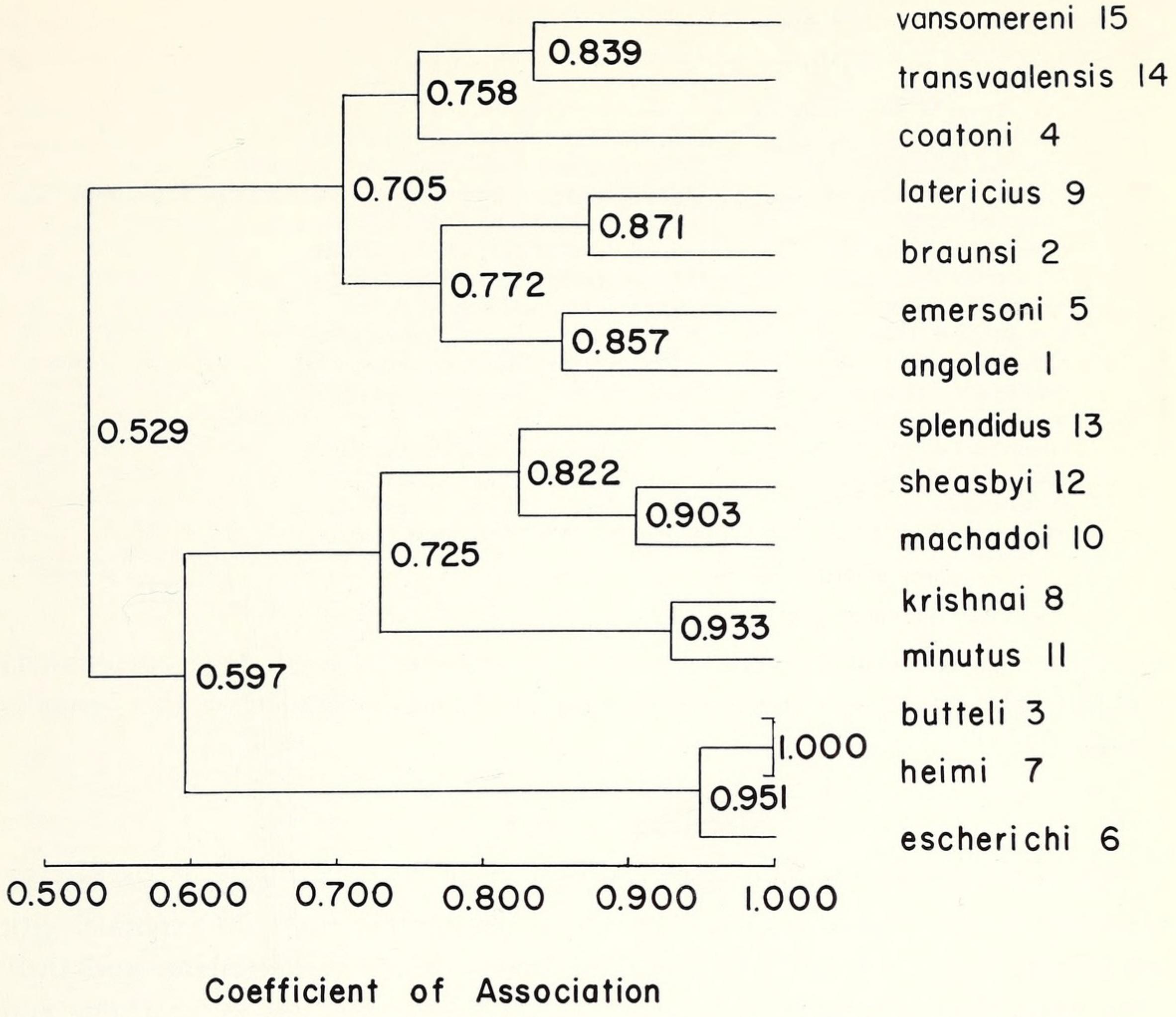


Fig. 42. Diagram of the phenetic relationships between the species of *Termitodiscus*.

The realtionships diagrammed in fig. 42 are probably less accurate as a phylogenetic scheme than the relationships shown in fig. 41. However, the information in fig. 42 is very useful as purely taxonomic information. It took only 45 minutes to put the problem through the computer and that 45 minutes saved hours of time in constructing the keys to species.

As the species are known now, there is complete host specificity. The host information is summarized in Table 2. If we make the assumption that the rates of evolution of the termites and termitophiles are about the same and that there were no accidental host changes in evolutionary history, both handsome assumptions, then we should expect that the termites would be related to each other in the same manner as the termitophiles. Thus we would expect *Odontotermes heimi* and *Odontotermes taprobanes* to be more closely related to each other than to *Odontotermes hainanensis*. We would expect the species *O. latericius* from S. W. Africa that is the host of *T.* **sheasbyi** to be more closely related to *O. interveniens* than to *O. latericius* from South Africa. It will be

TABLE 2. Host relationships of *Termitodiscus*.

Termitophile	Host
T. angolae Seevers	*Odontotermes nolaensis* Sjoestedt
T. braunsi Wasmann	*Odontotermes transvaalensis* Sjoestedt
T. butteli Wasmann	*Odontotermes (Hypotermes) obscuriceps* Wasmann
T. **coatoni** n. sp.	*Odontotermes badius* Haviland
T. **emersoni** n. sp.	*Odontotermes patruus* Sjoestedt
T. escherichi Wasmann	*Odontotermes taprobanes* Walker
T. heimi Wasmann	*Odontotermes obesus* Rambur
T. **krishnai** n. sp.	*Odontotermes hainanensis* Light
T. **latericius** n. sp.	*Odontotermes latericius* Haviland
T. machadoi Seevers	*Odontotermes interveniens* Sjoestedt
T. minutus Cameron	not known
T. **sheasbyi** n. sp.	*Odontotermes latericius* Haviland
T. splendidus Wasmann	*Odontotermes vulgaris* Haviland
T. transvaalensis Silvestri	*Odontotermes angustatus* Rambur
T. **vansomereni** n. sp.	*Odontotermes montanus* Harris

interesting to see whether either of the arrangements given here corresponds with the relationships between the species of *Odontotermes*, when this genus is revised.

BEHAVIORAL OBSERVATIONS

Two species were studied closely in the field, *T. heimi* and *T. escherichi*, especially to see what transpired when the termitophile came into contact with the termite host. To do this, living specimens of the termitophiles and their hosts were placed in petri dishes with moist filter paper on the bottoms and some pieces of fungus gardens. The termitophiles and termites were observed after a couple of hours had elapsed to give them time to accommodate to the container.

The chief behavorial adaptation of the termitophile appeared to be avoidance. The termitophile is small in relation to the size of the termite workers or soldiers, it has good eyesight whereas the termite does not, and it is fast on its feet whereas the termite is slow and clumsy. In every termitophile-termite encounter, the termitophile was able to maneuver out of range of the mandibles before the termite was even aware of its existence. We maneuvered some termites into position with a camel's hair brush and then tried to prevent the termitophile from escaping with another camel's hair brush, but in every instance, the beetle was able to crawl under or around the termite without getting caught or even attracting attention. We were thus unable to acquire any insight into the possible adaptive function of the limuloid body shape.

These same observations were confirmed in a limited way on *T. braunsi* in South Africa. However, future studies should be directed to see if there is any difference in the behavior of those forms with setae with bifurcated tips and those with straight tips.

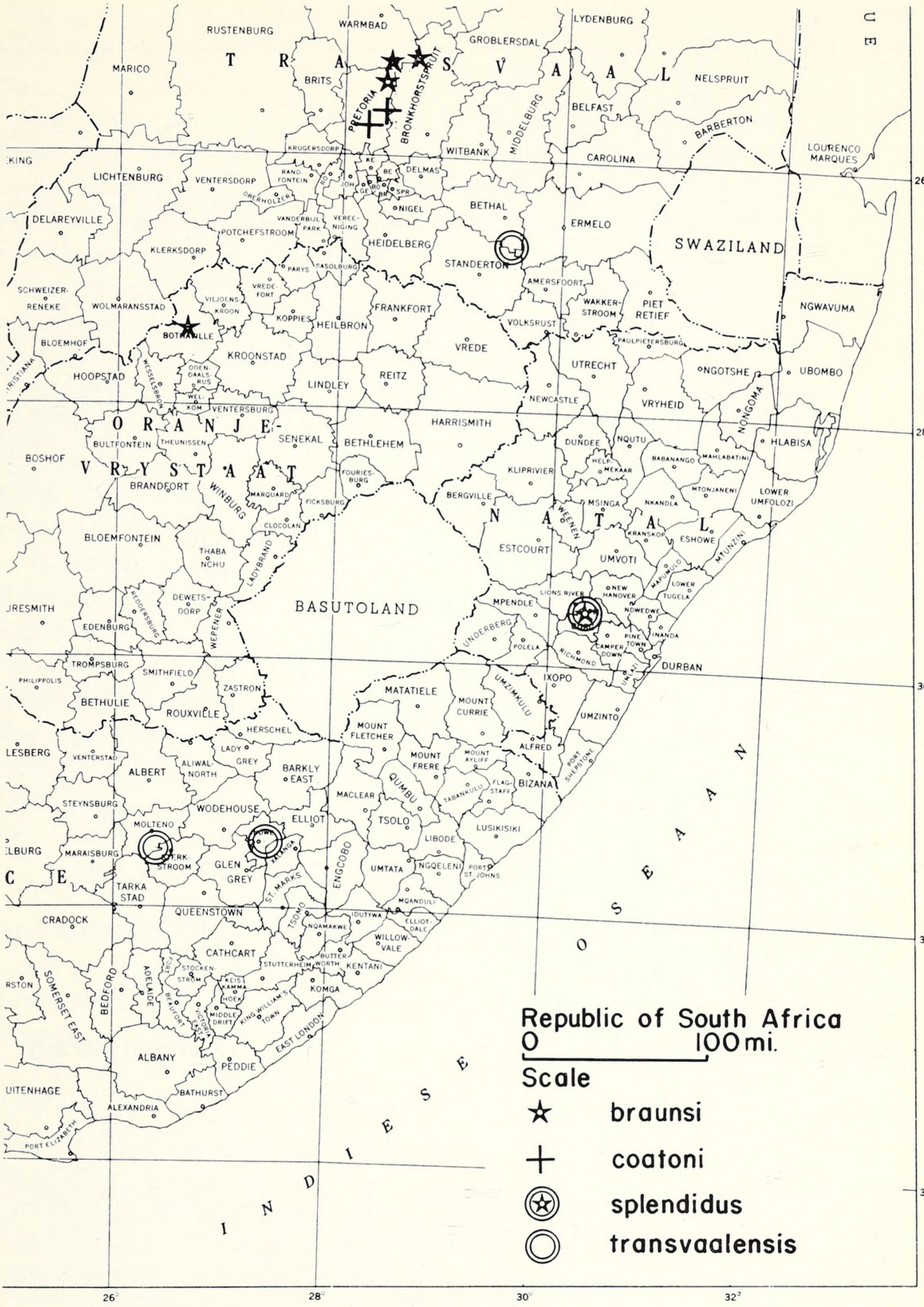


FIG. 43. Distribution of certain South African species of *Termitodiscus*.

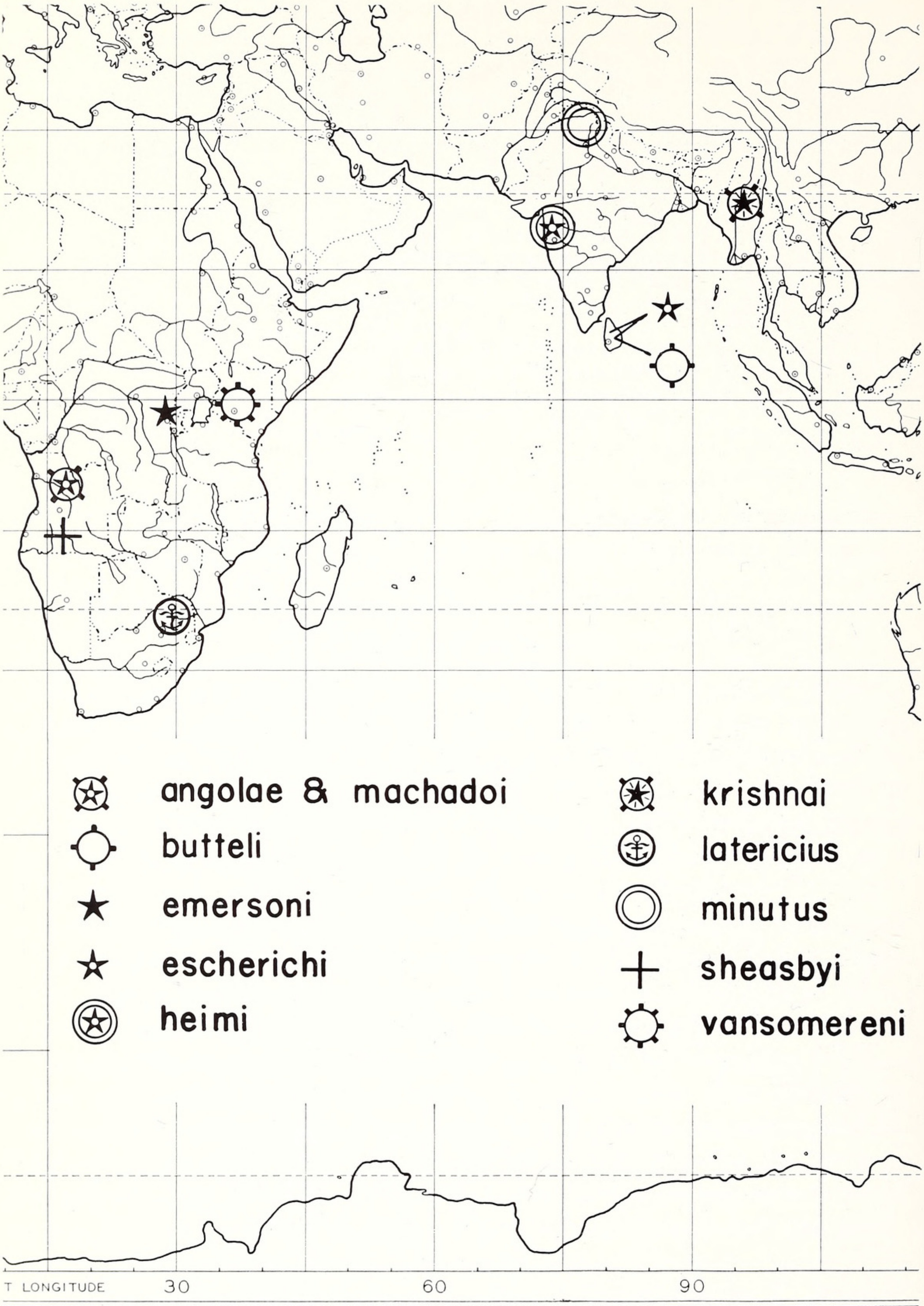


FIG. 44. Distribution of certain species of *Termitodiscus*.

Observations in the field of *T. heimi* and *T. escherichi* revealed that both species ate the fungus in the fungus gardens. Subsequent gut smears confirmed this.

The above observations should be combined with another field observation before any conclusions are drawn. Invariably, the most *Termitodiscus* were found in the fungus gardens immediately adjacent to the royal cell. These are the fungus gardens which contain the most eggs and young termites and hence there is more termite activity.

Termite activity decreases in the more peripheral fungus gardens and one seldom finds termitophiles in these. Termitophiles were never taken in the royal cells of *Odontotermes*.

Because of their association with the termites in areas of high termite activity, their perfect host specificity, and the fact that no accidental capture of *Termitodiscus* outside the termite nest has ever been made, I am interpreting the genus as integrated termitophiles whose principal adaptation to the termite hosts is avoidance of direct contact.

Wasmann (1895 and elsewhere) erected the category of "trutztypus" or defensive forms and placed the genus *Termitodiscus* in that category in 1912 and 1916 based on the morphology alone. There is no evidence that the termitophiles lead a harried existence in the nest. The avoidance of the termites under observation never led to a confrontation even when we tried to manipulate one. What seems to prevail is a kind of wary but completely dependent coexistence on the part of the termitophile and an unawareness on the part of the termites.

RELATIONSHIP OF THE TRIBE TO OTHER ALEOCHARINAE

The closest free-living aleocharine tribe to the Termitodiscini is the tribe Myrmedoniini. The following characters link the two tribes: (1) Nature of the teeth on the mandibles; (2) Structure of the legs; (3) Tarsal formula; (4) Structure of the prosternum; (5) The tri-lobed nature of the ninth abdominal segment.

The only termitophilous tribe that is close to the Termitodiscini is the subtribe Termitondina of the Myrmedoniini which may share common origins. More material of the Termitondina will be necessary before these relationships can be checked.

The relationship of the Termitodiscini to the Myrmedoniini does not destroy the tribal status of the Termitodiscini; it merely gives some idea of what the ancestral type must have been like.

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