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THE RELATIONS OF A RELICT SOUTH AFRICAN TERMITE (ISOPTERA, HODOTERMITIDAE, *STOLOTERMES*)

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Dr. Harold Kirby, during his African travels in 1935 on a John Simon Guggenheim Fellowship, found several colonies of a species of the primitive genus *Stolotermes* in Cape Province. Dr. M. F. Day also found the same species in 1938. The material turned over to me consists of six vials with many specimens of soldiers and nymphs. Unfortunately no alates or primary reproductives were found. However, the discovery of a species of this primitive genus so remote from its closest relatives in Australia, Tasmania and New Zealand is of considerable interest.

One is immediately reminded of the distribution of the genus *Porotermes*, also a rather primitive termite, which is known from one species in Australia and Tasmania [*P. adamsoni* (Froggatt) with *Calotermes convexus* Hagen, *P. froggatti* Holmgren and *P. grandis* Holmgren considered synonyms], one species in South Africa [*P. planiceps* (Sjöstedt), with *Calotermes amabilis* Sjöstedt considered a synonym and *Planitermes* considered a synonym of *Porotermes*], and one species in Chile [*P. quadricollis* (Rambur)]. *Porotermes* represents about the same level of termite evolution as *Stolotermes*. Such a distribution would seem to indicate a relict group formerly more widely distributed and now surviving in peripheral regions. One would guess that the ancestral genus must have been distributed through the connecting northern regions in Mesozoic times. There is also a possible explanation through a southern Antarctic distribution, but there is no more reason to assume such a connection than in the cases of the lung-fishes and marsupials. Connecting climatic conditions for termites were in all probability tropical or warm

temperate, the present northern and southern distribution of the order being near the 51°F. annual isothermal line. Only a few genera, such as those of the Termopsinae and *Reticulitermes*, are confined to temperate regions.

In view of the probable ancient ancestry of these living species of *Stolotermes* and *Porotermes*, the homologous parts indicate a stability of type through the ages that is noteworthy, although duplicated in numerous other instances. The persistence of a definite biological pattern with little modification through millions of years as other groups of animals spread and diversified demands explanation. One even finds a whole series of correlated characters, of no adaptive significance as such, persisting along with a general organization that is probably successful in certain ecological niches. Selection can hardly be conceived as acting directly upon many of these functionally trivial characters. It is also difficult to postulate a lack of hereditary variation when other types have become widely modified in the same length of time. One seems to be led to the conclusion that ancient adaptive characteristics selected because of their vital importance to the species become genetically so tied up and intermeshed with trivial secondary visible characters that variations in a trivial character are selected against because of the other effects of gene changes on the organism (Muller, 1940).

The correlations of characters of the genus *Stolotermes* with other genera indicate that the arrangement of the primitive genera in families and subfamilies at present recognized by students of termites is not wholly satisfactory, and I am suggesting a new arrangement of the known primi-

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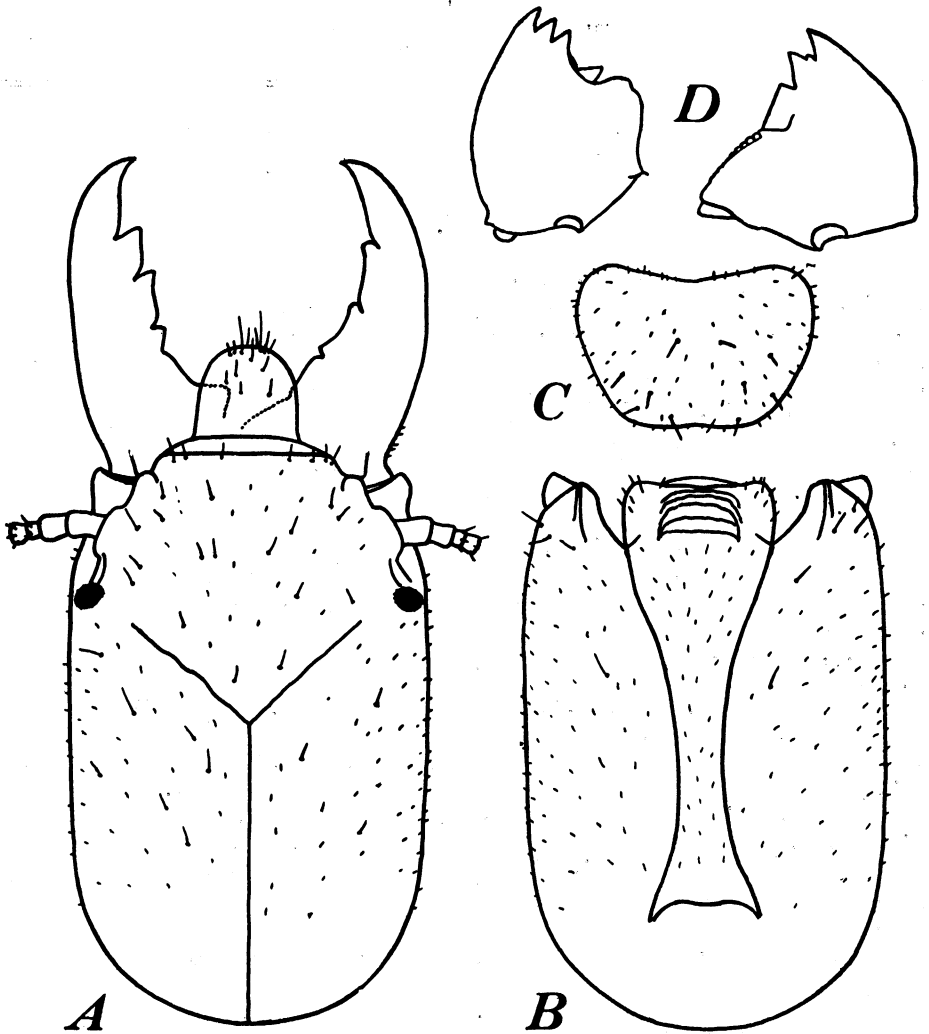


Fig. 1. *Stolotermes africanus*, new species. A—Head of soldier from above. B—Head of soldier without mandibles from below. C—Pronotum of soldier. D—Mandibles of nymph.

tive genera of both living and fossil termites exclusive of the more specialized families Rhinotermitidae and Termitidae.

The relation of the protozoans in the hind guts of these termites should prove most interesting. L. R. Cleveland and M. F. Day will soon report on their studies of these faunules. It is hoped that the ac-

cumulation of data on the relations of the protozoa and the relations of the termite hosts may ultimately give us a foundation for a critical comparison of evolutionary trends in two series of organisms, one asexual and the other sexual, and both moving together through time because of their symbiotic association.

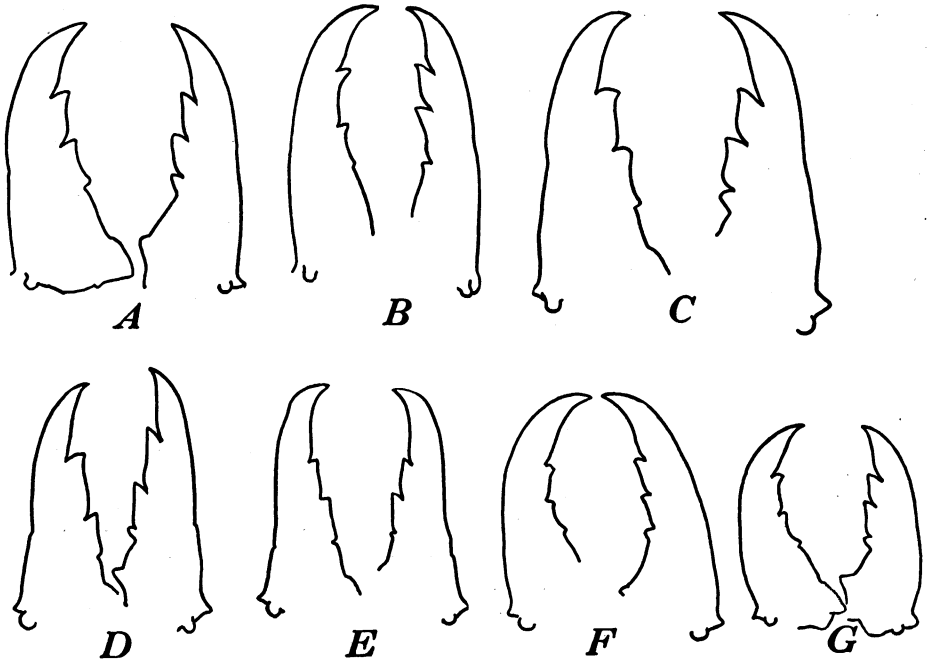


Fig. 2. Mandibles of *Stolotermes* soldiers from below (right mandible at left). A—*S. brunneicornis* Hagen. B—*S. australicus* Mjöberg. C—*S. queenslandicus* Mjöberg. D—*S. victoriensis* Hill. E—*Stolotermes* species, Kumara, Westland, New Zealand. F—*Stolotermes* species, Day's Bay near Wellington, New Zealand. G—*S. africanus*, new species.

ACKNOWLEDGMENTS

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Stolotermes africanus, new species

Figures 1, 2G

SOLDIER.—Head yellow-brown grading to lighter yellow behind, anterior half of mandibles dark red-brown. Head covered sparsely with short hairs and bristles growing more scarce toward the rear.

Head (Fig. 1A) flat, elongated, semi-quad-rangular to somewhat oval, sides fairly parallel to somewhat curved, hind margin rounded, projections above the base of the antennae, epicranial suture visible as a thin white mark; eyes pigmented, individual ommatidia visible at the edge of the eye; postmentum (Fig. 1B) ("gula") constricted in the middle with gradually expanded wide anterior end and less expanded posterior end, anterior end wrinkled. Labrum tongue-shaped, evenly rounded at tip, when fully extended reaching a little beyond the second marginal tooth of the left mandible. Mandibles (Fig. 2G) with curved outer margins; left mandible with three fairly prominent marginal teeth, the distance between the tips of the first and second marginal teeth about three-fourths the distance from tip of apical tooth to tip of first marginal tooth, first marginal tooth slightly shorter than second marginal tooth and third

marginal tooth about one-third the length of second marginal tooth; right mandible with two marginal teeth, the proportional distance from the tip of the first marginal tooth to the tip of the second marginal tooth about three-fifths to the whole distance from the tip of the first marginal tooth to the tip of the apical tooth and about equal to the distance between the two tips of the second marginal tooth, the cutting edge of the second marginal tooth evenly curved. Antennae with 14–18 articles, the third somewhat to much shorter than the second; articles near end in proportion of width to length are about 1.5:2.0 to 1.5:2.7 or .08–.09 mm. : .12–.14 mm.

Pronotum (Fig. 1C) about two-thirds the width of head with slightly indented front and hind margins, sides rounded and somewhat converging toward the rear. Meso- and metanotum often with short wing buds. Femora of legs swollen, the tibia about one-third the width of the femur from the side. Front and middle tibiae with 3 apical spines, hind tibiae with 2 apical spines. All tarsi with 4 articles, the fourth longer than the other three. A pair of styli present. Cerci with 4 or 5 articles, usually difficult to see more than 4.

NYMPH.—Mandibles (Fig. 1D) similar in dentation to those of *Archotermopsis*. Eye pigmented. No arolium ("pulvillus") between tarsal claws. Tibial spines as in the soldier.

Holotype and paratype series deposited in collection of The American Museum of Natural History, New York City.

TYPE LOCALITY.—Eight miles west of

Coldstream, Cape Province. Coll. H. Kirby, 16.III.1935, T-4106.

OTHER LOCALITIES.—Five miles west of Coldstream on Blaauwkrantz River, Cape Province, Coll. H. Kirby, 16.III.1935, T-4105. Tradouw Pass, seven miles west of Barrydale, Cape Province, Coll. H. Kirby, 25.III.1935, T-4148. Forty miles from Knysna, near Wilderness, Cape Province, Coll. H. Kirby, 18.III.1935, T-4108. Four miles from Wilderness toward George, Cape Province, Coll. H. Kirby, 23.III.1935, T-4214. The Wilderness, Cape Province, Coll. M. F. Day, 15.VIII.1938.

Every large series from South Africa contained nymphs or soldiers with reduced abnormal legs. Thirty-nine individuals had one or more legs reduced, and 279 had normal legs. There was no uniformity in the distribution of abnormalities in the different segments or sides, and both nymphs and soldiers had such abnormalities without distinction. At first I thought this queer reduction might indicate a genetic mutation. However, I also found one nymph of *S. brunneicornis* out of 49 individuals with the same abnormality. It seems as if the best explanation is regeneration of injured legs during early stadia.

COMPARISON WITH OTHER SPECIES OF *STOLOTERMES*

S. africanus seems to be closest to *S. brunneicornis*, the genotype species from Tasmania, although the specific distinctions of the species of *Stolotermes* are hardly sufficient to plot a phylogenetic system accurately. I have compared the African species with specimens kindly sent me by G. F. Hill collected at Adventure Bay, Brunni Island, Tasmania, and containing primary reproductives which I compared with the type imago at the Museum of Comparative Zoology, Cambridge, Mass. The mandibles of the soldier (Fig. 2A) were not so hooked at the tip as in most other species, including *S. africanus* (Fig. 2G). The inside edge of the apical tooth of the left mandible is more evenly curved and not so strongly sigmoid as in *africanus* and most other species except *S. victoriensis*. The postmentum is very similar to that in *africanus*. The penultimate article of

the antennae is similar to *africanus*. The fore and middle tibiae have three apical spines.

S. victoriensis Hill from the vicinity of Melbourne, Victoria, 2.II.1926, has rounder soldier heads than *africanus*, although Hill's figure does not show this to be a specific character. The mandibles (Fig. 2D) are straighter than in *africanus*. The first marginal tooth of the left mandible is proportionately longer. The distance from the tip of the first marginal tooth of the right mandible to the angle between the apical and first marginal tooth is definitely longer than in *africanus*. The sides of the anterior end of the postmentum are somewhat more parallel than in *africanus*. The fore and middle tibiae have 3 apical spines.

S. australicus Mjöberg, cotype from Cedar Creek, N. Queensland, IV.1913, has

the general shape of the head more similar to *africanus* than in the case of *S. queenslandicus*, but the mandibles (Fig. 2B) are proportionately longer. The penultimate antennal article is about two times as long as wide. The postmentum is proportionately narrower in the middle portion than in either *africanus* or *queenslandicus*. The fore and middle tibiae have 3 apical spines.

S. queenslandicus Mjöberg, cotype from Cedar Creek, N. Queensland, IV.1913, is larger with the head proportionately wider

than the pronotum compared to *africanus*. *S. queenslandicus* has straighter outer margins of both mandibles (Fig. 2C), and the distance from the apex to the first marginal tooth is proportionately greater than in *africanus*. All tibiae have only 2 apical spines. Holmgren (1911) gives 2 apical spines as a generic character, but the two species then known both have 3 spines on the fore and middle tibiae.

S. ruficeps Brauer is the only species so far recorded from New Zealand, but I have

TABLE OF MEASUREMENTS (IN MM.) OF SOLDIERS OF *Stolotermes*

		<i>S. africanus</i>	<i>S. brunneicornis</i>	<i>S. victoricensis</i>	<i>S. australicus</i>	<i>S. queenslandicus</i>	<i>S. sp., Kumara, N. Z.</i>	<i>S. sp., Day's Bay, N. Z.</i>
Total length	Range	5.84-7.33	—	7.01-11.56	7.90	11.09-11.28	8.27	7.80
	Number	20	—	3	1	3	1	1
Length head and mandibles	Range	2.76-3.09	4.06	3.37-3.78	3.90	4.64-5.08	3.82	3.84
	Number	30	1	3	1	3	1	1
Length head to side projection	Range	1.71-2.02	2.65	2.21-2.45	2.35	3.00-3.32	2.53	2.63
	Number	50	1	3	1	3	1	1
	Mean	1.874		2.32		3.14		
	σ	.0652						
	\pm s. e.	.0092						
Length left mandible	Range	1.10-1.25	1.71	1.39-1.61	1.76	1.94-2.17	1.43	1.47
	Number	50	1	3	1	3	1	1
	Mean	1.174		1.48		2.07		
	σ	.0393						
	\pm s. e.	.0056						
Width head	Range	1.14-1.34	1.73	1.68-2.03	1.49	2.29-2.32	1.43	1.38
	Number	50	1	3	1	3	1	1
	Mean	1.244		1.84		2.30		
	σ	.0427						
	\pm s. e.	.0060						
Thickness head	Range	.67-.75	1.03	.76-.79	.79	1.06-1.09	1.03	.97
	Number	30	1	2	1	3	1	1
	Mean	.715		.78		1.08		
	σ	.0198						
	\pm s. e.	.0036						
Length pronotum	Range	.41-.53	.69	.52-.69	.55	.65-.76	.63	.59
	Number	49	1	3	1	3	1	1
	Mean	.477		.59		.72		
	σ	.0293						
	\pm s. e.	.0042						
Width pronotum	Range	.74-.90	1.18	.85-1.14	.85	1.18-1.26	.94	.94
	Number	49	1	3	1	3	1	1
	Mean	.830		.99		1.23		
	σ	.0469						
	\pm s. e.	.0067						
Length hind tibia	Range	.67-.95	1.26	.94-1.29	1.18	1.59-1.77	1.06	1.18
	Number	50	1	3	1	3	1	1
	Mean	.822		1.15		1.69		
	σ	.0496						
	\pm s. e.	.0070						

single soldiers of what appear to be two species from New Zealand. These are unassociated with alates and I have no means of determining which may be *S. ruficeps* and which is a new species. One determined by G. F. Hill as *ruficeps* from Kumara, Westland, N. Z., 24.XI.1929, has a proportionately thicker head than the Australian species and *africanus*. The apical tooth is proportionately longer in both mandibles (Fig. 2E) than in *africanus*, and the mandibles are straighter. The cutting edge of the second marginal tooth of the right mandible is nearly straight. I do not know whether Hill has collections connecting this soldier with the alate of *ruficeps* or whether the determination rests upon the locality on the supposition there is a single species in New Zealand.

The other species from New Zealand is from Day's Bay near Wellington, 14.VIII.1914. The head is not so proportionately flat as the species from Australia, Tasmania and Africa. The head is somewhat longer than the other species in proportion to width. The mandibles (Fig. 2F) are about the same general curvature as *africanus*, but the apical tooth is proportionately longer than in *africanus*. The cutting edge of the second marginal tooth of the right mandible is curved as in *africanus*. The hind margin of the pronotum has a more definite notch than any of the other species.

KEY TO THE SPECIES OF *Stolotermes* Imagoes

- 1.—Hind margins of meso- and metanota broad, nearly straight.....2.
- Hind margins of meso- and metanota narrow with small notch.....*S. ruficeps*.
- 2.—Fore and middle tibiae with 3 apical spines, hind tibiae with 2 apical spines.....3.
- All tibiae with 2 apical spines.....*S. queenslandicus*.
- 3.—Pronotum wider, more than 0.9 mm.....*S. brunneicornis*.
- Pronotum narrower, less than 0.9 mm.....*S. victoriensis*.

Soldiers

- 1.—Head relatively flat, thickness less than two-thirds width.....2.
- Head relatively thick, thickness more than two-thirds width.....6.
- 2.—Fore and middle tibiae with 3 apical spines.....3.
- All tibiae with 2 apical spines.....*S. queenslandicus*.

- 3.—Larger species, length of left mandible over 1.30 mm.....4.
- Smaller species, length of left mandible under 1.30 mm.....*S. africanus*.
- 4.—Tips of mandibles not markedly hooked, cutting edges of apical teeth weakly sigmoid.....5.
- Tips of mandibles relatively hooked, cutting edges of apical teeth sigmoid.....*S. australicus*.
- 5.—Mandibles relatively curved.....*S. brunneicornis*.
- Mandibles relatively straight.....*S. victoriensis*.
- 6.—Mandibles relatively curved.....*S. sp.* (Day's Bay, N. Z.).
- Mandibles relatively straight.....*S. sp.* (Kumara, N. Z.).

SYNONYMY OF SUBFAMILY STOLOTERMITINAE

- < Family Termitina Hagen, 1858a, p. 4.
- < Subfamily Calotermitinae Silvestri, 1903, pp. 16, 17.
- < Subfamily Calotermitinae Froggatt, 1896, p. 516.
- < Tribe Hodotermitini Desneux, 1904a, p. 284.
- < Tribe Hodotermitini Desneux, 1904b, p. 14.
- = Subfamily Stolotermitinae Holmgren, 1910a, p. 285.
- = Subfamily Stolotermitinae Holmgren, 1910b, p. 137.
- = Subfamily Stolotermitinae Holmgren, 1911, pp. 34, 45.
- = Tribe Stolotermitini Handlirsch, 1930, p. 856.
- = Subfamily Stolotermitinae Hare, 1937, p. 475.
- = Tribe Stolotermitini Statz, 1939, p. 44, Tab. 4.

SYNONYMY OF GENUS *Stolotermes* HAGEN

- < Genus *Hodotermes* Hagen, 1858a, p. 81.
- = Subgenus *Stolotermes* Hagen, 1858a, p. 105.
- < Genus *Hodotermes* Hagen, 1858b, p. 13.
- = Subgenus *Stolotermes* Hagen, 1858b, p. 16.
- = Subgenus *Stolotermes* Girard, 1879, p. 273.
- = Genus *Stolotermes* Froggatt, 1896, pp. 517, 537.
- < Genus *Hodotermes* Wasmann, 1897, p. 149.
- = Subgenus *Stolotermes* Wasmann, 1897, pp. 149, 182.
- = Genus *Stolotermes* Desneux, 1904b, pp. 15, 17.
- = Genus *Stolotermes* Froggatt, 1905, p. 22.
- = Genus *Stolotermes* Holmgren, 1911, p. 46.
- = Genus *Stolotermes* Bugnion, 1914, p. 175.
- = Genus *Stolotermes* Mjöberg, 1920, p. 4.
- = Genus *Stolotermes* Hill, 1926, pp. 192, 193.
- = Genus *Stolotermes* Emerson, 1928, p. 405.
- = Genus *Stolotermes* Pongrácz, 1928, p. 114.
- = Genus *Stolotermes* Hare, 1937, pp. 460, 461, 474.

DIAGNOSIS OF THE SUBFAMILY STOLOTERMITINAE AND THE GENUS
STOLOTERMES

IMAGO.—Head, pronotum, wing scales and abdomen clothed with fairly long hairs, fewer on head.

Fontanelle absent; epicranial suture present; ocelli reduced; eyes medium size, oval, the front margin fairly straight, a little more than one-half their length from the lower margin; postclypeus very short and fused with the front, demarcation line marked by a depression with no visible suture, width about five times length; anteclypeus short, hyaline; labrum tongue-shaped, tip fairly straight; antennae with 15–17 articles; right mandible with 2 marginal teeth and a molar plate, a small subsidiary tooth on the anterior portion of the first marginal tooth near its base; left mandible with 3 marginal teeth of about equal size, the third separated from the others by a wide-angled notch. The arrangement of the teeth (Fig. 1D) is quite primitive and is about intermediate between *Archotermopsis* and *Hodotermopsis* in its degree of specialization and is more primitive in type than *Hodotermes*, *Poro-termes*, *Mastotermes* or *Kalotermes*.

Pronotum much narrower than the head, relatively flat with a shallow longitudinal depressed line in the middle and two shallow lateral depressed lines near the anterior edge, together making a Y-shaped depression, front margin rather evenly concave, sides somewhat rounded, hind margin rather wide and slightly emarginate. Hind margins of meso- and metanota either nearly straight and somewhat wider than the hind margin of the pronotum or (in *ruficeps*) sides converging and hind margin narrow with a small median notch. (This striking difference in *ruficeps* may warrant separation into a new subgenus, but I hesitate to take this step without specimens of the imagoes of all the species and without a better series of the New Zealand, Australian and Tasmanian species.) Tibial apical spines either 3:3:2 or 2:2:2 (in *queenslandicus*). Tarsi with 4 articles. Arolium absent. Tip of scale of forewing extends to or a little beyond the base of the scale of the hind wing, not extending to or much beyond the hind margin of the meso-

notum. Basal suture of the wing runs at an angle of roughly 45° from the costal border back to the anal region and is slightly sigmoid in shape, the costal border of the scale nearly twice the length of the anal border. Costal margin of the wing nearly straight for four-fifths the length of the wing; inner margin evenly curved. Shape of wing in general similar to that of *Archotermopsis* except for the scale. Veins *Sc*, *R*₁ sometimes, *R*₂₊₃, *R*₄₊₅, *M* and 2 or 3 branches of *Cu* distinct at or just beyond the basal suture. Wing membrane sometimes with a few weak cross veins or reticulations. Wing beyond the suture may have scattered bristles on the veins and membrane, especially near the tip. Wing membrane punctate with minute dots of chitin, giving a cloudy appearance viewed with the naked eye. As in the case of most other genera of termites, the wing venation is quite variable, making descriptions in more than general terms liable to numerous exceptions. The following description is taken from about 15 individuals of various species. In the forewing *Sc* runs to the costal border fairly close to the suture. If present, *R*₁ joins the costal border about one-twelfth the length of the wing from the suture. *R*₂₊₃ single or branched, joining the costal border from one-tenth to one-third the length of the wing from the suture. *R*₄₊₅ has about 7–11 branches reaching the border in the outer half or two-thirds of the wing. *M* is somewhat weaker than the radius and is closer to *Cu* than to *R*₄₊₅ a little beyond the suture, 9–14 branches reach the inner margin in the outer three-fourths to one-half of the wing. *Cu* has 4–6 branches reaching the inner margin in the basal sixth to half of the wing. The hind wing scale is roughly the same shape as the forewing scale but only about six-elevenths to seven-tenths the length of the forewing scale. *Sc* not distinct from the costal border beyond the suture. *R*₁ absent. *R*₂₊₃ with 1–3 branches joining the border from one-eighth to three-fifths the length of the wing from the suture. *R*₄₊₅ with 3–12 branches joining the border from one-third to one-half the length from the

tip. *M* is weaker than R_{4+5} and is joined with *R* just beyond the suture, running about midway between *R* and *Cu*, with 6–10 branches joining the inner margin about one-fourth to two-thirds the length of the wing from the suture, the outer branches close to the tip. *Cu* stronger near the base than *M*, 3–8 branches joining the inner margin in the basal half of the wing. A short and extending little beyond the suture along the inner margin.

Cerci with 4–5 articles. Styli absent in the female and present in the male, extending about to the tip of the abdomen.

SOLDIER.—Head, thorax and abdomen sparsely covered with hairs and longer bristles.

Head proportionately fairly large, elongated or oval, flat or fairly flat, front flat and evenly joined to the vertex; epicranial suture present; frontal gland absent; two rather sharp longitudinal ridges on the ventral side near the ventral condyle of the mandible; postmentum with a wide anterior region, the narrowest region less than one-half the width of the widest region; mandibles (Fig. 2) proportionately large and

well developed, the left mandible with three marginal teeth, four notches and a molar plate, right mandible with two marginal teeth, three notches and a molar plate, the second marginal tooth with a long cutting edge with a point at each end; eyes distinct, as long as the width of the antennal socket to longer than the widest diameter of the antennal socket, sometimes facettes visible externally; antennae with 14–18 articles; labrum widely tongue-shaped, anterior margin straight or curved; postclypeus fused with the front but the suture depression is still present.

Pronotum narrower than the head. Meso- and metanota often with short wing buds. Tarsi with 4 articles, arolium absent. Femora swollen, the tibia about one-third the width of the femur from the side, front and middle tibiae with 2–3 apical spines, hind tibiae with 2 apical spines.

A pair of styli present in both males and females. Cerci with 4–5 articles, usually difficult to see more than 4. Males and females distinguishable externally by the larger seventh sternite in the female.

THE RELATIONSHIPS OF *STOLOTERMES*

Stolotermes has always been considered a primitive termite from the time the genus was described as a subgenus of *Hodotermes* in 1858 by Hagen. With our more recent knowledge of evolutionary trends in termites we are able to place the group in its phylogenetic relationship with fair accuracy.

The imago-nymph mandible (Fig. 1D) is clearly homologous and very close to *Archotermopsis* and in type is between *Archotermopsis* and *Hodotermopsis* (Emerson, 1933). Other genera of the Termopsinae are derived forms from this mandibular type through various degrees of reduction of the second marginal tooth of the left mandible. The *Archotermopsis-Stolotermes* mandible is more primitive and closer to the Blattoid type than any other genus of primitive termites including *Mastotermes* (which has lost a visible second marginal tooth in the left mandible), and the Hodotermitinae (which have a nearly completely reduced

point of the second marginal tooth of the left mandible) and would also seem to be the ancestral type of the Rhinotermitidae (Hare, 1937, p. 461). The small subsidiary tooth at the base of the first marginal tooth of the right mandible does not seem to be present in the Blattoid types known to me and is not present in *Mastotermes* and *Kalotermes* but is characteristic of the Termopsinae, *Porotermes* and the Rhinotermitidae and is even present in the primitive Termitidae of the genus *Acanthotermes*. This subsidiary tooth is very small and often is practically invisible in the Hodotermitinae but is present in a reduced form in some of these termites. This peculiar character cannot conceivably be of any adaptive significance and is a good example of a trivial character from a functional standpoint persisting over a long period of geological history. The imago-nymph mandible of *Porotermes* is similar to that of *Zootermopsis*, and in this respect

Stolotermes is more primitive than *Porotermes*. The soldier mandible of *Porotermes* is closer to the Termopsinae than to *Stolotermes*. The relatively long anterior cutting edge which gives a blunt triangular shape to each tooth is a primitive character especially well seen in the soldier mandibles of *Archotermopsis* and in *Anacanthotermes*, and in this respect *Porotermes* is more primitive than *Stolotermes*.

The primitive termites had more joints in the various appendages than the later evolved types. (One imago of *Hodotermes* in my collection has 33 antennal articles and *Mastotermes* commonly has 30 or 31.) The Termopsinae, with 22-27 articles in the antennae, tarsi with 5 articles, and with 6-8 articles in the cerci of *Archotermopsis* (4-8 articles in the subfamily as a whole), must be considered more primitive. Also the kidney-shaped or lenticular eye of *Archotermopsis*, the longer styli in the male, the tibial spine arrangement, the presence of the arolium ("pulvillus") between the ungues ("tarsal claws") and the more simple suture of the wing indicate more primitive structural features in *Archotermopsis*. The presence of a subapical spine between the two apical spines on the hind tibiae of *Porotermes* must be considered a more primitive character than the arrangement of tibial spines in *Stolotermes*. Also the middle tibiae of *Porotermes adamsoni* sometimes have four apical spines, and the hind tibiae may have two or three apical spines as well as the single subapical spine of the inner row.

Certain characteristics of *Stolotermes* shared with the Termopsinae and other primitive termites must be considered as specialized. The reduction of the ocelli is one of the most noteworthy characters of this type. *Mastotermes*, *Prokalotermes*, *Proelectrotermes*, *Electrotermes* and *Kalotermes* have ocelli as well as the higher termites (with a few exceptions). The lack of ocelli in so many primitive termites including the Hodotermitinae, Termopsinae, Stolotermitinae and *Porotermes*, correlated with the pronotum narrower than the head and the presence of a subsidiary tooth at the base of the first marginal tooth of the right mandible, makes convergent reduction of

the ocelli less likely. It would appear that a primitive stock lost the ocelli and then branched out into several groups. The ocelli are much reduced in the Stolotermitinae, and in no case am I sure that I have seen vestigial ocelli. Holmgren (1911, p. 45) states the ocelli are absent, but Hill (1921, p. 433) states that the ocelli are invisible except in cleared preparations and are then very indistinct in *Stolotermes victoriensis*. In any case, groups with reduced ocelli cannot be considered ancestral types to groups with ocelli. This leaves a large gap in our knowledge of the ancestry of *Kalotermes* by eliminating all the primitive living termites except *Mastotermes*. A possible bridge connecting the Kalotermitinae with the Mastotermitidae (which shows many specialized features which indicate that it is a side branch from the common ancestry of termites) is the fossil genus *Prokalotermes* which possesses ocelli, mandibles of the *Mastotermes-Kalotermes* type, pronotum wider than the head and cerci with 4-5 articles. Some of the other fossil genera, such as *Electrotermes*, also show certain transitional characters, such as ocelli, pronotum wider than the head, an outer row of spines on the middle tibiae and cerci with 4 articles. *Prokalotermes* has a branched R_{2+3} vein in the hind wing, while *Electrotermes* has an undivided R_{2+3} in the hind wing. Because of the primitive condition of the cerci, I think it best to separate these fossil genera (*Proelectrotermes*, *Prokalotermes* and *Electrotermes*) as a subfamily of the Kalotermitidae which I call Electrotermitinae (new subfamily). The fossil genus *Eotermes* may be tentatively placed in this subfamily until more characters are discovered.

Mastotermes, the Termopsinae and the Kalotermitidae have the arolium (sometimes absent in some Kalotermitinae), thus indicating a more primitive ancestry in this respect than for either *Stolotermes* or *Porotermes*. The absence of the arolium ("pulvillus") in *Stolotermes*, *Porotermes* and the Hodotermitinae is a specialized character.

The fossil genus *Umerella* is described with pronota both wider and narrower than the head. In other characters, such as the four-jointed tarsus, the small eye, the seem-

ing absence of the ocelli and the characteristic wing venation, particularly in the unbranched Sc , the absence of R_1 , the presence of R_{2+3} (unbranched in the hind wing) and the inferior branches of the radial sector, *Ulmeriella* is similar to *Microhodotermes*. It is my opinion that *Ulmeriella* should be placed in the Hodotermitinae.

The pronotum seems to be different from that characteristic of the subfamily, but possibly the reëxamination of the fossil species may yet show the pronotum to be both narrower than the head and with the large, somewhat raised anterior lobe as in the Hodotermitinae. Statz (1939) places *Ulmeriella* in the Termopsini, but the characters described do not conform to this grouping as treated by Emerson (1933).

The wing venation of *Stolotermes* is fairly primitive and fairly close to that of the Termopsinae except for the peculiar and distinctive shape of the scales and wing sutures.

Most of the primitive termites show wide variation in the measurements of the soldiers, such as is characteristic of *Zootermopsis* and *Kalotermes*. The numerous specimens of *Stolotermes africanus* showed measurements in a narrower range than would be typical for such a series from a species of *Kalotermes*. Insufficient series of other species of *Stolotermes* make it impossible for me to know at the present time whether a narrow range of soldier size is characteristic of the genus.

Browman (1935), in his study of the female genitalia of termites, states that

Stolotermes is close to *Anacanthotermes* and *Zootermopsis*. He found "dorsal valves" present in *Mastotermes*, *Kalotermes*, *Reticulitermes* and *Pseudacanthotermes*, but absent in *Zootermopsis*, *Anacanthotermes*, *Stolotermes* and *Porotermes*. This character thus correlates with the presence of ocelli.

In summary, we should place *Stolotermes* as a genus of the Hodotermitidae somewhat more specialized than *Archotermopsis* and best considered as an offshoot from the Hodotermitid base and not ancestral to any other living termites but possessing many characteristics that are ancestral in type to other termite groups, notably the Rhinotermitidae. The only living termite which has a correlated series of more primitive characters that are ancestral in type to *Stolotermes* is *Archotermopsis*, but *Stolotermes* has so many characters distinctly specialized compared to *Archotermopsis* that it is best kept in a separate subfamily, the Stolotermitinae of the family Hodotermitidae, thus indicating a considerable gap between the species of *Stolotermes* and the species assigned to the different genera of the Termopsinae. Also *Stolotermes* is not close enough to *Porotermes* to be included in the same subfamily, and *Porotermes* is probably best considered as a separate subfamily, the Porotermitinae (new subfamily) of the family Hodotermitidae. The distribution of the various characters discussed would seem to necessitate a somewhat new arrangement of subfamilies and families of primitive fossil and living termites.

SUGGESTED CLASSIFICATION OF GENERA OF PRIMITIVE FOSSIL AND LIVING TERMITES

Family Mastotermitidae

- Genus *Mastotermes* (Eocene, Oligocene, Miocene, living)
- Genus *Pliotermes* (Miocene)
- Genus *Diatermes* (Oligocene)
- Genus *Miotermes* (Miocene)

Family Kalotermitidae

- Subfamily Electrotermatinae, new subfamily
- ?Genus *Eotermes* (Oligocene)
- Genus *Proelectrotermes* (Eocene)
- Genus *Prokalotermes* (Miocene)
- Genus *Electrotermes* (Eocene)
- Subfamily Kalotermitinae

Genus *Kalotermes* (Oligocene, Miocene, Pleistocene, living)

- Genus *Neotermes* (Pleistocene, living)
- Genus *Paraneotermes* (living)
- Genus *Rugitermes* (living)
- Genus *Procryptotermes* (living)
- Genus *Cryptotermes* (Pleistocene, living)
- Genus *Eucryptotermes* (living)
- Genus *Glyptotermes* (Pleistocene, living)
- Genus *Calcaritermes* (living)

Family Hodotermitidae

- Subfamily Termopsinae
- Genus *Termopsis* (Eocene)

Genus *Archotermopsis* (Eocene, living)
 Genus *Parotermes* (Miocene)
 Genus *Hodotermopsis* (living)
 Genus *Zootermopsis* (Miocene, living)
 Subfamily Porotermitinae, new subfamily
 Genus *Porotermes* (living)
 Subfamily Stolotermitinae
 Genus *Stolotermes* (living)

Subfamily Hodotermitinae
 Genus *Ulmeriella* (Oligocene)
 Genus *Microhodotermes* (living)
 Genus *Hodotermes* (living)
 Genus *Anacanthotermes* (living)
 Family Rhinotermitidae
 Family Termitidae

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