DISTRIBUTION AND BIOLOGY OF THE PRIMITIVE DRY-WOOD TERMITE *PTEROTERMES OCCIDENTIS* (WALKER) (KALOTERMITIDAE)[1]

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This summary of recent studies on *Pterotermes* is part of an irregular series of contributions to the biology and ecology of the relatively rich termite fauna of southwestern North America. The fact that such a large and primitive termite has been known from about a dozen rather poorly documented collections is indicative of the need for such knowledge in this rapidly developing region. Indeed, very little additional information on this species has beeen published since the important summary by Banks and Snyder in 1920. Most of the 25 new records have been accumulated by members, students and friends of the Department of Entomology at the University of Arizona, largely within the last ten years. The most extensive additions were made during a trip through Baja California in the late summer of 1959 by Floyd G. Werner and Keith W. Radford. Their almost nightly collections of this termite in a light trap indicate that their schedule must have coincided closely with the peak of the flight season. Although most of the records consist of alates taken in light traps, in seven instances one or more colonies have been found which have added much new biological information.

Distribution. This species has long been included in the large, cosmopolitan genus, *Kalotermes*. On the basis of careful morphological and taxonomic considerations, Krishna (1961) removed it to a previous place in the genus *Pterotermes*. Because of its probable key position in arising directly from ancestral kalotermitids and its apparent rarity, all readily available records have been brought together in Table 1 and plotted in Figure 1. Those in Mexico, particularly from the generally unfamiliar geography of Baja California, have been numbered to facilitate their location.

The distribution is thus found to conform closely to the Sonoran Desert as it has been delimited on the basis of the vegetation. A few marginal localities in southeastern Arizona and southern Baja California might be considered as local extensions of the region. A brief characterization of this, the richest of the four areas comprising the

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North American Desert, is pertinent to the discussions which follow. The physical features, vegetation and flora of this desert have been well reviewed by Shreve (1951). The Sonoran Desert lies in a region of plains, hills and mountains, and extends in elevation from approximately 3500 feet in eastern Arizona and northern Sonora to sea level on the coasts of Sonora and Baja California, and to below sea level in the vicinity of the Salton Sea in southern California. The Colorado River is the only permanently flowing stream in the entire region. A fairly uniform, continental type of climate prevails, in which the temperature varies from some of the highest records for North America to occasionally heavy frosts in the northern and eastern sections. Annual rainfall generally increases in amount from west to east, with less than 5 inches falling in the lower Colorado Valley and much of Baja California to slightly more than 15 inches in eastern Arizona and Sonora. The seasonal distribution of rainfall also varies importantly, with the extreme western areas receiving virtually all of their moisture during the winter from December to March. Going eastward the pattern shifts so that the eastern borders of the desert receive their major rainfall during a well-defined summer season from July to September.

In Arizona where more precise information is available, *Pterotermes* has been found from approximately 4000 feet on the lower slopes of a few mountain ranges, across the bajadas and onto the adjacent valley floors. It is apparently restricted to the more open foothills and bajadas rather than to the recesses of deep canyons. Here it is found in the larger woody plants of the desert scrub or spinose desert plant communities (Figs. 2 and 3). It is hardly necessary to point out that nearly all the collections from Baja California have been made in the lower, less rugged areas which are more readily accessible, either by sea or by the few passable roads over the peninsula.

Emerson (1955) has mentioned that temperature and moisture are the major physical factors limiting termite dispersal, largely by their effects in determining vegetation types. *Pterotermes* is a primitive, monotypic genus, apparently endemic to the hot, dry Sonoran Desert. Although almost pure speculation, it may be of interest to suggest that *Pterotermes* is so restricted not so much by high temperature and low moisture as by the higher rainfall of the surrounding regions. Approximately 12 vigorous and healthy colonies have been personally examined in extremely desiccated wood. A single large colony was completely removed from a dead palo verde tree in February, 1966, after a series of unusually heavy rains. This

colony contained a high percentage of individuals which had apparently succumbed in large terminal chambers to drowning and attack by fungi, bacteria, or both.

There is also limited evidence that *Pterotermes* may occupy a very narrow niche in this region where it only rarely comes into contact with other dry-wood termites. Two colonies have been found in wood previously or concurrently attacked by *Marginitermes hubbardi* (Banks). *Marginitermes* is itself a rather primitive, monotypic genus which is endemic to the southwestern United States and western Mexico. However, from the above evidence and wider field experience with the latter, it is my impression that *Pterotermes* is able to occupy even hotter and dryer situations than *Marginitermes*.

Comparative studies on water loss and cuticular structure (Collins and Richards, 1966) should provide a basis for explaining the adaptations of various species of termites to their particular environments. Indeed, Collins (1966, *in litt.*) has found that older and larger nymphs of *Pterotermes* have a comparatively low rate of water loss. She feels that the cuticular cement layer, which is particularly well developed in these forms, may be largely responsible for the ability of this species to conserve water and, hence, to occupy the severely dry environment of the Sonoran Desert.

As a result of very inadequate collecting there are a few broad discontinuities in the distribution. Further field work should be conducted to determine whether or not this termite has an essentially uninterrupted distribution generally within the Sonoran Desert. It may actually be absent over many of the intermont plains which are dominated by smaller and lower plants such as *Larrea* and *Franseria*. However, it is a strong flier and may well be able to cross narrowed valleys between adjacent mountain ranges — if not in one generation, then in several by way of relatively isolated trees and cacti, essentially as in island-hopping. After all, it does occupy a region where hosts are of necessity very widely spaced.

HOST TREES AND NESTING SITE. According to the meager records, *Pterotermes* has thus far been recorded nesting in the dead wood of only three plants: in the ribbed, woody skeletons of the giant or saguaro cactus, *Cereus giganteus* Engelm. (Fig. 2); one species of the green-stemmed palo verde tree, *Cercidium floridum* Benth.; and in the dead, flowering stalk of the non-arborescent Spanish bayonet, *Yucca Whipplei* Torr.

In the foothill areas of the Santa Rita Range Reserve and south of Oracle Jct., several colonies were discovered in dead palo verdes of this species from which the bark had long since slipped off. A

TABLE 1. Distributional and flight data for *Pterotermes occidentis*. Localities in Mexico are numbered for reference on map in figure 1.

LOCALITY	ELEVATION	DATE	NO. TAKEN IN FLIGHT	COLLECTOR OR REFERENCE
ARIZONA: COCHISE CO.				
"near Douglas"	ca. 4000′			Light, '29
PINAL CO.				
B. Thompson Arboretum (4 mi. W. Superior)	2400′	VIII-6-55	2	B. Benson
Oracle Jct., 3 mi. S, Hwy. 80-89	3200′		Colony	J. M. Nelson
PIMA CO.				
Sta. Rita Range Res. (10 mi. SE Sahuarita)	3600′	III-21-66	6 Colonies	W. L. Nutting
Sabino Can., Sta. Catalina Mts.	ca. 2800′	I-7-17	Colony	Banks and Snyder, '20
	2800′	VII-26-48	3	F. Werner, W. Nutting
Oracle Jct., 8 mi. S, Hwy 80-89	3000′	III-26-65	2 Colonies	R. Rush, W. Nutting
Tucson Mts., N. Slope	2450′	III-5-61	Colony	F. G. Werner
Tucson Mts., W. Slope (Desert Museum)	2800′	VIII-28-55	3	G. Butler, F. Werner
	2800′	VIII-1-16-62	1-45	W. Nutting, S. Oman
Coyote Mts.		VIII-4-7-17	"flights"	Banks and Snyder, '20
Baboquivari Mts.		VIII-7-9-17	"flights"	Banks and Snyder, '20
Baboquivari Can., Baboquivari Mts.	3550′	VII-17-49	4	F. Werner, W. Nutting
Ajo, 15 mi. S	1760′	VIII-24-49	4	F. Werner, W. Nutting
Alamo Wash, Organ Pipe Cactus Nat. Mon.	1960′	III-7-64	Colony	J. F. Burger
Ajo Mts., W. slope	2400′	II-15-59	Colony	F. G. Werner

TABLE 1. (Continued)

	LOCALITY	ELEVATION	DATE	NO. TAKEN IN FLIGHT	COLLECTOR OR REFERENCE
	MEXICO: SONORA				
1	Guaymas, 5 mi. N		VIII-16-59	Colony	F. Werner, W. Nutting
	"Westkuste von Centroamerika"			Colony	Hagen, 1858
	BAJA CALIFORNIA DEL NORTE				
2	Can. del Tajo, E. slope Sierra Juarez (ca. 30 mi. S. Rumorosa)	ca. 3000′	III-30-53	Colony	J. A. Powell, '66
3	San Felipe	ca. 30′	VIII-23-59	2	F. Werner, K. Radford
4	I. Angel de la Guarda				Banks and Snyder, '20
5	I. San Esteban		IV-19-20-21	Colony	Light, '33
6	Mezquital	ca. 1600′	VIII-25-59	8	F. Werner, K. Radford
7	Puerto de Sto. Domingo (S.D. Landing)		VI-1-27	Colony	Light, '29
	BAJA CALIFORNIA DEL SUR				
8	Bahia San Bartolomé		VI-1-3-25	Colony	Light, '33
9	San Ignacio, 4 mi. W	ca. 300′	VIII-26-59	2	F. Werner, K. Radford
10	Mulegé, 1 mi. S		VIII-27-59	4	F. Werner, K. Radford
11	Canipole, 10 mi. SW		VIII-28-59	34	F. Werner, K. Radford
12	I. Cármen, Bahia Marquer		V-23-21	Colony	Light, '33
13	I. Monserrate		V-24-21	Colony	Light, '33
14	I. San José				Krishna, '61
15	Pénjamo, 22 mi. NW	ca. 200′	VIII-29-59	26	F. Werner, K. Radford
16	La Paz, 25 mi. W	ca. 300′	VIII-30, IX-1	34, 8	F. Werner, K. Radford
17	La Paz		XII-'28	Colony	Light, '29
18	Todos Santos, 4 mi. N		IX-2-59	448	F. Werner, K. Radford
19	Santiago, 6 mi. SW	ca. 450′	VIII-31-59	4	F. Werner, K. Radford
20	Santa Rosa			Colony	Snyder, '66, *in litt.*
21	San José del Cabo, 10 mi. SW	ca. 100′	IX-1-59	2	F. Werner, K. Radford
22	Cabo San Lucas				Banks and Snyder, '20

few colonies were also noted in dead branches, down to one inch in diameter, on living trees in the same areas. An incipient colony was found by George Hofer in the sapwood of a dead palo verde (*Cercidium* sp.?) in Sabino Canyon (Banks and Snyder, 1920). The fairly large colony from Guaymas, Sonora, was from a short branch, one inch in diameter, on a living palo verde (species?). Burger took a very large colony in a fragment of palo verde (species?) trunk, about six feet long and 10-12 inches in diameter, partly buried in the sand of Alamo Wash. A colony in a "palo verde stump" was sampled by C. C. Lamb at La Paz, Baja California del Sur (Light, 1929).

There are three or four species of *Cercidium,* one or more of which are very abundant and characteristic trees in various parts of the Sonoran Desert. In the Arizona Upland, and probably elsewhere in their ranges, *C. floridum* is more abundant on upper bajadas and along drainageways, while *C. microphyllum* prefers hills, outwash slopes and plains. There seems to be no reason why *Pterotermes* should not utilize the wood of all these species wherever they occur.

In the Tucson Mts. Werner collected specimens from a colony in a disintegrating saguaro skeleton. The only other association with this wood was the small colony in a single rib, about one inch in diameter and a few feet long, found on the open desert floor in the Ajo Mts., also by Werner. *Cereus giganteus* is prominent over most of the Arizona Upland and the Plains of Sonora, but it is absent from the Foothills of Sonora and Baja California. Extensive collecting has been done in southern Arizona for termites and other xylophagous insects for many years. Since *Pterotermes* has not been found in any other wood (mesquite, *Prosopis juliflora,* and ironwod, *Olneya tesota,* for example) it is not improbable that the palo verdes and saguaro provide the most suitable nesting sites in this part of the desert.

In the remaining subdivisions of the Sonoran Desert, however, there is a different and even wider selection of woody plants which should be searched for *Pterotermes;* for example, the dead skeletons of other large, columnar cacti in the genera *Cereus* and *Pachycereus.* The only additional host data accompany the collection made by J. A. Powell from Canyon del Tajo, Sierra Juarez, in northern Baja California. "These specimens were taken in dry (1952) flowering stalks of *Yucca whipplei* on the trail down into the canyon probably at an elevation of about 3000 feet." Powell also added that "I have subsequently examined stalks of this host over a wide range in California from perhaps 40 or 50 localities in connection

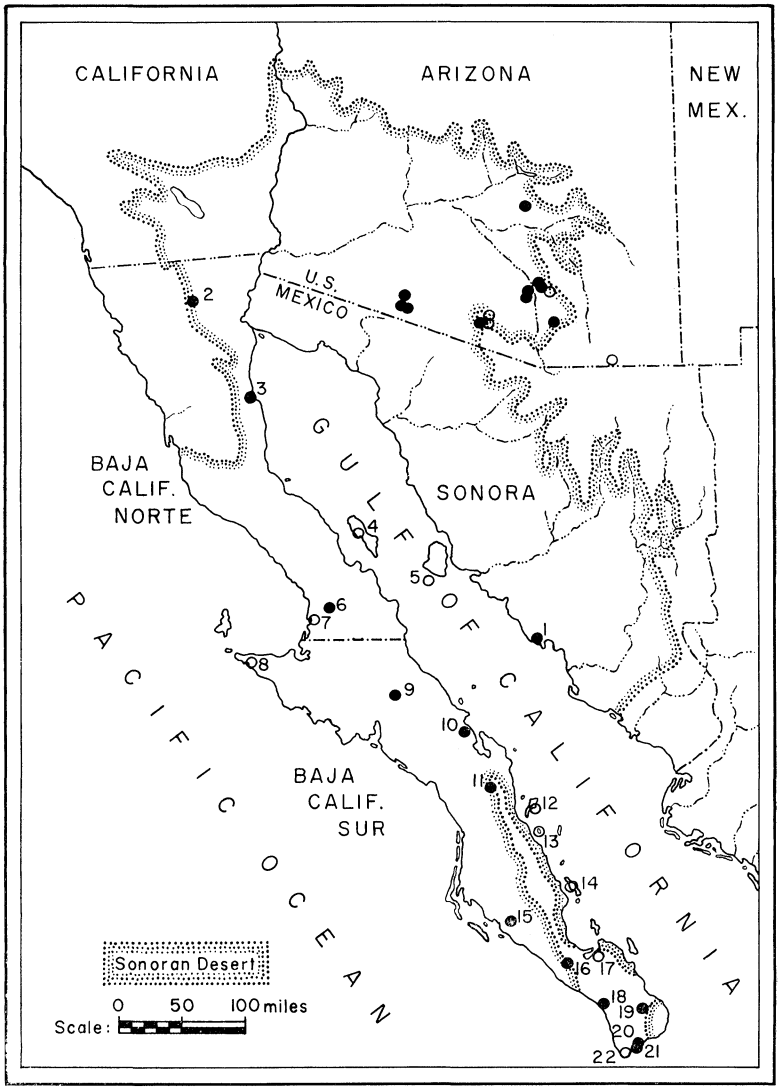


Figure 1. Map of the Sonoran Desert showing distribution of *Pterotermes occidentis:* open circles, previous records; solid circles, new records. See Table 1 for key to numbered localities in Mexico.

with studies of the moths associated with it and have never seen termites in the stalks elsewhere" (Powell, 1966, *in litt.*). A collection of nymphs was taken "in Yucca" by C. C. Lamb at Santo Domingo Landing, Baja California del Sur (Light, 1929). The fibrous or pithy tissues of yuccas would seem to be a rather unusual situation for the nest of a dry-wood termite.

The haphazard system of tunnels and chambers made by a colony of approximately 3000 individuals is shown in the longitudinal section of a dead palo verde in figure 4 B. In this and in one other standing palo verde, the colony had penetrated wood a few inches below ground level. The rough-surfaced galleries of *Pterotermes* could not be mistaken for those of any other termite in the desert. Although in a quite different environment, the workings of a large colony are nearly as large and extensive as those of *Zootermopsis* (Nutting, 1965). Galleries are generally driven in sound wood, although many palo verdes have been found where 50 to 75 percent of the wood has been previously tunneled by wood-boring beetle larvae. In this case the termites work through the tightly packed sawdust and even use the cleared tunnels for short distances. Since the soldier head is approximately 4 mm. wide and the abdomen of a large nymph may be nearly 5 mm. in diameter, the tunnels and access holes between chambers seldom measure less than 3 × 5 mm. Active galleries are nearly free of fecal spottings and pellets, but large dumps of loose pellets are found in abandoned chambers. In a caged palo verde colony, large quantities of fecal pellets were dumped from an old borer exit a few inches from the ground. Considerable use is made of semi-liquid fecal material in walling off old galleries and in plugging lateral tunnels made by borers to the outside.

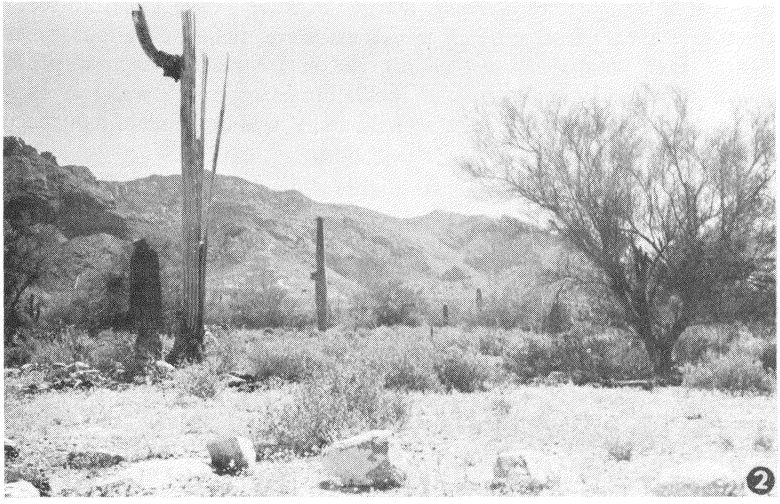
Colonizing flights. Previous flight records from Arizona had suggested that *Pterotermes* flies on a relatively few nights during late July and August. Alates from Baja California were taken in light traps in late August and early September by Werner and Radford (Table 1). Apparently the only observations on a flight in nature were made by the author on the night of August 7, 1963, in the Tucson Mts. A lantern was operated from dusk until midnight, and between 2235 and 2330 hrs. four males and four females flew rapidly in to the light on the ground. It was impossible to tell from what altitude or direction they had come. They were very active under the light but did not leave. The evening was quiet and nearly cloudless with the temperature between 22 and 23°C. The moon had risen about an hour before the flight and was just past full.

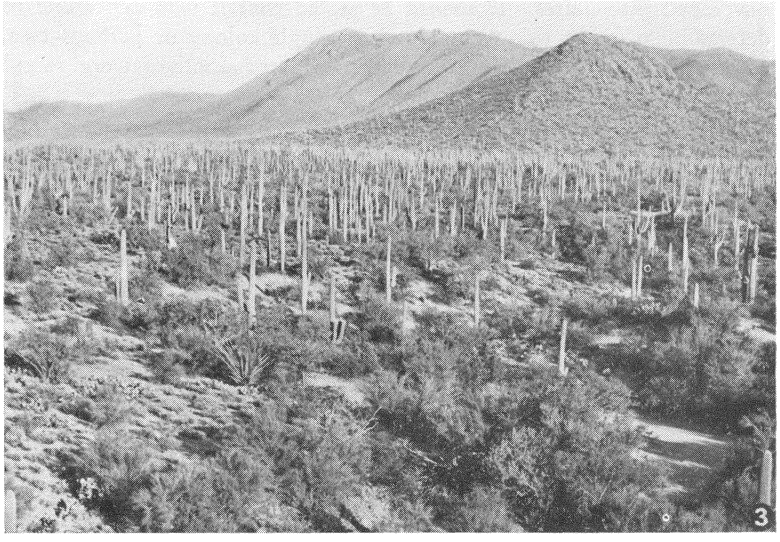
As part of a long-term study, flight and meteorological data were

collected from June through September, 1965, in Tucson, Arizona. A six-foot section of dead palo verde, containing what was probably a single colony of *Pterotermes,* was set in a field cage (6x12x6 feet) of 20-mesh Saran screen. Observations were made at various times nearly every night as well as for the entire period from dusk to dawn on a few other nights. A small black light trap was run each night in a corner of the cage so that there was reasonable assurance that practically all alates were captured.

The colony staged 40 separate flights during the 43 days beginning July 22 and ending Sept. 2. The smallest flight consisted of one alate, the largest 199, and roughly equal numbers of males and females were trapped. Twenty-five alates were later found to have escaped the trap and established themselves in cells within the same tree from which they flew. These plus those from the trap gave a total of 1688 alates produced by the colony. Nearly six months later the entire colony was removed from the tree and found to contain 4055 nymphs (Table 2, No. 3). Assuming that there were approximately 5600 nymphs in the colony during the spring of 1965 (number of nymphs produced since then not counted, but probably less than 200), this means that an impressive 30 percent of them developed into alates. It should be stated that it was impossible to determine whether this was actually a single colony or perhaps two, since a queen and a pair of replacement reproductives were found widely separated in the tree.

Although accompanying data have not yet been analyzed, a few generalizations may be made relating weather conditions to the flight season and the daily flight periods. The flight season began about three weeks after the highest weekly mean temperature of the year (30.5°C) was reached and continued for approximately six weeks with weekly means between 26.8 and 29.5°C. Individual flight periods took place with nighttime temperatures ranging from approximately 19 to 29°C. The flight season occurred while some of the highest weekly mean relative humidities of the year were recorded: 48-74%. Individual flight periods took place with nighttime relative humidities ranging between 39 and 100%. Flight periods began at temperature-relative humidity combinations between 29°C/39% RH and 24°C/100% RH. Nearly two inches of rain had fallen during the summer rainy season (June-September) prior to the flight season, and four significant rains (0.3 to 1.5 inches) occurred during the season itself. No flights took place on three nights during the 43-day season, apparently because of rain or considerably cooler temperatures. All flights were staged during dark-





NUTTING — PTEROTERMES

ness, from two hours or more after sunset until three-quarters of an hour or more before sunrise. A complete account of these flight studies on *Pterotermes,* including behavior of the alates, will appear as part of a separate series on the colonizing flights and associated activities of termites.

Table 2. Composition of five colonies of *Pterotermes occidentis* from Arizona. It was impossible to determine whether colonies No. 4 and 5 were fragments of a single colony in the same log, or whether No. 3 was actually made up of two colonies in the same tree. K and Q represent primary reproductives; Rep., replacement reproductives.

No.	*Nymphs*	*Soldiers*	*Reproductives*	*Eggs*
		Oracle Jct., 8 mi. S.		
1	721	37	K + Q	79
2	2867	42	K + Q	
3	4055	82	Q + 2 Rep.	ca. 30
		Alamo Wash		
4	591	21	2 Rep.	
5	1082	28	1 Rep.	

FOUNDING OF THE COLONY. About 30 incipient colonies have been collected in dead palo verdes in the vicinity of Tucson. Several were found 6 to 10 feet above the ground. Observations on these and on post-flight behavior of caged alates indicate that the alates use cracks and borer exits as primary points of attack. The initial chamber, or copularium, (Fig. 4 A) is usually hollowed out of sound wood less than one inch from the surface. A few captive pairs have been maintained in petri dishes containing a slice of wood on a layer of plaster of Paris, with a few drops of water occasionally added to the wood or plaster. Shrunken reproductives and nymphs become excited in the presence of moisture and will readily drink to repletion from free droplets or a cotton wick. However, laboratory colonies may die within two weeks where free moisture or even moderate humidities prevail. The pairs were kept in a study from September through May where temperatures varied from 13 to 27°C.

EXPLANATION OF PLATE 9

Figure 2. Scene in the foothills of the Santa Catalina Mts. north of Tucson, Arizona. To the left is the ribbed, woody skeleton of a saguaro cactus, *Cereus giganteus;* to the right, a palo verde tree, *Cercidium microphyllum. Pterotermes* has been found in these skeletons and in the dead wood of *Cercidium.*

Figure 3. *Cercidium — Cereus* association on the western slopes of the Tucson Mts. west of Tucson, Arizona. *Pterotermes* has been taken in this area which is typical of the Sonoran Desert in southern Arizona. Photograph by Peter J. Mehringer, Jr.

Perhaps because they were already enclosed, many of the pairs worked intermittently for as long as a month to construct the copularium: irregular grooves in wood beneath the cover of the dish or chambers within the wood, measuring roughly 5 × 10 × 6 mm. Semiliquid fecal material was used freely between wood and cover to encircle the grooves or to plug the chamber entrance. Some pairs produced up to six eggs within the first two or three weeks, while others produced no eggs during ten months of observation. The eggs are opaque, pinkish white and ultimately measure approximately 0.7 × 1.7 mm. Both sexes occasionally manipulated or cleaned the eggs with their mouthparts, but the eggs were not kept together in any particular place. No detailed observations were made on the progress of these incipient colonies, although most of the eggs had not hatched at the end of six months. Replacement reproductives of both sexes have been found in fragments of colonies in the laboratory and in natural colonies. In the latter case it has not always been possible to determine whether they were heading distinct colonies or were associated with remote parts of colonies headed by primary reproductives. They are pale yellowish-brown and possess very short wing pads. As would be expected, these preliminary observations show that captive colonies of *Pterotermes* provide good material for many types of biological studies.

COLONY SIZE AND OTHER BIOLOGICAL NOTES. Incipient colonies, probably within their first year, have been found consisting of barren pairs and pairs with as many as eight nymphs and five eggs. One colony, presumed to be in its second year, consisted of 13 nymphs, one small soldier and one egg. Another pair, perhaps in their second or third year, had produced 29 nymphs, 2 soldiers and 5 eggs. Data on the size of five older colonies are presented in Table 2. Assuming that all were single colonies, the soldier-nymph ratio varied from 1 to 20 in one of the smaller colonies to 1 to 68 in one containing nearly 3000 nymphs.

It should be of interest to mention the extremely high temperatures which *Pterotermes* must commonly meet in its exposed nesting sites. Temperature records were kept in connection with the flight studies made on the caged colony in Tucson from July through September, 1965. Temperatures were noted several times each day from a remote-reading thermometer, accurate to approximately ± 1°C. The bulb was fixed within the central galleries of the palo verde trunk, three feet above the ground. Brief excursions above 38° were common in the late afternoon and on one day reached 41.8°; the maximum air temperature (shade) on that day was 38°C. The

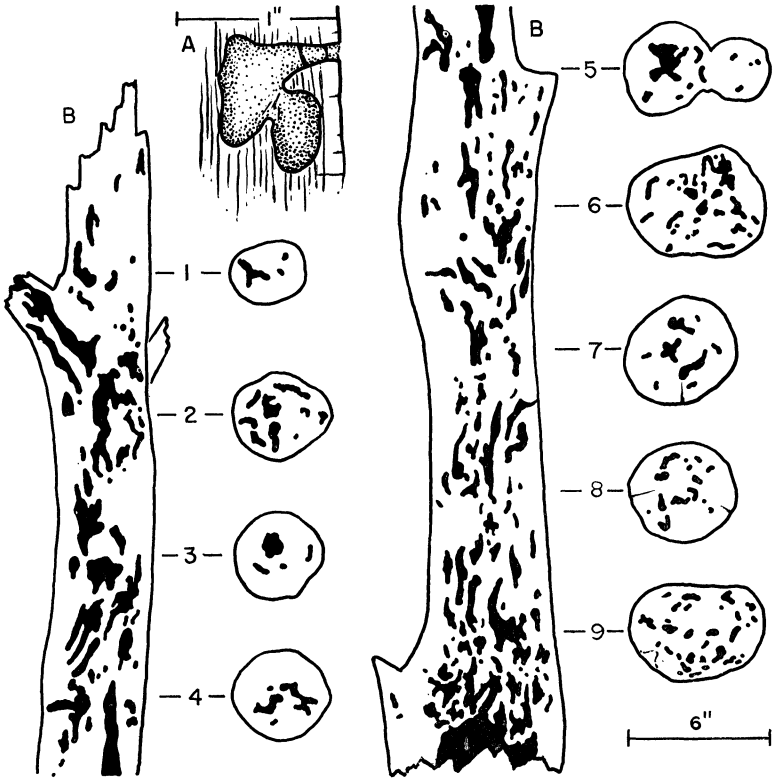


Figure 4. A. Longitudinal section through a copularium of *Pterotermes occidentis* in outer wood of a dead palo verde tree. This chamber contained a primary pair and four small nymphs. B. Longitudinal section showing the galleries of *Pterotermes* in a dead palo verde from the vicinity of Oracle Jct., Arizona. Cross sections 1-9 represent tracings of the galleries in adjacent cuts.

temperature rarely fell below 24°C in the early morning shortly after sunrise during the entire period. This tree received somewhat more than 50 percent shade for most of the day and complete shade early and late each day. Since colonies in nature are rarely in such shaded situations, these figures are certainly conservative. Further, for most colonies in branches and trunks from one to ten inches in diameter, there is no apparent escape from such temperatures.

ASSOCIATION WITH OTHER TERMITES AND INSECTS. In southern Arizona, *Marginitermes hubbardi* (Banks) has been found in palo

verde logs, and on two occasions in the same wood with *Pterotermes*. *Paraneotermes simplicicornis* (Banks) is the only other kalotermitid which is known to attack the palo verde. This unusual termite, which is essentially subterranean, generally infests the roots and stumps of dead trees in the desert. Both of these termites probably begin their attacks before wood has dried to the point where it is most favorable for *Pterotermes*. They are much more common in the skeletons of the saguaro cactus, where they appear shortly after the flesh has rotted and fallen off. They have never been found in saguaros inhabited by *Pterotermes*.

Heterotermes aureus (Snyder) is one of the most common subterranean termites in the Sonoran Desert region of southern Arizona. It commonly works in dead saguaros, particularly during periods of higher soil moisture following the winter and summer rains. On the north slopes of the Tucson Mts. its abandoned galleries were obvious in the saguaro stump containing *Pterotermes*. The only other insects commonly found in wood attacked by *Pterotermes* are buprestid and cerambycid larvae which are often very numerous in palo verde.

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