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STUDIES ON THE HABITS AND DISTRIBUTION OF *CRYPTOCERUS TEXANUS* SANTSCHI (HYMENOPTERA: FORMICIDAE)

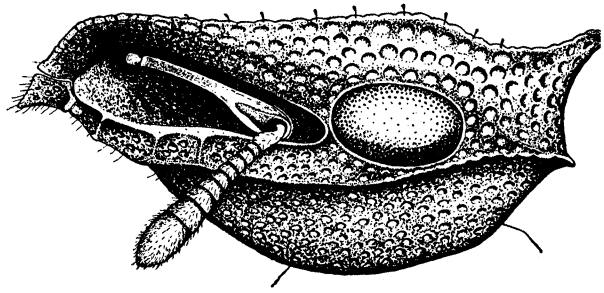
BY W. S. CREIGHTON, City College, New York
and
R. E. GREGG, University of Colorado

In recent years Dr. M. R. Smith (1,2) and Fr. W. W. Kempf (3,4) have published papers on the genus *Cryptocerus*[1]. These studies deal primarily with taxonomy and do not supply many data on the habits of the ants of this genus. The habits of *Cryptocerus texanus*, the only member of the group whose occurrence in the United States can be regarded as abundant, thus remain largely unknown. From the fall of 1951 to the spring of 1953 the senior author took twenty colonies of *C. texanus* in southern Texas and northeastern Mexico[2]. Three of these colonies were studied in artificial nests for several weeks and later three more colonies were sent to the junior author for further observation. One of this second group of colonies was still alive a year afterwards when this paper was sent to press. The habits recorded here were largely determined from studies made on these six colonies.

[1]The writers have appealed to the International Commission on Zoölogical Nomenclature to have Emery's use of the generic names *Cephalotes* and *Cryptocerus* sustained. Until a decision has been handed down we prefer to use Emery's system. The name changes advocated by Dr. Smith have already caused regrettable confusion in this group.

[2]Fieldwork done on a Guggenheim Fellowship.

Before discussing these studies it seems advisable to present certain general observations on *Cryptocerus texanus*. In the paper which Dr. M. R. Smith published on *texanus* in 1947(1) seventeen stations were listed. Only six of these carried notations as to the nest site of the



a.

b.

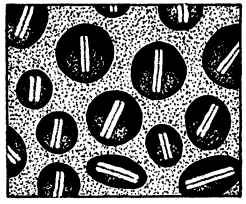


Figure 1. *Cryptocerus texanus*: a, lateral view of the head of the major; b, sculpture of the cephalic disc on the head of the major, showing the rectangular, silvery, longitudinally grooved hair in each foveola. Figure 1, a, is drawn to a scale twice that of plates 3 and 4.

colony. Of these six only one referred to a nest in a live-oak tree. On the basis of the above data it would be unlikely for anyone to conclude that *texanus* prefers to nest in live-oaks. Nevertheless, this appears to be the case. Presented below is a list of trees in which *texanus* has been found nesting. This is a composite of the data published by Dr. Smith and those more recently secured by the senior author. In two cases the information reported by Dr. Smith

has been interpreted on the basis of probability so that it fits into the list. Thus his nest reported from "persimmon" has been assigned to *Brayodendron* and that said to have come from a "live-oak" has been allocated to *Q. virginiana.*

1. *Quercus virginiana* (live-oak) 14 colonies
2. *Quercus fusiformis* (live-oak) 3 colonies
3. *Quercus stellata* (deciduous oak) 2 colonies
4. *Zygia flexicaulis* (Texas ebony) 3 colonies
5. *Brayodendron texanum* (Mexican persimmon) 2 colonies
6. *Xanthoxylum clava-herculis* (prickly ash) 1 colony
7. *Celtis pallida* (hackberry) 1 colony
8. *Prosopis juliflora* (mesquite) 1 colony

Of the twenty-seven colonies listed above seventeen (63%) came from live-oaks. It thus appears that *texanus* definitely prefers to nest in live-oaks, although it is sufficiently flexible in its nesting habits to accept other trees as well.

The size of the colony and the number of deälated queens present are also matters of interest. Four of the colonies taken by the senior author were plainly fragmentary and these have been omitted from the list below.

	Female	Major	Media & Minor	Total	Station
1.	1	8	22	31	Lapara Creek, Texas
2.	6	10	73	89	" " "
3.	1	19	56	76	" " "
4.	3	12	52	69	" " "
5.	5	25	61	91	Hochheim, Texas
6.	2	13	37	52	" "
7.	2	6	53	61	Floresville, Texas
8.	1	17	53	71	Gambel Creek, Texas
9.	22	13	115	150	Sealy, Texas
10.	5	18	55	78	Iturbide Canyon, Nuevo Leon
11.	3	8	25	36	" " " "
12.	0	46	186	232	" " " "
13.	0	9	28	37	" " " "
14.	1	8	31	40	El Pastor, Nuevo Leon
15.	7	10	32	49	Belmont, Texas
16.	2	1	26	29	" "

Two facts are shown by the above figures. The colonies of *texanus* are always small and they are often pleometrotic. It may be stated that most of the above colonies came from separate trees. The chance that a colony of *texanus* may be polydomus was constantly kept in mind. Hence colonies taken in closely adjacent limbs or at separated intervals in the same limb were treated as parts of a single nest. It may be, therefore, that the relatively large totals in colonies 9 and 12 represent more than a single colony.

The outstanding point of interest in the biology of *texanus* is the possibility that the major may serve in a phragmotic capacity. A good deal of what has been said on this subject seems to have been published without much idea of certain structural features which are involved. In order to make these features clear the junior author has prepared figures of the female, major and minor of *Cryptocerus texanus* (Pls. 3 and 4; text-figs. 1 and 2). Reference to these figures will show that the prominent cephalic disc present in the female and major of *texanus*, does not cover all of the upper surface of the head. Projecting rearward beyond this disc are two conspicuous occipital angles. Although these angles lie below the level of the rim of the disc they cannot be disregarded for they, and not the rounded posterior rim of the cephalic disc, determine the size of the aperture into which the head can be thrust. Behind these occipital angles stand the even more prominent humeral angles of the thorax. In the figure of the major considerations of perspective have made it necessary to show these angles as wider than the head, for the latter lies below and in front of them. But, even disregarding the matter of perspective, the maximum width of the dorsum of the thorax at the humeral angles equals or slightly exceeds the maximum diameter of the cephalic disc. It follows that the thorax of the major and the female of *texanus* (at least at the humeri) is fully as wide as the head and often a little wider than the head. It further follows that the diameter of a passage which the *texanus* major can occlude is determined as much by the width of the prothorax as it is by the size and shape of the cephalic disc. The failure of previous investigators to grasp this fact has been the cause of confusion in the past.

The first person to suggest a phragmotic function for the major of *Cryptocerus* appears to have been W. M. Wheeler. In 1905 (5) Wheeler stated that the nest entrance of several colonies of *Cryptocerus varians,* which he had found in hollow twigs in the Bahamas, was always exactly the size and shape of the cephalic disc of the major. Wheeler made no claim that the major blocks the nest entrance with its head, but the implication that it does so was clear and this seems to have been the basis for later views expressed by Wheeler in 1910 (6) and by Emery in 1922 (7) that the major of *Cryptocerus* is probably phragmotic. But no

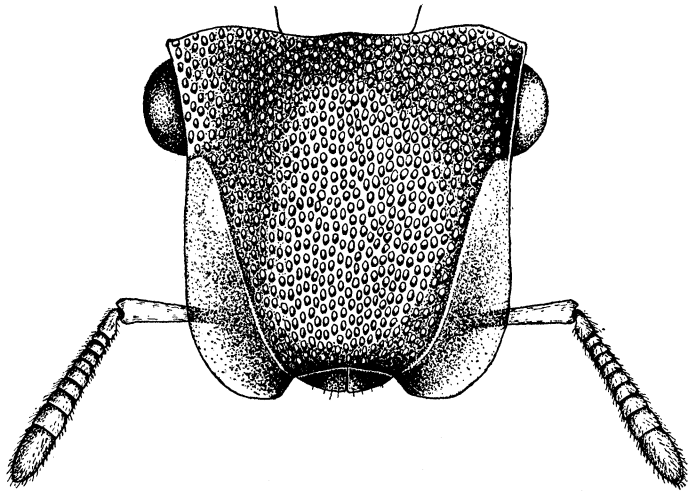


Figure 2. Dorsal view of the head of the minor of *Cryptocerus texanus.* Drawn to the same scale as figure 1, a.

positive statement was made on this point until 1942. In that year a posthumous paper by Wheeler (8) which had been prepared for publication by Dr. Joseph Bequaert, definitely made such a claim in the case of *Cryptocerus pallens* (the variety *porrasi*) and *C. setulifer.* The statement concerning *pallens* is as follows:

"Its habits are similar to those of *Colobopsis.* The elliptical nest entrance is guarded by one of the soldiers which occludes the orifice with its disc-shaped cephalic disc just as the *Colobopsis* soldier uses the truncated anterior sur-

face of the head for the same purpose. The cephalic disc in old soldiers and in the mother queen of the colony often becomes coated with dirt and extraneous particles so that it closely resembles the bark of the plant."

The most recent note on the phragmosis of *Cryptocerus* is that which Kempf published in 1952 (4). Kempf's single observation on *Cryptocerus maculatus* failed to show the behavior cited by Wheeler. It was not until Kempf had enlarged the small nest entrance that any majors were seen. These majors, which were well inside the nest, then tried to occlude the passage which Kempf had opened up by standing "side on side". Kempf recalled that a similar compound shield, consisting of the approximated heads of several minor workers, was reported for a colony of *Cephalotes atratus* by Santschi in 1919 (9). The date of this publication is incorrectly given by Kempf as 1929. Kempf was clearly aware that neither Santschi's observation on *atratus* nor his own on *maculatus* are comparable to Wheeler's statement of the phragmosis of the major of *pallens*. But the writers agree with Kempf that clarification is needed in the case of Wheeler's 1942 statement. The major of *Cryptocerus* is undoubtedly phragmotic, but it is misleading to say that it behaves just as does the *Colobopsis* major. The notable differences which mark the reaction of the *Cryptocerus* major are discussed in the following pages.

The junior author's colonies were housed in the modified Janet nests used in earlier studies on *Pheidole* (10). These nests gave little opportunity for studying the phragmosis of *texanus*, since they lacked restricting passages. In order to study this response two other types of nests were used, both of very simple construction. The first consisted of two glass vials with the bottoms removed. These vials were held together by a cork, which was forced into the neck of each vial until the two rims touched. On one side of this cork a groove was cut which approximated the size and shape of the cephalic disc of the major as closely as possible. The open end of each vial was plugged with cotton after the colony was installed. The second type of nest was a small, plaster one, cast over a microscope slide.

After the plaster hardened the slide was removed and suitable chambers and passages were cut in the plaster. The slide was then put back in place and held in position with rubber bands. In both these nests the action of the major in the passages could be easily observed and the passages could be enlarged when necessary.

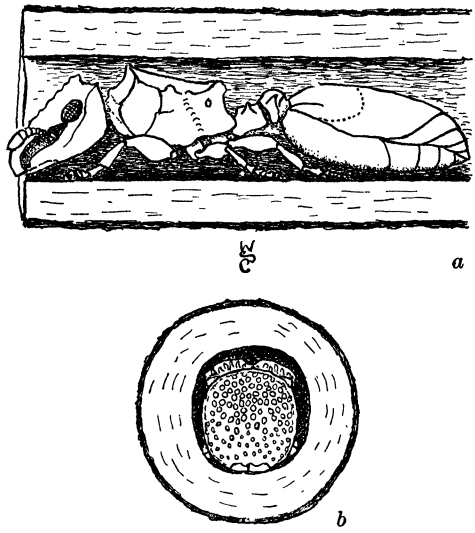


Figure 3. a, lateral view of the major of *Cryptocerus texanus* in the phragmotic position in a hollow twig; b, cephalic disc of above major seen in full-face view.

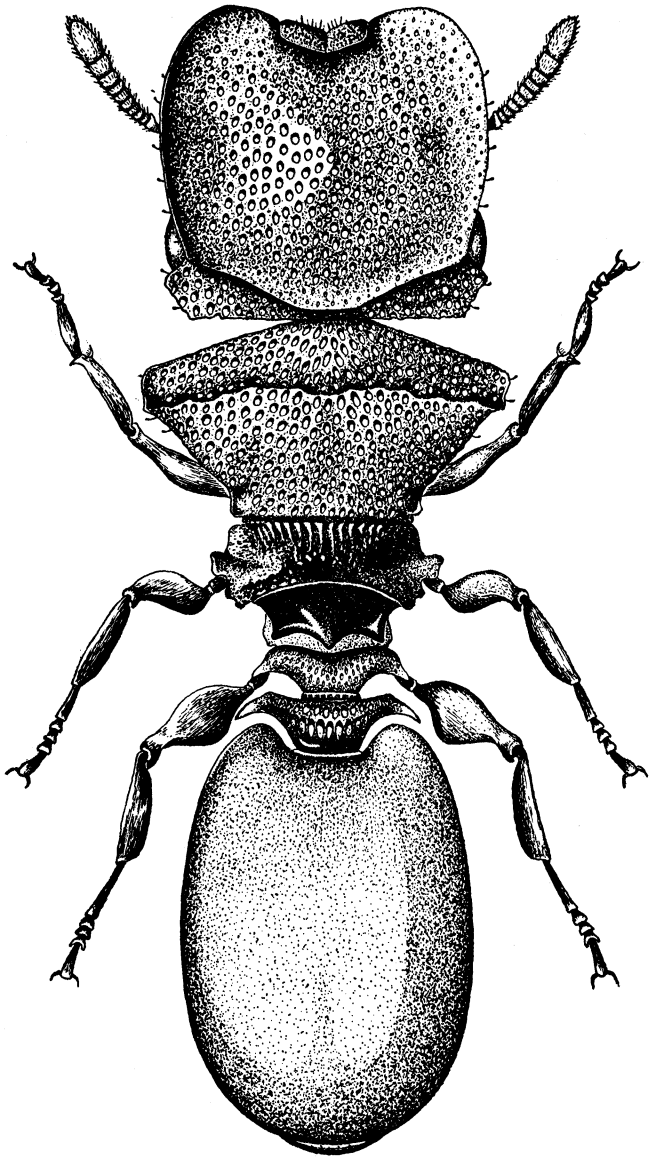
It soon became apparent that if the passages were made to fit the cephalic disc of the major closely, this caste would not enter them at all. Since the medias and minors would use such passages freely there was no reason to suppose that anything other than the size of the passage determined the refusal of the majors to use them. When such passages were enlarged the majors used them without hesitation. But this behavior indicated that the major of *texanus* cannot or will not go into a passage whose size and shape closely approximates that of the cephalic disc. The reason for this appears to lie in the fact that the major of *texanus* occludes the nest opening not only with the cephalic disc

but with the humeri of the thorax as well. The head of the major of *texanus* can be lowered until its long axis is at right angles to the long axis of the rest of the body. Although many majors die in this position it is rarely assumed by the living insect, presumably because in such a posture the anterior edge of the head is so far below the level of the coxae that the insect would have to stand on tiptoe to keep the mandibles clear of the substrate. Conversely, the head of the major can be raised until its long axis is parallel to that of the rest of the body. Under such circumstances the rim of the cephalic disc lies at the same level as the dorsum of the thorax. But in this position the head of the major does not occlude the passage for there is then a considerable space below the ventral surface of the head. To occlude the passage the major must lower the head until its anterior edge is on or near the floor of the passage. But when the head of the major is in this position, with its long axis forming an angle of approximately 120° with the long axis of the rest of the body, the posterior rim of the cephalic disc is well below the level of the humeral angles. Thus if a major of *texanus* is to occlude a passage, this passage must be large enough to accommodate not only the cephalic disc but also the humeral angles above and behind it. For if the head is lowered enough to form an effective barrier there is no way in which the humeral angles can be brought down to the level of the posterior rim of the cephalic disc. It would appear, therefore, that it is physically impossible for the major of *texanus* to occlude a passage whose size closely approximates that of the cephalic disc.

It may be readily appreciated that the situation just described is wholly different from that which marks the major of *Colobopsis*. In the cork-shaped head of the major of *Colobopsis* maximum occlusion occurs when the long axis of the head is parallel to that of the rest of the body. In this position the truncated anterior face of the head is presented to the exterior. Since the diameter of this truncated portion exceeds that of any other part of the

EXPLANATION OF PLATE 3

Cryptocerus texanus, dorsal view of the major.



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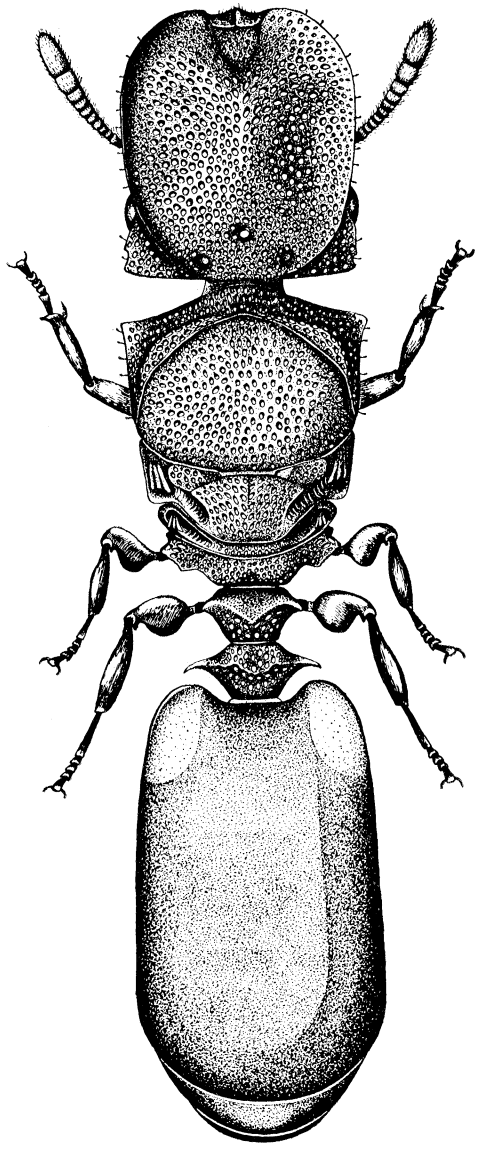
insect, it follows that the head of the *Colobopsis* major can be thrust into close-fitting apertures without putting the rest of the insect into an impossible posture.

We may now consider the method by which minors of *texanus* are admitted to the nest. When the guarding major has assumed the phragmotic position the lower rim of the head usually projects slightly beyond the edge of the nest entrance. The antennae are held at either side of the cephalic disc and are clearly visible from the outside. The returning minor may or may not touch the antennae of the guard, although it usually does so. Thereafter the guard crouches down. This brings the anterior rim of the head below the level of the floor of the passage or, if the guard stands completely inside the passage, the front of the head is raised as the guard crouches. The dorsum of the guard's thorax is now no longer close to the roof of the passage and the minor can, if it is sufficiently active, wriggle between the dorsum of the thorax and the roof of the passage. This action is seldom completed without considerable struggle on the part of the entering minor and at times the major will cease to crouch before the minor has gone through and pin the minor between its thoracic dorsum and the roof of the passage. The senior author has seen minors thus trapped who, perforce, remained in this awkward position for several minutes until the major would crouch again and release them. If the passageways are made large enough to accomodate two majors simultaneously, they ordinarily assume a position where they are back to back. Under such circumstances the two opposed cephalic discs form a V-shaped area. The bottom of this V is open but the space behind it is closed by the closely approximated thoracic dorsi of the two guards. When minors are admitted to the nest both majors crouch and the entering worker struggles through the narrow space between the thoraces of the guards. It seems scarcely necessary to state that there is no part of this behavior which at all resembles that of the *Colobopsis* major, which must back away from the nest entrance to admit the returning minor.

EXPLANATION OF PLATE 4

Cryptocerus texanus, dorsal view of deälated female.



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Two other habits of the major of *texanus* may be mentioned. It should be apparent that when a major is in a closely confining passage its head has much the position of the blade of a snowplow. The concave surface of the cephalic disc slopes forward and downward and its lower rim is close to the floor of the passage. When a major moves forward along a passage any minors which are in it are pushed ahead of the advancing major unless they are active enough to force their way between the thoracic dorsum of the major and the roof of the passage. This sometimes leads to rather surprising results for workers clustered within the nest entrance may be suddenly ejected from the nest by the advancing major. Before assuming its phragmotic position the major often comes out of the nest entirely. After exploring the area immediately around the entrance it backs into the passage. This is never true of minors who always go through the nest entrance head first.

Much remains to be learned about the feeding habits of *texanus*. In 1947 M. R. Smith published the statement that our species of *Cryptocerus* feed "largely on honey dew or the flesh of small arthropods"(2). This may be true but the writers were unable to discover any food for which the captive colonies showed much relish. They refused mealworms and termites, even when the latter were torn open to expose the tissues. High protein foods such as peanut butter and cheese were also refused. This would seem to indicate a distaste for a protein diet but other observations contradict such a view. While the ants refused pure honey they accepted honey mixed with egg yolk. In one instance an injured female was accidentally included when a colony was installed in an artificial nest. The gaster of this female had been broken open and her own workers promptly proceeded to eviscerate her. The gastric contents were completely cleaned out in a few hours. This action may have been due to some improper condition in the artificial nest and the food in this case can scarcely be the regular dietary staple of the insects. Yet it can be stated that was the only instance where the workers seemed at all interested in what they were eating. Other foods which were refused were pears, apples and

jelly. Bananas were accepted by some colonies but rejected by others. The most generally acceptable food seemed to be maple syrup. This suggests that the insects may possibly feed on the sap of the trees in which they live. If this is the case it is probable that such a diet is augmented by other food, for the workers of *texanus* forage on the surface of the ground, which they would scarcely do if the diet was entirely confined to sap. Whatever the natural food of *texanus* may be it seems certain that it is not sticky. Both writers found that it was inadvisable to leave sticky food in the nest for any length of time, since a number of minors were certain to get caught in it. The other workers make no effort to free their trapped nestmates, who ultimately die.

To judge from the captive colonies these ants are very sluggish in their nests. They often pack themselves together in a nest chamber or passage and remain immobile for hours. If disturbed both majors and minors may open their mandibles and keep them open. This is a preliminary to an attack on any intruder. When living termites were placed in the captive nests they were immediately attacked by both majors and minors. The attack was made with the open jaws of the attackers held close to the floor of the nest. As a result the termites suffered very little damage to any parts except their legs. These were rapidly cut off, but once the termites had been immobilized no further attention was paid to them.

The female of *texanus* lays a comparatively large egg and has considerable difficulty in doing so. The egg, which is from 1.3 to 1.5 mm. in length and about 0.5 mm. in diameter, is cylindrical with rounded ends. The senior author twice observed the process of egg-laying in this species. In both cases the egg was about one-quarter of its length out of the end of the gaster when first observed. Its extrusion was not a continuous process but proceeded by a series of slight motions which occurred at intervals. The entire process consumed about ten minutes. On one occasion the partially extruded egg was seized by a worker who pulled on it with sufficient force to haul the female backward without, however, releasing the egg from the gaster. Since only two instances of egg-laying were ob-

served the writers are not sure that the process described above is normal for *texanus*. But it should be remembered that the gaster of the *texanus* female is heavily sclerotized and because of this a large egg should be difficult to eject. Brood is tended by both minors and majors who, despite their clumsy heads, handle the eggs and young larvae with surprising gentleness.

The distribution of *texanus* is unusually interesting, since it is one of the few cephalotine ants which live outside the tropics. The structural relationship of *texanus* to certain Neotropical species is close but, because of the lack of records from northeastern Mexico, the spatial relation of *texanus* to the more southern species has been conjectural. In the following pages the writers have discussed the distribution of *texanus* and that of several other cephalotines which occur in eastern Mexico. The northern range of the latter species seldom agrees with the data published by Kempf in 1951 (3) and 1952 (4). In his important work with the cephalotine ants Kempf has been hampered by lack of adequate records from Mexico. This is particularly true of the region north of Mexico City, where the ranges of several Neotropical species terminate. Kempf cannot be blamed for the absence of records from this area but his attempt to supply distribution data from specimens intercepted at plant quarantine stations is far from satisfactory. Kempf's citation of Guerrero, Coahuila as a possible source of specimens of *C. minutus*, intercepted on orchids and labelled only "Guerrero" is a case in point. Guerrero, Coahuila lies four hundred miles outside the northern limit of the range of *C. minutus*. Moreover, the village is situated in a very arid part of the Rio Grande Valley where the ants are strictly xerophilous. That *minutus* could occur there is out of the question.

Most of the colonies of *texanus* secured by the senior author came from the area outlined by M. R. Smith in his 1947 publication. They were taken in what may be called the Brownsville-San Antonio-Houston triangle. The record from Sealy extends the known range of *texanus* about twenty-five miles to the east of its former limit (Columbus, Texas) but this extension is negligible and we agree with Dr. Smith that it is unlikely that *texanus* occurs east

of Texas. On the other hand the records from Nuevo Leon are a significant southern extension of the range. It may be recalled that Dr. Smith had specimens of *texanus* which came from Mexico but the source of these specimens was unknown. It is now clear that *texanus* occurs in the foothills of the Sierra Madre Oriental at least as far south as the latitude of Linares (24° 40′). Of the five colonies taken in Nuevo Leon, one came from El Pastor, a small village west of Montemorelos, and the remaining four from Iturbide Canyon, west of Linares. In this area the ant nests at elevations about the 2300 foot level, a considerable elevational rise over the stations in southern Texas, none of which were more than a few hundred feet above sea-level.

In addition to *texanus* the following cephalotine ants were taken in eastern Mexico:

Procryptocerus scabriusculus Em.
Cryptocerus scutellatus Sm.
Cryptocerus cristatus Em.[1]
C. (*Paracryptocerus*) *minutus* Em.

Because of the lack of reliable records from eastern Mexico a list of the localities where these species were taken is presented here:

SAN LUIS POTOSI:

Tamazunchale (600-800′) five colonies of *C.* (*Paracryptocerus*) *minutus;* one colony of *C. scutellatus;* Xilitla Ferry (200′) 22 miles north of Tamazunchale, one colony of C. (*Paracryptocerus*) *minutus;* Xilitla (1800′) one colony of *C.* (*Paracryptocerus*) *minutus,* one colony of *Procryptocerus scabriusculus;* 3 miles east of Xilitla (2000′) one colony of *Cryptocerus cristatus;* Axtla (200′) 23 miles northeast of Tamazunchale, one colony of *Cryptocerus scutellatus*[2]*;* 22 miles east of Ciudad del

[1]The single colony of *cristatus* which was taken consisted of eight majors and 330 medias and minors. Kempf believes that majors are seldom produced by *cristatus,* for he found none in the material which he examined. But since this material consisted of only 35 minors and 17 females coming from 11 stations, it seems probable that Kempf's conclusion is the result of inadequate series.

[2]This colony was observed in an artificial nest for a period of three weeks. These observations indicated that the habits of *scutellatus* do not differ significantly from those of *texanus.*

Maiz (3300′) one colony of *Procryptocerus scabriusculus;* El Salto (1400′) 30 miles west of Antiguo Morelos, one stray worker of *Cryptocerus scutellatus.*

TAMAULIPAS:

5 miles west of Altimira (300′) one colony of *C.* (*Paracryptocerus*) *minutus*[1].

The three northernmost records cited above (Ciudad del Maiz, El Salto and Altimira) all lie less than ten miles from Latitude 22° 30′. They are, thus, a little more than fifty miles south of the Tropic of Cancer. As has already been shown the present known range of *texanus* does not extend south of Latitude 24° 40′, which is approximately eighty miles north of the Tropic of Cancer. As things stand at present there is a gap of one hundred and thirty miles between the southern end of the range of *texanus* and the northern end of the range of the species cited above. Further studies in northeastern Mexico, particularly in the mountains southwest of Ciudad Victoria, may narrow or even close this gap. But if this happens it will not alter the fact that the distribution of *texanus* has little in common with that of the Neotropical species. For the range of *minutus* extends to southern Brazil and the other three species range into Colombia and Venezuela. It is safe to assume, therefore, that the area of maximum abundance for each of these species lies well within the tropics. This is certainly not the case with *texanus*, which is more abundant near the latitude of San Antonio, Texas than anywhere else in its range.

A comparable pattern of distribution has been reported by the senior author (11) for another "Neotropical" species, *Pseudomyrmex apache.* It would appear that the Neotropical component of the ant fauna in the southern United States is more complex from a distributional standpoint than has been previously supposed. Some of our representatives are northern fringes of species whose main range lies in the tropics. But others, like *Cryptocerus texanus* and *Pseudomyrmex apache* are more at home out of the tropics than in them. This last type of distribution

[1]Winged males and females were present in this colony and in one from Tamazunchale. Both colonies were taken in early April.

casts considerable doubt on the statement made by Wheeler in 1917 (12) and repeated by Emery in 1920 (13) that the major Neotropical additions to our ant fauna are relatively recent. If this northward migration was, as these authorities suppose, post-Pleistocene (Emery admits the possibility that it may have extended back to the Pliocene) at least there has been time for the development of marked changes in the ecology of some of the migrant species. No other conclusion is possible in the case of *Cryptocerus texanus* and *Pseudomyrmex apache.* The environmental preference of both these species has altered from that of their tropical ancestors to the extent that now neither of them seems capable of life in the tropics. This may, of course, be a recent phenomenon but more likely it indicates a long residence in the areas that they now occupy.

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