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IS THE ANT GENUS *TETRAMORIUM* NATIVE IN NORTH AMERICA?

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For some years, a controversy has continued concerning the distribution in North America of the ant genus *Tetramorium* Mayr. On opposite sides in this argument have been Dr. M. R. Smith (1943), who believes that all five of the *Tetramorium* species reported from North America have been introduced by man from overseas, and Dr. W. S. Creighton (1950), who thinks that the evidence points to prehistoric endemicity in the continent for at least two of the species mentioned; *T. caespitum* (Linnaeus) and *T. rugiventris* M. R. Smith. Apparently there is no serious disagreement about the origin abroad of *T. guineense* (Fabricius), *T. simillimum* (F. Smith) and *T. pacificum* Mayr. The first two of these are very likely African in origin, since they occur in wild parts of Africa and have their closest relatives among the species of that continent. *T. pacificum* is apparently from the Indo-Australian area, although its exact source has never been seriously tracked down. Certainly, it is Old World in origin.

The two species *caespitum* and *rugiventris* are therefore the central elements in the discussion, and it seems appropriate at this time to review the important facts in connection with these two forms and to add whatever significant observations are now available.

TETRAMORIUM CAESPITUM

This species is widespread in the Palaearctic region and in Africa, where it is extremely variable, as attested by an almost endless list of infraspecific variants. In terms of modern tax-

onomic practice, many of these entities would be considered good sibling species, as indeed some of them already have been treated by various European authors. Many others are mere synonyms of *caespitum* — individual or nest variants that do not represent natural, self-maintaining populations. No one has challenged the placement of the North American populations with the more nearly "typical" *caespitum* variants.

Creighton's assertion that *caespitum* is a native Nearctic ant rests on two principal pieces of evidence: first, the species was known at a very early date, i.e., 1895, from states as remote as Tennessee and Nebraska; second, there is present in North America, at least in the eastern states, a workerless parasite of *caespitum*, the aberrant species *Anergates atratulus* (Schenck), the transport and establishment of which would seem to present special difficulties.

The difficulty with the first piece of evidence is that the exact situation of the collections made in Tennessee, Nebraska and elsewhere in the "interior" of North America was never specified. All of these collections may have been, and probably were, made in or near "culture areas," that is, regions strongly disturbed by the presence of man. The experience of several practiced myrmecological field workers, including that of Dr. Creighton (personal communication) and myself, indicates that so far as known, *caespitum* in North America is known *only* from rather heavily disturbed localities, such as cities, towns, roadsides, farmyards, picnic areas and the like. I have been able to gather no records at all to show the existence of the species in places remote from the works of man in North America.

This situation contrasts with that holding in the Old World, at least so far as my own personal experience goes, and judging also from what I have been able to glean from various publications dealing with the species, and from personal communications with European myrmecologists. To sum up this information, it can be stated that *T. caespitum* in Europe and (although given various infraspecific names) in China is often abundant in and around human habitations, just as in North America. However, it is also to be found, often in abundance, in localities that show little or no trace of human disturbance, and that are far from the nearest humanly-occupied places. The contrast is very marked if one collects, as I have, at intermediate altitudes in

West China, in pine-oak forest, and then compares the collections of *Tetramorium* obtained with the results of a deliberate search for *Tetramorium* in similar vegetational zones in Pennsylvania, New Jersey or Massachusetts. In West China, *T. caespitum* tends to occur uniformly throughout the pine-oak forest, regardless of roads, villages, etc., which are very sparsely distributed in the areas I am recalling. In ecologically equivalent areas in the eastern United States, I have found the same species established only on or near the sites of more or less actively maintained human works. Clearly, the density of nests and individuals seen in North America is in large part proportional to the degree of urbanization of the area occupied, although the real extremes of urbanization, where almost all space is covered by concrete or asphalt, are certainly not favorable locales for colonization by this or any other ant species that lives largely in the open. In my opinion, the local, detailed distribution of *T. caespitum* in North America is that expected of an historically introduced, not a native ant.

The second point of evidence, that concerning the presence of the workerless, and therefore obligatory parasite, *Anergates atratulus,* certainly seems on the face of it a real sign of long occupancy of North America by both host and parasite. Creighton emphasizes the difficulties facing trial colonists of the parasite species: first, the species seems to be relatively rare in Europe; second, it is unlikely that the parasite female could survive a long trip; third, a female arriving in North America would be hard put to find a suitable nest of the host species to enter. To take these difficulties one at a time, we should first recognize that, while *Anergates* is not the commonest of ants in collections, it is nevertheless likely to be locally very common in restricted localities. Even in Europe, host populations are normally concentrated in gardens and waste places within towns and cities, including seaports, and these are accordingly very likely places for *Anergates* to occur unnoticed by primarily country-searching myrmecologists. In the United States, *Anergates* is known chiefly from East Coast localities in urban areas near the sea — exactly the kind of place from which colonists might be expected to be exported most easily. It should be added that *Anergates* females may be produced in very large numbers

from a single nest, so that a given locality may be heavily saturated with them during the period of nuptial flights.

The difficulty of transport of live *Anergates* propagules is real, but far from insurmountable. Females can be carried either as individuals carrying the necessary sperm, or as established inquilines in a *Tetramorium* colony. There is no reason why such a voyage might not be successfully made by a parasite queen, especially when one considers the evidence of Lindroth (ms., personal communication) for transport of faunal fragments to North America in ballast originating in Europe. Furthermore, there is no reason to believe that *Tetramorium* nests, with or without *Anergates,* cannot flourish on shipboard for at least the normal span of these species as colonies, a span which seems to be sufficient even for a long voyage under sail.

The third objection is the least difficult one, for there apparently has been no shortage of suitable host nests at close proximity to the waterfront in at least some of the major western Atlantic ports, perhaps as far back as colonial times. If a colony of the host parasitized by *Anergates* arrived in ballast or otherwise stowed-away, it had only to release its flight of fertile female imagines on the new shore to create a high probability of successful establishment.

A similar series of events may have led to the establishment of the workerless parasite *Xenometra monilicornis* Emery in the West Indies, together with or following the establishment of its host, *Cardiocondyla emeryi* Forel. A *Xenometra* of the same or a very closely allied species lives with *C. elegans* Emery in Italy; Menozzi (1919) thought this was the male of *elegans,* but specimens from his collection indicate instead its affinity with *X. monilicornis. Cardiocondyla* is a primarily littoral and riparian genus from the warmer parts of the Old World; records of several species from the New World seem to indicate rather clearly that it has been introduced by man on many separate occasions (M. R. Smith, 1944).

To conclude the discussion of the bearing of parasites on the distribution of *Tetramorium,* I think we may safely consider that introduction of an obligatory parasite, while less probable than the establishment of the host, is nonetheless entirely possible if the opportunities exist for a long enough time, and if a dense host population is available to the immigrant parasite.

TETRAMORIUM RUGIVENTRIS

The type series and only recorded sample of *T. rugiventris* was obtained from an upland ponderosa pine stand about ten miles south of Prescott, Arizona, and about one mile off the highway. In emphasizing his difficulty in accepting Smith's hypothesis, namely, that the ant was introduced with camel food or stores at the time when camels were imported from North Africa during the last century, Creighton wrote: "Entomologists frequently strain at gnats but it is seldom that they are asked to swallow a camel."

I have checked with care a syntype of *T. rugiventris* kindly sent by Dr. Smith. As a result of this examination, I can agree with Dr. Creighton that the ant in question is almost unquestionably endemic to the locality where it was found. However, I cannot agree with either Smith or Creighton that the species *rugiventris* belongs to the genus *Tetramorium* as it is now constituted. Instead, the type I have examined seems to me to be a clearcut, if somewhat aberrant, member of the genus *Myrmica,* closely allied to *M. striolagaster* Cole. *M. striolagaster* is recorded from several localities in Arizona and New Mexico, and I have specimens collected by E. O. Wilson at or near the type locality of *rugiventris,* in the vicinity of Prescott. Although the two species are separated by the extent and strength of the gastric sculpturing and by other characters as well, it seems clear that they are congeneric, and also that they run rather close to the *M. punctiventris* group of *Myrmica.*

The *rugiventris* type actually possesses minute barbulation on the posterior tibial spurs, as can be seen at magnifications of 90 × and better, so that in this character, the species would key to *Myrmica,* rather than *Tetramorium,* in the standard keys to tribes and genera of Formicidae. Actually, however, this spur barbulation is not worth much as a tribal character within the Myrmicinae, despite the faith that key-makers have placed in it. The false distinction between *Hylomyrma* Forel (tribe Myrmicini) and *Lundella* (tribe Tetramoriini) appears to have been based partly on this character (Brown, 1953), and the same may hold true of the supposed difference between *Cratomyrmex* Santschi, purportedly a member of tribe Myrmicini, and *Messor* Forel, of tribe Pheidolini.

Dr. Smith is fortified in his opinion that *rugiventris* belongs to *Tetramorium* by the presence in his species of raised cariniform lateral wings of the clypeus that border the antennal fossae in front, as in *Tetramorium;* but this character is shown with varying degrees of clearness in other, undoubted *Myrmica* species, both in North America and in southern Asia, so that it cannot be used as a point of separation between the two genera. The question comes to mind, of course, as to whether *Myrmica* and *Tetramorium* really are separate genera after all, and this is precisely the kind of question that most needs asking in ant taxonomy these days. In deciding this particular question, further study must be made of the males, since tetramoriine males (with the exception of a couple of African forms that require closer study) have several funicular segments fused in such a way as to reduce the number of antennal segments to ten in this sex.

Unfortunately, the males of *rugiventris* remain unknown at present, so that it is not known whether they meet the strong criteria of this caste. From the habitus and lesser details of the worker, however, I consider the relationship with *Myrmica* is close enough to call for a **new combination:** *Myrmica rugiventris.* Whether or not this combination finally proves to be the valid one, it at least helps to establish strong doubts as to the pre-Columbian existence of *Tetramorium* in North America.

In fact, were it not for *Tetramorium lucayanum* Forel and the *Xiphomyrmex spinosus* complex, the New World could be considered free of endemic members of tribe Tetramoriini. With the synonymy of *Lundella* under *Hylomyrma* (Brown, 1953), the New World lost its one endemic tetramoriine genus. *T. lucayanum* presents no special difficulty, because its distribution (Bahamas, Puerto Rico, etc.) is highly suggestive of introduced status. In its morphological characteristics, *lucayanum* seems closest to an African group of species, but the species itself has not been identified with any particular continental African population. However, our knowledge of African *Tetramorium* is in a very imperfect state, and it seems to me likely that *lucayanum* must have come from the Dark Continent, even though it may be rare there. A parallel case involving *Strumigenys rogeri* Emery has turned out to follow exactly this pattern (Brown, 1954).

The *Xiphomyrmex spinosus* complex (which may represent a single variable species) is the one example that cannot be explained away, and it is all the more remarkable, considering its isolated position in southwestern United States and through much of Mexico, far away from the remainder of the generic range, which is entirely Old World tropical and warm-temperate. Preliminary examination reveals no reason to consider this complex as other than bona fide *Xiphomyrmex,* and its distribution is almost certainly that of a long-established endemic group of populations, surely pre-Columbian in North America. *Xiphomyrmex* is separated from *Tetramorium* by a very minor character, 11 antennal segments in place of the 12 of *Tetramorium.* Future revisers could well fail to be impressed by the soundness of the generic split based on this difference, so that we may eventually see a systematic technicality bring back *Tetramorium* as a native American genus.

SUMMARY

Of the five species of *Tetramorium* so far reported as occurring in North America, only two are under dispute as possibly having existed on this continent prior to the advent of European colonists; these are the species heretofore known as *T. caespitum* and *T. rugiventris.* Evidence is presented to show that *T. caespitum* almost certainly was introduced by man from Europe, this evidence consisting primarily of the demonstration that *T. caespitum* in North America, unlike the Eurasian populations, is distributed exclusively in the manner of a man-accompanying "tramp" species. The species *rugiventris,* on the other hand, is removed from *Tetramorium,* where it does not fit well, and is transferred to *Myrmica.* The number of *Tetramorium* species occurring in North America is thus reduced to four, all of them likely introductions from the Old World within historical times. The only member of tribe Tetramoriini that can safely be considered as endemic to the New World at the present time is the *Xiphomyrmex spinosus* complex, widespread in southwestern U. S. and Mexico.

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