THE ANT TRIBE TETRAMORIINI (HYMENOPTERA : FORMICIDAE)

CONSTITUENT GENERA, REVIEW OF SMALLER GENERA AND REVISION OF *TRIGLYPHOTHRIX* FOREL

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SYNOPSIS

The generic composition of the myrmicine ant tribe Tetramoriini is revised and the tribe re-defined. Seven genera are recognized as valid, namely *Anergates* Forel, *Decamorium* Forel, *Rhoptromyrmex* Mayr, *Strongylognathus* Mayr, *Teleutomyrmex* Kutter, *Tetramorium* Mayr and *Triglyphothrix* Forel. The genus *Ireneella* Donisthorpe is synonymized with *Rhoptromyrmex*. The genera *Macromischoides* Wheeler and *Xiphomyrmex* Forel, and the subgenera *Lobomyrmex* Kratochvil and *Sulcomyrmex* Kratochvil are synonymized with *Tetramorium*. The genera *Eutetramorium* Emery, *Ireneopone* Donisthorpe and *Tetramyrma* Forel are excluded from the tribe. Keys to genera are given.

Tetramorium is defined and discussed as a preliminary to a world revision. The smaller genera are reviewed and a new species of *Rhoptromyrmex* described. *Triglyphothrix* is formally revised, 55 species being recognized as valid, of which 21 are new. Keys to species are provided for *Decamorium*, *Rhoptromyrmex* and *Triglyphothrix*. The species *Tetramorium opacum* (F. Smith) is transferred to genus *Romblonella* Wheeler (tribe Meranoplini), and *Xiphomyrmex flavigaster* Clark is transferred to genus *Chelaner* Emery (tribe Solenopsidini).

Genus *Atopula* is transferred from tribe Myrmecinini and synonymized with *Tetramorium*. Of the former species of *Atopula*, *belti* (Forel) is transferred to *Brunella* Forel, *longispina* Stitz is transferred to *Paratopula* Wheeler, and *hortensis* Bernard is synonymized with *Tetramorium sericeiventre* Emery.

INTRODUCTION

THIS paper is the first part of a projected revision of the ant tribe Tetramoriin and presents a review, with keys where possible, of all the smaller genera of the tribe and also gives a formal revision of the moderately sized genus *Triglyphothrix*. The genus *Tetramorium* is very large, larger than the rest of the tribe together, and will be dealt with separately in one or more papers which are now in preparation. The present paper only gives a definition and discussion of the genus and its synonyms.

The course of the study at the generic level has led to a number of interesting discoveries which make it possible to define the tribe accurately, but unfortunately it has also led to the conclusion that a number of quite well-known and old generic names have no validity. In this category come *Xiphomyrmex* and *Macromischoides*, both now relegated to the synonymy of *Tetramorium*. Other casualties include the spurious subgenera *Lobomyrmex* and *Sulcomyrmex* of *Tetramorium*, which are synonymized, and the monotypic *Ireneella*, based on a male, is sunk under *Rhoptromyrmex*. Three small and very poorly known genera which were formerly placed in the tribe, namely *Eutetramorium*, *Ireneopone* and *Tetramyrma*, are excluded from further consideration of the Tetramoriini and are assigned to different tribes elsewhere in the subfamily Myrmicinae.

In distribution most of the genera of the tribe Tetramoriini are primarily of the Old World tropics and subtropics, particularly the Ethiopian, Malagasy and Indo-Australian regions. A few Holarctic species of *Tetramorium* are known but only a single species is unquestionably endemic in the New World, *Tetramorium spinosum* (Pergande), which is found in the more arid regions of the southern U.S.A. and Mexico. The Palaearctic region has three endemic genera, *Anergates*, *Teleutomyrmex* and *Strongylognathus*. The first two of these are monotypic genera and are permanent social parasites without a worker caste. The last named is a dulotic genus with falcate mandibles. All the species of these genera utilize species of the

Tetramorium caespitum-group as hosts. The small genus *Decamorium* is restricted to the Ethiopian region but the larger genera *Rhoptromyrmex* and *Triglyphothrix* are found throughout the Old World tropics although no endemic species of these are known from either Madagascar or Australia. Finally, the huge genus *Tetramorium* is based upon the Ethiopian region but is also very strongly represented throughout the Old World tropics and subtropics. One group of this genus, the *T. caespitum*-group, has colonized the more temperate and Mediterranean zones of the Palaearctic region and numerous *Tetramorium* species are widely distributed across the Pacific island systems.

The tribe also contains some of the world's more successful tramp species, spreading mainly or solely by means of human commerce. Such species are found in *Triglyphothrix* (*Tr. lanuginosa*, *Tr. kheperra*) and *Tetramorium* (*T. simillimum*, *T. guineense*, *T. pacificum*) and are more or less commonly encountered in the temperate zones of the world where they are capable of surviving in hothouses or permanently heated buildings, and over wide areas of the world tropics where they are quite at home in nests away from human habitation or in places where the ground has been disturbed by agriculture.

In the free-living genera the vast majority of species are terrestrial or subterranean, with very few arboreal forms. Ground nesting species characteristically nest directly in the earth, in rotten twigs, in or under rotten logs or in compressed leaf litter, and foraging is normally carried on at ground level. A few species which nest in the ground are not averse to foraging on the stems and leaves of plants or even on trees. Of the arboreal species the most common nest sites include rot-holes or rotten areas beneath the bark of otherwise healthy trees, but a few species build rough fibrous nests under leaves or in branch forks, such nests being constructed of vegetable fibres, small twigs and pieces of leaf. Colony size is usually moderate, with a few hundred workers, but in some *Rhoptromyrmex* the nests may be enormous.

Most tetramoriines are generalized predators or scavengers but a few are more specialized and tend homopterous insects or visit plant nectaries. A few species have very specialized diets, for example all members of the *Tetramorium sericeiventre*-group are suspected of feeding entirely on other ants, particularly *Pheidole* species.

Previous studies of the Tetramoriini as a tribe are confined to a few works on a regional basis, such as those of Forel (1902*b*) and Bingham (1903) of the Indian fauna, Arnold (1917; 1926) of the South African fauna, Creighton (1950) of the North American fauna and Mann (1919; 1921) of the species of the Solomon and Fiji Islands. Apart from these there have been a number of reviews or revisions of some of the smaller genera, and these are noted under the discussions of the genera in question.

MUSEUMS AND INSTITUTIONS

ANIC, Canberra	Australian National Insect Collection, Canberra City, Australia.
BMNH	British Museum (Natural History), London, U.K.
CAS, San Francisco	California Academy of Sciences, San Francisco, California, U.S.A.
IE, Bologna	Istituto di Entomolgià del'Universita, Bologna, Italy.
MCSN, Genoa	Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy.

MCSN, Verona	Museo Civico di Storia Naturale, Verona, Italy.
MCZ, Cambridge	Museum of Comparative Zoology, Cambridge, Mass., U.S.A.
MHN, CdF	Muséum d'Histoire Naturelle, La Chaux-de-Fonds, Switzerland.
MHN, Geneva	Muséum d'Histoire Naturelle, Geneva, Switzerland.
MNHN, Paris	Muséum National d'Histoire Naturelle, Paris, France.
MNHU, Berlin	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (D.D.R.).
MRAC, Tervuren	Musée Royal de l'Afrique Centrale, Tervuren, Belgium.
NM, Basle	Naturhistorisches Museum, Basle, Switzerland.
NM, Bulawayo	National Museum, Bulawayo, Rhodesia.
NM, Hamburg	Naturhistorisches Museum, Hamburg, Germany.
NM, Vienna	Naturhistorisches Museum, Vienna, Austria.
UM, Oxford	University Museum, Oxford, U.K.
ZM, Munich	Zoologisches Sammlung des Bayerischen Staates, Munich, Germany.

MEASUREMENTS AND INDICES

Total Length (TL). The total outstretched length of the individual, from the mandibular apex to the gastral apex.

Head Length (HL). The length of the head proper, measured in a straight line from the anterior clypeal margin to the mid-point of the occipital margin, in full-face view.

Head Width (HW). The maximum width of the head behind the eyes, measured in full-face view.

Cephalic Index (CI).

$$\frac{HW \times 100}{HL}$$

Scape Length (SL). The straight-line length of the antennal scape excluding the basal constriction or neck.

Scape Index (SI).

$$\frac{SL \times 100}{HW}$$

Pronotal Width (PW). The maximum width of the pronotum in dorsal view.

Alitrunk Length (AL). The diagonal length of the alitrunk in lateral view from the point at which the pronotum meets the cervical shield to the base of the metapleural lobes or teeth.

All measurements are expressed in millimetres.

GENERIC COMPOSITION AND ORIGINS OF TETRAMORIINI

The earliest attempts at defining a tribe Tetramoriini were quite vague as to its limits and a number of unrelated genera which were excluded later were originally grouped together. The situation as it had been reached in the first decade of this century was summarized by Wheeler (1910) under a tribal name of Tetramorii. Beside the presently-included genera this agglomeration also contained the genera *Mayriella* Forel, *Calyptomyrmex* Emery, *Meranoplus* F. Smith, *Wasmannia* Forel and *Ochetomyrmex* Mayr.

A serious attempt to define the tribe more accurately was made by Emery (1914*a*) in a paper which gave a preview of his later massive works in the *Genera Insectorum* series. He presented a key to the myrmicine tribes as he defined them, and further restricted the Tetramoriini by removing disparate genera such as those noted above. A number of other genera were listed as tetramoriine by Forel (1917) and the genera thus included were more or less stabilized in the dual classifications of Emery and Wheeler, both of which appeared in 1922.

The only difference between these two systems as regards the tetramoriines lay in the treatment of *Tetramorium aculeatum*, which was treated under *Tetramorium* by Emery but which had been removed by Wheeler (1920) to a separate genus, *Macromischoides*. Later Wheeler (1922) defined this genus and placed it in tribe Leptothoracini where it has been retained by most authors (myself included; Bolton, 1973) despite the proof by Santschi (1924) that *Macromischoides* belongs in the Tetramoriini.

As the Emery-Wheeler classification was emerging, Forel (1922) described *Tetramorium* subgenus *Cephalomorium*, the single species of which was shown later by Santschi (1925) to be a member of genus *Pheidole*.

Despite these works the limits of tribe Tetramoriini were still rather vague, and subsequent to the Emery-Wheeler classification various authors added genera and subgenera to the tribe until by 1950 (after the addition of the last generic name but before any critical studies were undertaken) the generic composition of the tribe was as follows.

Decamorium Forel
Dyomorium Donisthorpe
Eutetramorium Emery
Ireneella Donisthorpe
Ireneopone Donisthorpe
Lundella Emery
Macromischoides Wheeler
Rhoptromyrmex Mayr
  R. subgen. *Acidomyrmex* Emery
Strongylognathus Mayr
  = *Myrmus* Schenk
Teleutomyrmex Kutter
Tetramorium Mayr
  = *Tetrogmus* Roger
  T. subgen. *Lobomyrmex* Kratochvil
  T. subgen. *Sulcomyrmex* Kratochvil
Tetramyrma Forel
Triglyphothrix Forel
Xiphomyrmex Forel

Since 1950 a number of modifications to this system have been suggested. Brown (1953) showed that *Lundella* was synonymous with *Hylomyrma* (tribe Myrmicini) and thus removed the Neotropical region's only claim to endemic tetramoriines (see also Kempf, 1973) and later Brown (1964) synonymized *Acidomyrmex* to *Rhoptromyrmex*. Ettershank (1966) showed that *Dyomorium* was a synonym of *Vollenhovia* and thus outside the Tetramoriini and he also pointed out that *Anergates* should be included in the tribe and not treated as a member of Solenopsidini or of a subtribe thereof, as had previously been the case (Emery, 1914*a*; 1922; Forel, 1917; Wheeler, 1922).

At generic level the results of the present study have confirmed the above suggestions and shown that *Eutetramorium*, *Ireneopone* and *Tetramyrma* are not tetramoriines; that *Ireneella* is a synonym of *Rhoptromyrmex* and that *Xiphomyrmex*, *Macromischoides*, *Lobomyrmex*, *Sulcomyrmex* and *Atopula* (from outside the tribe) are all synonyms of *Tetramorium*. These results are discussed in detail elsewhere in this study.

Thus the generic composition of the tribe is now as follows.

Anergates Forel
Decamorium Forel
Rhoptromyrmex Mayr
  Acidomyrmex Emery
  Ireneella Donisthorpe **syn. n.**
Strongylognathus Mayr
  Myrmus Schenck
Teleutomyrmex Kutter
Tetramorium Mayr
  Tetrogmus Roger
  Xiphomyrmex Forel **syn. n.**
  Atopula Emery **syn. n.**
  Macromischoides Wheeler **syn. n.**
  T. subgen. *Lobomyrmex* Kratochvil **syn. n.**
  T. subgen. *Sulcomyrmex* Kratochvil **syn. n.**
Triglyphothrix Forel

Amongst these seven genera *Tetramorium* is by far the largest, exceeding all the other genera combined in number of species. This is also the genus showing the least number of specialised characteristics and is most probably the stem from which the other genera originally radiated. It is difficult to make generalizations about such highly specialized forms as *Anergates* and *Teleutomyrmex*, but the other four genera cluster closely around *Tetramorium* and are obvious derivations from it, mainly through a process of reduction in characters (lower palp formula and antennomere count, reduced dentition, loss of cephalic and clypeal median carinae etc.) and only more rarely by the development of characters not seen in *Tetramorium* itself, such as branched hairs in *Triglyphothrix* and falcate mandibles in *Strongylognathus*.

Concerning the age of the tribe, Brown (1973) points out that the Tetramoriini may well be a recent group as it is unrepresented in any mid-Tertiary or earlier fossil deposits, whereas most other large myrmicine tribes, including nearly all those which have numerous living genera and species, are well represented or abundant in these deposits. Also, Tertiary fossil forms of numerous small myrmicine tribes are present in the deposits.

It can be argued that as the major Tertiary deposits which yield properly identifiable ants (as opposed to fragments or impressions) are in the form of amber, then only arboreal or subarboreal forms would be expected to occur in such locations, and as most tetramoriines are terrestrial or subterranean they would be excluded from such fossiliferous systems.

However, it is also true that the number of arboreal/subarboreal species of modern *Myrmica*, *Leptothorax* etc. are few when compared with the sizes of the genera as a whole but tree-dwelling forms have been represented throughout the history of these genera, and it is most probable that *Tetramorium* at least of the tetramoriines has as many arboreal/subarboreal forms as the other genera mentioned at the present time. It is difficult to envisage that if such forms were present in mid-Tertiary times they would not have been attracted to the resin oozing from the trees to the same extent as species from other genera. One is left with two possibilities: either the tetramoriines were scarce or absent at that time or they had not then developed arboreal species. In either case there remains the conclusion that the vast radiation of this tribe must have occurred since mid-Tertiary times as its members are now numerous or abundant throughout the Old World tropics and subtropics in all ecosystems, and are well represented in the southern Palaearctic region.

Wheeler (1914) was of the opinion that the members of the extinct Baltic amber genus *Nothomyrmica* resembled some species of *Tetramorium* but he did not include it in his section devoted to Tetramoriini, in which he actually placed *Parameranoplus*, *Stigmomyrmex* and *Enneamerus*, none of which are tetramoriine ants. I examined a Wheeler-determined specimen of *Nothomyrmica rudis* (Mayr) in MCZ, Cambridge and have reached the conclusion that the resemblances between this genus and the tetramoriines are superficial and do not indicate relationship. All this reinforces my belief that the tetramoriine radiation occurred after the formation of the Baltic amber deposits was concluded (i.e. post-Oligocene) and it is interesting to speculate upon whether the rise of the Tetramoriini was in any way responsible for the disappearance of earlier genera which originally occupied the environments now dominated by *Tetramorium* and its allies in the Old World tropics.

Concerning the relationships and derivation of the tribe as a whole it seems most probable, on grounds of habitus and morphology, that *Tetramorium* and *Myrmica* are descended from the same ancestral stock, and the more generalized leptothoracines also show similarities to these forms in construction of the body. Particularly interesting is the ease with which the relatively specialized dentitions of the leptothoracines and tetramoriines can be derived from the relatively generalized dentition of *Myrmica* in forms in which the general construction of the head and body are basically similar. In *Myrmica* the mandible has a long series of teeth which decrease in size from the apical to the basal and appear relatively unspecialized. In *Tetramorium* the number of teeth is usually less than in *Myrmica*, but not much less, and specialization has been achieved by reducing the basal series in size whilst maintaining the more apical 2–3 teeth as large. In generalized leptothoracines the trend has been towards a reduction in number of teeth rather than towards specialization of what is available, and the number of teeth has been reduced to a consistent count of five, in a decreasing size series from apex to base of the masticatory margin.

I consider the three tribes Myrmicini, Leptothoracini and Tetramoriini to be closely related and ultimately to have been derived from the same ancestral stock, which was most probably a creature closely resembling the modern genus *Myrmica*, but evidence proving or disproving this opinion is still very much incomplete.

Tribe **TETRAMORIINI** Wheeler

Tetramorii Wheeler, 1910 : 141. Type-genus: *Tetramorium* Mayr.
Tetramoriini Wheeler; Emery, 1914*a* : 38.

The definition of the tribe is rendered difficult by the presence in it of two degenerate, workerless parasitic species which occupy two monotypic genera and exhibit many of the changes listed by Wilson (1971) as the 'inquiline syndrome'.

Disregarding these two species for the moment the remaining vast majority may be diagnosed by the possession in combination of the characters noted below.

Diagnosis of worker and female Tetramoriini. Myrmicine ants in which:

1, either dentition of 2–3 teeth apically, followed by a row of 3–7 denticles; never with a graded series of teeth and never with fewer than 6 teeth; *or* mandibles edentate and falcate;
2, palp formula never exceeding 4, 3;
3, sting with an apical or apicodorsal lamelliform appendage of varying shape;
4, anterolateral portions of clypeus raised into a ridge or shield-wall in front of the antennal insertions.

Diagnosis of male Tetramoriini. Myrmicine ants in which:

1, antennae with second funicular segment an elongate fusion-segment usually consisting of 3–4 antennomeres;
2, mandible dentate or falcate and edentate.

DEFINITION. The following formal definition includes all members of the tribe.

Workers and females. Ants belonging to the subfamily Myrmicinae with thick, usually strongly sculptured integument. Mandibles usually triangular or subtriangular, the masticatory margin with 2–3 large teeth apically, followed by a series of 3–7 denticles, the most frequent dental arrangement being 3 teeth plus 4 denticles, but never with less than 6 in all. Exceptions to this occur in *Strongylognathus* where the mandibles are falcate and edentate, and in the workerless parasitic genera *Anergates* and *Teleutomyrmex* where the mandibles are edentate and reduced. Palp formula 4,3 at maximum, the vast majority of the tribe with this PF value but reductions to 4,2; 3,3; and 3,2 are known and in parasitic forms the PF is 1,1. Anterolateral portions of clypeus in front of the antennal insertions raised into an acute ridge or shield-wall which is confluent with the sides of the broad median portion of the clypeus as a ridge or sharp edge. This feature is a modification of the clypeus itself and is not merely the result of the impression of the head immediately posterior to the lateral parts of the clypeus. The ridge is eroded in *Decamorium* and reduced in *Anergates*.

Antennae 10, 11 or 12-segmented, the three apical antennomeres forming a club. Antennal scrobes often present, situated above the eyes. Ocelli present in females, absent in workers. Anterior lobes of frontal carinae widely separated, the distance across the lobes in a straight line up to twice the distance from the edge of the lobe to the genal margin in full-face view.

Most free-living species with a longitudinal cephalic carina running down the midline of the dorsum of the head and continued on the clypeus as a median clypeal carina. This character is reduced or absent in parasitic or dulotic forms and in some free-living species either the cephalic or the clypeal part of the carina may be absent, but it is rarely completely absent.

In workers the alitrunk without dorsal sutures although the metanotal groove is generally impressed (not in *Triglyphothrix*). Females always winged when virgin, the alitrunk with a full complement of flight sclerites. Wing venation as in males, discussed below. Propodeal spiracle circular or subcircular, the propodeum itself usually armed with a pair of spines or teeth but exceptions to this occur in most genera. Metapleural lobes present, often acute or dentiform but by no means universally so. Legs generally with the femora more or less swollen, and often with a single simple spur on each of the middle and hind tibiae, but these are reduced or absent in many species.

Petiole pedunculate, the node either squamiform or nodiform, subsessile only in the workerless parasitic forms; the node never armed with spines or teeth, never with a massive anteroventral process. Postpetiole very variable in shape. Sting well developed, with a lamelliform and translucent apical or apicodorsal appendage which may be spatulate, triangular, dentiform or pennant-shaped. Absent only in *Anergates* and *Teleutomyrmex* where the sting is reduced and non-functional.

Males. Amongst the Myrmicinae the tetramoriine males are defined by the following combination of characters.

Antennae 9-, 10- or 11-segmented, the second funicular an elongate fusion-segment composed of 3–5 segments fused together. The usual antennomere count in the tribe is 10, the fusion-segment thus containing 4. Mandibles dentate except in *Strongylognathus* (falcate) and the workerless permanent social parasites where they are edentate and generally reduced. Palp formula as in worker/female. Eyes and ocelli present. Alitrunk with flight sclerites, all males winged except in *Anergates* where the male is pupoidal. Wing venation is remarkably stable throughout the tribe and marked reduction is shown only in *Teleutomyrmex* and *Anergates* female. The usual vein-pattern is illustrated in Text-figs 8, 16, 30, 41 and the reductions in Text-figs 23, 26. In *Anergates* female and *Teleutomyrmex*, *m-cu* cross-veins are variably present, usually being weak, incomplete or absent, but in the former *m-cu* is generally visible. In most species *cu-a* has shifted well back along *Cu* towards the wing-roots, but in *Anergates* female this shift is not so well marked as elsewhere in the tribe.

Mesoscutum and scutellum strongly developed, in profile the former overhanging the pronotum. Notauli usually present, at least with the anterior arms of the Y-shape visible, more rarely the notauli very reduced or absent. Parapsidal grooves present or absent. Genitalia usually partially retractile, more rarely apparently fully retractile. Gonopalpi present.

GENERA NEWLY EXCLUDED FROM TETRAMORIINI

TETRAMYRMA Forel

Tetramyrma Forel, 1912*d* : 766 [as subgenus of *Dilobocondyla*]. Type-species: *Dilobocondyla* (*Tetramyrma*) *braunsi* Forel, op. cit.: 767; by monotypy.
Tetramyrma Forel; Forel, 1913*a* : 122. [Raised to genus.]
Tetramyrma Forel; Emery, 1914*a* : 42. [Transferred to Tetramoriini.]

There is little doubt that Forel's original placement of *Tetramyrma* outside the Tetramoriini was more accurate than Emery's (1914*a*) later transfer of this genus into the tribe, although it has since been retained there without question by later authors such as Wheeler (1922). On the present evidence the genus is certainly to be excluded from any further consideration of tetramoriine ants as both the included species lack all the basic tetramoriine characteristics. The palp formula is 5,3; the mandibles have five teeth in a decreasing-size series from apex to base; the sting lacks a lamelliform appendage apically and the clypeus is not raised into a ridge in front of the antennal insertions.

On the present evidence *Tetramyrma* shows affinities with the Ethiopian region species of *Leptothorax* in the construction of the head in general and the clypeus in particular, as this has a projecting, arcuate anterior margin which overlaps the base of the mandibles. On the other hand the metanotal groove is deeply impressed, a feature not encountered in other African *Leptothorax*. However, in overall appearance *T. braunsi* bears a striking resemblance to members of the *Leptothorax anacanthus*-group. I have examined a syntype of *L. maximus* (in MCZ, Cambridge) and compared it directly to the specimens of *T. braunsi* available; the similarities are obvious and it may be necessary to ask whether *Tetramyrma* can retain its identity or must be sunk as a synonym of *Leptothorax*.