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PART 1

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EDITED BY

J. H. MURGATROYD, F.L.S., F.Z.S., F.R.E.S.

WITH THE ASSISTANCE OF

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O. W. RICHARDS, M.A., D.Sc., F.R.E.S., F.S.B.E. W. H. T. TAMS

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# TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

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Part 1

## THE BRITISH ANTS ALLIED TO FORMICA RUFA L. (Hym., FORMICIDAE)

#### By I. H. H. YARROW, M.A., Ph.D.

(Department of Entomology, British Museum (Natural History))

#### CONTENTS

					P	xge
ı.	Introduction					Ī
2.	Definition of the rufa Group and Sync	onyniy of th	e specie	3		3
3.	Notes on the Synonymy:		•			_
_	(I) F. rufa Linnaeus					5
	(2) F. nigricans Emery					9
	(3) F. aquilonia nov. sp					10
	(4) F. lugubris Zetterstedt					10
4.	Distribution of the species					10
ġ.	Notes on distribution and biology					16
6.	Taxonomy of the rufa Group					22
7.	Keys to the species					29
	(I) Females					29
	(2) Workers					33
	(3) Males					36
8.	Appendix—Donisthorpe's collection as	nd book				ء 37
Ο.	Bibliography					15 15

#### INTRODUCTION

Since the day when Linnaeus described an ant as Formica rufa, the identity of this species has been an enigma and it has been the centre of a colossal nomenclatorial tangle ever since. This chaotic state of affairs has arisen in part as a result of the widespread belief that the specimen described by Linnaeus was indeed a worker of a wood ant species and in part from the great number of names with which each member of the rufa group has been generously endowed.

The belief that the original description of F. rufa must apply to a wood ant has led some myrmecologists to apply the name to whatever species in their opinion most closely approached that description, while others have applied the name to the wood ant species most commonly encountered by themselves, wherever in the world that may be, to all intents and purposes regardless of

the original description. The confusion has been increased by Forel's belief in hybrids and by the way in which subsequent workers have accepted, and indeed elaborated it. Finally, the characters which have been used to separate the several European species of the *rufa* group are of such a nature that all manner of misidentifications are possible, with the result that published records are of very little value unless the specimens themselves are accessible; even in our own limited fauna the four species of the *rufa* group have been thoroughly confused and one, to be described here as *F. aquilonia* nov. sp., has been treated as a hybrid between "*rufa*" and "*pratensis*." The present paper, which deals with the British species only, is complementary to a longer work on the Western palaearctic *rufa* group (to be published elsewhere in the near future) in which some matters will be treated at greater length than is here necessary.

For many years it has been customary to take Forel's Fourmis de la Suisse (1874) as the last word in European ant taxonomy and Donisthorpe's British Ants (1915 and 1927) was almost entirely an adaptation of this to "fit" the British fauna (in point of fact it turns out that the British fauna was to some extent "adapted" to fit Forel's conceptions of systematics!); Sweeney's Key to British Ants (1950) though largely following Donisthorpe, introduced several creditable innovations but failed lamentably in Formica and Morley's British Ants (1953) does nothing to improve the situation. During the course of several years' work I have come to the conclusion that Linnaeus's original description of Formica rufa worker (1758) does not apply to a wood ant as generally supposed but to a Camponotus worker presumably selected by mistake; now although this conclusion may not find general approval there is much to recommend it for it solves certain problems, for instance the impossibility of finding a rufa group species to agree with the original description, and the absence of a suitable worker "type" specimen in the Linnaean Collection; at the same time, however, its acceptance raises serious problems of nomenclature since F. rufa L. 1758 is the type species of the genus Formica. I propose to deal with this in some detail under the section "Synonymy" (p. 5) despite the fact that a paper on this subject has recently appeared in the Bulletin of Zoological Nomenclature (Yarrow, 1954b), because it is of vital importance to establish the identity of this keystone to both genus and species group. Furthermore, this paper is revolutionary in that Forel's "hybrids" are allowed no nomenclatorial status for reasons which will be found under the synonymy of rufa (p. 5).

An essential part of the work has been to study nest series from as many sources as possible and to this end I have personally collected in many counties of England, Wales and Scotland and also in several Continental countries, and I should like to express my gratitude to the Trustees of the Godman Fund for a financial contribution towards a visit to Scotland in 1952. Through the kindness of Museum authorities and private collectors both here and on the Continent I have been able to study a wealth of material, including a number of types, without which this and the forthcoming part would have been much less comprehensive. Due acknowledgement to those not directly concerned with the British fauna will be found in the paper dealing with the Continental species, and here I should like to thank the following for their help:

The Cartwright Memorial Hall, Bradford; the University Museum, Cambridge; The National Museum of Wales, Cardiff; Dorchester Museum; The National Museum of Ireland, Dublin; The University Museum, Edinburgh; The University Museum, Glasgow; The Tolson Memorial Museum, Huddersfield; The City Museum, Leeds; The Public Museums, Liverpool; The Manchester Museum; The University Museum, Oxford; Scarborough Museum; The Yorkshire Museum, York; Capt. D. B. Baker, Mr. R. B. Benson, Mr. M. Bibikoff, Mr. H. Britten, Mr. S. C. S. Brown, Dr. J. D. Carthy, Dr. V. H. Chambers, Mr. C. O. Clark, Mrs. J. A. J. Clark, Mr. C. A. Collingwood, Mr. J. Cowley, Mr. H. W. Daltry, Dr. C. D. Day, Mr. H. M. Hallett, Mr. P. Harwood, Mr. W. E. H. Hodson, Mr. S. J. Holt, Miss B. Hopkins, Mr. A. Ibbotson, Dr. T. T. Macan, Prof. F. O'Rourke, Mr. J. F. Perkins, Mr. W. Pickles, Prof. O. W. Richards, Mr. P. R. Richards, Mr. J. P. Rogerson, Mr. A. W. Stelfox, Mr. F. W. Waterhouse, Mr. L. H. Weatherill.

### DEFINITION OF THE RUFA GROUP AND SYNONYMY OF THE SPECIES

The rufa group contains those species of Formica in which the back of the head and the apex of the clypeus are entire or the former only very indefinitely emarginate, the maxillary palps fairly short and sturdy and with abundant hairs, the 5th and 6th segments each at most as long as the 2nd (cf. Yarrow, 1954a, figs. 5 and 6); male with eyes hairy and with hairs beneath the head; head of worker major usually broader than long, of worker minor usually longer than broad; workers vary greatly in size and are bicoloured, occasionally almost entirely reddish yellow or entirely black individuals occurring as rare aberrants in otherwise normal populations. These ants are the well-known wood ants, the large thatched nests of which are a feature of much of our countryside. In the British Isles there are four species, F. rufa Linnaeus and F. nigricans Emery in the south, F. lugubris Zetterstedt and F. aquilonia nov. sp. in the north and in Ireland. F. truncorum Fabricius, widely distributed on the Continent, and with close relatives in Spain, Tibet, China, Japan and N. America, is absent from our fauna: it belongs to a group of species with pronounced clypeal pits, long and narrow basal segments of the flagellum and with somewhat different nesting habits.

#### FORMICA RUFA LINNAEUS

F. rufa Linnaeus (1758); Fabricius 1793, 1804, Latreille 1798, 1802, Smith 1858, Saunders 1896, Donisthorpe 1915, 1927, Lomniki 1924, Karawajew 1930, Stitz 1939, nec Linnaeus (=Camponotus).

F. major Nylander 1849; Betrem 1953.

- F. rufa (Linnaeus) Nylander; Förster 1850 (\u03c4), Schenck 1852, Mayr 1855, 1861, Meinert 1861, nec Nylander 1846.
- F. polyctena Förster 1850; Bondroit 1918, Betrem 1953. F. truncicola Nylander; Förster 1850 (ξ), nec Nylander.
- F. piniphila Schenck 1852; Bondroit 1918.

F. rufa var. major Nylander; Mayr 1855, 1861.

F, rufa rufa i. sp. Linnaeus; Forel 1874, Adlerz 1885.

F. rufa var. rufo-pratensis Forel (nomen dubium) 1874; Ruzsky 1905, Emery 1909, 1925, Wasmann 1909, Donisthorpe 1915, 1927 in pt., Stitz 1939.

- F. rufa var. meridionalis Nasonov 1889; Ruzsky 1905, Emery 1909.
- F. pratensis var. rufo-pratensis Forel; Dalla Torre 1893.
- F. rufa Linnaeus (1758) s. str.; Ruzsky 1905, Holgersen 1943, rec Betrem 1953.
- F. rufa rufa Linnaeus (1758); Emery 1909, Wheeler 1913, Krausse 1929, Berland 1940, Gösswald 1942, Hölzel 1952.
- F. rufa rufa var. rufo-pratensis Forel; Emery 1909, Wheeler 1913, Krausse 1929.
- F. rufa rufa var. meridionalis Nasonov; Emery 1909, Wheeler 1913.
- F. rufo-pratensis Forel; Donisthorpe 1909, Stärke 1947.
- F. rufa rufa (Linnaeus) Nylander; Emery 1915, nec Nylander 1846.
- F. rufa rufa var. piniphila Schenck; Emery 1915, Soudek 1922.
- F. gaullei Bondroit 1917.

4

- F. rufa ab. emeryi Krausse 1926/7, Stitz 1939.
- F. rufa rufa rufa Lattreille; Krausse 1929.
- F. rufa rufa piniphila Schenck; Krausse 1929.
- F. rufa rufa polyctena Förster; Krausse 1929.
- F. rufa rufa emeryi Krausse; Krausse 1929.
- F. rufa var. nuda Karawajew 1930; Stitz 1939, Holgersen 1943.
- F. rufa var. piniphila Schenck; Stitz 1939.
- F. rufa rufo-pratensis major Gösswald 1942; Hölzel 1952.
- F. rufa rufo-pratensis minor Gösswald 1942; Hölzel 1952.
- F. rufa polyctena Förster; Stärcke 1944, van Boven 1947.
- F. rufa polyctena var. piniphila Schenck; Stärcke 1944, van Boven 1947.
- F. rufa polyctena ab. rufo-pratensis Forel; Stärcke 1943b.
- F. rufa polyctena var. piniphila ab. pratensoides Forel; Stärcke 1943b.
- F. rufa polyctena ab. bondroiti Stärcke 1944.
- F. polyctena var. piniphila Schenck; Stärcke 1944.
- F. rufa Linnaeus 1761  $\varphi$ ; Yarrow 1954b (nec  $\varphi = Camponotus$  sp.).

#### FORMICA NIGRICANS EMERY (NOV. STAT.)

- F. congerens Nylander; Förster 1850, Mayr 1855 1861 Saunders 1880 in pt., White 1884 in pt., Betrem 1953, Yarrow 1952, nec Nylander 1846.
- F. congerens Förster? Nylander; Schenck 1852.
- F. pratensis Retzius; Roger 1863 et auct. nec Retzius 1783.
- F. rufa var. rufo-pratensis Forel 1874 (nom. dub.) in pt. et auct. in pt.
- F. rufa pratensis De Geer; Forel 1874, Adlerz 1885, Saunders 1896 in pt., Donisthorpe 1912, nec De Geer 1771.
- F. pratensis Göze; Dalla Torre 1893, Bondroit 1918, Stärcke 1944, van Boven 1947, nec Göze 1779.
- F. rufa pratensis var. truncicolo-pratensis Forel 1874 in pt., Wasmann 1891 et seq. in pt., Emery 1909, Wheeler 1913.
- F. rufa pratensis Retzius; Emery 1909, Wheeler 1913, Karawajew 1930, Berland 1940, Gösswald 1942, Hölzel 1952, nec Retzius 1783.
- F. rufa pratensis var. nigricans Emery 1909, 1916, Wheeler 1913.
- F. rufa pratensis pratensis Retzius; Krausse 1929.
- F. rufa pratensis nigricans Emery; Krausse 1929.
- F. pratensis ab. thyssei Stärcke 1942b.
- F. pratensis ab. nigricans Emery; Stärcke 1943b.
- F. pratensis var. nigricans Emery; Stärcke 1944.

F. (rufa rufo-pratensis) minor pratensoides Gösswald 1951 (SYN. Nov.).

FORMICA AQUILONIA NOV. Sp.

- F. rufa Linnaeus (1761); Nylander in pt.
- F. rufa var. rufo-pratensis Forel 1874 (nom. dub.) in pt.; Donisthorpe 1915, 1927 in pt., ? Karawajew 1930, Holgersen 1943.
- F. rufa rufa var. rufo-pratensis Forel; ? Wheeler 1913 in pt.
- F. rufa (Linnaeus) Nylander, Schenck; Bondroit 1918 in pt.
- F. rufa rufa Nylander; ? Stärcke 1947 (boreal form).

#### FORMICA LUGUBRIS ZETTERSTEDT

- F. rufa Linnaeus 1761; Nylander 1846 in pt. Q nec Q, Schenck 1852, Bondroit 1918 in pt. nec Linnaeus.
- F. lugubris Zetterstedt 1840.
- F. congerens Nylander 1846; Smith 1858, Saunders 1880 in pt., White 1884 in pt. (SYN. Nov.).
- F. rufa var. rufo-pratensis Forel 1874 (nom. dub.) in pt.; Donisthorpe 1915, 1927 in pt., Holgersen 1943 in pt.
- F. rufa pratensis De Geer; Forel 1874? in pt., Adlerz 1885 in pt., Saunders 1896 in pt., Donisthorpe 1912 in pt., nec De Geer 1771.
- F. rufa var. alpina Santschi 1911; Donisthorpe 1915, 1927, Krausse 1929, Stärcke 1944.
- F. rufa rufa var. rufo-pratensis Forel; Wheeler 1913.
- F. rufa rufa var. santschii Wheeler 1913, Kutter 1919, Krausse 1929.
- F. pratensis Retzius; Donisthorpe 1915, 1927 in pt., ? nec Retzius 1783.
- F. rufa (Linnaeus) Nylander, Schenck; Bondroit 1918 in pt.
- F. alpina Santschi; Bondroit 1918.
- F. rufa var. nylanderi Bondroit 1919.
- F. pratensis var. alpina Santschi; Lomniki 1924.
- F. rufa rufa var. nylanderi Bondroit; Krausse 1929.
- F. rufa rufa Nylander; Stärcke 1942a.
- F. rufa rufa ab. tir Stärcke 1942a.
- F. rufa var. santschii Wheeler; Holgersen 1943.
- F. rufa pratensis Retzius; Holgersen 1943.
- F. rufa rufa var. alpina Santschi; Stärcke 1944, 1947.
- F. rufa rufa Nylander; Stärcke 1947, alpine form.
- F. rufa Linnaeus 1758 s.s. Betrem 1953 nec Linnaeus.
- F. rufa var. nigricans Emery; Betrem 1953 nec Emery.

#### NOTES ON THE SYNONYMY

#### A. FORMICA RUFA

1. F. rufa Linnaeus 1761, nec 1758.

I need not here go into the minute details of my reasons for rejecting rufa Linnaeus 1758 as these have already appeared in print (Yarrow 1954b) but it is of great importance that the reasons be fully appreciated. In the first place I find it impossible to reconcile the 1758 description of the worker with any Formica (modern sense) for to what species can "thorace compresso... capite abdomineque nigris" apply?—or the 1761 supplementary description "squama intergerina ferruginea, acuminata"? Linnaeus gives in fact a very creditable diagnosis of a worker of what is now known as Camponotus

herculeanus, the apterous female of which he had described immediately before. On the other hand, his female of F. rufa described for the first time in 1761 is very evidently a Formica and not a Camponotus and the type of nest he mentions is not at all in agreement with a Camponotus species. It seems clear enough to me that in 1758 Linnaeus believed he had before him a specimen of the rufa group when he described Formica rufa but by accident had selected a superficially similar though in fact abundantly distinct species from which to make the description. Now Formica rufa Linnaeus 1758 has been pronounced to be the type species of the genus Formica and if the Rules of Nomenclature were to be rigidly applied, then the enormous genus Camponotus would have in future to be known as Formica and Formica as we know it would require another name; such a change is extremely undesirable and nothing short of chaos would ensue if it were put into effect, and I have therefore applied to the International Commission on Zoological Nomenclature to have the name Formica rufa Linnaeus 1758 put on the list of names permanently rejected in Zoological Nomenclature; if this is done, Formica rufa Linnaeus 1761 becomes an available name for one of the rufa group species, but since it was not included in the original description of Formica 1758 it cannot be treated as the type of the genus without the sanction of the "Commission." For the time being these matters are sub judice. question of a type specimen is quite easily solved without recourse to a neotype for in the Linnaean Collection in London are certain specimens from which a lectotype can be chosen. It may be asked why these specimens have not come to light before and indeed, considering their importance, at first sight it does appear strange; but here again the explanation is simple: there is no specimen in that collection which could be the type of F. rufa Linnaeus 1758 if this species is interpreted in the usual way. But if F. rufa Linnaeus 1758 is interpreted as a worker Camponotus, then the specimens in the collection fall into place: a wingless female Camponotus as the type of F. herculeana, a worker Camponotus as type of F. rufa (1758) and two winged females and three males of Formica (modern sense) to include the male and female of F, rufa (1761). (The description of the worker (1761) is merely an elaboration of that given in 1758 and accentuates the "Camponotus" element.) The type specimen of Formica rufa (1761) could be a male or a female and as females show the more definite morphological characters I have temporarily selected one of the two females as lectotype. Both females belong to what is probably the commonest and most widely distributed of the European species of the group, because of which, rather than by design, it is the species most frequently attributed to rufa Linnaeus by European authors.

2. The validity of Forel's hyphenated names in zoological nomenclature.

Although I shall have more to say about these names in my second paper I cannot avoid reference to them here because Donisthorpe set the lead in this country, but I believe that Forel's whole hypothesis was misunderstood by him (and others). The problem set by rufo-pratensis (and the other hyphenated names too) must be considered from three angles: first, what did Forel himself intend by them, secondly, to what did he apply the name, and thirdly, how have subsequent workers applied the names. Information regarding the first can be obtained from his Fourmis de la Suisse (1874), regarding the second from his collection in the Museum at Geneva and from

specimens elsewhere which carry his determination. Forel's conception of species, races and "formes intermédiaires" are quite clearly given (1874: 16, etc.) and although they do not necessarily correspond to modern taxonomic categories the principle behind Forel's technique is obvious enough, i.e. different species do not interbreed though different races of the same species do, or can do, producing a hybrid population; the terminology Forel used to distinguish the hybrids followed the Swiss botanist Monsieur D. Rapin, who had adopted an abbreviated way of denoting the parentage of hybrids (cf. Forel, 1874, p. 15, footnote) with the result that Forel's F. rufa var. rufopratensis was in effect a short way of writing F. rufa rufa x F. rufa pratensis; Forel's belief that hybrids exist in nature is apparent from time to time in his text, as, for example, when he says, "Je suppose qu'une ? truncicola ait été fécondée par un of pratensis... Ses descendants seront des F. truncicolopratensis" (Forel, 1874, p. 419). Forel varied these names in order to show which parent the hybrid most resembled, producing such names as rufa pratensoides, pratensis rufoides, etc., except on one occasion (p. 368) written without the connecting hyphen; a study of his table (p. 17) (reproduced in toto in Donisthorpe, 1927, p. 305) will show that although written without hyphen, these names are of the same standing as those with hyphen. It is not perhaps appreciated that these "formes intermédiaires" are to some extent hypothetical—witness the name Leptothorax affino-nigriceps (p. 86) for the hybrid of two supposed races of L. tuberum of which he said, "Je n'ai pas encore trouvé des formes affino-nigriceps, mais je ne doute pas de leur existence." I need not deal here with the genetical aspects of Forel's hypothesis but I should perhaps remark that Mendel's work on inheritance was not available to him in 1874. Some years later Wasmann bravely applied the Mendelian theory to "mixed" colonies of ants and between the years 1881 and 1915 published a number of papers on the analysis of three such colonies; I have been able to study specimens from these colonies and am of the opinion that Wasmann himself became more "mixed" than his ants! (I shall deal more fully with this matter in my second paper but would just add here that his "intermediates" appears to be such only on the trivial characters (of colour and pilosity) which he used to separate the "races.")

According to Forel, a community maintains its status as a pure race on the one hand or as the product of two pure races on the other, by not accepting back into the parent nest any female which has mated with a male from another colony (1874: 17) and that females mated away from the parent nest are very unlikely to find their way back to it (1874: 398). The morphological continuity of the community is retained, in fact, through inbreeding, even in the hybrid community (1874: 419), an hypothesis which can scarcely be accepted in view of modern knowledge of segregation, but the importance of Forel's belief is that if his observations are accurate and these supposed hybrid colonies do in fact maintain their morphological continuity over a period of years, then it is extremely improbable that these colonies are hybrids.

We have established, I think, that Forel applied a hyphenated name to a specimen not only because it looked, for example, like a rufa or pratensis hybrid (i.e. more hairy than rufa yet less darkly marked than pratensis or as dark as pratensis but as hairless as rufa) but because he believed that it really was such a hybrid. It is important to establish this point because his use of

the word "variety" as in rufa var, rufo-pratensis does not imply an aberration or abnormality as Donisthorpe in part (p. 306) and most other authors have taken it to be. Now how did Forel himself apply the name rufo-pratensis? I regret that I have not been able to study his collection but Dr. Betrem of Holland has very generously sent me notes made by himself when he visited Geneva, and although he and I do not entirely agree over the taxonomy of these ants it is evident that Forel's series of rufo-pratensis contains examples of all or nearly all the species of the European rufa subgroup and includes, as Donisthorpe's did nearly fifty years later, the species aquilonia, the workers of which, in colour and pilosity, fall between rufa and on the one hand nigricans and on the other lugubris. Whether or not rufa and the other species ever interbreed I do not know; in Great Britain the areas where cross breeding could take place are limited to one small part of Dorset where rufa and nigricans occur within about a half-mile of each other and in parts of Scotland such as the Black Wood of Rannoch where nests of aquilonia and lugubris are often only a matter of yards apart. At Rannoch I spent ten days sampling at the time the sexuals were in the nests and on no occasion did I encounter mixed populations. The whole problem of mixed nests in ants is a very complicated one, for if ants will accept mated females of other species into their nests as some authors claim, then mixed populations could occur without any question of cross-breeding and they would maintair, themselves as mixed populations for so long as the female or females remained fertile. A female of one species mated with the male of another would presumably produce hybrid workers and females, the latter probably sterile, but males of her own species, and since the cross-mated female is more likely to be received into an existing nest than to start on her own, her hybrid progeny might pass unnoticed. (There is ample scope for research here but for reasons of distribution it could be carried out on the Continent more easily than in Great Britain.)

It is necessary now to deal with Donisthorpe's use of Forel's names. Apart from transcribing Forel's table already mentioned, and being at great pains to point out the value of it, Donisthorpe showed a singular disregard for the very essence of Forel's hypothesis, that is, to repeat, that races of a species but not species themselves can interbreed and produce intermediates, for according to Donisthorpe rufo-pratensis could be produced either by direct variation from rufa itself (as in the Isle of Wight where "pratensis" has never been known to occur) or (as in parts of Scotland where he believed both rufa and pratensis to occur) by "crossings between rufa and pratensis males and females" (p. 306), both rufa and pratensis being treated as distinct species. An examination of Donisthorpe's collection shows that his rufo-pratensis from S. England are all rufa, the series from Parkhurst Forest upon which he particularly commented consisting almost entirely of pseudogynes, a fact which he omitted to mention; from Scotland his specimens belong to a species which, although occurring not uncommonly in Scandinavia and the Alps, has been "lost" under the name rufo-pratensis and I am obliged to describe it here as new.

There remains the problem of the nest found by King at Nethy Bridge from which Donisthorpe (1927: 299) identified females of both pratensis and rufo-pratensis, the workers being rufo-pratensis "much nearer to pratensis than

to rufa"; in the University Museum, Glasgow, in the J. J. F. King Collection there are numerous specimens from Nethy Bridge of both aquilonia and lugubris determined by Donisthorpe as rufa, rufo-pratensis and pratensis but it is not indicated which specimens came from the same nest. Donisthorpe would have identified first the workers and these, from experience, one would expect to have been aquilonia, but as he does not include rufo-pratensis in his key to females it is impossible to guess why he separated King's examples into two groups. The specimens themselves are helpful, however, for there is no date on which females of both forms and workers of rufo-pratensis were taken; on the 12th of July, 1911, however, King captured four females determined as pratensis (=lugubris), one female as rufo-pratensis (=lugubris) and twelve workers as rufo-pratensis (=lugubris). I think there can be little doubt that these specimens are the ones referred to by Donisthorpe and they explode this example of mixed nests.

I can see no justification for allowing the hyphenated names any status in nomenclature: they are hypothetical names for hypothetical hybrids, the hybrid "quality" of which is related to appearance rather than to fact; they are scattered through many ant genera where they may either mask undetected species or restrict our knowledge of species variation. It would be desirable to have some, if not all, of these names permanently rejected, for the fact that the *rufa* group ants named by Forel are not racial hybrids but sympatric species does not lend any validity to these names.

#### B. FORMICA NIGRICANS

In 1771 De Geer published the description of an ant which he called the "Fourmi rousse des prés," pointing out that it differed so little from the "Grand fourmi des bois" (F. rufa s.l.) that he was able to distinguish it on biological but not on morphological characters. In 1783 Retzius latinized De Geer's name as Formica pratensis. In 1846 Nylander described the worker of a species close to rufa under the name Formica congerens, and in 1850 Förster described the female of what he believed to be congerens; in 1863 Roger synonymized congerens Nylander with pratensis Retzius. The confusion that today surrounds this species was by then well under way, for Förster's female was not of the same species as Nylander's worker and quite probably neither of them was De Geer's "Fourmi rousse des prés." However, support for Förster's species can be claimed on the grounds that the nest of this species is usually out in the open away from woods, is (therefore) usually thatched with grass stems rather than with twigs, pine needles, etc., and frequently has grass stems growing through it; all this agrees well with what De Geer wrote of his "fourmi rousse des prés" and his inability to distinguish this ant from his "grand fourmi des bois" would not be at all surprising, especially if the latter were F. lugubris. On the other hand, the description of the nest applies equally well to Formica exsecta or F. pressilabris or even to F. suecica, species likely to be more abundant than Förster's congerens, though here one is faced with a considerable difference in head shape which I find hard to believe De Geer would not have noted. Dr. Betrem has pointed out to me that De Geer's "fourmi noir et luisant" is most probably Lasius (Dendrolasius) fuliginosus and that if this is correct, then De Geer failed to comment on the remarkable head of that species also. Now if De Geer's descriptions are inaccurate to this extent there can be very little point in IO [March

trying to establish anything definite about either of his species. The transfer of the name pratensis from the rufa group to the exsecta group would be most undesirable yet its retention in the rufa group can lead only to further confusion; it seems advisable, therefore, that the name should be suppressed by its inclusion in the "Official index of rejected and invalid specific names in Zoology." The next available name is nigricans Emery 1909, originally described for a southern "form" of "pratensis."

This species was first recorded as British from Bournemouth, under the name *F. congerens* Nylander (Smith, 1865) and thus, due to Förster's interpretation of that species, immediately confused with the species recorded under that name from Scotland.

#### C. FORMICA AQUILONIA

The discussion on Forel's hyphenated names leaves little to be said regarding this species. It is unfortunate that a new name must be created for a species which has been known for so long and it will probably be found that similar action is required when the various interpretations of some other Forellian hybrids are investigated. Although Donisthorpe from time to time identified specimens of this species as "rufa" and "pratensis," rufo-pratensis is the most common and lugubris was not included in the series of rufo-pratensis in his collection (cf. p. 38).

#### D. FORMICA LUGUBRIS

The type of this species is a male from Ofoton jiord, N. Norway, in Zetterstedt's Collection at Lund. So far as we are concerned in the British Isles, this species has been known as F. rufa, F. rufa var. alpina (later var. santschii), F. congerens and F. pratensis; most records of these names from Scotland apply to this species while those that do not, apply to aquilonia but in no case to rufa. The species was first recorded as British under the name F. congerens (Smith, 1858) from a male taken near Loch Rannoch, Perthshire, and later confused with what was believed to be F. pratensis from the extreme south of England.

#### DISTRIBUTION OF THE SPECIES

The distribution of the four species in the British Isles is of extreme interest but cannot be properly assessed except as a part of their whole range. This I propose to illustrate in my second paper and here I propose to discuss the subject only briefly.

In the map and the lists which follow I have indicated by means of an\* the localities from which I have actually seen examples, either alive in the field or as museum specimens: some of the localities such as Kensington Gardens and Hampstead Heath are taken from very old publications and it is certain that in some of these the ant colonies no longer exist. In certain parts of the country, for example the south, south-west, south midlands and East Anglia, experience has led me to believe that all published records, no matter under what name, must refer to F. rufa, with the exception of the Bournemouth district of Hampshire and the Wareham district of Dorset, where some old records refer to F. nigricans. Similarly in the extreme north of England, with the exception of a small area north of Keswick in Cumberland, I believe all records refer to F. lugubris. In Scotland the position is not so simple, for both F. lugubris and F. aquilonia are now known to occur together in a number of

localities and may well do so in others; I have therefore listed the localities from which each species is known from specimens and I have added, as a separate list, the localities from which the exact identity remains unknown. In this way I hope that subsequent collectors may be able to reach more definite conclusions than I am able to do now. In Ireland the position may be somewhat similar and I have treated it as though it were but at the present time aquilonia is known only from Armagh in the north. I should point out that although Donisthorpe listed records of F. rufa from both Scotland and Ireland and indeed identified specimens from those countries as such, this species is not known from either country and why he did not treat these as "pratensis" remains a mystery.

#### I. F. RUFA

Bedfordshire. Clophill\*, Moulden.

Berkshire. Aldermaston, Bradfield, Burghfield\*, Crowthorne\*, Finchampstead\*, Mortimer\*, Padworth\*, Penny Hill\*, Tubney\*, Windsor Forest\*, Wokingham.

Brecon. Ystradfelte\*.

Buckinghamshire. Brickhill\*, Burnham Beeches\*, Stoke Green\*.

Cardiganshire. Devil's Bridge\*.

Cornwall. Bishop's Wood\*, Blackdown Lane\*, Grampound Road, Idless\*, Truro.

Cumberland (see also under F. lugubris). Bassenthwaite\*.

Devonshire. Ashton\*, Bickley Vale, Bovey Tracey\*, Bridford Wood, Buckfastleigh, Buckland in the Moor\*, Budleigh Salterton\*, Clifford Bridge, Croyde, Dawlish\*, Exeter, Exmoor\*, Exmouth\*, Gidleigh Park, Haldon Moor, Holne Bridge, Kingsteignton\*, Lustleigh\*, Lustleigh Cleave\*, Marsh Mills, Shaughbridge, Stoke Wood, Teignmouth\*, Virtuous Lady Mine, Webburn Valley.

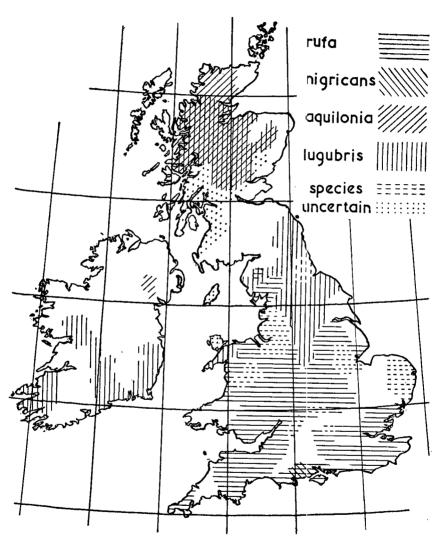
Dorset (see also under F. nigricans). Affpuddle, Bere Heath, Blandford\*, Bloxworth Broadstone, Branksome Chine\*, Bovington Heath, Bushey, Cannon Hill\*, Clyffe, Cold Harbour Common\*, Coombe Heath, Coombe Keynes, Corfe, Dudsbury, East Stoke, Galton, Glanvilles Wootton, Gore Heath\*, Grange Woods, Godlingstone Heath, Higher Brockhampton, Highwood Heath, Holme Heath, Holnest, Hyde, Lulworth, Lytchett Minster\*, Middlebere Heath, Morden\*, Newton Heath, Osmington\*, Owermoigne Heath, Parley Heath, Poole\*, Puddletown Heath, Redbridge, Rempstone Heath, Sandbanks\*, Slepe Heath, Stoborough Heath, Studland Heath, Wareham\*, Warmwell, West Knighton, West Moors, Wimborne\*, Wool Barrow, Wool Heath, Wytch Heath, Yellowham Heath.

Essex. Billericay\*, Birdbrook, Chantry Wood\*, Colchester\*, Hockley, Houghton\*, Lee-on-Sea\*, Lingwood Common, Little Baddow, Southend, Sparkey Wood\*, Walthamstow, Wickham Bishops\*, Woodham Walter Common.

Flint. Llangollen\*.

Glamorgan. Briton Ferry, Castell Coch\*, Cwrt-y-ala, Portneath, Swansea, Taff's Well\*.

Gloucestershire. Bailey Brooke\*, Birdlip, Chalford, Cheltenham, Cirencester Park, Coldwell Rocks, Daglingworth\*, Dean Forest\*, Great Doward,



Map showing the distribution of Formica rufa and its allies in the British Isles.

Dursley, Gorsley, Micheldean, Newent Woods\*, Much Marcle, Sapperton, Sheepscombe\*, Slad Valley, Stinchcombe Hill, Symonds Yat\*, Westbury, Woodchester\*, Wooton-under-Edge\*.

Hampshire (see also under F. nigricans). Amberwood\*, Avon Heath, Barnsfield Heath\*, Basingstoke, Beaulieu\*, Boldre Wood, Bournemouth\*, Bransgore\*, Brockenhurst\*, Broomy, Burley\*, Chandler's Ford\*, College Woods\*, Denny, Eastleigh, Farnborough, Fleet, Fordingbridge, Godshill, Harewood Forest\*, Hartley Wintney, Hasley, Hawley, Headley, Highland Water, Holiday Hill, Holmhill, Holmsley, Hurn, Island Thorns\*, Knightwood, Lady Cross\*, Little Linford\*, Long Sutton, Lyndhurst\*, Mark Ash\*, Marlboro' Deeps, Milkham\*, Minstead\*, Oakley, Pamber Forest\*, Petersfield, Picket Hill, Pound Hill\*, Ramnor Enclosure, Rhinefields\*, Ringwood\*, Roe Wood, Royden, Swanmore, St. Leonard's, Sloden, Sopley Heath, Southampton, Sway\*, Talbot Woods\*, Tunworth, West End\*, Wilverley Enclosure, Wolmer Forest, Woodforde.

Hereford. Buckton\*, Haugh Wood\*, Hollybush Hill, Leominster, Woolhope.

Isle of Man. Mentioned but without reference in Nelmes, 1938.

Isle of Wight. Firestone Copse, Landslip\*, Norton, Parkhurst Forest\*,

Shanklin Chine, Ventnor, Woolton\*.

Kent. Benenden\*, Bexley Heath, Biddenden\*, Blean Wood, Bredhurst, British Camp\*, Brogues Wood\*, Canterbury, Chatham, Chattenden, Chiddingstone, Darenth\*, Fox Cross\*, Goddard's Green\*, Hawkhurst, Hempstead Woods, Herne Bay, Huntingfield, Kingsgate, Maidstone, Oldbury\*, Rainham Park, Rochester, Sheppey Cliffs, Swanscombe, Throwley, Westerham\*, Whitstable\*, Yelstead Woods.

Lancashire. Brathay Hall Woods\*, Carnforth, Grange over Sands\*. Winder-

mere\*, Holker Hall, Satterthwaite, Silverdale, Warton Woods.

Leicestershire. Buddon Wood\*, Charnwood Forest.

Lincolnshire. Coningsby\*, Doddington Wood, Horncastle Spa, Skellingthorpe, Tumby.

Merioneth. Barmouth, Fairbourne, Towyn\*.

Middlesex. Enfield, Hampstead Heath\*, Highgate, Kensington Gardens, Stanmore\*, Wanstead, Winchmore Hill\*.

Monmouth. Cussop Dingle, Llandogo\*, Penhow, Stoke Edith, Tintern\*, Trelleck\*.

Northamptonshire. Harlestone\*, Helpstone, Thornhaugh.

Nottinghamshire. Sherwood Forest, Thorney Wood, Wigsley Wood\*.

Radnor. Stanner Rocks\*.

Shropshire. Bridgenorth, Farley Common, Lyth Hill\*, Shirlett, Wyre Forest (west part)\*.

Somerset. Bristol, Brockley, Horner's Wood\*, Limpney Stoke, Longthorn Woods\*, Minehead, Porlock\*, Stonehouse, Street.

Staffordshire. Burnt Wood\*, Cannock Chase, Eccleshall, Hopwas Wood, Moddershall.

Ashstead, Bagshot, Blackheath, Byfleet\*, Camberley\*, Catford, Chobham\*, Cobham\*, Elsted\*, Esher Common\*, Farnham, Holmbury, Horsell, Jumps Estate, Guildford, Limpsfield\*, Long Cross, Milford\*, Ockham\*, Oxshott\*, Pyrford, Reigate, St. George's Hill, Shere, Thursly Common\*, Weybridge\*, Wisley\*, Woking\*.

Sussex. Ashling, Balcombe Forest\*, Battle, Bexhill, Bolney Woods, Brighton dist., Champs\*, Coldwaltham\*, Cross in Hand, Crowborough, Eridge, Felcourt Heath, Fittleworth, Graffham, Guestling, Lewes, Midhurst, Hastings, Pulborough, Storrington\*, Tilgate Fores:\*, Tunbridge Wells\*, Vetching Wood, West Hoathly, Worth Forest.

Warwickshire. Edgbaston, Hay Wood\*, Knowle, Sutton Coldfield, Tamworth.

Westmorland. Arnside, Storth\*.

Wiltshire. Rabley Wood and West Wood, Marlborough, Selwood Forest, Whetham.

Worcestershire. Bewdley\*, Shrawley, Trench Wood\*, Wyre Forest (east part)\*.

Counties from which wood ants, presumed to be F. rufa, have been recorded but from which no specimens have been seen:

Cambridge. Gamblingay.

Cheshire. Delamere Forest, Dunham Park.

Norfolk (East). Edwards' MS., 1911, locality unknown.

Oxfordshire. Caversham, Elsfield, Shotover Hill.

Suffolk. Assington Thicks, Bentley Wood, Holbrooke Park, Ipswich.

#### 2. F. NIGRICANS

Dorset. Bloxworth, Morden\*. Hampshire. Bournemouth\*.

#### 3. F. AQUILONIA

A. Scotland.

Aberdeen. Bannockbui Forest\*, Braemar\*, Linn o'Dee\*.

Inverness. Aviemore\*, Kincraig\*, Nethy Bridge\*, Rothiemurchus\*.

Nairn. Culbin Sands\*, Dunphail\*.

Perth. Chuallaich\*, Pass of Leny\*, Rannoch\*, Tyndrum\*.

Ross. Baddagyle\*, Inverpolly\*.

Sutherland. Shin Valley\*.

B. Ireland.

Armagh. Churchill\*.

#### 4. F. LUGUBRIS

A. England and Wales.

Carnarvon. Beddgelert, Bettws-y-Coed, Llanberis, Trefiew, Crafnant\*. Cumberland (see also under F. rufa). Ashness Wood\*, Coldbeck, Dunnerdale\*, Lodore\*.

Denbigh. Deganwy, Taly-Cafr\*.

Derbyshire. Alderwasley\*, Ambergate\*, Chesterfield\*, Cromford\*, Grindleford, Hathersage\*, Little Eaton, Longshore Woods, Via Gellia\*, Wirksworth\*.

Durham. Chopwell Woods, Gateshead, Gibside, Hov/gill, Shotley Bridge, Staindrop, Winlaton.

Northumberland. Broomley, Corbridge\*, Dipton, Dilston, Harbottle, Holystone, Lemmington Wood, Morpeth, Hexham\*, Slaley, Styford, Whitley, Yardhope.

Yorkshire. Baysdale, Bingley, Commondale\*, Dalby Valley, Denby Dale\*, Farndale, Fryaton, Glaisdale, Grassington, Hardcastle Crags\*, Hebden

Bridge, Pickingill, Ravensgill, Riccal Dale\*, Scarborough, Silpho Moor\*, Langdale End, Levisham Woods, Littlebeck, Newton Dale\*, Pateley Bridge, Pickingill, Ravensgill, Rical Dale\*, Scarborough, Silpho Moor\*, Sprotboro Woods\*, Upper Wharfdale, Wakefield dist., Wentbridge, West Ayton, Wharncliffe Crags, Wilsden.

Not seen but presumably this species: Anglesey. Garth Ferry-Beaumaris Road.

B. Scotland.

Aberdeenshire. Balmoral\*, Braemar\*, Linn o' Dee\*.

Inverness. Aviemore\*, Greenloch\*, Loch Garten\*, Nethy Bridge\*.

Nairn. Brodie\*.

Perth. Rannoch\*.

Ross. Corrie Valighan\*, Garve\*, Inchbae\*.

C. Ireland.

Galway. Woodford\*.

Kerry. Derrycunniny\*, Muckross\*.

Tipperary. Ballinacourty\*.

Waterford. Kilmacomma\*.

Wexford. Killoughrum Forest\*.

Wicklow. Devil's Glen\*.

Recorded Scotch localities from which specimens have not been seen:

Aberdeen. Ballater, Brig of Gairn, Craig Gowan, Deeside, Garmaddie, Glen Lui, Invercauld.

Argyll. Ardnamurchan, Armidale Wharf, Colintraive, Loch Awe, Loch Riddon, Loch Tyne, Loch Sween, Strontian, Sunart, Tighnabruaich.

Ayshire. Auchincruive, Barrhill, Dalmellington, Dunure, Kilmarnock, Mauchlin, Mochrum, Girvan Water.

Dumbarton. Inchtavrennach.

Elgin. Grantown, Logie.

Forfarshire. No exact locality.

Inverness. Abernethy Forest, Ben Nevis, Fort William, Glenmore Forest, Glen Urquhart, Loch an Eilean, Loch Hourn, Loch Ness, Strathglass, Strath Affric.

Kinross. Blair Adam Estate, Cleish Castle.

Perthshire. Aberfoyle, Brig o' Turk, Cambusmore, Cammorhauren, Comrie, Coninish Glen, Glen Suie, Killiekrankie, Killin, Loch Ard, Loch Tummel, St. Filans, Trossachs.

Renfrew. Paisley.

Ross. Loch Scalpey, Norvar.

Stirling. Rowardennan.

Sutherland. Annat Woods, Glen Alladale, Inveran, Invershin, Loch Shin, Strath Vaich.

Recorded Irish localities from which specimens have not been seen:

Kerry. Killarney, Parknasilla, Rossbehy, Valentia.

Waterford. Clonmel.

Wicklow. Annamore, Clara.

## NOTES ON THE DISTRIBUTION AND BIOLOGY OF THE SPECIES

#### I. F. RUFA

F. rufa occurs over a large part of Europe extending south to Central Spain and north to Scandinavia where it seems that it does not extend further north than the 64° parallel, about 10° further north than it does in England. It is a common object of the countryside in many of our southern counties but in the Midlands it occurs only sporadically and only just overlaps the more northern F. lugubris in Cumberland; in Wales it is really abundant only on the wooded slopes of the Wye Valley although it occurs here and there throughout that country. It is generally looked upon as an insect of sandy conifer-clad country but it is not at all restricted to such places and is equally, if not more, abundant in birch and oak scrub and occurs also, though perhaps less frequently, in beech, holly, hazel and mixed woodlands. Very damp badly drained woodlands are not suitable for this species, nor are very dense coniferous woodlands, where the canopy obscures sunlight and in such places nests are found only at the sides of rides or in clearings. Soil type does not seem to be unduly important so long as drainage is good but I do not know of any nests on chalk. Hillsides facing south are probably the most favoured situations except in the sandy heaths of S. England where even flat land drains quickly and is exposed to the warmth of the sun throughout the day. The occurrence of F. rufa in Cumberland is extremely interesting; the locality, Bassenthwaite, on the SW. facing lower slopes of Skiddaw, overlooking the northern extremity of Derwentwater is quite unlike the slightly more southerly and rugged Ashness Wood and Lodore where lugubris abounds; the rufa colonies at Bassenthwaite are relatively low down, some in fact are in the hedge beside a meadow at the same level as the lake. The nearest rufa nests I know are beside Lake Windermere, several miles to the south. In four different places I have climbed these slopes, so steep in places that one progresses slowly from tree to tree, but wood ants do not occur at any altitude and my hope of finding rufa and lugubric side by side was not gratified; here, in a "pocket" of rufa surrounded (albeit at some distance) by lugubris, there seems little likelihood of the type of "crossing" that Forel and Donisthorpe claimed. It will be seen from the map that the more northern species, lugubris, extends down the Pennines almost to Derby and one might expect peripheral areas of overlap here and also around Snowdonia but my experience is that rufa never does occupy territory sufficiently close to that of lugubris to make hybrids even a remote probability. I have been unable to see any specimens from S. Lancashire and Cheshire but there seems no reason to believe them other than rufa. It is possible that there will be found specimens from these areas in Willoughby Gardner's collection recently arrived at the National Museum of Wales. The number of wingless and therefore presumably mated and returned females in rufa nests can be very great and in a fair sized nest 100 or more is nothing unusual but whether these all lay during the same season I do not know. The nest dome may be of almost any shape or size dependent very largely upon the site and the available material—broad flat nests in open places when bracken is the major element of the thatching material, narrower and more conical domes when twigs and pine needles are used, taller when this is an advantageous way of

obtaining more sunlight, smaller when in situations exposed to wind and rain. (This applies to aquilonia and lugubris also and any attempt to separate these three species by the shape of their nests is doomed to failure, as Creighton (1940) found for North American species.) Gösswald in Germany on the other hand correlates nest shape and certain other biological observations with various forms of rufa; for instance the nest of rufa rufa usually stands by itself, is tall, made of coarse twigs in deciduous or mixed woods and usually has no pathways, has but a single female and is consequently only sparsely populated; the nest of rufa var. rufo-pratensis major is flatter, often somewhat elliptical in outline, is most frequently in coniferous woods, the nest material is finer than in rufa-rufa and there is sand thrown out from the subterranean part of the nest, there are usually some branch nests and broad pathways to nearby trees, there are several females (up to 20) and consequently the nests are well populated; in rufo-pratensis minor, Gösswald recognizes a pine and a spruce race, the former making flat nests in open places, but tall ones in more shaded situations; there are rarely pathways to trees but often very broad ones connecting the often very numerous branch nests, between which there occurs exchange of females, brood and workers. The spruce race on the other hand builds steeper sided domes below which the ground is much excavated with consequent throwing out of sand; pathways run to trees but are not so pronounced as in rufo-pratensis major and there are numerous branch nests and as in the pine race there are many females (200-5,000) and workers. Gösswald's work is very interesting but it does not fit in at all nicely with rufa in Great Britain, where as I have stated earlier, nest shape seems to be a function of the habitat and not of the ant. Furthermore, our rufa, on account of the large number of females present together in a nest could be only Gösswald's var. rufo-pratensis minor (presumably the pine race, because native spruce does not exist in this country and the ant does not, or apparently does not, occur in the cultivated stands of that tree) which, however, most populations cannot be on account of the thoracic markings. Gösswald kindly sent me several samples of rufa rufa and rufopratensis minor but I am unable to distinguish them structurally from our rufa. Now while I do not dispute the value of biological observations as recorded by Gösswald and others, they should not be allowed to override morphological affinities nor to dictate the limits of systematic entities; for example. Gösswald's rufa pratensis and rufa rufo-pratensis minor pratensoides are in my opinion morphologically identical and very distinct from his rufa rufa and rufa rufo-pratensis minor; "pratensoides" is linked to rufa (rufopratensis) rather than to "pratensis" on account of its nest-dome which was constructed largely of spruce needles in the manner of rufa; if populations which behave somewhat aberrantly (and this can be measured only by our knowledge of the species over its whole range) require names then those names must be based on the species and not on the behaviour or the value of the observations will be lost without access to the specimens.

The fascinating problem of colony founding in these ants is still very imperfectly understood and speculation based on very doubtful evidence has done little to assist, while laboratory experiments on queen acceptance show only what can happen under laboratory conditions. One thing, however, that must be evident to all who study these ants in nature, is that no matter

in what way or by what means new nests are begun, their number in any locality must be infinitesimal compared with the number of virgin females available as potential nest starters. When Wheeler (1904) put forward the theory that rufa group females were incapable of starting up nests on their own but would prove to be temporary parasites in nests of F. fusca and allied species, he could little have guessed how quickly it would become acclaimed an established fact; it is not an established fact even today and if colonies can start in this way there must be some very great barrier to their success or the distribution of the nests in many areas would take on a very different appearance. The occasional discovery of rufa group females presumed to be about to enter fusca nests or even established with broad within fusca nests proves only that under certain (but unknown) conditions nests might be established in this way but I do not know that any of these embryonic rufa nests has been followed into maturity. The presence of large numbers of dealate females together in isolated nests implies that some at any rate of the mated females must either return to the parent nest or perhaps never leave it but it is very improbable that those which fly away ever find their way back. The peculiarly restricted distribution of nests in one small part of an apparently homogeneous area has brought forth the very plausible theory that some of these nests must be of off-shoots or branch nests of others and are populated by females and workers which have moved out from the parent nest; that such groups of nests are closely related I think there can be no doubt, for they live on peaceful terms with each other and are frequently connected by pathways, but that these branch nests arise in the way just described is not I think proven and at least as likely a way is for mated females which have descended within the foraging range of the group of nests to start up new nests with the aid of the workers which will have been attracted to them; such a method would, however, produce a far greater rate of increase than is ever the case unless here also is some barrier to successful establishment, for example if the workers were to desert the new nest and return whence they had come.

The artificial introduction of wood ants has been used to explain their existence in private parks and such places where the cocoons are dug out and fed to pheasants but I think such a theory must be viewed with suspiction, for although transplanted colonies will sometimes appear to settle down for a short time, they do not survive for long (especially when being fed to pheasants, one would imagine) and it is hard to believe that a gamekeeper armed with a sack and a spade can succeed where forest hygiene experts on the Continent encounter so many difficulties. The little "pocket" of rufa in Cumberland at first thoughts might be explained as an artificial introduction but further consideration makes this seem very improbable for why should this species have been introduced instead of the locally abundant lugubris? Continental workers have progressed a long way towards being able to establish at will colonies which will thrive but the fact remains that we still do not know in what manner the original member of a group of nests comes into being under natural conditions. Not one of the European species of the rufa group has the reduced body-size of the females of the North American microgyna group which are proven temporary social parasites, nor the remarkable pilosity of certain females of the rufa group in that country

which are to be suspected, if not conclusively proven, temporary parasites nor the agility of the diminutive females of proven parasitic species in this and certain other genera, necessary no doubt for self-preservation during the initial stages of colony founding in this way. The answer to this intriguing and important problem will be found only by observations in the field, not, I think, by laboratory experiments and very definitely not by writers prepared to embellish and present as facts the umproved theories of their predecessors.

#### 2. F. NIGRICANS

On the Continent this species has a distinctly southerly range, being rare in south Scandinavia and south Finland but abundant throughout France, the Channel Islands (where it is apparently the only representative of the group), Holland, Western Germany, Switzerland, Austria and parts of northern Italy. Its occurrence in Hampshire and Dorset but nowhere else in Great Britain suggests that here it is at the western extremity of its climatic tolerance and the fact that it is today known from a single colony only in the same wild open heathland where, if older authors were correct, it was at one time abundant, suggests that before long we shall lose this relic of a warmer climate. British F. nigricans is an ant almost certainly absent from most modern collections and even in those made at the end of the last century and early in the present one it was rarely represented; its occurrence in the Bournemouth district was first recognized in 1864 and thirty years later Farren White (1895) referred to it as being "the common wood ant at Bournemouth"; he was mistaken, however, for many of the supposed pratensis workers are no more than rather hairy rufa. My rediscovery of this species in 1951 is an interesting example of good luck—I visited Dorchester Museum in order to see a female taken in Dorset about forty years ago by the late Dr. F. H. Haines; on seeing the locality on the date label I at once visited Dr. C. D. Day, who I knew had been a collecting companion of Haines, and who was able to tell me which part of the enormous heathland near Wareham was particularly favoured by Haines. The same afternoon I went to this area and within a few minutes found a small nest among the coarse grass and low gorse. My next visit was in the following spring when I found a second but somewhat aberrant colony only a few hundred yards from the original nest but although I have visited the area many times since and have spent many hours searching I have failed to find another. The first nest was very small and I could cover it completely with my hat and it might not have been very old; during the late summer of 1953 it moved about five yards and on opening up the grass-stem dome I found a female which, perhaps unfortunately, I took; when I visited the area in late summer of 1954 the nest and its occupants had disappeared entirely. I suspect that this colony had but a single female and being either very young or in the process of dying out, was unable to stand the loss of the queen. During the summers of 1952 and 1953 the nest contained worker pupae but I never saw a sexual pupa or adult whereas in the aberrant colony there were hundreds of both males and females in June of both years. The aberrant nest is of very different appearance for it is in a bank with only scanty thatch on the top but plenty down the side of the bank into the ditch bottom. The material of the dome is largely heather flowers. It is a very populous nest and although for very obvious reasons I have never dug into it to look for females I find it hard to believe that there

are not several (I have experienced great difficulty in finding the old females in nests of this and an allied species, F. cordieri Bondroi, both in France and in Spain, though in both countries nearby nests of rufa contained large numbers of females). There is no doubt, I think, that nigricans nests, which on the Continent are frequently found singly though often not far from a rufa nest (nigricans frequently nests in the roadside grass verge), are reluctant to accept back fertilized females, yet from the large numbers of young females they produce and the frequent occurrence of single nests it appears that they do not or only rarely increase by branch nests, and likewise newly mated females either alone or in small groups find it difficult to start up new nests in the vicinity of the mother nest. For all his experience of this species, Donisthorpe had no female in his collection and his remarks about the nest founding, number of females, etc., all refer to lugubris. Donisthorpe quotes Wheeler (1910) regarding the existence of covered pathways leading from one nest to another in southern Europe but he makes no reference to their presence in the group of nests he found at Bournemouth in 1925; pathways ran from the first nest I found in Dorset where the nest was in very thick herbage beneath which a stream of ants could be followed to a nearby tree: the second nest on the other hand was in much more open ground and I saw no such pathways. It has been said that this species has perhaps the most irregular swarming period of all ants (Forel, 1875); in Dorset males and females were together in the nest in June, 1952 and 1953, and Beck found males in Donisthorpe's 1914 nest in the same month.

#### 3. F. AQUILONIA

This species appears to have an even more northerly range than lugubris and although it occurs in the Alpine regions of Europe as well as in Scandinavia and Finland, from the very few specimens I have seen it seems likely to be much less abundant. In Ireland it is known from a single locality in Armagh (1896 and 1933) which is the most northerly rufa group record for that country; Stelfox (1927) points out that these specimens are much smaller than all others in the Dublin Collection. It does not penetrate into England at all. In Scotland, where at Rannoch I have been able to study it living side by side with lugubris, I was unable to detect any constant difference in position, size, shape, etc., of nest, though I could always recognize lugubris by the black mass of large workers protecting the top of the nest, an interesting example, perhaps, of division of labour between large and small workers not shared by aquilonia. Through the kindness of Mr. S. J. Holt, then of the Nature Conservancy and stationed in Edinburgh, I was able to visit an area of the old Caledonian Forest near Tyndrum in Perthshire where every nest sampled proved to belong to this species. 'The majority of the nests were about three feet tall with a basal circumference of about ten feet and pointed at the top, unlike most of the nests of lugubris at Rannoch, the tops of which were flat or even somewhat concave and of about six inches diameter. I have not seen aquilonia away from trees and the nests at Rannoch in open country all proved to be *lugubris*.

Since a detailed diagnosis of this species will be found in my keys and illustrations I see no necessity to give a formal description of the holotype female; this specimen is in the British Museum (Natural History) and is one

of a series of fifty females and a greater number of workers from a nest in the Black Wood of Rannoch, Perthshire, Scotland, 10.6.1952.

#### 4. F. LUGUBRIS

On the Continent this species has a much more northerly distribution than rufa, occurring in Scandinavia, Finland and the great mountain ranges of France, Italy, Switzerland and Austria. It is the "rufa" of Snowdonia, northern England, southern Ireland and Scotland, where it shares with aquilonia the honour of clearing the relics of the Old Caledonian Forest of many insect pests. Ouite obviously its requirements of sunlight and its tolerance of long cold wet winters are very different from those of rufa; evidently it can survive several months under deep snow and in the Black Wood of Rannoch, if not elsewhere, summers whose rainfall exceeds all imagination. It will be seen from the distribution map that the more southerly records of wood ants in Scotland are unsupported by specimens; there seems no reason to doubt that both *lugubris* and *aquilonia* will be found to occur in the areas north of the Clyde but in the West Ayrshire localities recorded by Clark (1910) the possibility of rufa itself occurring cannot be overlooked; all attempts to locate Clark's collection have failed and I was unable to find a nest in any of these places when I visited them in 1952; it would be extremely interesting to see specimens from this area because it differs in several respects from the rugged mountainous more northern parts of Scotland and is I think the only part of that country in which rufa is at all likely to occur. Nests of lugubris are usually smaller than those of rufa and their occupants spend a great deal of their time repairing damage due to wind and rain; in Yorkshire and Derbyshire I noticed that the average size of nest was well below that of rufa in most southern localities but this I believe to be entirely due to lack of shelter and nests in the lea of rocks and trees were usually well above the average. The nests vary a great deal in size and shape, are frequently partly overgrown with Vaccinium and are frequently in extremely damp marshy places where the investigator requires waders rather than "Wellingtons." In June, 1952, males and females were in the nests in abundance, unlike neighbouring nests of aquilonia from which most of the males had already flown; pronounced pathways run from the nests when these are in close herbage (heather or coarse grass, etc.) but are absent when the nests are on a carpet of pine needles (this probably accounts for Donisthorpe's statement (1927: 308) that there were no pathways running from the nest of rufa var. alpina (=lugubris) which he found at Rannoch in 1911). In Derbyshire I found a small nest containing nine wingless females and perhaps three hundred workers placed in the bed of a stream, the subterranean part of the nest being sodden. In Riccaldale in Yorkshire many of the domes were large and constructed of bracken and could not have been distinguished from the rufa nests of south England, while at Helwith Bec in the same Riding the nests were all very small, about eighteen inches in diameter and not more than twelve inches tall. This species seems particularly fond of nesting near water but it will thrive well away from it, perhaps because the rainfall of the mountainous districts it inhabits is sufficient for its humidity requirements.

The mating of this, and of the other *rufa* group species, remains a mystery; For all their long experience of these ants, the most Forel and Donisthorpe

could do was to offer certain suggestions and that is as much as I can do now; Forel had never seen copulation taking place but believed that it did not take place in the air but probably in the tree-tops and on the hill-tops, while Donisthorpe recorded having seen it on one occasion only, when it took place in the middle of the afternoon on a heap of sawdust at Aviemore in Scotland. As Forel pointed out, if copulation takes place on the nest-dome itself then females of one nest would be obliged to mate only with males from the same nest, for the workers would not tolerate a male from another (and therefore the hybrids in which he so firmly believed could never come into being). Now since it is so rare an occurrence for even the most persistent observer to see these ants copulating, I think it may be assumed that this act must take place at a time or in a situation inconvenient to the observer, and perhaps inconvenient also to the ants themselves, for a great wastage of females through failure to achieve fertilization would to a great extent account for the relative stability of the number of nests in any one area; Forel's suggestion of tree-tops as a likely site would be well worth following up for if copulation does take place up above the parent nest or group of nests, as it very well could in rufa, aquilonia and lugubris, it is easy to see how fertilized females could return, at any rate to the same group of nests, while in the case of migricans whose nests are frequently well removed from the nearest tree, and the isolated single nest is the rule rather than the exception, how very remote indeed would be the chance of the flying females encountering the males at all, let alone being able to return to the parent nest after fertilization.

#### TAXONOMY OF THE RUFA GROUP

The morphological characters used in this paper are very different from those used by Forel and Donisthorpe and some explanation for such a radical change seems necessary. At the time when the rufa group was considered to consist of the races rufa and pratensis with intermediates rufo-pratensis (and on the Continent also race truncicola with intermediates rufo-truncicola and truncicolo-pratensis) the separation of the races was believed to be a simple one based upon differences of colour and pilosity. For so long as myrmecologists adhered to Forel's methods all was straightforward and any "difficult" individuals were placed in the limbo of rufo-pratensis, etc., but with the appearance of the Belgian artist and entomologist Jean Bondroit the position altered very considerably. Bondroit's Fourmis de France et Belgique in 1918 paid scant attention to Forel's hybrids, applied the name rufa to a species which Forel had either overlooked or failed to recognize, and brought forward a number of names at that time considered to be synonyms, using such characters as leg pilosity of the workers and gastric sculpture of the queens to distinguish them; the followers of Forel were up in arms at once and retaliated by means of some somewhat scurrilous reviews in which sound criticism, of which there was some need, became all but lost in a welter of trivial objections. Bondroit, who unhappily was a most unconventional and uncompromising personality ready to support his theories at scientific meetings with the revolver which it has been said he habitually carried in his pocket, seems to have collapsed under the treatment his work received and to have retired into the oblivion which his critics desired. For all its faults, Bondroit's work was a distinct advance in ant taxonomy for it showed, in the

rufa group at any rate, where characters other than colour and pilosity could be found, particularly in the until then almost ignored female caste. Stärcke and Betrem in Holland and van Boven in Belgium have been considerably influenced by Bondroit in their approach to this group of ants, but in Great Britain his name as a myrmecologist is unknown save for a brief reference to the defects of his Fourmis de France et Belgique in the Preface to the second edition of Donisthorpe's British Ants and a lengthy criticism of his work in The Entomologist's Record (Donisthorpe, 1920).

#### Morphological Characters used by earlier workers

Before turning to the separatory characters used in the present paper it is necessary to investigate those used by Forel and others.

#### 1. Dark marking of worker thorax.

The worker pro- and meso-nota may be entirely red or one or both may be dark-marked and it has been claimed that according to the extent of these markings various species or races can be separated; the several categories in which these markings can be grouped and a graphic method of recording their representation in a nest population are shown in fig. 1. Many populations of the different species have been analysed in this way and a number of them shown as histograms in figs. 2-18. According to Donisthorpe (1927) groups 1, 2 and 3 (but not 4) occur in rufa while 3, 4, 5, 6 occur in "pratensis," 3, 4 and perhaps 5 in rufo-pratensis; according to Gösswald (1944, etc.) for medium to large workers 1 and 2 occur in rufa rufa, 3 and 4 occur in rufa rufo-pratensis major, 5 occurs in rufa rufo-pratensis minor. Figs. 2-6 show four nest samples of rufa from each of four localities, from which it will be seen that 2, 3 and 4 occur in some numbers in most populations while 1 and 5 are either poorly represented or absent. No population examined from very many British samples would agree with Gösswald's rufa rufa and the variation in most would cover both rufo-pratensis major and minor. Bearing in mind that Donisthorpe's rufa, rufo-pratensis and pratensis each contain more than one species it is not very surprising that his descriptions proved difficult to follow.

Since but one nest of *F. nigricans* was known to the writer, little can be shown of colour variation in this species. This one nest was sampled in 1951, 1952 and finally in 1953, when it died out (fig. 7). For comparison a sample from north-west France taken by my colleague Mr. J. F. Perkins is included (fig. 8). In 1952 a nest of what I think must be an aberrant *nigricans* (aberrant in pilosity, intensity of dark markings in workers and gastric sculpture of females, though apparently normal in males) was found a few hundred yards from the *nigricans* nest in Dorset. This nest was sampled in 1952, 1953 and 1954 (fig. 9) and it will be seen that all show very slight variation only and in this respect both Dorset nests differ fundamentally from *rufa* populations about a half-mile away (fig. 2).

While in Scotland in 1952 I was able to take samples from many nests of both F. aquilonia and F. lugubris shown in figs. 11, 12, 13 and 14; lugubris is much darker than aquilonia not only in the extent of the dark markings but also in the "tone" of the red parts. Samples of lugubris from northern England and north Wales (figs. 15, 16, 17, 18) produce occasional lightly marked specimens of categories 1 and 2 as well as very dark individuals of 5 and 6.

Unfortunately I have had no long series from Ireland but specimens on loan from the National Museum in Dublin suggest that *lugubris* populations at any rate do not differ from British ones.

It is not difficult to see that single specimens of our four British species could not be separated on thoracic markings with any degree of accuracy and even large samples might perplex any but the most experienced, though the very restricted range of variation in nigricans should make identification of that species fairly simple. Qualitatively as well as quantitatively nigricans stands apart from the others (in the British fauna) for the dark parts are black and lustreless and are sharply defined, particularly on the pronotum where there is no gentle grading into the red such as is seen in the other species; F. lugubris approaches nearest to nigricans in the intensity of the black markings while in aquilonia and rufa the colour is often brownish. The small and very small workers frequently encountered do not prove good taxonomic subjects, being frequently completely infuscate, and there is rarely any need to make use of them rather than larger individuals for identification purposes.

#### 2. Pilosity.

Older authors placed great faith in the presence or absence of erect or semi-erect hairs (as distinct from flattened pubescence) on various parts of the body, especially the eyes, rufa having naked eyes, "pratensis" (and truncorum) having hairy eyes; British and north European rufa can be recognized in this way, though I have seen what are probably much abraded aquilonia and nigricans in which the eyes showed scarcely a hair and conversely, F. rufa from central Spain may have quite distinctly hairy eyes while even British examples may have an occasional very short hair. Comment on the pilosity of the worker head has been restricted to the gula region, piniphila Schenck (=rufa L.) having some hairs there but polyctena Förster (?=rufa L.) being bare: I have seen no British samples in which some of the workers did not have hairs on the underside of the head. Outstanding hairs on the thoracic dorsum have also been given prominence but perhaps due to abrasion (in life and in careless handling after death) populations show too much variation for this character to be of much value. More recently Bondroit (1918) drew attention to the hairs on the legs, particularly on the hind legs, and I shall have more to say about these shortly.

#### 3. Pubescence.

Females of "pratensis" have long been separated from those of "rufa" by the dull densely pubescent gaster; this is such a striking feature that it is surprising that Donisthorpe, who presumably had seen females of nigricans from Bournemouth, should include with them the far more shining females of lugubris from Scotland under the name pratensis.

It has been the custom to use workers for taxonomic purposes, often to the complete exclusion of sexual forms, presumably because workers represent the bulk of specimens both in nature and in cabinet drawers. I have made it my purpose to collect sexuals (and workers of course) from very many nests and I have found that in the *rufa* group, at least, far better separatory characters exist between the females of the different species than can be found among the corresponding workers. I do not suggest that every nest a collector wishes to identify should be thoroughly excavated (and perhaps

exterminated) but most nests contain very many females which in early summer at any rate are easily found up in the dome. (This does not apply to nigricans, however, which may have but a single female and the colony is very easily destroyed therefore: collectors in Dorset beware!) The keys which follow are all based on nest series in which more than one caste is represented, an essential in working out the differences between aquilonia and lugubris for example, and I consider it possible now to determine correctly a high proportion of the single individuals so often found in collections. Males have received practically no attention before and if retained at all in collections are usually to be found lumped together as unidentifiable; rather to my surprise I discover that there is no great difficulty in distinguishing the British males and the characters used can be seen under very modest magnification.

#### Description of the Specific Characters used in the present paper

The Palaearctic species of the *rufa* group divide at once into two subgroups, those associated with *F. rufa* in which the basal flagellar segments are less than two times as long as broad and the clypeus depressed laterally, the depression running somewhat obliquely to the anterior margin of the clypeus, and those associated with *F. truncorum* in which the basal segments of the flagellum are long and narrow, at least two times longer than wide, the clypeus much more abruptly depressed laterally, the depressions forming lateral pits which are separated by a transverse raised area from the anterior clypeal margin; this second group does not concern us here but is represented on the Continent by *truncorum* Fabricius throughout Europe, *dusmeti* Emery in Spain, *sinensis* in China, *yessensis* in Japan and by certain other species in North America.

#### The Head.

I have pointed out elsewhere that the shape of the head of worker and female has no specific significance and that the long narrow head attributed to rufa var. alpina occurs sporadically in most species; it may, as Santschi suggested, be due to some form of parasitism. The pilosity of certain parts of the head affords good characters, for while the front of the head appears subject to abrasion (evinced by the stumps of broken off hairs which can be found on most specimens) the back region of the head seems to be free from such injury; here long outstanding hairs may form a fringe round the back of the head extending from eye to eye as in workers of nigricans (fig. 24) and lugubris (fig. 26) or may be fewer in number and at times short and difficult to detect as in aquilonia and a form of nigricans. The females show the same hair arrangement as the workers but the hairs are frequently even more reduced, especially in individuals which may have been in the nest for several years. Rufa itself differs from the other species in having no outstanding hairs round the temples in worker or female, and in having the eyes with at most a very few very short hairs only visible under high magnification. (Spanish examples which seem to agree with rufa in all other respects have rather more hairy eyes but never reach the condition of the other species.) The male head is hairy behind in all four species and so are the eyes but less so in rufa than in the others; the cheeks afford no characters in workers and females but in males the absence or abundance of outstanding hairs between

eve and mandible can be used to good purpose. The presence or absence of outstanding hairs beneath the head has been used on the Continent to separate workers of rufa var. piniphila Schenck and var. polyctena Förster: no sample that I have seen could claim to be the latter for there is great variation in this region and if apparently hairless specimens are subject to careful scrutiny hair stumps are frequently discovered. The shape of the male head is rather variable but in aquilonia and lugubris there is a distinct narrow flattened area surrounding the eye which produces a very different outline from that of rufa and nigricans, in which species it is either absent or very much reduced. The shape of the clypeal margin varies considerably in all castes as does the prominence of the median longitudinal keel. I can detect no difference in the mouth parts nor in the antennae. The carinae which lie above the antennal sockets (the lateral carinae) and the area between them show differences which have been used by Betrem (1953) for separating certain Dutch species and I have found that the sculpture of the frons in this region can be used to separate the workers though not the females of the four British species. In figs. 31-50 I have shown diagrammatically the relation between puncture and interspace on various parts of the head and body and I should point out that the presence or absence of microsculpture on the interspaces, not shown in the diagrams, very considerably affects the appearance of the sculpture when viewed under poor magnification and badly arranged lighting; nevertheless the shining interspaces and rather large punctures of the lower frons of lugubris will distinguish it at once from the completely dull from of nigricans and from the less shining and more finely punctured from of aguilonia; rufa itself is nearest to aguilonia in this character but is more shining and the fine punctures are wider apart. The sculpture of the frontal triangle varies in all species from quite copiously punctured (though never to the extent of the Continental uralensis Ruzsky) to impunctate and is always to some extent shining, often brilliantly so, though with a rather oily appearance.

#### The Thorax.

The profile of the worker thorax varies to some extent, especially in the posterior dorsal angle of the epinotum (the epinotum is strictly speaking part of the abdomen but it is so fused with the thorax and so disassociated from the gaster or apparent abdomen that it is convenient to treat it with the thorax) and I have been unable to find any constant differences. It is perhaps not generally appreciated that in some if not all worker Formicines the pronotum and mesonotum are not fused into one position, there being a little up and down movement between the two; thus when in the depressed position, frequently seen in preserved specimens, a rather pale area can be seen around the base of the pronotum and it is this which frequently separates the black prothoracic mark from that of the mesonotum. The profiles of both females and males of all species are very similar. The sculpture of the thorax of the females suggests separatory characters but with the exception of the scutellum I can find no character which is not so subject to variation that overlap between species does not occur, though the general appearance of the mesonotum of nigricans is much the most dull. The sculpture of the scutellum is variable but there seems to be little overlap; in rufa it is most

variable, ranging from completely shining and impunctate to copiously punctured and with fine longitudinal striae yet shining, all forms occurring within the same nest; in nigricans there is no shine at all and owing to the completely matt surface, punctures are difficult to detect but in both aquilonia and lugubris punctures are easily seen, much smaller and finer, the interspaces dull, though not matt, and with conspicuous longitudinal striae in aquilonia, larger and wider apart, the interspaces on the discs shining and with scarcely any longitudinal striae in lugubris. In the males the thorax is always hairy though in rufa these hairs are the shortest and least abundant. In the females there may be very long fine hairs in *lugubris* (and in the Continental *cordieri*) but these are absent in rufa, nigricans and aquilonia. In the worker the hairs of the thoracic dorsum are so liable to abrasion that their apparent absence is of little significance but the outstanding hairs on the mesopleuron appear to vary specifically, and viewed from above, the sides of nigricans and lugubris are very hairy but in rufa and aquilonia they are not, in the latter the long hairs being almost restricted to the ventral region (figs. 27-30). The closeness of the decumbent pubescence of the worker thorax is to a large extent responsible for the dullness of the thorax in nigricans. The presence or absence of upstanding hairs on the thorax is another character used on the Continent to distinguish rufa var. piniphila from var. polyctena but I have seen no sample from anywhere which was completely devoid of such hairs.

#### The Scale.

The outline of the upper margin of the scale in workers and females has no significance whatsoever and it may be flat, elevated or incised in the middle within a single population and is frequently bilaterally asymmetrical; seen laterally it appears to be thinner in *aquilonia* than in *lugubris* but owing to the degree of variation in other respects I am prepared to disregard this. The hairiness of the scale of the worker varies enormously within nest samples but in females provides an easy way of recognizing *lugubris*, in which species it has long outstanding hairs, frequently curled at the tips (fig. 22).

The Legs.

Bondroit was the first to recognize that the leg hairs have specific significance. The absence of outstanding hairs on the extensor (upper) margin of the hind femur and tibia affords a certain way of recognizing rufa; Stärcke (1944) has used the approximate number and angle of these hairs as a separatory character but I think variation makes this impracticable.

The Wings.

The wings provide no character except the degree of infuscation and the wings of males and females of *nigricans* being almost completely clear, distinguish this species from the others in which the wings are considerably darkened in the apical half.

#### The Gaster.

The sculpture and pubescence of the gaster of worker and female, especially of the first tergite, provides an instant means of separating *rufa* from all other species; in *rufa* the pubescence is very scanty and short and the punctures are wide apart in the female (fig. 31) and though closer together in the worker (fig. 39) are shallow and towards the apex of the segment tend

to become elliptical in outline; everywhere they are clearly visible through the scanty decumbent pubescence. The females of all species but rufa are very finely and closely punctured and in nigricans (fig. 32) the punctures and the pubescence are close and the latter thick, so that the gaster has a very matt appearance. The quantity of outstanding ventral hairs in the female varies considerably but only in lugubris do these hairs extend from the sternites on to the tergites in any numbers; dorsally there are no hairs except towards the apex and the anus is surrounded by a circle of hairs. In males the gaster becomes progressively more hairy (as does the rest of the body) in the order rufa, aquilonia, lugubris, nigricans and larger in the order aquilonia, rufa,

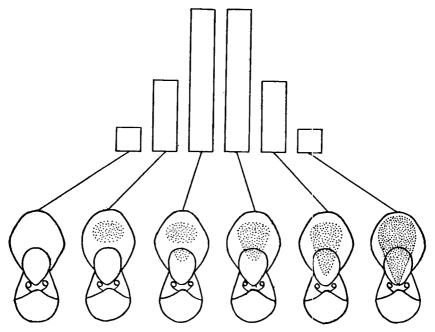


Fig. 1. The extent of the dark markings of the worker thorax and its relation to the histograms (figs. 2-18) showing frequency distribution in nest populations, expressed as percentages of the sample.

lugubris, nigricans; this is largely comparative I admit but the species are easily separated on other characters. Donisthorpe (1927) separated the males of rufa (=rufa+aquilonia) and pratensis (=nigricans+aquilonia+lugubris) thus:

4. Slightly more robust; body and eyes more hairy.....pratensis

While hymenopterists as a whole are accustomed to find good specific characters in the male and even the female (Bombus) genitalia, the

myrmecologist is unlucky so far as *Formica* is concerned, particularly unfortunate perhaps since the male organs are normally extruded and visible without any special attention. I have examined the genitalia of very many males of all species, and I am convinced that no character of specific value can be found. Clausen (1938) has already demonstrated that although in the allied genus *Lasius* the male genitalia and terminal sternite provide excellent differences, in *Formica* even the different species groups cannot be separated.

Before concluding this section it is perhaps worth saying a word about the collecting and preparation of specimens. The old method of mounting flat on a card, like a postage stamp, may make a collection look neat but that is its only attribute. Specimens must never be collected in alcohol (they become discoloured and their hairs become brittle and are easily abraded, making identification by keys based on dry specimens difficult if not impossible). They should be mounted on "tips," not on cards and not on celluloid (for the underside is no better seen than through a card), and a fair sized sample should be taken from every nest; the histograms shown in figs, 2-18 are based on approximately 100 individuals per sample, a dozen or so of which are mounted for the collection, the remainder retained in labelled tubes; for normal purposes a dozen workers should prove sufficient and if females are wanted the collector must be prepared for formic acid injury to his hands. In 1952 in Scotland I excavated seventy-two nests in ten days and by the last day my hands were without skin and it became a matter of great discomfort to touch another nest for several weeks; Donisthorpe comments upon the effect the acid had on his hands (1927:294) and many years earlier (1901) had exhibited at a meeting of the Entomological Society the acidburned gloves which he wore when opening up nests of these ants.

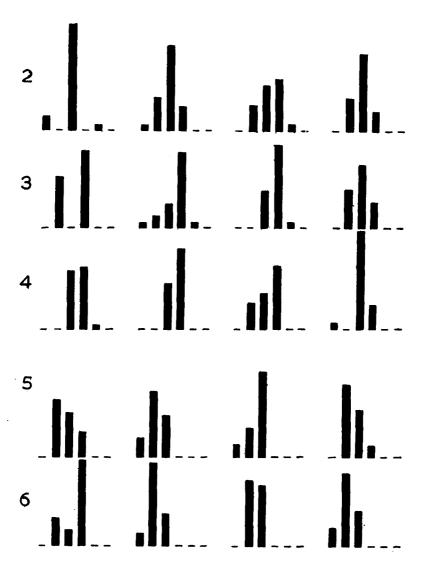
When identifying populations of these polygynous communities it is essential to bear in mind that some slight genetic divergence in even one of the females may be magnified many thousand times in the workers she produces and in this way a community may take on an appearance quite out

of proportion to its importance.

#### KEYS TO THE SPECIES

#### 1. FEMALES

I. Punctures on disc of first gaster tergite fine and shallow, the interspaces sometimes with fine microsculpture and except at the sides considerably greater than the diameter of a puncture (fig. 31); general appearance of gaster shining, often brilliantly so but depending upon the amount of microsculpture. Temples (cf. fig. 23 (\(\frac{1}{2}\))) and declivous part of first gaster tergite (fig. 19) never with outstanding hairs (occasionally on the former there may be one or two somewhat outstanding short hairs but these give the impression of being ruffled out of place and the back of the head in no way resembles that of those species in which it is normally hairy). Scutellum considerably shining, the sculpture on the disc varying from almost entirely smooth to punctate with a few very fine longitudinal striae, the punctures being of irregular size and distance apart. Extensor surface of femur and tibia never very hairy, at most with one or two outstanding hairs



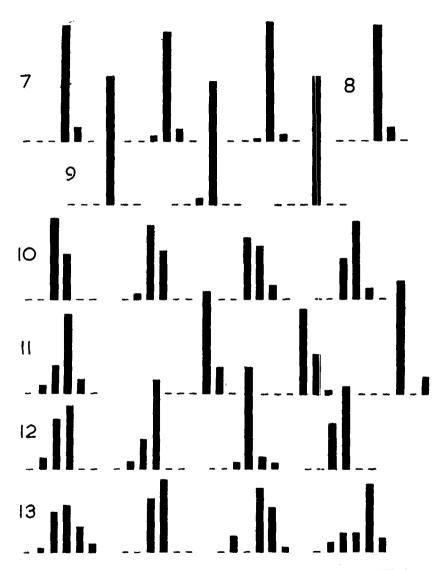
Figs. 2-6. F. rufa. 2, Morden, Dorset; 3, Finchampstead, Berks.; 4, Daglingworth, Glos.; 5, Bassenthwaite, Cumberland.

- Punctures on disc of first gaster tergite smaller, deeper and closer together (figs. 32, 33, 34), the pubescence in one species sufficiently dense as to make the general appearance dull. Temples (cf. figs. 24, 25, 26 (♥)) and declivous part of first gaster tergite (figs. 20, 21, 22) normally with outstanding hairs which may be long and easy to detect or short and at times exceedingly difficult to find. Eyes normally conspicuously hairy. Legs normally much more hairy than in previous species, particularly on extensor surface of hind femur and tibia..... 2
- 2. Gaster shining although frequently with copious but fine microsculpture; decumbent pubescence of first gaster tergite neither sufficiently long nor dense to obscure the underlying sculpture. Scutellum somewhat shining, always considerably punctured and often with conspicuous longitudinal striae. At least some of the anterior four tergites of the gaster with outstanding hairs ventro-laterally which, however, do not arise dorsad of the spiracles (figs. 21, 22).... 3

(A less hairy form with the punctures of the first gaster tergite not so close together and with copious microsculpture between those on the disc is known to occur in Dorset near the typical nigricans; this is perhaps the pratensis ab. Thyssei Stärcke described from Holland. The specimen from Bournemouth which E. Saunders marked as his "type" female of rufa race congerens appears to be this form.)

3. Scale without long outstanding hairs except for those beneath and one or two near the spiracles (fig. 21). No long fine hairs on body or appendages, even in fresh examples. Temples (cf. fig. 25) and declivous part of first gaster tergite (fig. 21) with for the most part short outstanding hairs, those on the former sometimes very few in number or form tufts. Tergites 1-4 with a few rather short outstanding hairs which arise close to their ventral margin. Scutellum little shining, finely longitudinally striate and with copious very fine punctures....

aquilonia nov. sp.

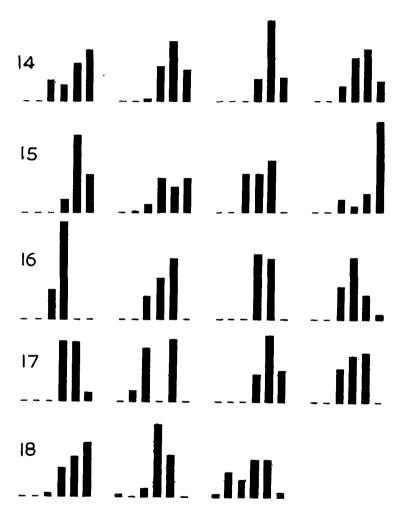


Figs. 7-9. F. nigricans. 7, 1 nest Morden, Dorset, 1951, 2, 3; 8, 1 nest Huelgoat, NW. France; 9, 1 nest of nigricans ab. Morden, 1952, 3, 4.

Figs. 10-13. F. aquilonia. 10, Rannoch; 11, Tyndrum; 12, Pass of Leny, Perth. 13, Linn o' Dee, Aberdeen.

#### 2. Workers

- The small punctures on disc of first gaster tergite coarse though somewhat ill defined, not very close together except at the sides and near apical margin, everywhere clearly visible beneath the rather scanty decumbent pubescence; large punctures from which upstanding hairs (bristles) arise very distinct (fig. 39). Temples never fringed with outstanding hairs although an occasional short hair may project as described in key to females (fig. 23). Frons between the lateral carinae somewhat shining, exceedingly finely and in parts rather remotely punctured (fig. 35). Hind femur and tibia with at most a few outstanding hairs on extensor surface (fig. 51) and never with a continuous row of such hairs. Eyes completely bare or at most with a few very short irregularly spaced hairs which can be seen only under great magnification. Pilosity of mesopleuron rather variable though there are often a few irregularly placed long hairs (fig. 27) which, however, are rarely sufficiently numerous to make the sides appear conspicuously hairy when the insect is viewed from above. Thorax varying in colour from entirely red to dark marked on both pro- and mesonotum, the markings not dead black and matt but brownish and somewhat shining and merging gradually into the red. Head, above and below, thorax, scale and gaster with varying (within the same nest) degree of pilosity, sometimes almost entirely bare. Head sometimes slightly excised behind, clypeus often with a dark median area, a little keeled, frons, vertex and temples usually dark but occasionally showing an almost entirely red or black head ......rufa



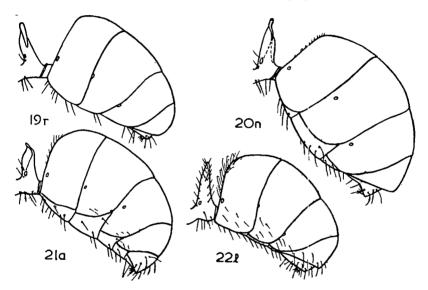
Figs. 14-18. F. lugubris. 14, Rannoch, Perth; 15, Via Gellie, Derby; 16, Lodore, Cumberland; 17, Riccaldale, Yorks.; 18, Crafnant, Carnarvon.

2. Frons between the lateral carinae somewhat shining and with perceptible sculpture in which punctures are fairly easily seen. Thorax and gaster with a close but fine and regular pubescence giving these parts a distinct shine, and on the first gaster tergite allowing the underlying punctures to be seen without much difficulty. Dark markings of thorax merging gradually into the red through an area of intermediate colour and frequently with a small antero-lateral extension of the dark mark... 3

- Frons between lateral carinae dead matt, almost without traceable sculpture in which are rather widely separated and exceedingly small punctures (fig. 36) (these, however, can be detected only under very high magnification and with very carefully adjusted lighting; for the purposes of this key the frons may be considered impunctate). Temples always with some outstanding hairs, though occasionally these may be much reduced both in size and number. Long hairs of mesopleuron rather fine and pale and arise over its whole surface (fig. 28) so that when viewed from above the sides of the insect appear very hairy. Thorax and gaster matt, with an abundant and rather coarse pubescence which on the first gaster tergite almost completely obscures the underlying punctures. Dark markings on thorax usually very clearly defined, and not merging gradually into the red through an area of intermediate colour. (In this species the "black" is extremely black and so matt that from lack of contrasts it is almost impossible to make out any surface structure.) Legs hairy but not excessively so, the hind femur and tibia in normal specimens with numerous outstanding hairs on extensor surface (fig. 52) ...... nigricans (Some workers of the less hairy aberrant form can be very difficult to distinguish from rufa on characters of pilosity and intensity of dark thoracic markings but the sculpture of the first gaster segment and the apparent lack of punctures on the matt lower frons should make it possible to place such specimens correctly.)
- Frons between the lateral carinae clearly punctured, the punctures relatively large and the interspaces to a large extent without microsculpture and shining (fig. 38). Temples usually with copious long outstanding hairs forming a conspicuous fringe which extends forward

#### 3. MALES

1. Cheeks with decumbent pubescence but without long outstanding hairs (fig. 55). Frons somewhat shining and distinctly punctured (fig. 43). Mesonotum with somewhat scanty upright black hairs and



Figs. 19-22. Scale and gaster of female.

Note—In this and the following plates, the figure numbers are followed by the letters r, n, a or l, indicating rufa, nigricans, aquilonia or lugulris respectively.

 Cheeks always with outstanding hairs (figs. 56, 57, 58). Hind femur and tibia more hairy, the extensor surface always with numerous short

- 2. Gaster distinctly shining, temples compressed and eyes rather swollen so that seem from above there is a very pronounced angle between eye and head capsule (figs. 61, 62). Wings usually considerably infuscate. 3
- Gaster scarcely shining, with abundant close golden decumbent pubescence and numerous erect hairs which arise over the whole of each tergite. First tergite with extremely fine punctures which are difficult to detect even under high magnification (fig. 48). Cheeks exceptionally hairy (fig. 56). Frons, mesonotum and scutellum for the most part so completely matt that surface sculpture is extremely difficult to analyse due to lack of contrasts. Frons between the lateral carinae broad, the carinae not very abruptly raised (fig. 64). Temples not compressed and the eyes not swollen, there being no very pronounced angle between the head capsule and the eye (fig. 60). Wings slightly infuscate only in the region of costal vein. Mesonotum with abundant but not very long upstanding hairs......nigricans (Males from the aberrant nest do not differ from the above.)

#### APPENDIX

### DONISTHORPE'S COLLECTION AND BOOK

Donisthorpe's collection of British ants and beetles which was purchased by the British Museum (Natural History) in 1934 with an agreement that it should be retained intact until 1958 and after that if possible, is little known to those outside the Museum. One might imagine it to be some vast accumulation of specimens but Donisthorpe was no believer in numbers and his series are lamentably small and few in number, at least in part due to his generosity to other collectors at home and abroad. All specimens are beautifully mounted flat on cards, as was the tradition of the times and owing to excessive use of gum, especially on the head, have lost a great deal of their value for taxonomic purposes.

His rufa group series are as follows:

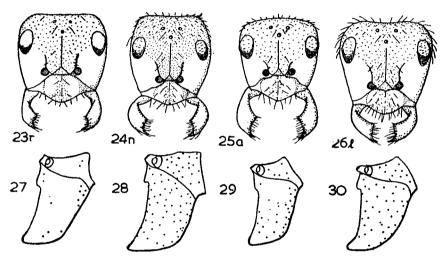
 F. rufa: I ♂ rufa, I ♂ lugubris from Northumberland, 3 ♀ rufa, 14 ♀ rufa, I ♀ lugubris Rannoch.

2. F. rufa var. rufo-pratensis: 1 ♂ rufa, 2 ♀ rufa, 9 ♀ rufa, 3 rufa pseudogynes, 3 ♀ aquilonia, 5 aquilonia pseudogynes Nethy Bridge.

3. F. rufa var. alpina:  $4 \supseteq Rannoch$ , 20  $\supseteq Rannoch$ , lugubris.

4. F. rufa subsp. pratensis: 2 ♂ Rannoch, 3 ♀ Rannoch, x ♀ Northumberland, lugubris, 4 ♀ Bournemouth, genuine nigricans, 16 ♀ Rannoch, lugubris.

Donisthorpe's book, *British Ants*, is full of interesting biological data but without his own collection and his identifications of certain other collections for reference it is often impossible to know to which species his remarks apply.



Figs. 23-26. Head of worker (the four heads have been selected to illustrate variation in shape, all of which may be found in populations of each species).

Figs. 27-30. Distribution of long hairs (shown by dots) on the mesopleuron.

So that these observations may not be wasted I have marked in my own copy of his book (second edition) the name of the species wherever it has been possible to correlate preserved specimens with text or for other reasons to feel certain of the identity. The paragraphs in question I have now abstracted and present here for those who wish to make similar notes in their own copies.

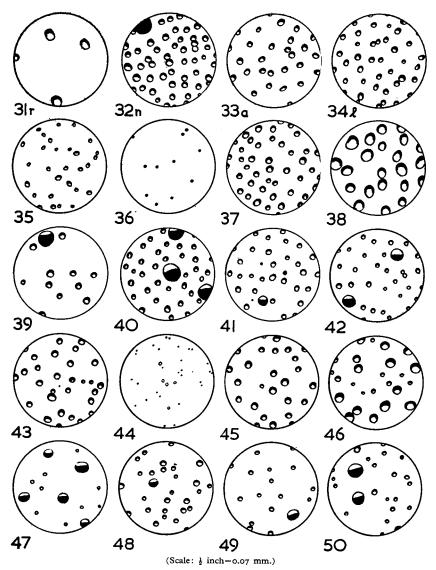
# I. F. Rufa.

p. 290, etc. "This species nests in woods in shady places, in clearings, and on the borders of woods and forests—but also in the interior—on heaths and commons but never far from trees, being more generally associated with fir trees, though it also occurs in oak, birch and other woods."

- p. 290. "Its nests principally consist of the well-known mounds or hillocks forming a conical structure on the ground, covering an earth mound crater at the base, these structures being built up of pine needles, bits of stick, leaves, dried grass or any other vegetable refuse, small shells, pebbles, etc."
- p. 290. "In Dean Forest where this ant is abundant, its nests were found to be constructed of grass; holly twigs and leaves; and beech buds; respectively."

Plate XIII. Upper photograph only.

- p. 291. "Bignell in describing a large nest near Plymouth which he had known for ten years and which he stated would measure forty feet in circumference at its base . . ."
- p. 291. "Joy records rufa nests situated in very thick undergrowth near Bradfield . . ."
- p. 292. "F. rufa occasionally makes its nests in stumps and posts, carving out chambers in the wood, these stumps being often wholly or partly covered with vegetable refuse."
- p. 292. "It was situated all round a gate-post, and the materials of the nest were piled right up to and on the top of the post, and the space between the post and the gate was also filled up with the same."
- p. 292. "I have seen *rufa* colonies at Bagshot situated in tree stumps on a high bank; no materials were present over the stumps except a quantity of sawdust which the ants had accumulated in boring out their galleries in the stumps."
- p. 292. "A single colony may have a number of nests connected with one another by runs, paths and tracks . . ."
- p. 296. "On April 17th, 1912, I found *rufa* males out on fir posts, some distance from any nest, at Wellington College; but on March 21st, 1920, when at Oxshott, I found a winged *rufa* female out at some distance from her nest, which is the earliest date of which I am aware for either of the winged sexes of this species."
- p. 297. "On May 9th, 1922, a single winged female was seen running in a sand-pit in the new Forest . . . in Dean Forest in June, 1923, winged females were observed . . . on 13th and 16th, and a few dealated females on the latter date. A male was captured on the wing on the 14th."
- p. 297. "On March 29th, 1912, Crawley and I found a very large rufa nest at St. George's Hill, Weybridge, which measured six feet in diameter, and it contained vast quantities of large (male and female) larvae and cocoons, but in 1913 all rufa nests examined by me were very backward, only eggs and very small larvae occurring as late as May 4th."
- p. 297. "I have found eggs in nests as late as August and worker cocoons present in a nest at Wellington College on Sept. 28th, 1912, but no eggs, larvae nor pupae occur in the winter."
- p. 298. "... and on Sept. 5th, 1913, I obtained a number of naked worker pupae in a rufa nest at Weybridge."
- p. 300. "On May 15th, 1910, when in Parkhurst Forest . . . I observed a rufa female making her way into a fusca nest."

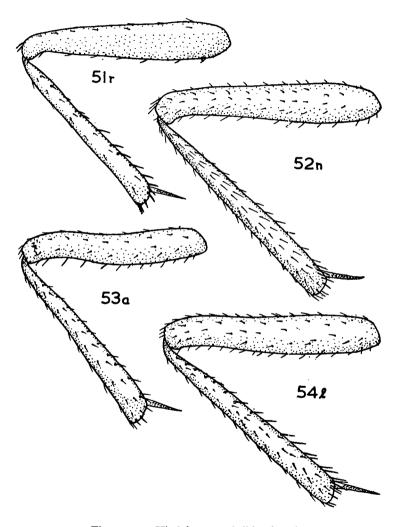


Figs. 31-50. Punctation and relation of puncture size to interspace, shown diagrammatically: 31-34, first gaster tergite of female; 35-38, frons of worker; 39-42, first gaster tergite of worker; 43-46, frons of male; 47-50, first gaster tergite of male.

- p. 300. "On August 21st, 1910... visited Parkhurst Forest and during the day we found in an enclosure of young fir trees a very small *rufa* nest, which consisted of a small mound only eight or nine inches in diameter and about three inches high, but built of *rufa* materials in the usual way."
- p. 306. "On Sept. 8th, 1912, I found two nests of this variety (rufo-pratensis) at Parkhurst Forest... which were situated on a bank, constructed of finer materials than the rufa nests in the neighbourhood, and in fact looking more like exsecta nests."
- p. 306. "Several nests of *rufo-pratensis*, superficially like *exsecta* nests were again found in Parkhurst Forest, on June 29th, 1913, which were situated in clumps of grass. A dealated female was taken but only worker cocoons were present, and in August another dealated female and a male were found in the same locality."

## 2. F. nigricans.

- (p. 310 (facing), Plate XV, specimens from Rannoch and are lugubris.)
- p. 311. "F. pratensis is very like rufa in many ways and has similar habits."
- p. 311. "F. pratensis certainly used to occur more commonly near Bournemouth as there are many specimens in the Dale and F. Smith collections from that locality, but it had not been found there for many years until I found a single colony in June, 1914. I have examined hundreds of woodants' nests in that neighbourhood, all of which, with the exception of the one just mentioned, have proved to belong to F. rufa."
- p. 311. "It would seem that the latter (rufa) had nearly replaced F. pratensis in this locality; but in September, 1925, I found several nests of F. pratensis, situated near to the spot where I found a colony in 1914."
- p. 312. "... and Farren-White found it acting as a miner in a turf bank at Bournemouth, and he says its nests, though often seen in the pine woods in that locality are as often found on the open heath. He discovered a large nest on a sloping bank of fern and heather and gorse, on the margin of a running stream, the depth at the crown of the nest measuring twelve inches, and eighteen inches down the slope of the bank seven inches across the nest; from the upper part to the base on the declivity seventy-two inches; and a foot from the crown, fifty-three inches across; the circumference measuring eighteen feet and four inches."
- p. 312. "The colony I found at Bournemouth on June 15th, 1914, was situated in the grass by the side of a road. Their hillock, which was nine or ten inches high and fifteen to eighteen inches in diameter, was built at the foot of a small gorse bush, but not among trees, and was composed of coarse materials—long twigs, bits of straw, etc.—and the ants had collected a number of wooden matches, and small pebbles from the footpath near the road, which they had mixed with the other materials of the nest. These ants were mostly large in size and brightly coloured as in Continental specimens."
- p. 313. "The colonies of this ant are usually smaller than those of *rufa* and they may occur singly or near to each other". (This may be based upon observations on *lugubris* made in Scotland.
- p. 315. "Beck found males present in my Bournemouth nest on June 14th, 1915."



Figs. 51-54. Hind femur and tibia of worker.

1955] 43

p. 318. Plate XVI is probably perfectly correct.

# 3. F. aquilonia.

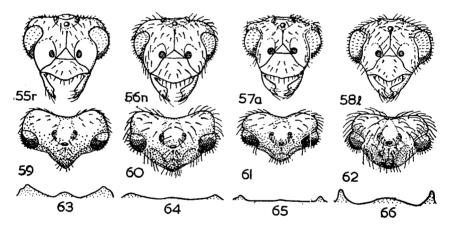
- p. 290 (under F. rufa). "At Nethy Bridge I have seen a nest formed entirely of juniper leaves and twigs . . ." Plate XIII shows this nest.
- p. 295 (under F. rufa in his book but the actual specimens are in his collection under var. rufo-pratensis). "Pseudogynes are sometimes abundant in colonies of this species; I first found these curious forms in a nest of F. rufa at Nethy Bridge, a large proportion of the inhabitants of the nest consisting of them, and subsequently other colonies in the same district were found to possess them, and in both 1911 and 1912 nearly all the rufa nests examined at Nethy Bridge contained pseudogynes."
- p. 306 (under rufa var. rufo-pratensis). "In 1909 I recorded rufo-pratensis from Nethy Bridge, the colouring of the ants being darker than rufa but they did not possess the hairiness of pratensis and I mentioned that the nests differed somewhat from those of rufa, being more compact, the dome-shaped surface smoother and flatter and the nest material not so loose—capable of being moved in layers."

## 4. F. lugubris.

- p. 291 (under F. rufa). "In Northumberland and Scotland these ants collect large quantities of yellow resin-"ant amber"-from the fir trees. I have seen nests full of it and Latreille states that in Sweden the inhabitants gather the resin of juniper trees accumulated by F. rufa in its nests and burn it to purify the air."
- p. 293 (under F. rufa). "On June 12th, 1911, I observed a branch nest of rufa in the Black Wood at Rannoch. Two nests were found to be in connection one hundred and twenty-eight yards apart, one a large mound about seventy-two inches in diameter and fifty-four inches in height, a few yards below the path, and the other a small hillock about the same distance from the path on the other side of it . . . a dealated female was trying to get to the smaller nest . . . some winged females were on the top of the large mound."
- p. 300 (under F. rufa). "On June 10th, 1911, in the Black Wood at Rannoch, I found a dead dealated rufa female in a fusca nest under a stone, which had evidently entered the fusca nest and had been killed by the workers and on June 14th in the same locality, high up on a mountain where no rufa nests occur, I observed a dealated rufa female walking round a stone over a fusca nest."
- p. 308 (under rufa var. alpina). "On June 11th, 1911, I found at Rannoch, on the edge of a moor, a small mound made of heather, etc., which was superficially very like a nest of F. exsecta; the workers running about on the mound, according to the habit of that species, were mostly small in size and very red in colour, and might easily have been taken for it, nor were there any tracks to and from the nest such as are found with F. rufa." (These were the specimens named by Forel.)
- p. 308 (under F. rufa var. alpina). "On July 13th, 1913, when again at Rannoch . . . we visited the same spot where I originally discovered alpina

and some seven colonies were observed; dealated females were found, three in one nest and two in others and pseudogynes were present in one nest, but no winged ants were seen. The nests were all small hillocks, chiefly composed of heather, and were distributed over a small area of the moor and its borders."

- p. 310. Plate XV shows male, female and worker of *lugubris*, not of *pratensis* as stated; the specimens are recognizable in Donisthorpe's collection.
  - p. 308. Plate XIV. The two nests figured are probably both lugubris.
- p. 313 (under pratensis). "In June, 1911, I discovered two pratensis nests situated close to each other among the fir trees near the loch at Rannoch, the one a small, rather flat hillock, the other considerably larger built over a pine stump, both being constructed of pine needles, bits of heather, etc."



Figs. 55-58. Head of male; 59-62, ditto from above; 63-66, elevation of lateral carinae of male through apex of frontal triangle.

- p. 313 (under pratensis). "In July, 1913, a number of colonies were found in this same spot—which consisted of rough hilly ground, some parts of it swampy, with higher dry places and paths winding round the stumps of cut-down trees among the heather, with a number of large Scots Firs scattered about—the workers travelling long distances on the paths to some of the nests."
- p. 315 (under pratensis). "On June 3rd, 1906, I took a winged female pratensis at Corbridge in Northumberland, near a rufa nest, and on June 11th and 12th, 1911, I captured a very few males in, and also away from, the nest, at Rannoch, but on July 17th, 1913... males and winged females were found to be abundant in one nest in that locality, only sex pupae occurring in another."
- p. 315 (under *pratensis*). "... and I found four queens in one nest at Rannoch in which nest pseudogynes were also present."

There are a number of biological data referring to ants in Scotland which cannot be associated with a particular species but which are worth recording:

- p. 288. Buchanan-White writes in 1872: "It (rufa) does not appear to occur in Scotland south of a line beginning at Arran in the south-west, and then passing in a north-easterly direction along the line of the Grampians, through Ben Lomond, Dunkeld, and Dee-Side, and reaching the east coast probably somewhere in Aberdeenshire. It is certainly very remarkable that it does not appear to occur between Dumbarton and Stirling and the English border."
- p. 291 (under rufa). "... and Buchanan-White mentions nests four feet in height and twenty-five feet in circumference in Scotland, but I have seen some narrow cone-shaped nests quite five feet high at Aviemore."
- p. 297. "On June 15th, 1911, I actually witnessed the coupling of the sexes at Aviemore in the middle of the afternoon. A number of *rufa* males and females were seen flying about in a timber-yard, running about on a large mound of sawdust in the hot sunshine, flying off and settling on it, the males appearing to rise more easily than the females. Copulation took place on the mound; I never saw a single pair together in the air."
- p. 298 (under rufa). "Naked pupae also occur; many such pupae, which were evidently pseudogynes, were present in a nest at Nethy Bridge in June, 1911..."

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