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A morphometric comparison of three closely related species of *Myrmica* (Formicidae), including a new species from England

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ABSTRACT. In the course of a population study on *Myrmica sabuleti* Meinert a miniature queen was found in some colonies. This paper describes the form as a new parasitic species, *Myrmica hirsuta* sp.n., and shows how an analogous male was identified. Twelve measurements were then made on a sample of males and females of this new species and these were compared with *M. sabuleti* and *Myrmica scabrinodis* Nyl. using a multivariate discriminating technique. The status of the new species is discussed.

Introduction

This paper is divided into three parts. In the first part a new species, belonging to the *scabrinodis*-complex of the genus *Myrmica*, is described and in the second part a morphometric comparison is made between the new species with two other species belonging to the *scabrinodis*-complex. In the third part the new species is compared with similar *Myrmica* and its status is discussed.

In spring 1973, thirty-one colonies of *Myrmica sabuleti* Meinert were collected from an area of limestone grassland at Durlston, Purbeck, Dorset, U.K., for a population study that has been published by Elmes (1974); eight of these colonies contained miniature queens that at that time were called microgynes of *M.sabuleti*. Apart from their small size these queens could be distinguished easily from normal *M.sabuleti* queens by possession of much more body hair and an enlarged post-petiole. Subsequently, males that possess characteristics comparable to those of the small queens were found in some of these *M.sabuleti* colonies. This has led me to consider the small queens and analogous males as a separate species that is described below. Since the first discovery of the new species I have collected specimens from three other sites in Dorset. These were chalk grassland in the Purbeck Hills, 10 miles from the Durlston site; wet heathland on Hartland Moor, National Nature Reserve, 10 miles from either of the two other sites; and from Lyscombe Down, an area of chalk downland in Central Dorset that is a considerable distance from any of the Purbeck sites. This shows that the form is widespread in Dorset and may well be common throughout Britain.

M.sabuleti is very close taxonomically to the species *Myrmica scabrinodis* Nylander so that for many years *M.sabuleti* was treated as a variety of *M.scabronodis* rather than as a separate species. The worker forms are very hard to separate although males are easily separated by relative scape length. The purpose of the second part of this paper is to investigate these three species by morphometry in an attempt to show that they are well separated by their morphology. Initially, a large sample of queens was investigated using four body measurements which were compared directly; later, a larger number of measurements were made upon a smaller sample of queens and males and these were compared by a discriminant analysis.

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Myrmica hirsuta sp.n.

(i) *Material examined.* 145 queens were discovered living in eight colonies of *Myrmica*

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sabuleti from Durlston Country Park, Purbeck, Dorset (50° 36′ N, 1° 58′ W). The populations of these colonies were analysed in May 1973 and the results have been published by Elmes (1974). Forty-seven of these queens were mounted and placed in my collection, one of these has been designated as holotype while the others form paratypes. The holotype came from a nest containing three queens and 2641 workers of *M.sabuleti* along with forty-six other *M.hirsuta.* Twenty-eight *Myrmica hirsuta* males were collected from three of these colonies in 1974. These also form paratypes. The holotype, two female paratypes and three male paratypes have been deposited in the British Museum (Natural History).

(ii) *Holotype:* author's reference number D1–B total length 5.50 mm. A female without wings.

Head: light, ginger brown, moderately sculptured and covered with erect bristles that are conspicuous at the rear side of the head. The mandibles are normal for *Myrmica,* having a large apical tooth and others reducing in size. The eyes appear to be large but in fact tend to be isometric with headwidth compared with *Myrmica sabuleti.* The antennae have twelve segments and a distinct bend of the scape near to the base that is typical for the *Myrmica scabrinodis* group; there are lateral projections at the bend but these are reduced and could be confused with the scape of *M.scabrinodis.* (Headwidth 1.02 mm, head length 1.12 mm, frons width 0.40 mm, eye length 0.28 mm, length of a typical bristle 0.15 mm; see Fig. 1 for details of measurement.)

Thorax: the thorax is moderately sculptured and slightly darker than the head, the parapsidal furrows are distinct. The spines are relatively short and blunt, curved inwards.

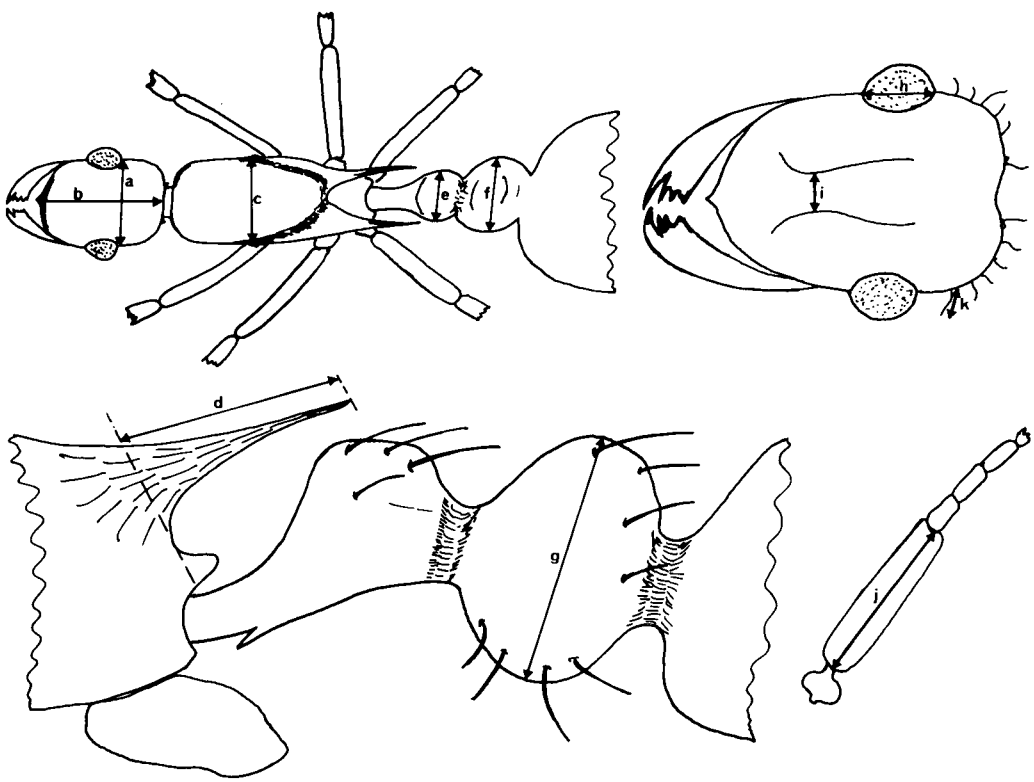

FIG. 1. Diagram showing the measurements made on specimens: (a) headwidth behind eyes, (b) head length excluding mandibles, (c) maximum thorax width, (d) spine length, queens only, (e) petiole width, (f) post-petiole width, (g) post-petiole height, (h) eye length, (i) minimum frons width, (j) scape length, males only. Measurements were made, using a binocular microscope and scaled eyepiece, accurate to 0.02 mm for measurements (a), (b) and (c) and 0.01 mm for all other measurements.

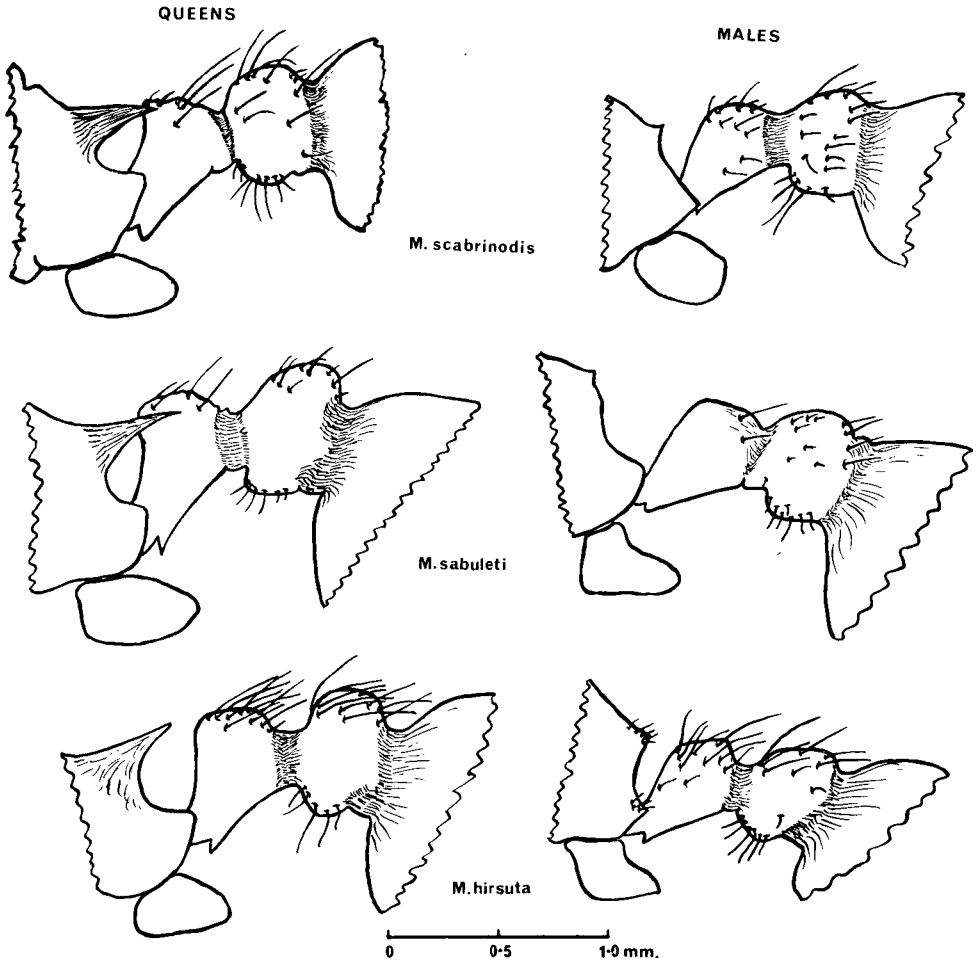

FIG. 2. Scale diagram of the petiolar region, seen in lateral profile, of a queen and male *Myrmica scabrinodis, Myrmica sabuleti* and *Myrmica hirsuta*. Note the shorter epinotal spine and increased hairiness of *M. hirsuta*.

Bristles are obvious, especially on the pronotum and scutellum. The legs are normal for the genus *Myrmica*, having large pectinate spurs on the tibia of the first pair and reduced pectinate spurs on the remaining pairs. (Thorax width 0.96 mm; thorax length 1.70 mm, spine length 0.32 mm; see Fig. 1.)

Abdomen: the gaster is lighter in colour than the head. The petiole is wide and the post-petiole is very wide. Bristles are obvious especially on the petiole region (Fig. 2). The post-petiole is wider than it is high and there is a tendency for the surface of the petiole node (seen in lateral profile) to slope backwards when compared with that of a *Myrmica sabuleti* queen (Fig. 2). A sting is present. (Post-petiole width 0.62 mm, post-petiole height 0.53 mm, post-petiole length 0.44 mm, petiole width 0.38 mm, petiole length 0.50 mm; see Fig. 1.)

(iii) *Paratype:* a winged male; author's reference number D1–10, total length 5.30 mm.

Head: is shiny black, finely punctuated with erect hairs that are easily visible at the back of the head. The clypeus is smooth and shiny and the mandibles have a large apical tooth and several equally small teeth. The eyes are isometric with head width but appear to be large and protruding. The antennae has thirteen segments, the scape is short with a bend near to the base. (Head-width 0.82 mm, head length 0.90 mm, frons width 0.24 mm, eye length 0.28 mm, scape

length 0.50 mm, length of a typical bristle 0.14 mm; see Fig. 1 for measurement.)

Thorax: is the same colour as the head having fine striations. The wings are as *Myrmica* with a closed discoidal and partially dissected cubital cell. The legs are yellowish brown with large pectinate spurs on the tibia of the first pair and reduced pectinate spurs on the other two pairs. The spines are rudimentary and have some bristles. (Thorax width 0.8 mm, thorax length 1.80 mm; see Fig. 1.)

Abdomen: is black and shiny with obvious long hairs. These are particularly visible on the petiole and post-petiole. The post-petiole is wide compared to headwidth and is wider than it is high, contrasted with *M.sabuleti* where the post-petiole is higher than it is wide. (Post-petiole width 0.56 mm, post-petiole height 0.56 mm, post-petiole length 0.46 mm, petiole width 0.42 mm, petiole length 0.44 mm; see Fig. 1.)

(iv) *Position in current keys.* It was first thought that these specimens were microgynes of *M.sabuleti* for they possess many obvious *Myrmica* characters and appear to be very microgyne like in size and range compared to *M.sabuleti* queens (Elmes, 1974). However, the larger petiole size and the obvious hairiness are definite parasitic characters that can be seen in many inquilines and parasites of *Myrmica* species (Kutter, 1973). It will be shown later (Fig. 4) that although hairiness is one of the most obvious characters of this species, hence the name, it is a very viable character. No worker form has yet been discovered and evidence presented later will suggest that no worker form exists for this species. If it is attempted to key the species out using the key given by Collingwood (1958) the queens would key out at couplet six as *Myrmica scabrinodis.* They could then be split at this stage by inserting a division which would read 'specimens small with many upright hairs easily visible, having relatively large post-petioles and a wide frons, frontal index FI about 40', giving *Myrmica hirsuta* then: 'specimens with relatively few hairs and a normal width petiole and post-petiole', go to 7. Couplet 7 would then read as couplet 6 of Collingwood (1958). Similarly males would key out at couplet 5 as *Myrmica sabuleti* which separates *Myrmica scabrinodis* from *Myrmica schencki* Emery; *M.hirsuta* could be separated at couplet 5 from these others by the width of the post-petiole and their hairiness. Using the more recent key by Bolton & Collingwood (1975), *M.hirsuta* 'keys out' as *M.scabrinodis* or *M.sabuleti*; it then can be easily separated from these in the manner outlined above. If Kutter's classification (Kutter, 1973) is used the female of the species can be coded as A1, B3, C5, D9, E12, F16, G19, H22, I26, K29, M33, N38, O41, Q48?, host *M.sabuleti.*

(v) *The separation of the male form of M.hirsuta.* In 1974 211 males were collected from five of the colonies at Durlston, three of these colonies were known to contain *M. hirsuta* queens. All the specimens were weighed and a small number from each colony was mounted. Fig. 3 shows the distribution of fresh weights of these males; this distribution is best described by two normal curves that are shown superimposed, giving a fit of 0.90 by χ^2. The means are 2.9 ± 0.4 mg and 4.1 ± 0.6 mg. Examination of the mounted sample showed that a proportion of the specimens were much more hairy than the others and that these all come from the colonies known to contain *M.hirsuta* queens; the histogram of weights of the hairy specimens (dotted) and the less hairy specimens (vertical hatching) are shown superimposed on Fig. 3. A glance at Fig. 3 shows that the hairy specimens are associated with the normal curve having the smaller mean and comparison with specimens from other sites shows that the less hairy individuals are the typical form of *M.sabuleti.* It seems reasonable to conclude that the smaller hairy form of the male which is associated with colonies that contain the miniature females of *M. hirsuta* is the male of that species.

(vi) *Evidence for a worker form of M. hirsuta.* The data in this section have all come from the thirty-one colonies that were collected from Durlston (Elmes, 1974). There is no positive evidence that shows whether *M.hirsuta* has a worker form or not but all the indirect evidence points to the absence of a worker form. First, the frequency distribution of headwidths of 196 workers from *M.sabuleti* colonies containing *M. hirsuta* and 575 workers from normal *M. sabuleti* colonies were examined and it was found that both distributions were best

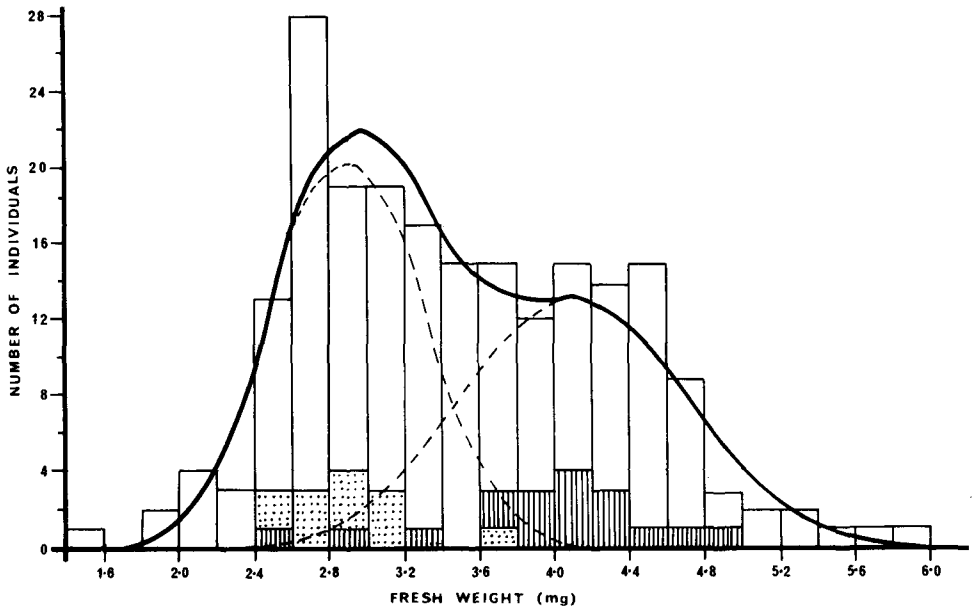

FIG. 3. The frequency histogram of the fresh weights of 211 *Myrmica sabuleti* males sampled from five nests at Durlston, Dorset; two nests were normal and three contained *Myrmica hirsuta* queens. The data are best described by two normal curves (means 2.9 mg and 4.1 mg) that are shown superimposed. The shaded areas represent individuals that are mounted and placed in the author's collection; hairy specimens are shown as stippled and normal specimens as vertical hatched areas. Note the association of the hairy specimens, which all come from the *M.hirsuta* nests, with the smaller size distribution.

described by a single normal curve and that the means of the two distributions were not significantly different. This showed that if *M.hirsuta* produces workers there is no significant difference in size between these and *M.sabuleti* workers. Secondly, a sample of 100 workers from each type of colony was examined carefully and no obvious *M.hirsuta* character, such as hairiness or large post-petiole width, could be detected. Finally, laboratory tests have not yet resulted in any workers being produced although eggs have been reared to the third instar diapause larval stage; these were most likely to have become sexual individuals after a low temperature period. It is hoped that details of the laboratory experiments will be published elsewhere.

Morphometric analysis

(i) *Material examined and measurements used*

The queens that have been measured for this paper are all preserved in the author's collection. Specimens were obtained in two ways: first, from collection of whole colonies for the population studies that have been published elsewhere (Elmes, 1974) and secondly, from among the contents of pitfall traps that have been used for studies on spider populations. Consequently I have a total of 170 *M.sabuleti* queens, 106 of which were obtained from pitfall traps at three Dorset sites and sixty-four from the nests that were collected from Durlston, Dorset. There are fifty-four *M.hirsuta* queens in my collection, forty-seven were collected from *M.sabuleti* nests at Durlston and seven from the pitfall traps. *M.scabrinodis* is represented by 143 queens, 101 collected from the pitfall traps in Dorset and forty-two from population studies on colonies from Bodmin Moor, Cornwall, and Dartmoor, Devon. I have many fewer males in my collection than queens. The *M.scabrinodis* males consist of nine collected from pitfall traps in Dorset and fourteen collected from Studland National Nature Reserve in the 1930s by Capt C. Diver, whose collection is held at Furzebrook Research Station. A further four were collected

from a colony in Denmark. Nine *M.sabuleti* males were available from pitfall and one from the Diver Collection, the remaining eighteen being taken from colonies at Durlston. Twenty-eight males of *M.hirsuta* were collected and mounted from the Durlston colonies.

The following characters were measured on a sample of queens and all the males from each of the three species (see Fig. 1 for way in which measurements were made). Head characters were: headwidth, head length, frons width, eye length and scape length (the last was measured only for males because the curvature of the female scape makes measurement difficult). Frons ratio has been used by other authors to separate *M.sabuleti* from *M.scabrinodis* (Collingwood, 1958) and this is calculated here as frons width/headwidth x100. Thorax width and epinotal spine length were the thoracic characters measured (spines are essentially a female character and were not measured for males). The measurements of the petiolar region were petiole width, post-petiole width and post-petiole height (petiole height was not measured because it is difficult to standardize between species).

An attempt was made to assess the hairiness of an individual in two ways. First, the length of a typical bristle on the back of the head was measured (although the bristles on an individual are quite variable a distinct difference between the species was hoped for). Secondly, the number of hairs on the petiole were counted (the petiole was chosen because it is an easily definable region and has sufficient hairs to make a count worthwhile but not enough to make counting too difficult). The variability in the number of hairs on the petiole for specimens of the three species is illustrated in Fig. 2 and Fig. 4

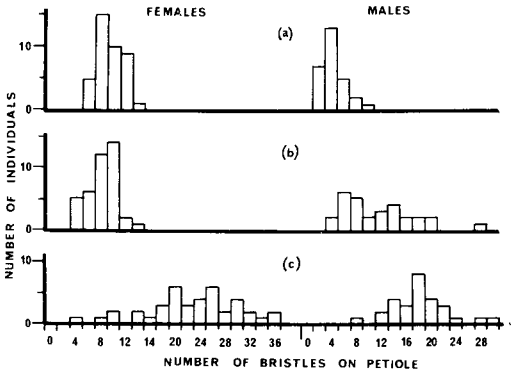

FIG. 4. Frequency histogram of the numbers of bristles on the petiole of the samples of queens and males (grouped in twos): *M.sabuleti* (a), *M.scabrinodis* (b) and *M.hirsuta* (c).

(ii) *Examination of all the queens*

Initially four measurements were made on all the queens available to see whether the three species could be distinguished by morphometrics. The measurements used were headwidth, head length, frons width and post-petiole width. The means and standard deviations of these four measurements are given in Table 1; comparisons between the species using the '*t*' test shows that the mean measurements of headwidth, head length and post-petiole width are significantly different ($P < 0.001$). There is no significant difference between the mean frons width of *M.scabrinodis* and *M.sabuleti* but the frons width of *M.hirsuta* differs slightly from the other two ($P = 0.015$). Comparison of subsets of the data for the different species collected from the different sites shows that specimens from every site tend to conform to the following observations. In order to save space the tables of measurements are not given here but if head length is plotted against headwidth, head length appears isometric between the three species. There is an indication that

TABLE 1. Means and standard deviations of the four measurements made on the 143 *M.scabrinodis* queens, 170 *M.sabuleti* queens and 54 *M.hirsuta* queens

	M.scabrinodis (143 individuals)		*M.sabuleti* (170 individuals)		*M.hirsuta* (54 individuals)	
	Mean	SD	Mean	SD	Mean	SD
Headwidth (mm)	1.097	0.033	1.195	0.036	1.024	0.054
Head length (mm)	1.216	0.034	1.308	0.034	1.100	0.048
Frons width (mm)	0.414	0.022	0.414	0.022	0.425	0.027
Post-petiole width (mm)	0.568	0.025	0.626	0.028	0.648	0.038

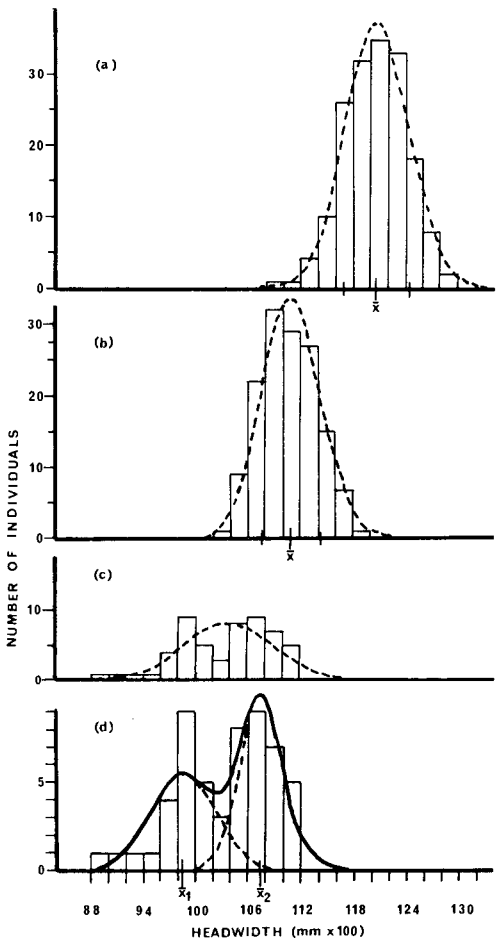

FIG. 5. Frequency distribution of headwidth for all the individuals measured. Best fit normal curves are superimposed. *M.sabuleti* (a), *M.scabrinodis* (b) and *M.hirsuta* (c) and (d). In (d) the scale has been enlarged and the data are best described by two normal curves.

M.scabrinodis has a relatively slightly longer head than the other two species. Overall a moderate separation of the three can be made on head size alone. Fig. 5 shows the frequency histograms of headwidth of the three species with superimposed normal curves that are described by the means and standard deviations given in Table 1. χ^2 tests show that a normal curve fits the data for *M.sabuleti* (P = 0.99) and less well for *M.scabrinodis* (P = 0.85). Surprisingly, a normal curve is a bad fit to the data for *M.hirsuta* (P = 0.30); however, if the data are divided into two, approximately equal portions, two normal curves can be calculated that fit with a probability of 0.72. These have means of 1.064 ∓ 0.024 mm (mean of thirty individuals) and 0.974 ∓ 0.036 mm (mean of twenty-four individuals). The implications of two sizes of *M.hirsuta* will be considered later.

If the distribution of frons width relative to headwidth is examined the three species form distinct clusters and while there is a positive correlation of frons width with headwidth within each cluster there is no overall isometry. The regressions through the three clusters are:

M.sabuleti

Frons width = 0.310 Headwidth + 0.022 ($P < 0.001$)

M.scabrinodis

Frons width = 0.340 Headwidth + 0.021 ($P < 0.001$)

M.hirsuta

Frons width = 0.395 Headwidth + 0.013 ($P < 0.001$)

The frons ratios, calculated from the means, are 34.6 for *M.sabuleti*, 37.7 for *M.scabrinodis* and 41.5 for *M.hirsuta* which agree well with other estimates (e.g. Collingwood, 1958). Unfortunately from the data we can calculate that if an individual with a frons ratio of >37 is called *M.scabrinodis* and one with a ratio of <35 is called *M.sabuleti* we have misidentified 15% of *M.sabuleti* and 3% of *M.scabrinodis* while a further 27% of the *M.sabuleti* and 20% of the *M.scabrinodis* fall between the two limits and cannot be identified confidently; yet if we consider the clusters formed by frons width plotted against headwidth, only about 5% of the *M.sabuleti* and 3% of the *M.scabrinodis* obviously fall amid the wrong cluster. Therefore, when considering individuals, frons ratio is a useful guide but a fallible one, whereas plotting the value of frons against headwidth amid a body of data is much more reliable. The same argument applies to the separation of *M.scabrinodis* from *M.hirsuta* but *M.hirsuta* can be separated well from *M.sabuleti* on frons ratio.

If the frequency distribution of the values for post-petiole width are plotted against headwidth it is apparent that although the values for *M.sabuleti* and *M.scabrinodis* form two distinct clusters, taken together post-petiole width is isometric with headwidth.

TABLE 2. Means and standard deviations of the twelve characters measured on males and females of *M.scabrinodis*, *M.sabuleti* and *M.hirsuta*. Forty specimens of each type of female; twenty-seven male *M.scabronidis* and twenty-eight male *M.sabuleti* and *M.hursuta* were measured.

		M.scabrinodis				*M.sabuleti*				*M.hirsuta*			
		Mean	SD	Mean ratio to head-width	SD	Mean	SD	Mean ratio to head-width	SD	Mean	SD	Mean ratio to head-width	SD
Headwidth (mm)	♀	1.077	0.034	1.000	0	1.197	0.030	1.000	0	1.026	0.052	1.000	0
	♂	0.828	0.070	1.000	0	0.886	0.073	1.000	0	0.838	0.023	1.000	0
Head length (mm)	♀	1.214	0.034	1.128	0.034	1.300	0.026	1.086	0.029	1.105	0.044	1.080	0.055
	♂	0.872	0.070	1.053	0.038	0.932	0.075	1.053	0.031	0.875	0.028	1.045	0.026
Frons width (mm)	♀	0.414	0.025	0.384	0.019	0.421	0.016	0.352	0.013	0.424	0.022	0.414	0.017
	♂	0.223	0.021	0.270	0.018	0.259	0.025	0.292	0.018	0.250	0.012	0.299	0.015
Eye length (mm)	♀	0.295	0.014	0.274	0.011	0.323	0.011	0.270	0.010	0.270	0.015	0.263	0.009
	♂	0.316	0.022	0.382	0.028	0.324	0.026	0.367	0.018	0.286	0.014	0.342	0.017
Scape length (mm)	♂	0.317	0.027	0.384	0.032	0.516	0.050	0.583	0.038	0.474	0.025	0.566	0.029
Thorax width (mm)	♀	1.025	0.031	0.952	0.029	1.110	0.026	0.931	0.033	0.969	0.057	0.944	0.025
	♂	0.981	0.078	1.185	0.054	1.008	0.044	1.138	0.049	0.935	0.022	1.116	0.036
Spine length (mm)	♀	0.419	0.032	0.389	0.029	0.427	0.030	0.357	0.024	0.314	0.027	0.306	0.023
Petiole width (mm)	♀	0.374	0.016	0.348	0.015	0.430	0.018	0.359	0.015	0.414	0.026	0.404	0.027
	♂	0.349	0.047	0.420	0.034	0.381	0.045	0.434	0.028	0.396	0.022	0.473	0.027
Post-petiole width (mm)	♀	0.563	0.026	0.523	0.023	0.630	0.027	0.526	0.024	0.650	0.034	0.635	0.029
	♂	0.486	0.057	0.590	0.041	0.523	0.044	0.594	0.031	0.561	0.022	0.669	0.020
Post-petiole height (mm)	♀	0.564	0.023	0.524	0.021	0.633	0.028	0.517	0.079	0.588	0.086	0.574	0.045
	♂	0.499	0.058	0.602	0.045	0.546	0.045	0.618	0.036	0.550	0.017	0.664	0.068
Bristle length (mm)	♀	0.111	0.014	0.103	0.013	0.121	0.019	0.101	0.017	0.154	0.017	0.151	0.018
	♂	0.119	0.034	0.136	0.043	0.043	0.013	0.048	0.014	0.126	0.023	0.150	0.028
Bristle number	♀	8.2	2.4	7.60	2.30	9.3	2.1	7.76	1.74	22.9	7.6	21.84	7.08
	♂	11.8	5.8	14.20	7.52	4.4	2.0	4.96	2.34	18.2	4.6	21.66	5.58

M.hirsuta do not conform to this pattern and form a cluster that is very distinct from those of the other two.

(iii) *Analysis based on twelve measurements*

In the previous section it was demonstrated that a few measurements were sufficient to illustrate that the three species differ morphologically. In this section more measurements, made on smaller samples, are investigated for both males and females. The mean values for these measurements are given in Table 2. Comparisons of Tables 1 and 2 show that the measurements based on the smaller samples agree well with those based on all the specimens and that the small samples are thus representative.

These measurements can be examined in either of two ways. First, the mean values for the measurements (Table 2) could be compared between the species, but, as we have already shown that there is a distinct size difference and because most of the measurements are correlated with size, relative differences will tend to be masked. One way of overcoming this problem is to standardize all the measurements for size; and this is done by considering headwidth to be a good measure of size and adjusting each specimen to a headwidth of 1 mm. The standardized size is then a ratio which makes strict statistical comparison difficult; however, the distributions of the standardized measurements, or ratios, are approximately normal, thus means and the associated variances can be calculated for each species (Table 2). The mean ratios can then be compared by the '*t*' test and the results of this comparison are given in Tables 3 and 4. A second, better, way is to use a multivariate analytical technique to discriminate between the species taking account of all the measurements simultaneously. Canonical variate analysis is suitable for this purpose and has been carried out on the measurements made for both males and females of the three species. A canonical analysis assumes pre-established groups and then maximizes the ratio of the variance between the groups to the variance

TABLE 3. Comparison of measurements made for *M.scabrinodis* males and females (standardized for headwidth, see Table 5) with those for *M.sabuleti*. 0 means *M.scabrinodis* show no relative difference, + means relatively bigger and − means relatively smaller compared with *M.sabuleti*. The number of plus and minus signs indicate the level of significance when the measurements are compared by the '*t*' test; three signs show a difference at the 0.0001 level, two signs at the 0.001 level and one sign at the 0.01 level.

	Female	Male
Head length	+++	0
Frons width	+++	− − −
Eye length	0	+
Scape length		− − −
Thorax width	+	++
Spine length	+++	
Petiole width	− −	0
Post-petiole width	0	0
Post-petiole height	0	0
Bristle length	0	+++
Bristle number	0	+++

TABLE 4. Comparison of the values of the various measurements (relative to headwidth, see Table 5) of *M.hirsuta* with *M.scabrinodis* and *M.sabuleti*. 0, + and − mean that *M.hirsuta* have relatively no difference, bigger or smaller body characters than the species at the head of the column. Three plus or minus signs indicate a difference at 0.0001 by chance, two signs at the 0.001 level and one sign at the 0.01 level.

	Females		Males	
	M.scabrinodis	*M.sabuleti*	*M.scabrinodis*	*M.sabuleti*
Head length	− −	0	0	0
Frons width	+++	+++	+++	0
Eye length	− − −	− −	− − −	− − −
Scape length			+++	0
Thorax width	0	0	− − −	0
Spine length	− − −	− − −		
Petiole width	+++	+++	+++	+++
Post-petiole width	+++	+++	+++	+++
Post-petiole height	+++	+++	+	+++
Bristle length	+++	+++	0	+++
Bristle number	+++	+++	+++	+++

TABLE 5. Summary of the canonical analysis on the twelve measurements made on males and females of the three species. The weighting values given in part 1 can be used to calculate canonical vector values for new individuals and the weightings in part 2 can be compared directly to show the relative importance of each variable in the interpretation of the canonical vector.

	Part 1: Canonical vector normalized to give unit within-group SD (weighting values)				Part 2: Canonical vector standardized to have unit total variance and scaled to have maximum weighting of unity			
	Weighting values, first vector		Weighting values, second vector		Weighting values, first vector		Weighting values, second vector	
Original variable	♀	♂	♀	♂	♀	♂	♀	♂
Headwidth	0.039	−0.033	−0.214	−0.117	0.196	−0.035	−1.000*	−0.188
Head length	0.189	−0.094	−0.058	−0.043	1.000*	−0.104	−0.287	−0.072
Frons width	−0.269	0.120	0.366	0.099	−0.353‡	0.100	0.451‡	0.125
Eye length	0.256	−0.223	−0.180	−0.229	0.394‡	−0.197‡	−0.261	−0.306
Scape length		0.324		0.005		1.000*		0.022
Thorax width	0.085	−0.173	0.091	−0.151	0.364‡	−0.225†	0.367	−0.296
Spine length	0.095		0.205		0.342‡		0.694†	
Petiole width	0.018	−0.030	−0.240	−0.025	0.033	−0.044	−0.424‡	−0.055
Post-petiole width	−0.237	0.095	−0.109	0.375	−0.681†	0.167	−0.294	1.000*
Post-petiole height	0.071	0.074	−0.020	−0.177	0.194	0.119	−0.052	−0.433‡
Bristle number	−0.127	−0.095	−0.139	0.302	−0.194	−0.143	−0.200	0.687†
Bristle length	−0.062	−0.082	−0.086	0.242	−0.153	−0.098	−0.200	−0.438‡

* First most important variable contributing to canonical vector.
† Second most important variable contributing to canonical vector.
‡ Third most important variable contributing to canonical vector.

within the groups to give a set of canonical vectors (cv). There will at most be one less vector than the number of groups, thus, in this case, three species will produce two cv's. If each cv is normalized to give unit within-group SD, then for any set of measurements the cv can be thought of the sum of those measurements each adjusted by a weighting value: or cv = $\Sigma_1^N (a_i X_i)$ where X_i is the ith measurement of N measurements and a_i is the weighting value applied to that measurement. Table 5 (part 1) gives the weighting values (a) which can be used to work out cv values for individuals or group means from the individual measurements or group mean measurements. Note that in this paper the morphometrics (X), with the exception of the count of hair number, have been multiplied by 100 (= mm × 100) before being used to calculate the cv value: this simply makes the cv values larger and more manageable. In order to interpret the canonical variates in terms of these original measurements the vectors have to be standardized so that each variable has a unit total variance and then scaled to give a maximum weighting of unity. These weightings can then be compared directly to see which contributes the most to the canonical variant (see part 2 of Table 5).

The values of the cv's for each individual of the three species have been calculated from part 1 of Table 5 and Figs. 6 and 7 show the values for the first variate (cv_1) plotted against those for the second (cv_2) for queens and males respectively. A glance at these figures shows that for both queens and males the three species are all well separated by the two variates; each set of individuals forming a distinct cluster for each of the species. The centroid, calculated from the mean values for the original measurements, is marked for each species by a star and a circle that corresponds to the 99% confidence limit around this centroid is also shown. The numbers of individuals in each species group is relatively large compared to the number of measurements made therefore the confidence regions in the two dimensions defined by cv_1 and cv_2 can be approximated to χ^2 with two degrees of freedom. Thus, a 99% confidence interval for each species would be a circle of radius $r = \sqrt[2]{\chi^2}\ (2; 0.01) = \sqrt[2]{9.21} = 3.03$. Fig. 7 shows that the 99% confidence circles for males do not overlap

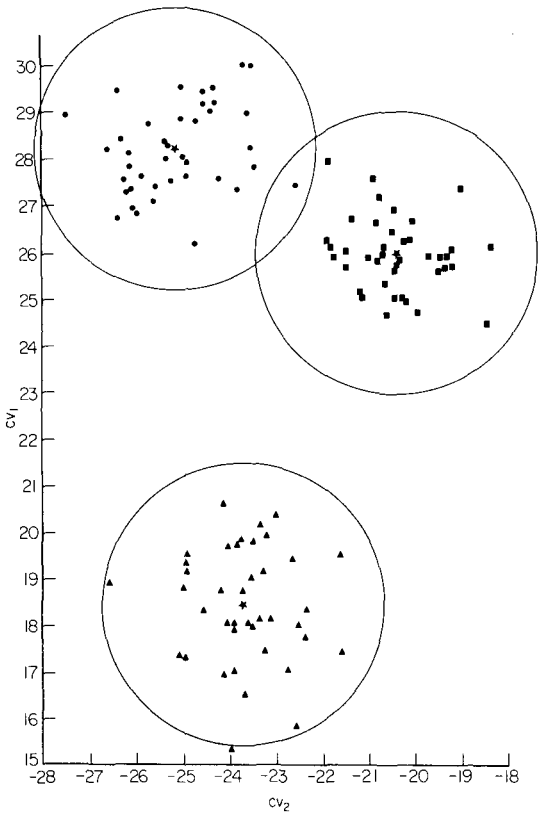

FIG. 6. The values for individual queen component scores (cv_1 and cv_2) plotted against each other: *M.sabuleti* (circles), *M.scabrinodis* (squares) and *M.hirsuta* (triangles). The centroids are marked by a star, and the 99% confidence circles are shown.

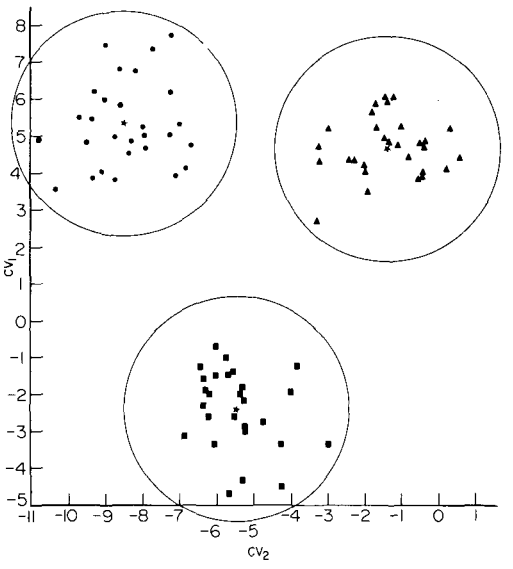

FIG. 7. The values for individual male component scores (cv_1 and cv_2) plotted against each other: *M.sabuleti* (circles), *M.scabrinodis* (squares) and *M.hirsuta* (triangles). The centroids are marked by a star, and the 99% confidence circles are shown.

for any of the species; in Fig. 6 although *M.hirsuta* queens do not overlap there is a slight overlap of the 99% confidence circles for *M.scabrinodis* and *M.sabuleti*. However, it is possible to calculate that of the 99% of individuals that are expected to fall in each circle only 0.3% of these are expected to fall within the region of overlap. Conversely, if the distance between any two centroids is halved (d) and this is taken as the value that will be used to discriminate between unknown new individuals then the confidence of a separation based on this value will be that for a $\chi^2 = d^2$. Thus in the present case it would be possible to draw a key based on the canonical variate values as shown at the foot of this page.

Compare this for the separation of *M. scabrinodis* from *M.sabuleti* based on the ratio of two measurements, headwidth and frons width (section 2 and Fig. 5). There, up to 40% of each of the species could not be assigned to either group with any degree of confidence. Even using graphical interpolation up to 10% can be misclassified, compare this to the very high levels of confidence of correct classification using the canonical variates.

Having shown that the three species can be separated with a high degree of confidence by canonical variates it is usual to attempt

Queens	1.	cv_1 value < 22.2	..... *M.hirsuta*	(confidence > 99.9%)
		cv_1 value > 22.2	 2	
	2.	cv_2 value > −22.8	..... *M.scabrinodis*	(confidence 99.0%)
		cv_2 value < −22.8	..... *M.sabuleti*	
Males	1.	cv_1 value < 1.5	..... *M.scabrinodis*	(confidence > 99.9%)
		cv_1 value > 1.5	 2	
	2.	cv_2 value > −4.9	..... *M.hirsuta*	(confidence >99.9%)
		cv_2 value < −4.9	..... *M.sabuleti*	

to interpret the variates in terms of the original measurements. If part 2 of Table 5 is examined it can be seen that high values of cv_1 are expected from queens that have long heads, narrow post-petioles, large eyes, wide thorax, narrow frons and long spines, in decreasing order of importance; and from males that have long scapes, narrow thorax and small eyes, in decreasing order of importance. Similarly, high values of cv_2 are expected from queens that have narrow heads, long spines, wide frons and narrow petioles, and from males that have wide post-petioles, low post-petioles and many long hairs. Thus as was seen in Fig. 6, *M.hirsuta* queens have low values for cv_1 showing that this species tends to have short (rounder) heads, wide post-petioles, small eyes and spines with narrow thorax and wide frons compared to *M.sabuleti*. *M.scabrinodis* queens differ from *M.sabuleti* by higher values for cv_2 (i.e. not such big negative values) showing they have narrower heads, wider frons, narrower petioles and longer spines compared to *M.sabuleti*. Similarly, *M.scabrinodis* males differ from *M.sabuleti* males by low values of cv_1 (Fig. 7) showing that they have relatively short scapes, wide thorax and big eyes; *M.hirsuta* males have larger (not such big negative) values of cv_2 compared to *M.sabuleti* and thus differ by having relatively wide, low post-petioles and more and longer hairs.

(iv) *Validity of the canonical analysis*

If the above interpretation of the canonical variates given in Table 5 are compared with the results of the simple comparison between species, Tables 3 and 4, it can be seen that *M.hirsuta* queens are shown to differ from the others in much the same way whichever method is used; except that hairiness seems to be more important in Table 4 than it does in Table 5. *M.scabrinodis* queens are shown to differ from *M.sabuleti* queens in much the same way using either type of analysis in Table 3 or Table 5. In Tables 3, 4 and 5 *M.scabrinodis* males differ from the other two species, mainly by scape length, and in both Tables 4 and 5 *M.hirsuta* differs from the others, principally by hairiness and post-petiole width. It will be remembered from part (v) of the descriptive section that scape length, hairiness and post-petiole size were important in separating the males in the first instance, hence it is hardly surprising that these are shown to be important in the subsequent analysis; this illustrates the caution that should be taken against possible circularity of argument when using this type of analysis. However, in the case of queens initial classification was mainly on ecological considerations and scape shape, which have not been quantified, and hence the morphometric characters that are shown to be important in their separation are much more independent of initial prejudice than in the case of the males.

It might be asked what is the value of the canonical analysis if it shows what can be demonstrated from a simple two-way comparison (Tables 3 and 4) and if it has dangers of circularity. The answer is that it enables an unknown individual to be assigned to a group with a known confidence based upon many characters taken simultaneously. Here, it also demonstrates a very good separation of three closely related species in a way that cannot be done otherwise and yet is easily interpreted biologically. In due course it is hoped that this type of analysis can be applied to a similar set of data for many more *Myrmica* species, for then multivariate analysis becomes essential as simple two-dimensional comparisons become an almost impossibly cumbersome task.

Size seems to be relatively unimportant in the canonical analysis unlike a principal components analysis which would be expected to take out a size component first. This was checked by comparing the weightings given to the canonical vectors with similar weightings of the major components of a principal component analysis. Further, in the case of *M.hirsuta* queens an analysis of headwidths suggested two size classes of queen (Fig. 5) yet detailed examination of the cluster in Fig. 6 shows that the individuals from the two size classes are mixed together. This is important when true microgynes are considered; these should be perfect reductions of the normal queen and thus, if size is ignored, should be classified with the normal queens. It is hoped that a canonical analysis would only separate microgynes from the normal queens if they differed relatively in other respects than size.

Taxonomic position of *M.hirsuta*

There seems little doubt that *M.hirsuta* is a workerless parasite that has evolved from its host species, *M.sabuleti*. There are several routes that can lead to social parasitism; one is through a process of slave-making that has led to a complete absence of worker forms in the slave-maker. Another is by a degeneration of a symbiosis or a temporary parasitism to obligate–temporary parasitism then further to obligate–permanent parasitism. Yet another method is by a process of mutation within a colony to produce a form that achieves breeding isolation within that colony and eventually becomes a parasite of the normal form; this has been discussed by Buschinger (1970). I believe that *M.hirsuta* has evolved by this last method.

If the idea of rapid mutation within a colony is examined in more detail, several aspects of the colony structure would seem to be important in order that speciation can be achieved. The original host species should by polygynous and tolerate the recruitment of young queens into its colony who can be considered to act as a sort of parasite (Elmes, 1973); this faculative polygyny seems essential, for it is hard to see how a monogynous society that will not normally tolerate other fertilized females, even originating from their own colony, will tolerate the recruitment of many parasitic-like queens that are derived from itself. Monogynous colonies are more likely to be parasitized by species evolved through the faculative temporary parasitic route, for example the parasitism of *Tetramorium* by *Strongylognathus*. Faculative polygynous species are most likely to produce microgyne forms and the mutation that enables the establishment of a microgyne variety is probably not far removed from the mutation required to produce a truly parasitic variety. In the case of *M.rubra* microgynes are known to have a slightly aberrant breeding biology (Elmes, 1976), and if such a species produced a microgyne form that never contributed to the worker population of the colony, it could be considered as parasitic and it is easy to imagine how breeding isolation of the new form could occur within the original colony. This would be especially so if microgyne forms tend to mate within the nest and do not need the stimulus of a nuptial flight.

Brian & Brian (1955) suggested that the spread of the microgyne form of *Myrmica ruginodis* Nyl. is chiefly by colony division; therefore if microgyny occurs spontaneously in different geographically isolated populations of the parent species it could lead to simultaneous evolution of parasitic forms peculiar to the local host population. If, once a parasitic form has been established for a long time, it still retains the capacity to spread by flight, then it could become widespread in the host population. I consider that *Sifolinia*, the satellite genus of *Myrmica* (Kutter, 1973), has probably evolved in this way from a microgyne form that has retained its proclivity for nuptial flight or a parasitic form such as *M.hirsuta*. *M.hirsuta* may indulge in nuptial flights as is suggested by the occurrence of queens in pitfall traps, although an alternative explanation might be that they mate in the nest and then later wander off on foot in search of a new host colony.

I have unpublished morphometric evidence that suggests that *M.scabrinodis* is very typical for the *Myrmica* genus as represented in Western Europe; and if this is compared with a *Sifolinia* species such as *Sifolinia karavajevi* Arnoldi, which I consider to be fairly representative of *Sifolinia* it is seen that: *Sifolinia* typically has no worker caste and is a parasite of a *Myrmica* host, there being very little chance of interbreeding with the host; the males have only twelve antennal joints compared with *Myrmica* which has thirteen; the spurs on the tibia of legs II and III are absent or simple compared with the reduced pectinate spurs of *Myrmica*; the petiole and post-petiole are relatively wide, this is a character that can only be recognized after a degree of familiarization with *Myrmica*; *Sifolinia* have wings that have a partially open discoidal cell and no division of the cubital cell as opposed to *Myrmica* where the cells are closed and partially divided respectively; finally, again a more comparative character, *Sifolinia* tend to have longer more dense hairs on the body compared to *Myrmica*.

To summarize, I believe that the genus *Sifolinia* has evolved by a fairly direct route from microgyne-like ancestors through parasitic *Myrmica* forms; the path of this evolution seems to be associated with a degeneration of *Myrmica* characters until the end product is a form that resembles *S.karavajevi*, differing

from *Myrmica* as outlined above. Thus the different species of *Sifolinia* could be phylogenetically closer to their host *Myrmica* species than to each other, the morphological similarities resulting from convergence due to their pattern of evolution. If this is so, the generic name of *Sifolinia* is unnecessary and *Sifolinia* species would best be called *Myrmica.* However, until more convincing morphological proof or proof obtained, for example, by electrophoretic studies of *Sifolinia* species and their hosts is available, the generic status of *Sifolinia* is best left alone; although the concept of a satellite genus (Kutter, 1973) should be more fully appreciated. As long as the two genera are recognized as being separate there exists the difficulty of placing those species that are intermediate between the typical forms, *M.hirsuta* being such a species: this can only be resolved by placing them in the genera to which they bear most resemblance. Although this is not satisfactory, if the close relationship of the genera is borne in mind it makes very little difference in practice.

There are only four species of parasitic *Myrmica* known at this time and *M.hirsuta* is the fifth, assuming that it is not a microgyne of *M.sabuleti* nor a species of *Sifolinia*; multivariate analysis of the morphometry rejects the former, and presence of pectinate tibial spurs and absence of *Sifolinia* like wing venation and post-petiolar lobes reject the latter supposition. The four species are *Myrmica bibikoffi* Kutter (1973), *Myrmica myrmicoxena* Forel (1874), *Myrmica lampra* Francoeur (1968) and *Myrmica faniensis* van Boven (1970). *M.lampra* is a North American species that is parasitic on *Myrmica kuschei* Wheeler; the female has curved antennal scapes with no projections and the male has only twelve antennal joints, this is quite different from *M.hirsuta*. The female of *M. myrmicoxena* resembles the *rubra*-group (Bernard, 1968) whereas the female of *M. hirsuta* falls in the *scabrinodis*-group; the male of *M.myrmicoxena* has *scabrinodis*-group characters but it differs from *M.hirsuta* in several ways according to Kutter (1973). *M.faniensis* has been found with *M.scabrinodis* and is quite different from *M.hirsuta* especially in the possession of *Sifolinia*-type characters shown by the female (van Boven, 1970).

M.bibikoffi is the only other parasitic *Myrmica* and this is the species that most resembles *M.hirsuta*; the females are slightly larger than *M.hirsuta* and rather less hairy, also their tibial spurs are either indistinctly or not pectinate (Kutter, 1973). In common they have broad post-petioles with no ventral projections, males that have thirteen antennal joints and a shared host, *M.sabuleti*. Another very similar form is *Sifolinia lemasnei* (= *M. lemasnei* Bernard, 1968) which is parasitic upon *M.sabuleti* and is very similar to *M.hirsuta* in general description. However it is smaller than *M.hirsuta* and has sufficient *Sifolinia* characters, the most notable of which is a male that has only twelve antennal joints, to be considered a member of that genus.

The parasites of *M.sabuleti* show a range as follows: *M.sabuleti* microgynes (unknown and hypothetical); *M.bibikoffi* which is microgyne-like but has been found free-living with its own workers; *M.hirsuta* a parasitic form without workers; *S.lemasnei* an obligate parasite with many characters normally associated with parasitic ants; and *Sifolinia laurae* Emery a true and widespread parasite. These then illustrate a hypothetical evolutionary range from the widspread host species through locally distributed parasitic forms to a widespread parasite. *M.scabrinodis/Myrmica alboa* Forel, *M.faniensis, Sifolinia cabylica* Cagniant (1970) and *Sifolinia karavajevi* (Arnoldi) show a similar though less well defined range. At the present time, with the exception of the nearctic *M.lampra*, few parasites have been discovered from the *M.rubra/ruginodis* group although microgynes are well known for these two species. It seems likely that as more nests are examined in detail more parasitic forms will be reported, for since the first discovery of *Sifolinia* in Britain myrmicologists have become more alert to its likely occurrence and subsequently it has been reported on several other occasions (Barry Bolton, personal communication).

Earlier in this paper it was suggested that *M.hirsuta* queens might show a bimodal frequency distribution of size. Elmes (1976) discussed variations iu queen size for *M.rubra* and suggested that normal queens have a size range that reflects trophic variations during their larval stage. It was suggested that microgynes of *M.rubra* not only have a smaller size as a result of genetic variation but also show trophic variation in the same manner

as the normal queens. Elmes (1976) pointed out that the smaller microgynes of *M.rubra* tended towards intercastes and were frequently unfertilized; *M.hirsuta* could likewise show trophic variation and the smaller queens are likely to be incapable of fertilization. Preliminary laboratory experiments have shown that the smallest *M.hirsuta* have no effect upon *M.sabuleti* workers whereas the larger *M.hirsuta* queens have a queen affect that is akin to that of *M.sabuleti* queens. This suggests that there is some difference between large and small *M.hirsuta* queens, not of genetic origin, and that the bimodal size distribution is not an artifact.

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