

BIOMETRICAL STUDY ON INTERSPECIFIC DIFFERENCES AND AFFINITIES OF THE GENUS *FORMICA* L. (HYM. FORM.)

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ABSTRACT

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1) A sample at random of 50 ♀♀ individuals has been proved to be big enough to ensure the representativeness for the whole caste of an ant hill.

2) As the growth for both the thorax length and head size is proportional, it is sufficient to get one of these measurements to ascertain the variation between species.

3) Different ant hills may show a more or less strong variation in size. In spite of this scattering between separate ant hills, which could well hint at the ununiformity of the species, nevertheless a species is quite different from the other in the range of size.

4) The standard deviation (σ) and the coefficient of variation (V), especially their averages, have been proved to be characteristic for each species.

5) The extreme values resulting from the 3σ rule are also of specific meaning. Thus *F. truncorum* shows the greatest range, while *F. exsecta* a distinctly small one in variability which indicates unequivocally for the exclusiveness of the species.

6) Particularly characteristic, however, are the measurements of petiolus. These show that each species has its own growth proportion. To quote only the case of *F. aquilonia* and *F. lugubris*, although these species are from the same biotope and often very difficult to distinguish morphologically, they exhibit in this respect even an inverse proportion in their growth tendency.

7) The affinity results so far obtained indicate that there are three distinct groups among the *Formica* species, namely, the morphologically more or less intermediary group of *F. polyctena*, *F. rufa* and *F. aquilonia* and the two lateral ramifications represented by *F. exsecta* on one side and by *F. lugubris*, *F. nigricans* as well as *F. truncorum* on the other side.

One may readily divide the genus *Formica* L. into red ants, robber ants, meadow ants, worker ants and kerf ants on account of morphological, ecological and biological differences. A further differentiation within these groups would be, however, rather difficult, as it was already known

nearly 40 years ago (Gösswald 1932). So far van Boven (1947), Betrem (1953), Lange (1954, 1956, 1958, 1959), Yarrow (1955) *et al.* have been seeking after a morphological separation of the genus *Formica*. Owing to its importance in the forest economy the group red ants has been studied in a particularly

intensive and extensive way. But as yet the morphological study of the group has been proved to be unsatisfactory. Gösswald and Schmidt (1959) have, therefore, begun their differentiation work on a biochemical basis. The result is that the species may be further differentiated. Thus 5 different biochemical forms have been found in both *F. rufa* and *F. polyctena*. Arnoldi (1927, 1928, 1932), Huxley (1927, 1932), Wilson (1955), van Boven (1958), Otto (1959) and others have successfully adopted the biometrical method in their studies on polymorphism and taxonomy of the family Formicidae. In applying the same method to his present work the author seeks to answer the following questions, namely, whether there are systematic differences between various species of the genus *Formica* and, if so, what would be their phylogenetical relationships. From the work of Wilson with the genus *Lasius* it may well be expected that this method will throw a new light also on the above problems concerning the *Formica* species.

MATERIALS & METHODS

1. Materials

The author of the present paper has made his study mainly on the Middle European species of the red ants except for *F. uralensis* of which no sufficient specimens were at his disposal. The morphologically close affinity of the meadow ant *F. nigricans* and the kerf ant *F. exsecta* has motivated the author to include also these two species for his comparative study. All materials have been kept in 70% alcohol and in no way deformed. The species studied are as follows:

- Formica aquilonia* Yarr.
- F. (Coptof.) exsecta* Nyl.
- F. lugubris* Zett.
- F. nigricans* Em.
- F. polyctena* Först.

F. rufa L.

F. truncorum Fabr.

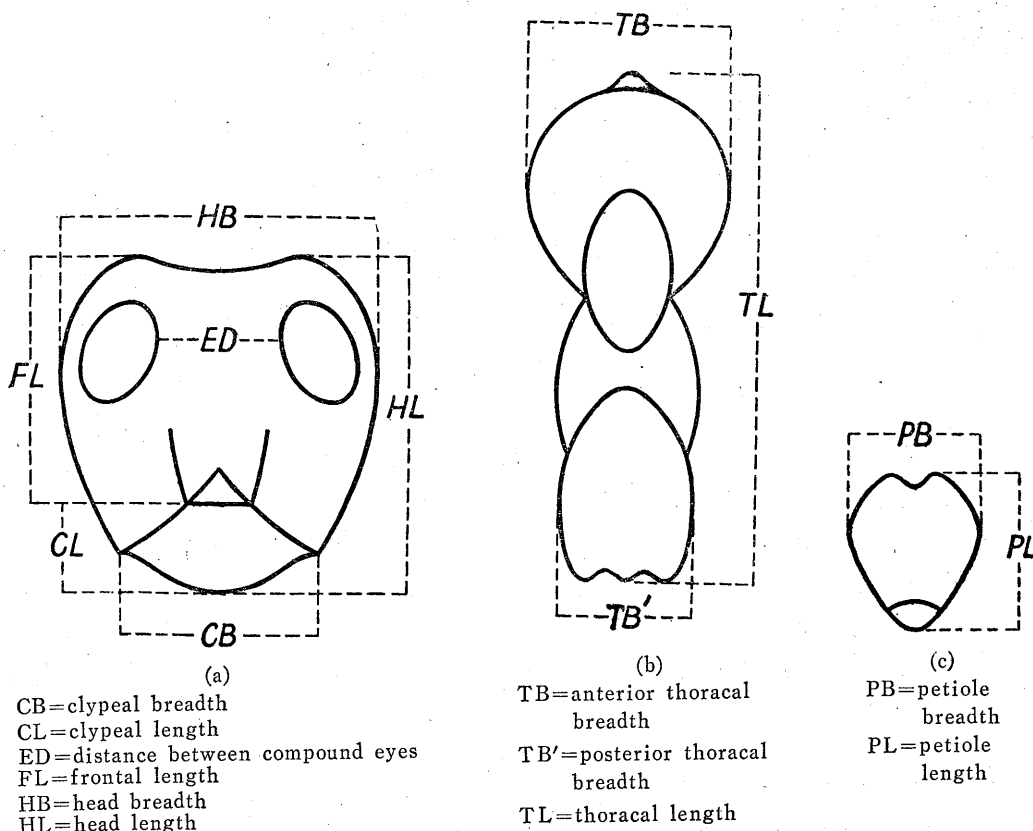
2. Methods

It is from biostatistical viewpoint that the author has approached his problems. The primary task of this method is to transform the objects to study into numerical data and to describe them in a numerical way. This is done by measuring different body parts of the ants. The measuring technique is given below.

A pre-treatment of the materials was necessary to make the measuring work easier and consequently to come to a greater exactness of the measurements obtained. The gaster as well as the appendages of head and thorax are removed, and the head, thorax and petiolus are then separately put on the slide with some water-soluble adhesive substance. The polyvinyl-alcohol-lactophenol mixture¹ is the most suitable one owing to its flexibility which would allow a correction of the object position.

The binocular with the corresponding micrometer used is the model of the firm Hensoldt/Wetzlar, and the tungsten-point light source served the purpose of illumination. All measurements are given in 20 times the natural size (in mm). In taking the thoracal measurements the author has disregarded those of the height, since already the smallest change of position may affect the measuring work so that serious errors would arise. On the other hand, the measurements of the thoracal length and breadth are to be considered as fairly exact. The same precision may apply to the remaining measurements of both the head and petiole. Accordingly, the measurements taken into consideration are as following (Fig. 1):

1. 10g polyvinyl alcohol, 35cm³ lactic acid, 25cm³ of 15% phenol, 10cm³ glycerine, 20g chloral hydrate, 40-60cm³ aqua destillata (Heinze 1952).



CB=clypeal breadth
 CL=clypeal length
 ED=distance between compound eyes
 FL=frontal length
 HB=head breadth
 HL=head length

TB=anterior thoracal breadth
 TB'=posterior thoracal breadth
 TL=thoracal length

PB=petiole breadth
 PL=petiole length

Fig. 1. Diagrammatic representation of the measured distances on head (a), thorax (b) and petiolus (c).

In order to give the numerical data a deeper meaning, the author has proceeded further to their allometrical analysis. Etymologically the word allometry is of Greek derivation and composed of *ἄλλοιος* (different) and *τὸ μέτρον* (measure), meaning different measure. Biologically it refers to the variation of proportion of a certain body part in relation to the size of the other body parts or of the body as a whole. So, what is to be stressed here is not the proportion as such but rather the variation of proportion. Here we have to deal with the so-called law of allometric growth¹; in

other words, with the morphogenetic regularity, according to which every body part has its own growth rate and is consequently in a definite relation to other body parts. If the growth rate of a body part is greater than that of the other, so its growth shows a positive allometry vis-à-vis another body part, which is slower in its growth, hence shows a negative allometry. When two organs or two body parts keep pace with each other in their growth, we call it isometry, a case which is rather rare. What is important here is the equation $Y=b.X^{\alpha}$, i.e. $organ_1=b.organ_2^{\alpha}$, where the exponent α means the measurement of correlative proportion and is known as allometric exponent; b is the constant which

1. Known also as the law of heterogonic growth (Huxley & Teissier 1936).

depends on the selected measurement system. Should this constant be related to a point $Y_0 = b \cdot X_0^a$, then $\frac{Y}{Y_0} = \left(\frac{X}{X_0}\right)^a$. The constant, however, has the value 1 in the application of relative values and is dependent on a number of factors such as age and sex.

In addition to the abbreviations listed in Fig. 1, the following abbreviations are also used in the present paper:

- a) *Abbreviations for morphometrical indices*
 CI (Clypeal Index)=CB.100 : CL
 FI (Frontal Index)=ED.100 : FL
 HI (Head Index)=HB.100 : HL
 PI (Petiolar Index)=PB.100 : PL
 TI (Thoracal Index)=TB.100 : TL
- b) *Abbreviations for specific names*
 aq=*F. aquilonia*
 ex=*F. exsecta*
 lu=*F. lugubris*
 ni=*F. nigricans*
 po=*F. polycтена*

ru=*F. rufa*

tr=*F. truncorum*

Owing to the fact that the worker caste of the red ants is much more variable in the body size as compared with other castes, the author has attached a particular significance to it in the course of his study. One of the most important presuppositions is, however, the selection of a sufficiently large and truly representative sample at random for the whole population of an ant hill. Therefore the author has taken at random of 50 individuals of the worker caste from each ant hill respectively for study.

From previous testing it was determined that the number of 50 corresponds in fact to the needs of the experiment. 5 random samples of every 50 individuals have been measured and the variation of these samples shows such a uniformity that the selected number of 50 is suitable to be taken for biostatistical analysis. This is shown in Table 1.

TABLE 1.

Variability in head breadth of 5 samples taken at random and at the same time (50 of the worker caste each) from an ant hill of *Formica rufa*. (Ant hill F_{II}, F.A. Hadamar, West Germany).

No	n	M	VI-Vn	σ	σM	V
1	50-1	37.3	26-42	4.76	0.67	12.77
2	50-1	37.4	25-41	4.20	0.59	11.24
3	50-1	37.5	27-42	4.48	0.63	11.94
4	50-1	37.2	26-43	4.35	0.61	11.69
5	50-1	37.4	27-41	4.38	0.62	12.03
mean value		37.2	26.2-41.8	4.43	0.62	11.93

Explanation of the lettering

n number of ants
 n-1 number for the degrees of freedom (used only when $n < 100$)
 M arithmetic mean (in mm)
 VI-Vn range or extreme values (minimum and maximum in mm)

σ standard deviation; $\sigma = \pm \sqrt{\frac{\sum \delta^2}{n-1}}$

σM mean error of the average;

$$\sigma M = \frac{\sigma}{\sqrt{n}}$$

V coefficient of variation; $V = \frac{\sigma}{M} \times 100$

RESULTS

1) Interspecific Differences

The question here is to what extent do the body measurements vary and whether there are different growth tendencies between the

Formica species. For this purpose the author presents his numerical data above all in form of two frequency tables, the first for the measured ranges (Tab. 2), the second for the computed ones (Tab. 3). Table 3 results form $M \pm 3\sigma$ (Fig. 2):

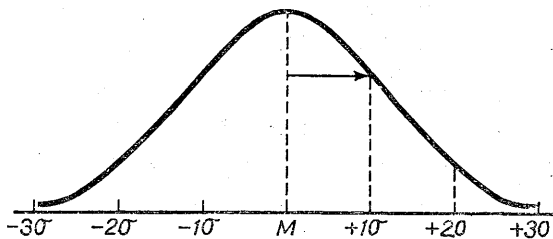


Fig. 2. The normal distribution.

TABLE 2.

The measured ranges (V1-Vn) of the 7 ant species in their different body parts.

	aq	ex	lu	ni	po	ru	tr
CB	15-28	17-22	14-28	18-31	15-29	15-31	17-30
CL	6-13	7-10	6-14	7-17	7-14	7-14	8-15
ED	13-26	15-20	12-27	16-34	14-26	14-24	15-27
FL	16-30	17-24	15-29	18-33	18-31	18-33	18-31
HB	20-38	21-29	20-38	23-48	21-39	21-43	24-42
HL	23-41	24-33	22-41	26-47	25-42	26-46	28-44
TB	14-27	15-21	14-28	18-29	15-28	16-29	16-28
TB'	12-23	13-17	11-22	16-25	12-23	13-24	14-25
TL	32-59	34-47	31-62	40-64	35-59	36-65	40-64
PB	12-20	9-14	14-18	12-21	11-20	12-21	10-19
PL	13-23	10-15	14-20	14-23	12-21	13-22	12-19

The mathematical expression of normal distribution is

$$\frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{1}{2}\left(\frac{x-M}{\sigma}\right)^2}$$

with 68.27% for $M \pm 1\sigma$, 95.45% for $M \pm 2\sigma$, and 99.73% for $M \pm 3\sigma$ (Weber 1948). This

means the overstepping probability by using the 3σ rule is only 3‰.

Since the arithmetic means (M) as well as the standard deviations (σ) and the coefficients of variation (V) can bring out some other specific points, a tabular presentation of these values should also be given their space.

TABLE 3.

The computed ranges (VI-Vn) of the 7 ant species in their different body parts.

	aq	ex	lu	ni	po	ru	tr
CB	14.5-29.5	16.5-22.6	13.0-30.2	16.7-33.9	15.4-31.0	16.7-35.3	14.3-32.3
CL	6.5-13.7	6.2-11.0	5.8-14.0	6.5-15.7	6.2-14.6	7.3-16.6	6.4-15.0
ED	12.5-27.5	13.6-20.8	10.8-27.8	14.5-32.3	13.1-28.7	15.0-33.0	11.1-30.7
FL	15.6-30.0	15.4-23.8	15.0-30.6	18.4-34.8	17.3-35.7	19.4-35.8	14.7-34.3
HB	18.8-40.6	20.8-30.4	16.9-41.3	21.5-47.5	20.1-43.3	22.9-48.9	17.7-46.1
HL	22.9-42.9	23.3-33.3	21.5-43.9	26.1-49.3	24.2-45.8	27.7-51.3	21.6-48.2
TB	13.9-28.9	13.1-21.9	12.2-29.4	17.7-31.3	14.6-31.8	16.1-34.1	8.9-32.5
TB'	12.1-23.5	11.6-18.0	9.5-24.3	15.0-25.4	12.2-25.8	13.5-28.1	11.5-27.3
TL	31.4-60.2	32.6-49.0	28.8-61.6	41.1-66.7	33.6-67.8	38.0-74.4	32.5-69.1
PB	10.7-20.3	8.5-13.9	11.9-19.7	11.8-21.4	10.0-21.8	11.8-24.2	7.4-21.6
PL	11.8-22.4	9.3-15.9	12.3-20.5	14.1-24.3	10.7-23.7	12.8-24.0	9.0-22.8

TABLE 4.

The arithmetic means (M) of the 7 ant species in their different body parts.

M	aq	ex	lu	ni	po	ru	tr
CB	22.0	19.1	21.6	25.3	23.2	26.0	23.3
CL	10.1	8.6	9.9	11.1	10.4	11.9	10.7
ED	20.0	17.2	19.3	23.4	20.9	24.0	20.9
FL	22.8	19.6	22.8	26.6	26.5	27.6	24.5
HB	29.7	25.6	29.1	34.4	31.7	35.9	31.9
HL	32.9	28.3	32.7	37.7	35.0	39.5	34.9
TB	11.4	17.5	20.8	24.5	23.2	25.1	20.7
TB'	17.8	14.8	16.9	20.2	19.0	20.8	19.4
TL	45.8	40.8	45.2	53.9	50.7	56.2	50.8
PB	15.5	11.2	15.8	16.6	15.9	18.0	14.5
PL	17.1	12.6	16.4	19.2	17.2	18.4	15.9

TABLE 5.

The standard deviations (σ) of the 7 ant species in their different body parts.

σ	aq	ex	lu	ni	po	ru	tr
CB	2.51	1.16	2.88	2.88	2.61	3.09	3.01
CL	1.21	0.79	1.37	1.52	1.41	1.55	1.44
ED	2.52	1.21	2.84	2.97	2.60	2.99	3.27
FL	2.40	1.40	2.60	2.73	3.06	2.72	3.25
HB	3.62	1.61	4.06	4.28	3.87	4.32	4.75
HL	3.35	1.67	3.75	3.88	3.60	3.92	4.42
TB	2.50	1.47	2.85	2.26	2.87	2.99	3.92
TB'	1.89	1.07	2.47	1.73	2.28	2.42	2.63
TL	4.80	2.73	5.45	4.28	5.71	6.05	6.11
PB	1.58	0.90	1.30	1.59	1.98	2.07	2.37
PL	1.78	1.08	1.37	1.69	2.16	1.87	2.31

TABLE 6.

The coefficients of variation (V) of the 7 ant species in their different body parts.

V	aq	ex	lu	ni	po	ru	tr
CB	11.4	6.1	13.3	11.4	11.3	11.9	12.9
CL	12.0	9.1	13.9	13.7	13.5	13.1	13.4
ED	12.6	7.0	14.7	12.7	12.4	12.5	15.7
FL	10.5	7.1	11.4	10.3	11.5	9.9	13.3
HB	12.2	6.3	13.9	12.5	12.2	12.0	14.9
HL	10.2	5.9	11.5	10.3	10.3	9.9	12.7
TB	11.7	8.4	13.7	9.2	12.4	11.9	18.9
TB'	10.6	7.2	14.6	8.6	12.0	11.6	13.6
TL	10.5	6.7	12.1	7.9	11.3	10.8	12.0
PB	10.2	8.1	8.2	9.6	12.4	11.5	16.4
PL	10.4	8.6	8.3	8.8	12.5	10.2	14.5

From the data we may draw our inferences. First of all, the parameter σ and the computed range (VI-Vn) are interconnected (Tab. 3, 5). Thus being the largest value (Tab. 4) with the widest range (Tab. 2, 3), the thoracic length (TL) has the

largest deviation (σ); and the clypeal length (CL), being the smallest value (Tab. 4), with mostly the narrowest range (Tab. 2, 3) contrary to the thoracic length (TL) has the smallest deviation (Tab. 5). Second, the correlation between σ and V does not

necessarily mean that σ is the cause of V (compare and contrast Tab. 5 and 6.) Third, the head breadth (HB) is positive to the head length (HL), as will be seen in both Tab. 3 and 6. Fourth, as compared with the head breadth (HB), the distance between compound eyes (ED) shows a still stronger growth tendency (Tab. 6.) Fifth, the distance between compound eyes (ED) is of positive allometry to the frontal length (FL) except for *F. exsecta* (Tab. 6). Sixth, the thoracal length (TL) is negative to both the anterior and posterior thoracal breadth (TB, TB'; Tab. 6). Seventh, the clypeal length (CL), however, is positive to the clypeal breadth (CB; Tab. 6). Eighth, a glance at the arrayed figures in Tab. 6 informs us that the values for coefficients of variation (V) of *F. exsecta* are strikingly small, especially those of the head and thorax. Ninth, in spite of the fact that the σ values of both *F. rufa* and *F.*

truncorum fall within more or less the same ranges (Tab. 5), their corresponding V values, however, show some remarkable divergences, particularly those of the frontal length (FL), thoracal breadth (TB), petiolus breadth (PB) and petiolus length (PL; Tab. 6).

In addition, the author has made a comparative study of allometric growth on both the small and big individuals of the worker caste from each and all species under discussion. Thus he has selected the smallest and the biggest ones from each ant hill of a species and 15 extreme values for each category, as a rule. The indices are then calculated from the corresponding arithmetic means. These are given separately in Tab. 7. The signs between two values denote their respective growth tendencies, such as quasi-isometry, isometry, negative and positive allometry.

TABLE 7.

Comparison of the indices between small and big individuals (\checkmark \checkmark) of the 7 ant species.

	CI	FI	HI	PI	TI
	small big	small big	small big	small big	small big
aq	219.6 \approx 219.1	84.2<89.4	88.5<92.2	91.7=92.1	45.9<47.4
ex	240.5>214.4	88.4 \approx 87.8	89.8<91.3	84.3=84.4	42.5<43.9
lu	217.5<219.6	82.1<89.6	86.9<91.6	100.0>94.7	45.8<47.2
ni	236.2>223.2	84.5<90.5	87.7<93.3	82.9<89.4	44.9<46.1
po	232.1>216.1	84.1<86.3	88.1<92.1	92.3=92.1	44.3<45.9
ru	223.0>214.3	83.0<87.4	86.4<92.1	95.9 \approx 95.3	44.7<45.9
tr	214.9 \approx 214.0	82.6<88.4	87.1<92.9	85.7<95.8	43.0<45.4

Key to the signs

= isometry, difference less than 5%

\approx quasi-isometry, difference between 5% and 9%

> negative allometry, index of the small \checkmark \checkmark > index of the big ones

< positive allometry, index of the small \checkmark \checkmark < index of the big ones

TABLE 8.
Differences of the indices

	CI	FI	HI	PI	TI
aq	- 0.5	+5.2	+3.7	+0.4	+1.5
ex	-26.1	-0.6	+1.5	+0.1	+1.4
lu	+ 2.1	+7.5	+4.7	-5.3	+1.4
ni	-13.0	+6.0	+5.6	+6.5	+1.2
po	-16.0	+2.2	+4.0	-0.2	+1.6
ru	- 8.7	+4.4	+5.7	-0.6	+1.2
tr	- 0.9	+5.8	+5.8	+10.1	+2.4

For our better orientation, differences have been worked out of the above indices in the way that the index of the big individuals served as minuend and that of the small ones as subtrahend. The + sign means the positive difference (allometry) and the - sign the negative difference (allometry).

When the head indices (HI) of the small ants are compared with those of the big ones, it will be clear that the small individuals always show a relatively narrower head than the big ones of a small ant hill. The same may be stated of all the species studied, with the conclusion that by the increasing body size the head breadth (HB) shows a positive allometric tendency as compared with the head length (HL); in other words, the head breadth (HB) grows relatively quicker than the head length (HL). This positive allometry in the breadth growth of head will become more evident after a transformation process as shown in Table 9.

TABLE 9.

The transformed mean values (in mm) of the head breadth (HB) and head length (HL) of the small and big worker individuals and of the female ones.

	small	♀ ♀	big	♀ ♀
HB	36.8		39.1	41.3
HL	42.4		42.4	42.4

Transformed are here the measurements of the small ♀ ♀ and those of the ♀ ♀. The head length (HL) of the big worker individuals serves thereby as reference measurement. The thorax of all species shows a positive allometry in its breadth growth (Tab. 7). Whereas the frontal indices (FI) of 6 species are of positive allometry, *F. exsecta* yields a difference of -0.6 and is, therefore, to be considered as quasi-isometric (Tab. 8). On the contrary, the petiolus is quite changeable in its growth tendency: positive in *F. nigricans* and *F. truncorum*, negative in *F. lugubris*, quasi-isometry in *F. rufa*, isometry or harmony in the remaining three species, namely, *F. aquilonia*, *F. exsecta* and *F. polycytena* (Tab. 7). The clypeal indices (CI) are also variable: except for positive allometry in *F. lugubris*, quasi-isometry in *F. aquilonia* and *F. truncorum*, all other species exhibit a negative allometry (Tab. 7).

A comparison of indices between the small and big individuals of various species, as seen in Table 7 and particularly in Table 8, shows that characteristic differences can be worked out for each species, even though they might be insignificant in separate cases. This proves that the species differentiation may be ascertained by means of allometric study on growth.

Through a further method one may compare the allometric proportions of the separate species likewise.

The allometric exponent, α , known also as somatic exponent (Klatt 1919) will in this case have to indicate different growth ratios of the head breadth and length between every 2 groups. Table 10 has as its basis the mean values of the corresponding head measurements (HB, HL) of the 7 ant species (♀ ♀), not, however, the head indices. The allometric exponent α has the formula (Rensch 1954)

$$\left(\frac{HL_1}{HL_2}\right)^\alpha = \frac{HB_1}{HB_2} \quad \alpha = \frac{\log HB_1 - \log HB_2}{\log HL_1 - \log HL_2}$$

In case the exponent α is equal to 1, we have to deal with isometry. If the exponent α is bigger or smaller than 1, we will have then to do with positive and negative allometry, respectively. The negative exponent means that the proportion of the breadth is just the opposite of the length (compare *F. truncorum* : *F. polycytena*).

Since the values are symmetrical to the diagonal, the other half of the table will not be repeated.

TABLE 10.
Allometric exponent α of the 7 ant species (\checkmark \checkmark).

α	aq	ex	lu	ni	po	ru	tr
tr	1.21	1.05	1.41	0.98	-2.08	0.95	—
ru	1.04	1.01	1.11	0.91	1.03	—
po	1.05	1.01	1.26	1.10	—
ni	1.08	1.03	1.23	—
lu	3.35	0.89	—
ex	0.99	—
aq	—

With the help of the allometric factors one could make a comparison between proportions of the head breadth and length of 2 species. If one takes as basis the same head length, so the factor $\beta=1$ (in our case $\beta \approx 1$, as for po:ex=1.0012 or ex:po=0.9988) means that also the head breadths are the same as goes without saying. If the factor $\beta > 1$, so the head shows an excess towards the breadth, as seen in entry II of Table 11. If the factor $\beta < 1$, so the species with the same head length in entry I has excess with regard to the head breadth.

The mathematical formula is

$$\frac{HB_1}{HL_1} \beta = \frac{HB_2}{HL_2}$$

TABLE 11.
Allometric factor β for the head indices of the 7 ant species (\checkmark \checkmark).

β	aq	ex	lu	ni	po	ru	tr	II
tr	0.9876	0.9897	0.9735	0.9982	0.9909	0.9943	—	
ru	0.9832	1.0047	0.9791	1.0039	0.9965	—	1.0056	
po	1.0033	1.0012	1.0178	1.0074	—	1.0034	1.0091	
ni	1.0107	1.0087	1.0253	—	0.9926	0.9960	1.0017	
lu	1.0144	0.9838	—	0.9752	0.9825	1.0212	1.0271	
ex	0.9979	—	1.0165	0.9914	0.9988	0.9953	1.0104	
aq	—	1.0021	0.9858	0.9893	0.9967	1.0067	1.0125	
I								

To facilitate the reading of Table 11, one may transform all the measurements after the head length of *F. polycytena* as in Table 12.

TABLE 12.
Measurements of the ant species transformed after the head length of *F. polycytena* (in mm).

	aq	ex	lu	ni	po	ru	tr
HB	31.6	31.7	31.1	31.9	31.7	31.8	32.0
HL	35.0	35.0	35.0	35.0	35.0	35.0	35.0

2) Interspecific Affinities

It would be of interest in this connection to try also for a classification of the *Formica* species according to their phylogenetical relationships. This may be done on the basis of the primary different characters of morphological nature as shown in Table 13.

TABLE 13.
Morphological different characters of the 7 ant species.

characteristic features	aq	ex	lu	ni	po	ru	tr
1. occipital margin and scale deeply notched	-	+	-	-	-	-	-
2. occipital margin with scattered hairs	±	-	+	+	-	-	+
3. thoracal back either bare or with few bristles	-	+	-	-	+	-	-
4. thorax with many bristles (cf. Tab. 11)	-	-	+	+	-	±	+
5. thorax pigmentation limited to the margin	-	-	-	+	-	-	-
6. genae with hairs	-	-	-	-	-	-	+

Key to the signs: + yes, ± more or less, - no

In order to give the above morphological features a quantitative expression, one may transform these in figures in the following way:

TABLE 14.
Quantitative valuation of the different characters enumerated in Table 13.

characteristics	aq	ex	lu	ni	po	ru	tr
1	0	10	0	0	0	0	0
2	5	0	10	10	0	0	10
3	0	10	0	0	10	0	0
4	0	0	10	10	0	5	10
5	0	0	0	10	0	0	0
6	0	0	0	0	0	0	10

On the strength of Tab. 13 and 14 one is in a position to produce the following affinity table.

A family tree may be sketched on the basis of the above affinity table (Fig. 3).

This family tree is not, however, intended to point at the relationship between an ascendant and its descendants. It ought solely to inform us about the grouping of the species. The broken line indicates that the *F. exsecta* might not belong to the genus

TABLE 15.

Affinity table based on the morphological characteristics listed in Tab. 13/14. For the formula $A^2 = \frac{\sum \delta^2}{\sum C}$ see Schilder (1951).

A ²	aq	ex	lu	ni	po	ru	tr
tr	37.5	83.3	16.7	33.3	66.7	37.5	-
ru	8.3	20.8	20.8	37.5	20.8	-
po	20.8	16.7	50.0	66.7	-
ni	37.5	83.3	16.7	-
lu	20.8	66.7	-
ex	37.5	-
aq	-

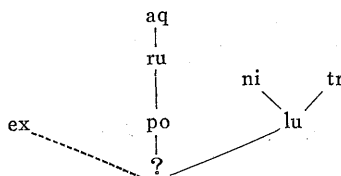


Fig. 3. Family tree of the 7 *Formica* species.

Formica L.¹ The three main ramifications should hint at the three ant groups. That *F. exsecta* is a group sui generis, is shown already by the typical deep notching on its occiput. The similar bristle density on

1. In fact, this species has once been called *Copto-formica exsecta* (see p. 70) and perhaps with more reason.

thorax and the progressive hairy condition on occiput are the main reasons why *F. polycтена*, *F. rufa* and *F. aquilonia* should be grouped together. The sequence is based on stages of development with an increasing tendency (see Tab. 16).

TABLE 16.

species	ex	po	aq	ru	lu	ni	tr
	→						
	increasing density of the hairy condition on thorax						

The criterion for the third category is to be sought in the distinct hairy condition on occiput and on back of the thorax, a condition which is common to all the remaining three species, the principle of sequence being the same as above. Should the three groups be compared with one another, then both the group of *F. exsecta* and that of *F. lugubris*, *F. nigricans* and *F. truncorum* would present two lateral ramifications, whereas the morphologically more or less intermediary group of *F. polycтена*, *F. rufa* and *F. aquilonia* occupies a middle position. Their stem form is, however, not known as yet.

From Table 15 it would follow that *F. rufa* has the greatest morphological similarity to *F. aquilonia*, since their A^2 -value, an expression of global difference, is the smallest one (8.3). The next affinity group is formed by *F. lugubris* and *F. nigricans*. With the same degree related to each other would be *F. lugubris* and *F. truncorum*, resp. *F. polycтена* and *F. exsecta* (all of them with an A^2 -value of 16.7). That *F. exsecta* is well distinguished from all other species except *F. polycтена*, is a phenomenon which would justify making out of it a separate group.

The result obtained about the affinity has, however, only the value of a working hypothesis. It should not be expected to correspond completely to the reality, since

many other morphological features (such as the different gaster pubescence of ♀♀ which is of great importance indeed and may induce a quite different conclusion) are not studied. It would be, therefore, necessary to refer, inter alia, to the paleontological data, in order to construct a better founded affinity picture.

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