EVOLUTION OF POLYETHISM IN ANTS :

OBSERVATIONAL RESULTS AND THEORIES

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SUMMARY

Reports to date concerning social evolution in the family Formicidae leed us to distinguish the most primitive subfamilies (Ponerinae and Myrmeciinae) from the higher subfamilies (Myrmicinae, Formicinae and Dolichoderinae). Generally speaking, the most primitive subfamilies are characterized by some particular traits like reduced number of individuals by colony and a very slightly marked caste polymorphism. Conservely, societies in evolutioned subfamilies are generally constituted by a higher number of individuals, with more evident polymorphism. The question we tried to answer is if the taxonomic belonging to a subfamily (exepting particular cases of regressive evolution as social parasitism) is more representative of a higher level in social evolution than those characteristics of a society, concerning its size and the degree of caste polymorphism. This study was carried out by comparing to the genus *Neoponera* two other genus : a «primitive» one (*Ectatomma* : subfamily Ponerinae), and an «evolutioned» one (*Myrmecina* : subfamily Myrmicinae). In fact, *Ectatomma* constitutes relative important societies and presents a marked polymorphism between the queen and workers, while *Myrmecina* constitutes societies with a small number of individuals, characterized by slight morphological difference between the queen and workers. The study of ethograms and sociograms by using methods of data analysis led us to conclude that social characteristics (number of

individuals, polymorphism) might be better than the taxonomic criterion to appreciate the degree of social evolution of an ant genus.

RÉSUMÉ

La bibliographie actuelle concernant l'évolution sociale dans la famille Formicidae distingue classiquement les sous-familles primitives (Ponerinae et Myrmeciinae) des sous-familles les plus évoluées (Myrmicinae, Formicinae et Dolichoderinae). On admet généralement que les sous-familles les plus primitives sont caractérisées par des traits particuliers tels que le nombre réduit d'individus par colonie et un polymorphisme de caste peu marqué. Inversement, il est admis que les sociétés, dans les sous-familles évoluées, sont populeuses et présentent un polymorphisme de caste accentué. La question que nous nous sommes posée est de savoir si l'appartenance taxonomique à une sous-famille est un meilleur indice du degré d'évolution sociale que d'autres caractéristiques de la société, comme la taille ou le polymorphisme de caste (exception faite des cas particuliers d'évolution régressive comme le parasitisme social). Cette étude consiste à comparer le genre *Neoponera* (sous-famille Ponerinae) à deux autres genres : l'un «primitif», *Ectatomma* (sous-famille Ponerinae), l'autre «évolué», *Myrmecina* (sous-famille Myrmicinae). En fait *Ectatomma* présente des sociétés assez importantes et un polymorphisme marqué, tandis que *Myrmecina* présente des sociétés peu populeuses où le polymorphisme est faiblement marqué. L'examen des éthogrammes et des sociogrammes en recourant aux méthodes de l'analyse des données permet de conclure que les caractéristiques sociales (nombre d'individus et polymorphisme) peuvent être meilleures que les critères purement taxonomiques pour apprécier le degré d'évolution sociale d'un genre de fourmi.

INTRODUCTION

The work so far published concerning the phylogenetic organization of ants indicates that certain subfamilies are less evolved than others.The criteria used in making this distinction concern mainly morphological characteristics. The theorical reviews by Brown (1954 and 1960) are fairly representative of this approach. This leads to a classification in which the subfamily Ponerinae contains genera considered to be more primitive than those contained in the subfamily Myrmicinae. This statement must however be modified because within the Ponerinae subfamily there are different levels of evolution. The *Amblyopone* are for the moment considered to be the most primitive living genus. This has been confirmed by the study of those few fossil finds such as those of the ancestral ant *Sphecomyrma* (Wilson, Carpenter and Brown, 1967). Based on the anatomical characteristics of this fossil ant, these

authors haved proposed a phylogenetic organization of the Formicidae, based on two different directions of evolution developped :
1 – The «Poneroïd complex» includes, for example, the subfamilies Dorylinae, Pseudomyrmicinae and Myrmicinae. These later are considered to have developped from the Ponerinae. At the base of the complex, the *Amblyopone* represents the most primitive genus.
2 – The «Myrmecioïd complex», which includes the Dolichoderinae and Formicinae is thought to have developped from the primitive subfamily Myrmeciinae. The recent report by Taylor (1978) concerning the rediscovery of the fossil living ant *Nothomyrmecia macrops* suggests that important modifications are needed in this branch of evolution and leads the author to place the genus *Nothomyrmecia* at the base of the Myrmecioïd complex.

Much information concerning the biology of ant colonies shows appreciable differences between the species. For example, the *Amblyopone*, classed amongst the most primitive species, live in colonies with only a modest cast polymorphism between the queen and workers, as it was shown by Brown, Levieux and Gotwald (1970), Gotwald and Levieux (1972), Levieux (1972). On the other hand, the Myrmicinae, an evolved subfamily, found colonies with many individuals, in which cast polymorphism is very noticeable, see for example Wilson's review (1968). These factors should logically influence the social organization of labour (polyethism). It is now generally admitted that the division of labour is a function of both the age and size of the workers. We know that the young workers are most likely to be nurses whereas the old ones are foragers, as demonstrated for Myrmicinae by Buckingham (1911), Heyde (1924), Goetsh and Eisner (1930), Weir (1958) ; or for Formicinae by Buckingham (1911), Kiil (1934), Okland (1930), Otto (1958), Dobrzanska (1959). Polymorphism of workers also appears to have a determining role in task distribution. This difference in size is sometimes such that the workers are divided into subcasts of minors and medias for the nest (eg. Goetsh and Eisner, 1930, Weber, 1972, and Wilson, 1968). There appears also to be joint determinism by these two factors in a number of evolved species (Oster and Wilson, 1978).

Little is known about the social organization of «primitive» species. There is a suggestion of continuous polymorphism amongst the workers of certain species of *Myrmecia* (Wilson, 1971), whereas Bonavita and Poveda (1970) have noted the probable existence of age Polyethism (in the absence of polymorphism), in *Mesoponera cafraria*. We must reserve judgements on this issue, however, because Traniello (1978) has concluded that there is no age polyethism in the very primitive genera *Amblyopone pallipes*. Our aim is to utilize a new method to examine the social organization of three genera selected for their evolutionary affiliation within the poneroid complex. These

genera are caracterized by low numbers of individuals in each colony, which makes individual analysis possible. The genera we have studied are :

– *NEOPONERA* (subfamily Ponerinae) caracterized by polygyny (at least for the species studied) and the absence of clear polymorphism between queen and workers ;

– *MYRMECINA* (subfamily Myrmicinae), generally monogynous, caracterized by clear polymorphism (Baroni Urbani, 1968) ;

– *ECTATOMMA* (subfamily Ponerinae). According to Wilson, Carpenter and Brown (1955), this genus is the most advanced of the Ponerinae because they consider the tribe Ectatommini to be the ancestors of Myrmicinae. Since Taylor's recent suggestions (1978) do not call this affiliation into question, we will attempt to test the value of this hierarchy from the point of view of social organization.

METHODS

After collection, each society was installed in the same type of artificial nest. It consisted of a nest made of plaster maintained in the dark, and an artificially lighted foraging area. Each member of the colony was marked with small number, easy to identify during observations (Fresneau and Charpin, 1977).

An observation consists of noting the location and activity of each ant at the moment it is identified. The observation is finished when all members of the society have been identified and scored. It takes between 5 and 20 minutes for this operation, depending of the size of the colony. The observation is repeated 8 to a 10 times per day over a period of 7 to 12 days. This procedure allows one to establish a schema of the activities of each of the individual members of the society during the same period of time. After the observational period, the results of the scoring were summed for each individual, which allows one to reconstruct the social activity of the colony ; it also constitutes a sufficiently rich data set to establish a social ethogram or sociogram. In this respect, we have the same goal as Wilson (1973) in his study of *Zacryptocerus varians*. Our method, based on individual analysis, allows us both to establish the repertoire of behavioural acts of the species and the distribution of the individual roles around these activities. To this end, we have used a different mathematical treatement from that used by Wilson. Our data are particulary suited to the «correspondances factorial analysis» method, described by Benzecri et al. (1973). This method has previously been used in the study of ants by Lenoir and Mardon (1978) in *Lasius niger* placed in a test situation. In the present context, this test and the use of taxonomic analysis method allow us to produce a simplified but rigorous picture of the social organization of a colony in a normal situation (Fresneau and Dupuy, in preparation).

This purely descriptive technique gives no information concerning the variability that could result from testing a sample of colonies ; one must therefore be careful not to overgeneralize the results. This test, however, constitutes a useful basis for the subsequent analysis of strictly quantitative data that are presently being collected. For this reason, we have chosen to present for each species the results of a typical colony from the sample of colonies so far observed, while taking into account the factors highlighted by the results of all the colonies so far analysed.

RESULTS

First species : Neoponera fœtida

This species is restricted to the neotropical forests. All the societies studied were collected in different areas of the Lacandon forest in Chiapas state, Mexico. One frequently observes polygyny, or at least the integration of winged females (out of six colonies collected only one was monogynous). The colony for which we will report the results included seven wingless females. Their dissection after the observational period revealed that three of them were inseminated. There were also 57 workers, 15 larvae, 8 cocoons and eggs. Sixty sets of observations recorded over eight days thus resulted in a total of 3840 individual scores. These observations allowed us to establish 36 behavioural categories distributed between the nest and the foraging area. In order to facilitate subsequent comparisons, however, we pooled together those categories which were highly correlated in the factorial analysis ; for example, the category «care of eggs» combines licking and transport of eggs, and the category «care of larvae», combines licking, transporting and feeding larvae. The results we report do not therefore constitute an ethogram of the behavioural categories, but a slightly simplified grid of 24 behaviours which highlights the social role existing in the society. Benzecri's correspondances factorial analysis allowed us to produce figure 1, which simplifies the relationships between the behaviours on the one hand and the individual ants on the other. At a subsequent stage, one may establish the correspondance between these two groups of variables and verify the social roles.

The analysis based on the behaviour. In figure 1, the two axes shown are those which most effectively classify the data. Each of them represents a continuum between two extremes ; thus, axis F1 (the horizontal axis or factor 1) allows the separation of two groups of behaviours :

– behaviours concerning care of the brood (especially care of eggs) are found at the negative end of this axis.

– a varied set of behaviours, all situated in the foraging area, constituting the

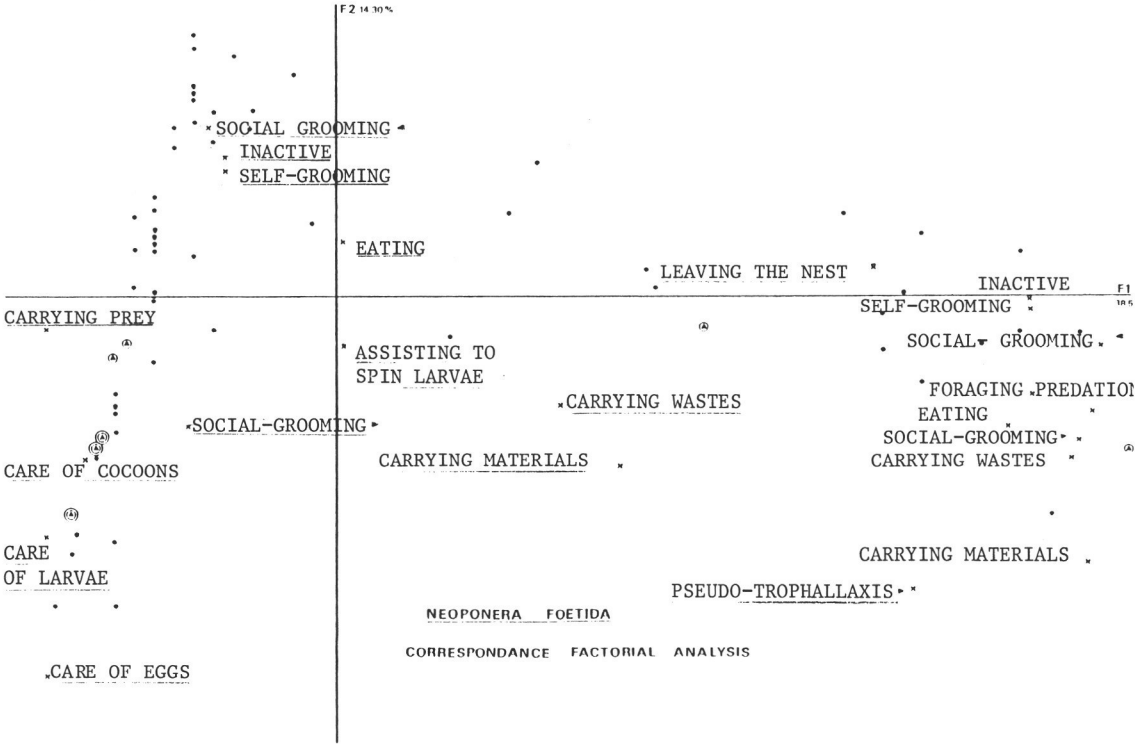

Fig. 1 – Graphic representation of 24 behavioural categories within the framework of the first two axes. ◉ queens (3) ; ▲ females (4) ; ● workers (57). The underlined activities (e.g. self-grooming) are activities performed inside the nest. The behaviour not underlined are the outside activities. An arrow → indicates an instigator of that social behaviour. An arrow ← indicates a recipiant of that social behaviour.

Fig. 1 – Représentation des 2 premiers axes. 64 individus, 24 comportements. ◉ reines (3) ; ▲ femelles (4) ; ● ouvrières (57). Les comportements soulignés sont situés dans le nid (ex. : «self-grooming») les mêmes comportements non soulignés ont été observés à l'extérieur du nid. Les comportements sociaux comportant une flèche →désignent le fait d'être actif ou donneur dans cette interaction. La flèche ←indique le fait d'être passif ou receveur.

outside tasks of the society, especially food supply. These behaviours are found at the positive end of this axis.

This first continuum «represents» or «explains» 38,5 % of the total variance of the data. The axis F 2 (vertical axis or factor II) represents 14 % of the total variance. It contrasts the behaviours concerning the care of the brood, at the negative end, with the set of activities located outside the nest, at the positive end (such as inactivity, feeding, self-grooming, etc.). This set represents the activities common to all the ants and we have called them non-specific activities, in contrast to those activities previously separated by axis F 1. These behaviours are quantitatively significant and represent the «center of gravity» of the social structure of *Neoponera*, which can be summarized by the existence of three extremes : a) care of brood ; b) non specific behaviours in the nest ; c) the outside tasks supplying provisions.

Certain other classes of behaviour are categorized separately. These are the domestic tasks which include the transport of the material needed by the larvae for spinning the cocoon, as well as tidying and transferring waste or the remains of prey. One may observe these behaviours either inside the nest (underlined) or outside (not underlined). In figure 1, these behaviours occupy an intermediate position between non specific activities and the outside tasks. In fact, the domestic tasks are characterized by the axis F 3, which clearly separates them from all the other activities. They are, however, close to the non specific activities. The domestic tasks are in general quantitatively unimportant, and axis F 3 represents only 10 % of the total variance. For simplicity this axis has not been shown on the figure. The same applies to the 20 other axes, which each represents very little of the total variance (less than 3 %). We do not report them here.

Analysis based on individuals. The distribution of the ants (shown as black dots or triangles) is very similar to the organization of activities and show clear polyethism. One can assume that two ants that are close on the figure have a similar behavioural profile. At the same time, the proximity of individuals to each extreme allow one to assume (provided certain precautions are taken) a correspondance between the two sets of variables. For example, the data points found near the «care of eggs» section represent a group of ants who are strongly characterized by that behaviour. On the other hand, these ants are a long way from the outside tasks : they never engage in these behaviours. One may distinguish another class of ants characterized by «non specific» activities, and a further class which engages predominantly in predation and foraging. As a result, figure 1 gives a picture of the behavioural profile of each ant, and allows one to describe the relationships between behaviours. It is however not easy to clearly delimit those groups that are specialized in one task. A complementary analysis allow us to treat this

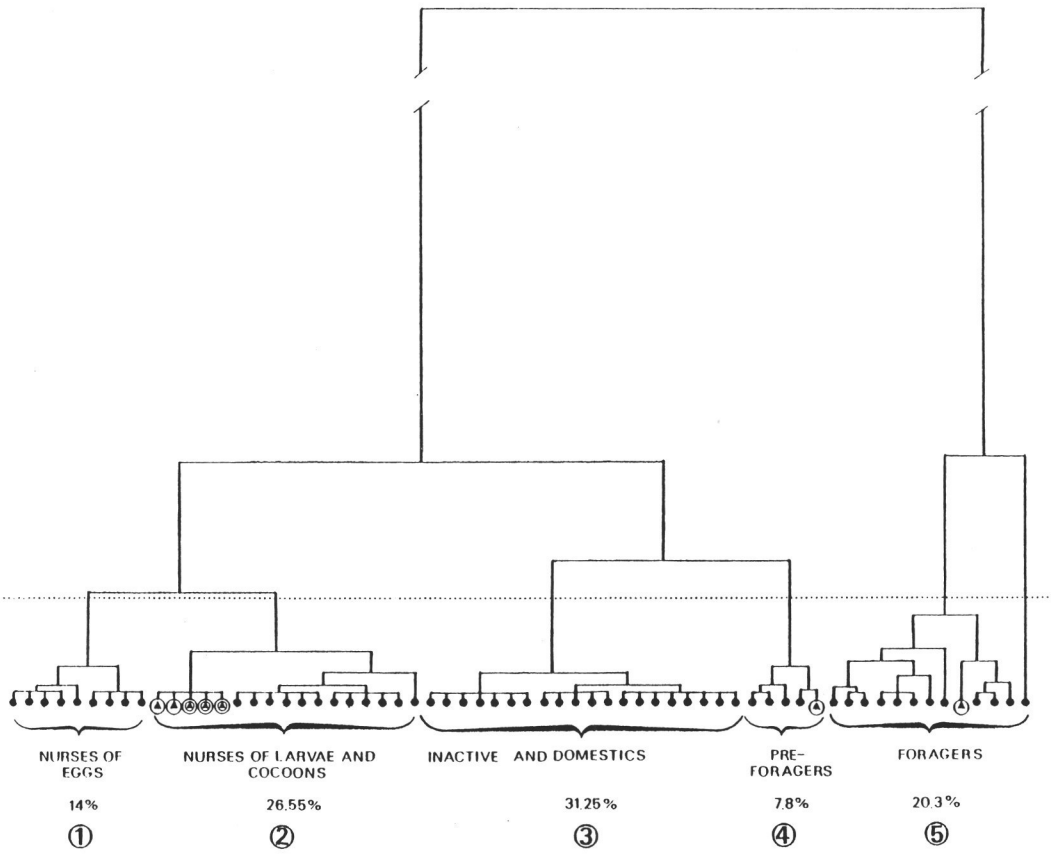

Fig. 2 – Hierarchical Cluster Analysis : dendogram of regrouped individuals obtained by an aggregation criterion of moment of order two. ◎ queens ; ▲ infertilized females ; ● workers.

Fig. 2 – Analyse de classification hiérarchique. Dendrogramme des individus regroupés à partir d'un critère d'agrégation de moment d'ordre deux. ◎ reines ; ▲ femelles non fécondées ; ● ouvrières.

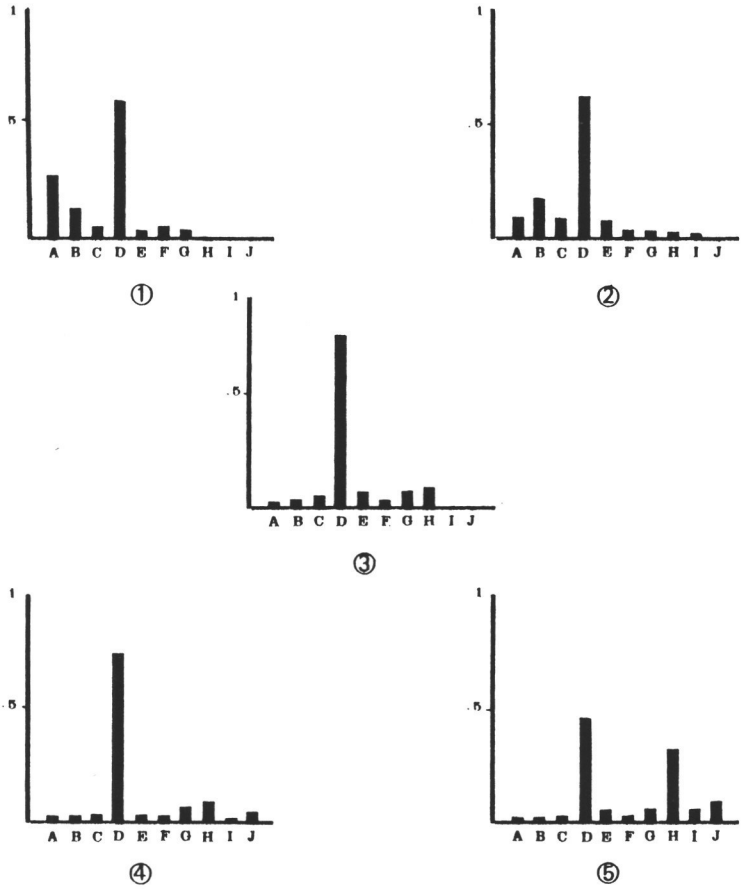

Fig. 3 – Behavioural profile for each group defined by the dendrogram. For convenience we have grouped the behaviour into 10 categories : A – care of eggs ; B – care of larvae and assisting larvae to spin ; C – care of cocoons ; D – non specific activities in the nest : inactive, self-grooming, eating ; E – social grooming →inside and outside the nest ; F – social grooming ←inside and outside the nest ; G – domestic activities in the nest : carrying of materials, carrying wastes, carrying prey, transporting liquids and pseudo-trophallaxis ; H – non specific activities outside the nest : leaving the nest, foraging, self-grooming, eating ; I – domestic activities outside : carrying materials and carrying of wastes ; J – supply : predatory behaviour, carrying prey and transporting liquids. The height of the bars represents the relative frequencies in each class of activity over the total number of activities shown by the group.

Fig. 3 – Profils comportementaux des groupes isolés par le dendrogramme. Afin de faciliter les comparaisons nous nous sommes limités à 10 activités : A – soin des œufs ; B – soins des larves et assistance au tissage du cocon ; C – soin des cocons ; D – activités non spécifiques dans le nid ; E – toilettes sociales →dans et hors du nid ; F – toilettes sociales ←dans et hors du nid ; G – activités domestiques dans le nid : transport des déchets, des matériaux, des proies et pseudotrophallaxies ; H – activités non spécifiques hors du nid : quitter le nid, exploration, toilette individuelle, manger ; I – activités domestiques à l'extérieur : transport des matériaux et des déchets ; J – approvisionnement : chasse, transport des liquides. Les valeurs des graphiques représentent les fréquences relatives de chaque classe de comportement sur le total d'activités présenté par le groupe.

question : it is based on automatic classification techniques or cluster analysis. This consists of grouping together individuals as a function of the similarity of their behavioural profiles. We have used an ascending hierarchical classification based on the distances of X^2.

Figure 2 shows the set of clusters for the ants of this colony. The distance between individuals or groups of individuals represents their degree of similarity. A short distance indicates a considerable resemblance, a long distance indicates little resemblance or even an opposition between the elements connected. This is the case, for example, between the ants in group 1 to 4, and those of group 5. Two further pairs of groups may be dissociated : 1 and 2 on the one hand, and 3 and 4 on the other. A higher level of analysis allows one to distinguish each of the five groups. It seems reasonable to limit the analysis to a significant degree of similarity (indicated here by the dotted line). Beyond that, interpretation becomes fragmented and approaches the continuous distribution obtained in figure 1. When this limit is used, the classification permits to separate five groups of ants. The roles played by them may be appreciated by calculating, for each group, the relative frequency of each behaviour over the total of all behaviours of the five groups, for ten categories of activity (Fig. 3) :

– Group 1 includes the workers dedicated to the care of the brood. Their nursing activities are primarily directed towards the eggs (f = .20 the highest frequency recorded this type of caring behaviour). We have named the ants of this group egg-nurses.

– Group 2 includes three queens, two unfertilized females and 12 workers. Their level of non-specific activities is higher than in the preceding group (f = .55), and they care for the cocoons (f = .21) and the larvae (f = .12). However, they assume little care for the eggs (f = .03), which are cared for exclusively by the ants of group 1.

– Group 3 contains workers with no apparent role ; they are characterized by a high level of non-specific activities (f = .85). We have called them «inactive» because of their low level of involvement in the ergonomic tasks described in figure 1.

– Group 4 contains four workers and a unfertilized female. These ants are relatively inactive in the nest, apart from various transport tasks, but they explore the foraging area for most of the waste removal from the nest to the exterior.

– Group 5 finally, contains 12 workers and a unfertilized female specialized in foraging (f = .55). They provide food for the society (f = .20), and display little behaviour towards the brood.

One individual is placed separately on the right of the graph : this is a worker specialized in the transport within the nest, of material that

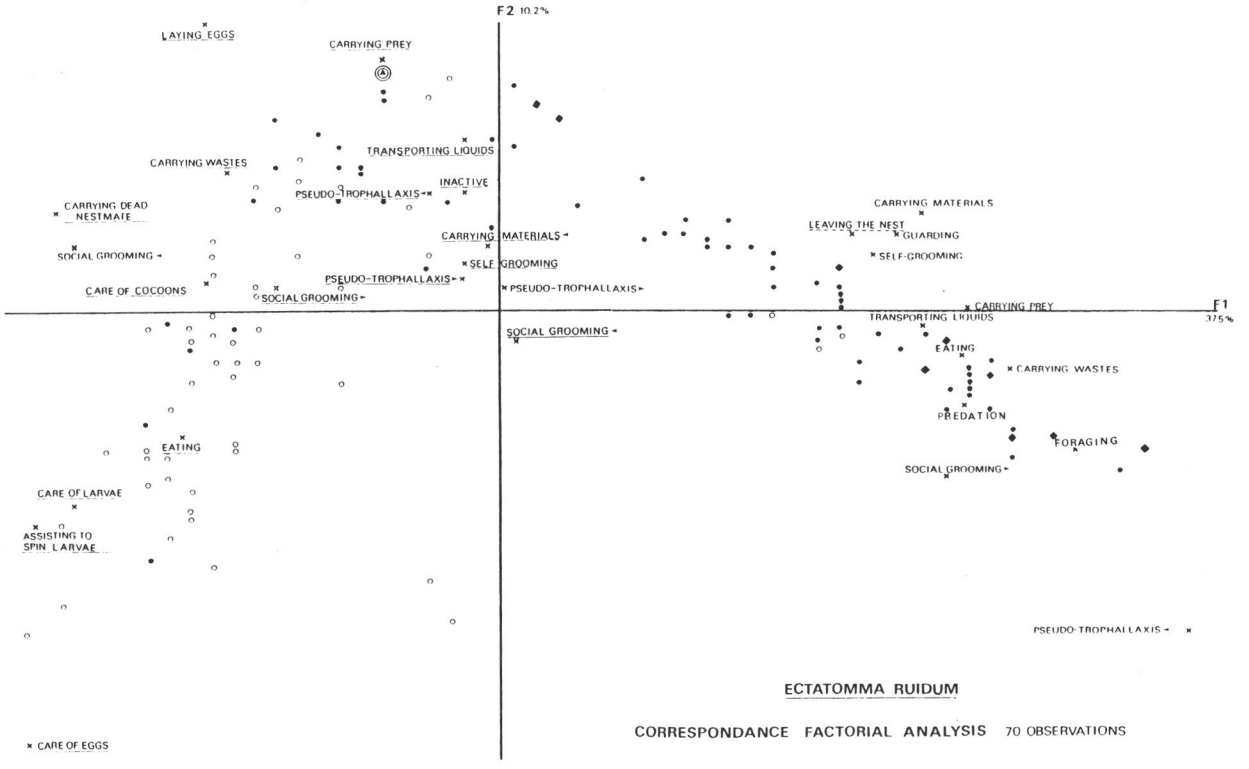

Fig. 4 — Graphic representation of 31 behavior types within the framework of the first two axes 127 individuals. ◉ queen (1) ; ○ young workers (49) ; ● mature workers (68) ; ◆ dead workers (9).

Fig. 4 — Représentation graphique des 2 premiers axes : 127 individus, 31 comportements. ◉ reine (1) ; ○ jeunes ouvrières (49) ; ● ouvrières adultes (68) ; ◆ ouvrières mortes (9).

subsequently serves as a support for the spinning larvae. This result has also been obtained for a close species, *Neoponera apicalis* (Fresneau and Dupuy, in preparation). As a result of this information, figure 3 shows a very clear distinction between the behavioural profiles of those ants that remain most of the time inside the nest (Group 1 to 4) and those that supply provision (Group 5). Among the sedentary ants, two sets may be distinguished : the nurses, and those ants, without a particular role, who deal with the domestic tasks. We thus again demonstrate the three poles described in the correspondance analysis. The presence of queens and the unfertilized females amongst the nurses, and the presence of the other unfertilized females in the last two groups demonstrates the remarkable integration of the unfertilized females in the division of labour. It is not an isolated case, because we have observed unfertilized females participating in food-supply in a natural setting. We consider that this is a distinctive feature of the *Neoponera*.

Second species : Ectatomma ruidum

This neotropical species lives in open biotopes. The colonies were collected near Tuxtla Gutierrez, Chiapas, Mexico. The society we present here included one queen, 126 workers, eggs, larvae and cocoons. The colony was observed 70 times, which revealed a broarder behavioural repertoire. This included a «guarding» function and more frequent pseudotrophallaxis. This latter consists of transporting droplets of sugary liquids between the mandibles, and «giving» them to other workers in the foraging area, or in the nest, (the *Neoponera*, prefer to transport fruit fragments directly into the nest). Figure 4 shows the repertoire of 31 behavioural classes projected onto the first two axes of the factorial analysis. The axis F 1 (or first factor) represents 37 % of the total variance. As in the previous cases, it contrasts the activities in the foraging area (not underlined), with those in the nest (underlined). Amongst the latter, care of the eggs is located at the negative pole of axis F 1. The second axis (F 2) represents 10 % of the total variance and separates inactivity in the nest (at the positive end) from care of eggs and larvae (at the negative end). However, egg-laying and receiving pseudotrophallaxis are perfectly characterized by the third axis (F 3), which represents 4,8 % of the variance. This axis strongly contrasts these behaviours with all of the others, and especially care of eggs. It seems that this axis is representative of the queen's activity. The fourth axis (F 4) represents 4 % of the variance. Within the nest, it contrasts care of cocoons with care of eggs and larvae. Outside the nest, it clearly separates predatory behaviour and food supply from waste disposal and the transport of material. Summarizing, the ethogram for *Ectatomma ruidum* seems broadly similar to the organization

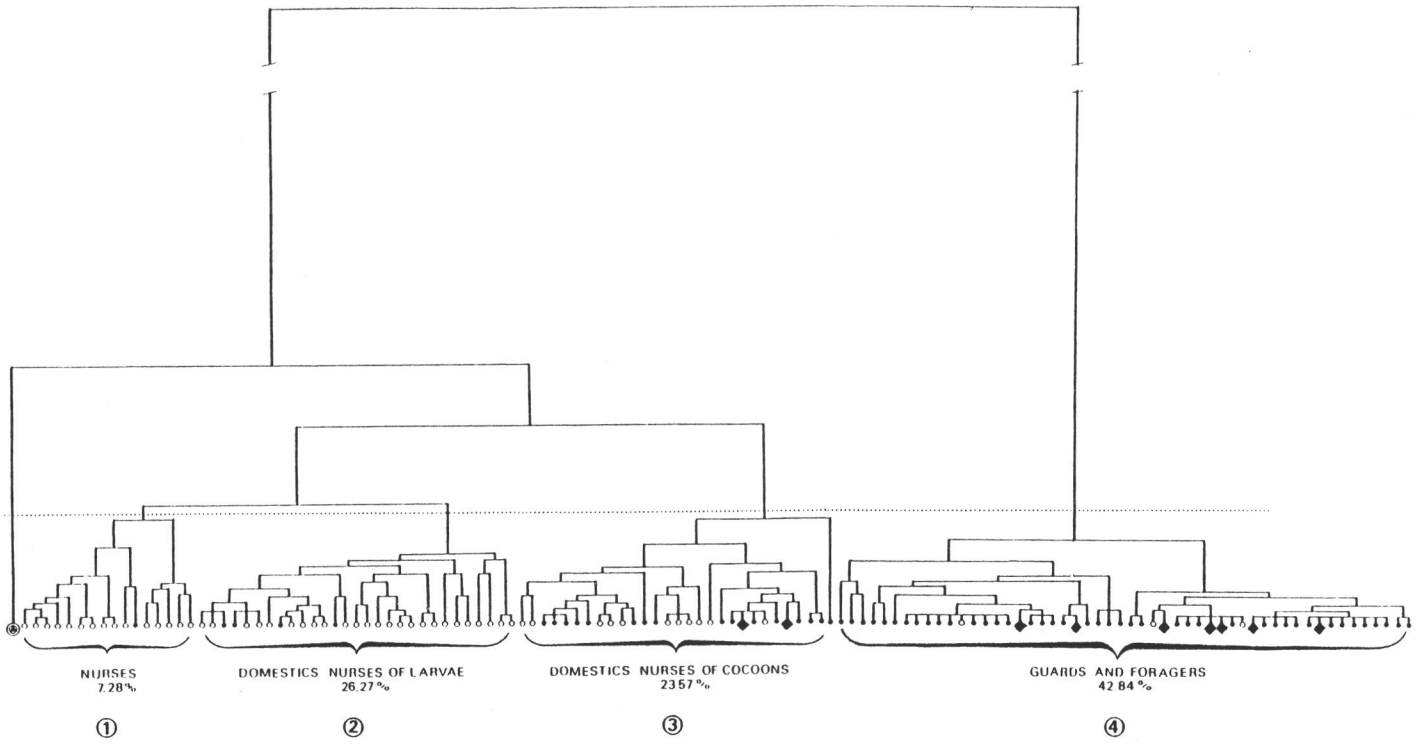

Fig. 5 – Hierarchical Cluster Analysis : Dendogram of regrouped individuals obtained by an aggregation criterion of moment of order two. ▲ queen ; ○ young workers ; ● matures workers ; ◆ dead workers.

Fig. 5 – Analyse de classification hiérarchique : dendrogramme des individus regroupés à partir d'un critère d'agrégation de moment d'ordre deux. ▲ reine ; ○ jeunes ouvrières ; ● ouvrières adultes ; ◆ ouvrières mortes.

described for *Neoponera*. Three primary poles control the activities of the colony :
– The food supply outside the nest and all those activities situated in the foraging area, including guarding the nest entrance.
– Non specific activities within the nest, combined with domestic tasks and the care of cocoons.
– Care of the eggs and larvae, dissociated from the second pole, and constituting the exclusive activities of the nurses.

The distribution of the ants is perfectly continuous between the three poles. The young workers, aged between 8 days and 1 month during the observational period, are represented by open circles on the graph. These circles are massively grouped around the nursing and non specific activities in the nest. After an examination of the individual cases, it appears that the youngest are significantly specialized in the care of the larvae, but we also observe some in non specific activities and even guarding of the nest entrance. The adult workers (identified by filled circles), at least 1 month old during the observation period, are divided between non specific activities and outside tasks ; few of them are nurses. Nine workers, identified by black diamonds, died during the observation period ; their position amongst the outside tasks indicates that ants spend more and more time outside the nest at the end of their lives. Polyethism related to age is therefore highly probable.

The queen is located near the non specific activities. In *Ectatomma ruidum* she is above all inactive. Confinated to the egg chamber, she remains very passive receiving pseudotrophallaxis from the workers. She is, in fact, characterized by the axis F 3 (not shown here), associated with egg-laying and receiving pseudotrophallaxis. The taxonomic analysis shown in figure 5 clarifies and confirms the preceeding remarks, separating four groups of individuals :
– Group 1, consisting of 16 workers (of which 15 are young), is characterized by nursing activities (see figure 6). These are furthermore the only ants to care for the eggs (f = .10). As opposed to *Neoponera*, the low level of care for the eggs suggests that for *Ectatomma* the eggs require little attention from the workers.
– Group 2, containing 29 workers (of which 23 are young), is characterized by care of the larvae (f = .22).
– Group 3, also contains 29 individuals of all ages (only 11 young). This group distinguishes itself by care of cocoons (f = .60) and provides little care of eggs (f = .006) or of larvae (f = .08). For this reason, group 3 is clearly separated from the first two on figure 5.
– Group 4, is quantitatively the largest (52 workers of which 3 are young), and is distinct from the 3 other groups. The behavioural profile reveals that

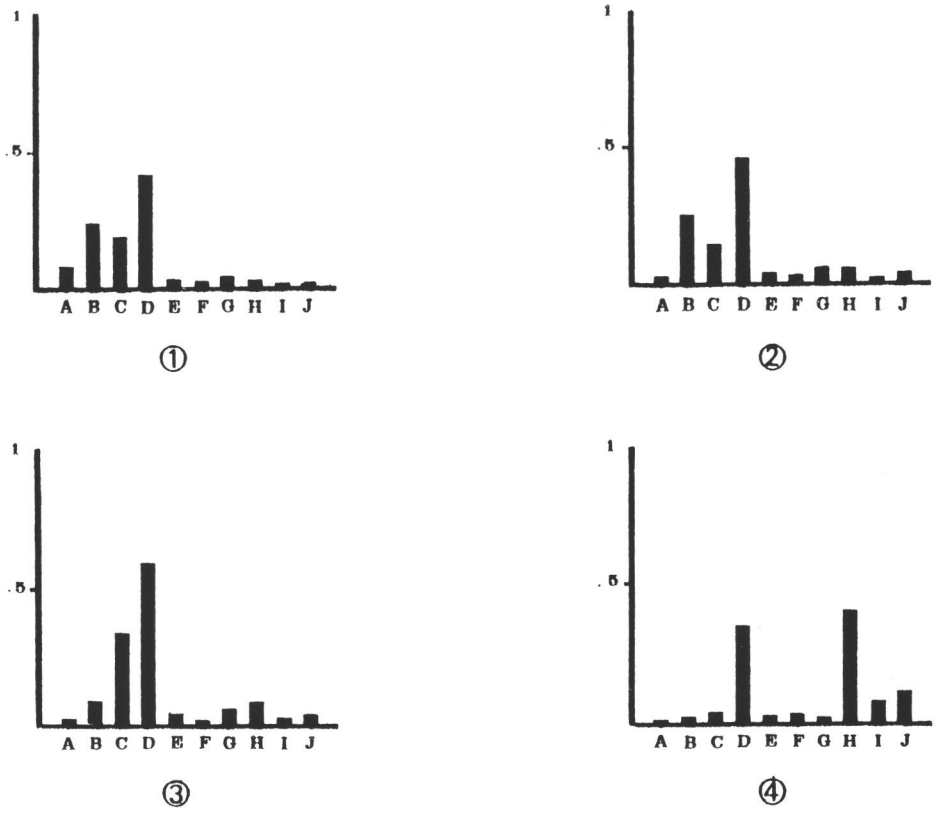

Fig. 6 – Behavioural profile for each group defined by the dendrogram. A – care of eggs ; B – care of larvae and assisting larvae to spin ; C – care of cocoons ; D – non specific activities in the nest : inactive, self-grooming, eating ; E – social grooming → inside and outside the nest ; F – social grooming ← inside and outside the nest ; G – domestic activities in the nest : carrying of materials, carrying wastes, carrying prey, transporting liquids and pseudo-trophallaxis ; H – non specific activities outside the nest : leaving the nest, foraging, self-grooming, eating ; I – domestic activities outside : carrying materials and carrying wastes ; J – supply : predatory-behaviour, carrying prey and transporting liquids.

Fig. 6 – Profils comportementaux des groupes isolés par le dendrogramme. A – soin des œufs ; B – soin des larves et assistance au tissage du cocon ; C – soin des cocons ; D – activités non-spécifiques dans le nid : inactivité, toilette individuelle, manger ; E – toilette sociale → dans et hors du nid ; F – toilette sociale ← dans et hors du nid ; G – activités domestiques dans le nid : transport des matériaux, des déchets, des mortes ; H – activités non-spécifiques hors du nid : exploration, quitter le nid, toilette individuelle, manger et garde hors du nid ; I – activités domestiques : transport des matériaux, transport des ordures, transport des mortes ; J – approvisionnement : prédation, transport des proies, transport des liquides et pseudo-trophallaxies.

the outside activities are well represented : this foraging group includes up to 50 % of the members of the colony. This proportion, which was observed with other colonies, may constitutes a characteristic trait of *Ectatomma*.

The queen is logically categorized separately because she does not participate in the main activities of the society, but is connected to the set of ants that rarely, if ever, leave the nest. This result is notably different from that we obtained for *Neoponera*, and the non-integration of the queen in the social activity seems to characterize *E. ruidum*. We must also note the existence of a complex polyethism related to age. In this organizational system, the three types of brood are separated according to a model which Wilson (1976) has termed «temporal continous caste system», in which sensitivity and responsiveness of the ants to stimulation evolues progressively with age.

Third species : Myrmecina graminicola

Although this paleartic species belongs to the evolved subfamily Myrmicinae, polymorphism is less pronounced than in *E. ruidum* and the number of individuals in the observed colonies is also typically much less than for *Ectatomma*. The colony presented here was collected near les Eyzies, Dordogne, France. During the observation period it consisted of 1 queen, 52 workers of which 21 were less than 10 days old, eggs, 20 larvae and 4 nymphs. Ninety observations were taken over a 12 days period. The ethogram is slightly different from the previous species, and we never observed predation. It seems that the food supply occurs in an episodic manner (only twice during the observational period, whereas food was available in the foraging area). When the food supply does take place, a short but massive recruitment of the members of the colony occurs, and trophallactic exchanges become widespread. Constantly, one or two foragers wander about close to the nest entrance, where one or two guards remain immobile and beat with their antennae any individual trying to enter. Similarly, there is a guard, within the nest, at the entrance of the chamber containing the queen and the brood. In this species, the nymphs are naked and copiously licked, as are the large larvae. The eggs and small larvae are licked much less, and are often covered by totally immobile nurses. Sometimes they are isolated from the floor by the nurses, who suspend them in bunches between their legs, and by the queen, who helps with this task. All of these activities (protection, transport, licking) have been regrouped according to the type of brood, in order to facilitate comparisons with the previous species. The ethogram is represented on fig. 7.

Axis F 1 (37,5 % of the total variance) clearly contrasts the outside activities (at the positive end) with the care of the brood (negative end).

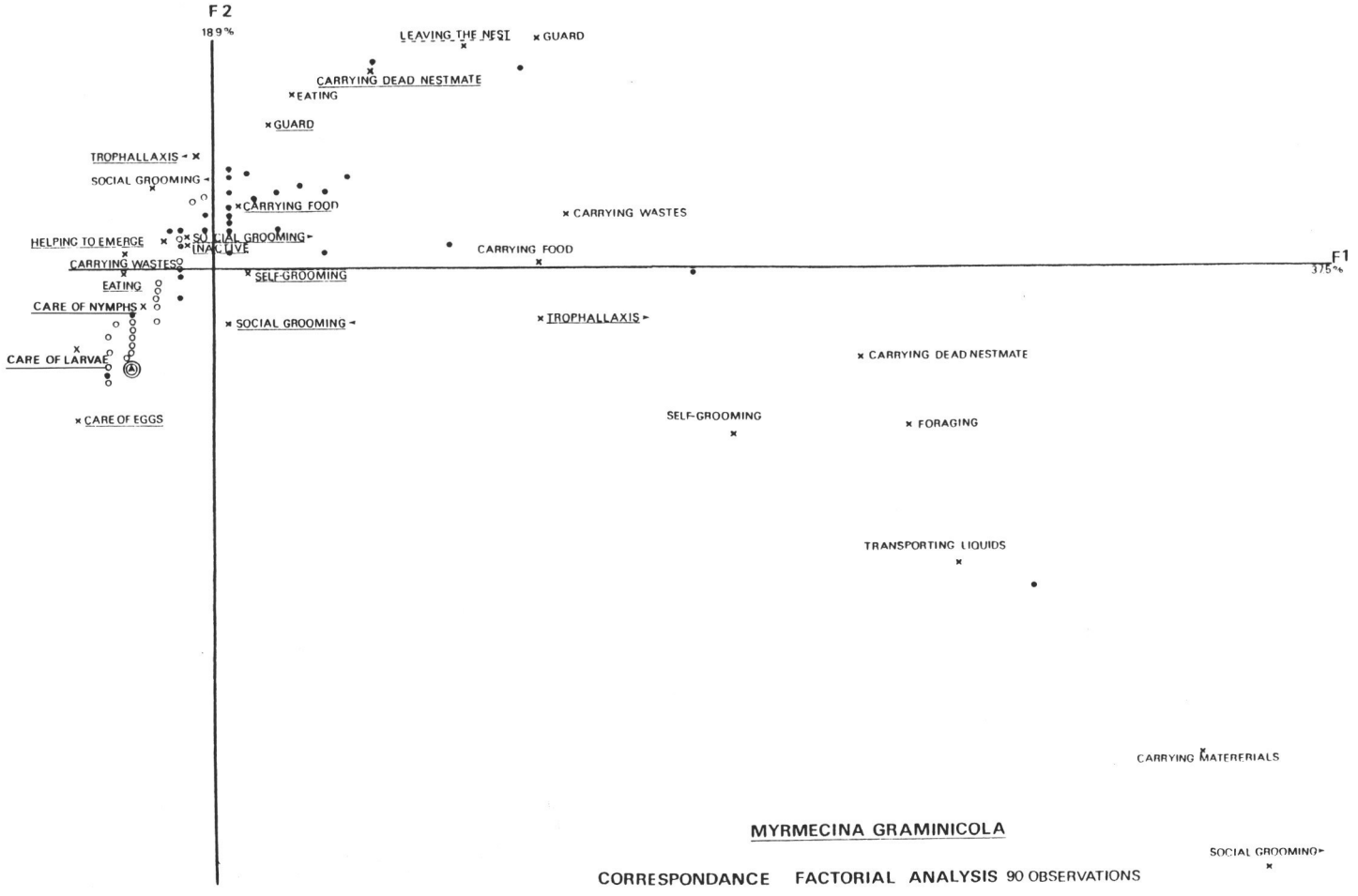

Fig. 7 – Graphic representation of 28 behavioral categories whitin the framework of the first two axes. 52 individuals ◉ queen (1) ; ○ young workers (21) ; ● mature workers (30).

Fig. 7 – Représentation deux premiers axes. 52 individus, 28 comportements. ◉ reine (1) ; ○ jeunes ouvrières (21) ; ● ouvrières adultes.

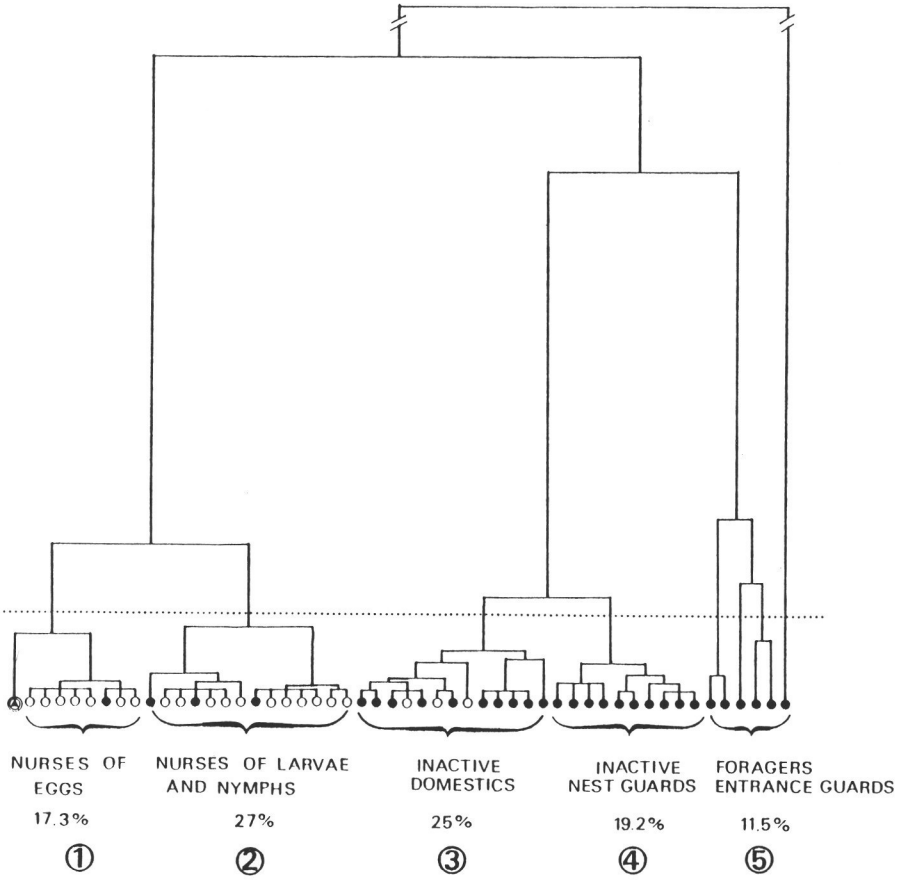

Fig. 8 – Hierachical Cluster Analysis. Dendogram of regrouped individuals obtained by an aggregation criterion of moment of order two. ◎ queen ; ○ young workers ; ● mature workers.

Fig. 8 – Analyse de classification hierarchique : dendrogramme des individus regroupés à partir d'un critère d'agrégation de moment d'ordre deux. ◎ reine ; ○ jeunes ouvrières ; ● ouvrières adultes.

It must be emphasized that foraging and domestic activities are the only significant outside tasks.

The axis F 2 (18 % of the total variance) contrasts outside domestic tasks with nonspecific activities in the nest and, to a lesser degree, care of eggs. The non-specific activity pole also contains nest-guarding behaviour and the act of leaving the nest. Finally, food supply is also located near this pole, which implies that the food supply is done by a significant proportion of the

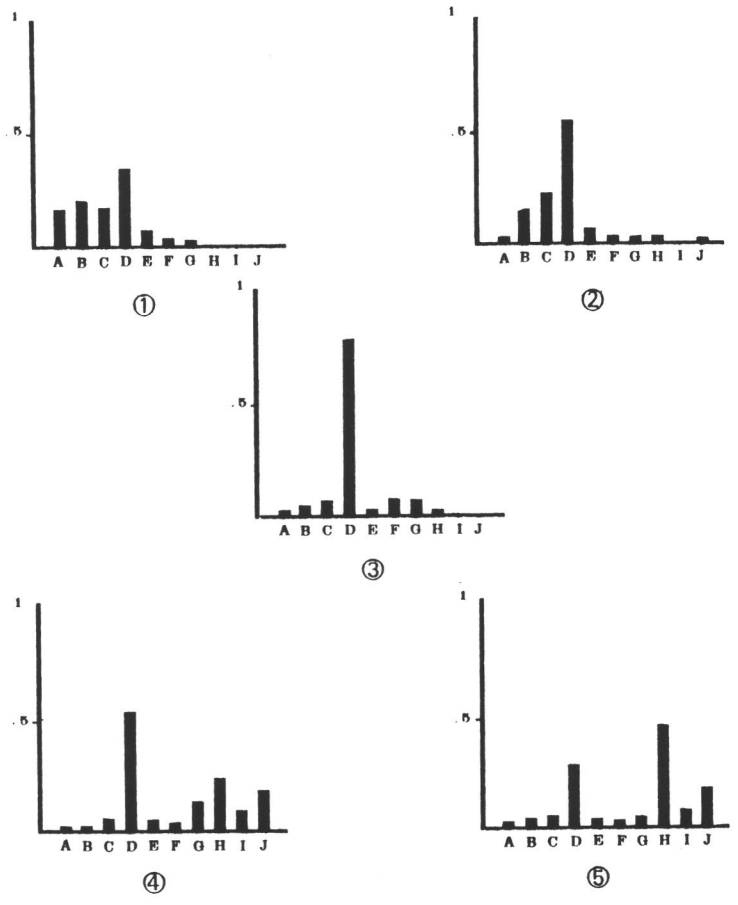

Fig. 9 – Behavioral profile for group defined by the dendrogram. A – care of eggs ; B – care of larvae ; C – care of nymphs and assitance to emerge ; D – non specific activities in the nest : inactive, self-grooming, eating and guarding inside the nest ; E – social grooming → inside and outside the nest ; F – social grooming ← inside and outside the nest ; G – domestic activities in the nest : carrying materials, carrying wastes, carrying dead nest-mate ; H – non specific activities outside : foraging, leaving the nest, self-grooming, eating, guarding ; I – domestic activities outside : carrying materials, carrying wastes, carrying dead nest-mate ; J – supply : carrying food, transporting liquids and trophallaxis.

Fig. 9 – Profils comportementaux des groupes isolés par le dendrogramme. A – soin des œufs ; B – soin des larves ; C –soin des nymphes et soins lors de l'éclosion ; D – activités non spécifiques dans le nid : toilette individuelle, manger, garde de l'entrée de la chambre aux œufs ; E – toilette sociale → dans et hors du nid ; F – toilette sociale ← dans et hors du nid ; G – activités domestiques dans le nid : transport de matériaux, des déchets et des mortes ; H – activités non spécifiques hors du nid : exploration, quitter le nid, toilette individuelle, manger et garder ; I – activités domestiques hors du nid : transport de matériaux, des déchets et des mortes ; J – approvisionnement : transport de nourriture et des liquides, trophallaxies.

domestic workers, or those that are inactive in the nest. This function could occur in an episodic manner after a recruitment initiated by the foragers.

The axis F 3 (11 % of the variance, and not shown here) dissassociates «leaving the nest» and «guarding the entrance» with the nest of the non-specific activities. Axis F 4 (5 % of the variance) contrasts the care of eggs with the care of larvae and nymphs, which corresponds to a similar organization to that of *E. ruidum*.

The distribution of individual ants on figure 7 closely follows the organization of activities. The young workers are massively grouped around the nursing activities ; the queen is integrated with this group, being an egg-nurse. The older workers are spread out between the non-specific activities and the outside tasks. The taxonomic analysis, represented on figure 8, confirms and refires this categorization : virtually, all the young workers (18 out of 21) are found in the first two groups. Group 1 contains the queen and the egg-nurses. Group 2 includes the nurses of larvae and nymphs, that we could separate as two subgroup, as with *E. ruidum*, but the degree of specialization is less pronounced. The rest of the colony includes the workers engaged in non-specific activities in the nest, guarding and foraging. Among the foragers (group 5) a worker which permanently explores the foraging area is set appart ; if we combine this ant with the guards, it appears that only 11 % of the members of the colony usually explore outside the nest. This low proportion (also obtained in another colony) is notably different from *E. ruidum*, in which half the colony is permanently outside the nest.

To summarize, it appears that the *Myrmecina* constitute limited societies in which all the workers spend most of the time in the nest. This increases their unobtrusiveness in the field, while the episodic character of the food supply implies the massive distinction in the cluster of figure 8 between the nurses (groups 1 and 2) and the rest of the colony. Figure 9 confirms and explains this dichotomy : groups 1 and 2 present behavioural profiles which are very similary to those of individual nurses (the same level of inactivity is observed in both cases, f = .55), but a difference is that group 1 preferentially cares for the eggs (f = .27), whereas group 2 directs its nursing activity (f = .83), principally the domestic tasks. It would therefore be reasonable to assume that these two groups constitute a reserve that can be called upon for a short time to forage. This is especially the case for groups 4, which shows a higher level of «leaving the nest». The last group (5), less homogenous, is characterized by non-specific activities outside the nest (foraging and guarding the nest entrance, f = .45), and domestic tasks that are always outside (f = .12). The foraging is part of the behavioural repertoire of these workers. At the appropriate time, these workers, which spend most of their time outside, locate the food and then recruit the inactive workers in the nest. The low level

Table I – Behavioural profile of queens belonging to three species studied. Relative frequencies of activities displayed by the queens over the observational period.

Tableau I – Profils comportementaux des reines appartenant aux trois espèces étudiées. Fréquences relatives des activités présentées par les reines sur le total d'observations effectuées.

	Care of Eggs	Care of Larvae	Care of Cocoons	"Non-specific" Activities	Social-grooming	Trophallaxis	Egg-laying	Total
NEOPONERA FOETIDA 3 ♀ , 60 Obs.	.058	.222	[.362]	[.350]	.006	-	-	1
ECTATOMMA RUIDUM 1 ♀ , 70 Obs.	.030	.007	-	[.856]	[.077]	-	.030	1
MYRMECINA GRAMINICOLA 1 ♀ , 90 Obs.	[.306]	.031	.006	[.544]	.094	.019	-	1

of foraging unfortunately prevented us from quantitatively studying this recruitment behaviour. After *Neoponera* and *Ectatomma*, the organization of *Myrmecina* constitutes a third original solution. The main points to be remembered are the integration of the queen in the care of the eggs, and the innovation of the significant function of foraging to a section of the inactive workers.

DISCUSSION

Is it possible to establish an evolutionary hierarchy based on polyethism, as a result of proceding analysis ?

Many limiting factors make it difficult. First of all, it is possible that the descriptive analysis used does not account for the total behavioural repertory of each species. Certain distinct but in frequent activities could have eluded our investigation due to the observational method used. Perhaps by extending this research, we could in the future, to pool the results of several colonies into the same factorial analysis. This would increase our chances of observing the influence of these rare behaviours. A new systematization for each species could then be drawn up. On the other hand, it would be useful to complete and enlarge the set of evolutionary levels studied by carrying out similar studies on other species selected on the basis of recent taxonomic findings. This diversification of the levels of investigation would permit a more coherent interpretation of the results. Three levels of investigation therefore constitute a minimal initial sample. Partial results reveal a considerable stability in polyethical organization. Summarizing, in all cases the division of labour is based on three poles of inactivity : nursing towards the brood (in the nest), non-specific activities common to all ants (in the nest) and the activities that occur outside the nest. The domestic tasks, both inside and outside the nest, are spread between the second and third poles. The distribution of individuals between these poles is always perfectly continuous. This characteristic must be very wide spread amongst the social Hymenoptera, because Brothers and Michener (1974) came to the same conclusion for semi-social colonies of primitive bees.

On the basis of the results we have reported here, *Neoponera* represents the most primitive reference point, with the ants being divided equally between the three poles, although the foragers are nevertheless the smallest group. The *Myrmecina* have a broadly similar organization to the *Neoponera* (the same proportion of nurses) and there are even fewer foragers. In both species many inactive individuals constitute a reserve available according to the needs of the society. In the case of *Myrmecina*, for example, the inovation of recruitment

permits a restricted number of foragers to recruit, if necessary, the normally inactive sedentary ants, for the provision of a massive and rapid food supply. The case of *Ectatomma* is somewhat different, because the permanent foragers constitute the largest group. As opposed to the preceding species, the societies are more populous and the organization of labour is both less adaptable and more specialized. The absence of recruitment in a populous society with and abundant brood could explain the permanent investment in a large number of foragers. The size of the societies and the ability to recruit would therefore be key elements in the social organization.

In an earlier study the integration of unfertilized females into the social roles of the species *Neoponera apicalis*, was demonstrated (Fresneau and Dupuy, in preparation), and we report here the same thing in *Neoponera foetida*. Furthermore, subequent dissection allowed us to identify which of these females were fertilized. Here, it seems possible to compare the behavioural profiles of the queens of the three species. The results are shown in table 1, in which the main valves are framed. Generally, the queens play no role in the domestic and outside tasks. In each case, however, they show a much higher level of inactivity and non-specific activities than the workers. The participation of the queens in the division of labour concerns principally the care of the brood. For example, the queens of *Neoponera* spread their nursing activities accross the eggs, larvae and cocoons, whereas the queen of *Myrmecina* preferentially cares for the eggs and the small larvae. The *Ectatomma* queen, the most passive, is submitted to intensive grooming by the workers. It is the only queen that we have observed ovipositing, and from the behavioural point of view, the *Ectatomma* queen strongly resembles the queens of evolved species, who are totally dedicated to egg-laying, abandoning the other behaviours in which they engage during the foundation of the colony. On the other hand, it is frequently considered that the Ponerine queens continue their nursing activities in the adult society (Le Masne, 1953). Thus, the level of the queen'inactivity, or alternatively, her role in the care of the brood, would be a good indication of the species'evolutionary level. In this respect, *Ectatomma* would be placed at the top of the classification of these three species, *Neoponera* the bottom, and *Myrmecina* paradoxically in an intermediate position. We have attempted to test the value of this classification by studying the degree of polymorphism of the three genera reported here. Two biometric indices were used : the width of the head (between the eyes) and the maximum length of the thorax.

The measures were taken from a fairly large sample of females and workers coming from all the colonies reared in the laboratory. Then, we established a relationship between the workers and females. The results, portrayed in table 2, show that the same type of categorization is obtained on

Table II – Estimation of polymorphism between castes in the three species studied. The biometric measurements were obtained from samples obtained in various colonies.

Tableau II – Profils comportementaux des reines appartenant aux trois espèces étudiées. Fréquences relatives des activités présentées par les reines sur le total d'observations effectuées.

		HEAD Interocular width (mm)	THORAX Prothoracic width (mm)
NEOPONERA FOETIDA	♀ (7) $\bar{X}$	2.145	1.761
	♂ (57) $\bar{X}$	2.040	1.445
	♀/♂	1.052	1.219
ECTATOMMA RUIDUM	♀ (2) $\bar{X}$	3.00	2.780
	♂ (46) $\bar{X}$	1.960	1.450
	♀/♂	1.531	1.917
MYRMECINA GRAMINICOLA	♀ (4) $\bar{X}$	0.860	0.700
	♂ (46) $\bar{X}$	0.738	0.460
	♀/♂	1.165	1.521

the basis of both types of biometric index. Low values indicate little polymorphic difference (near to 1), which is the case for *Neoponera*, and for many Ponerine species and in general for the «primitive» species. On the other hand, higher values reflect a pronounced polymorphism. This is the case for *Ectatomma*, whereas *Myrmecina* yields intermediate values, which are closer to those of *Neoponera* than to those of *Ectatomma*.

Although belonging to the subfamily Myrmicinae, *Myrmecina graminicola* form societies in which there is little difference between queen and workers either behaviourally or morphologically. The paradoxical position of *Myrmecina graminicola* in the hierarchy is confirmed by these two results. One may therefore assume that the polymorphic separation between queens and workers is also a good indication of the polyethic separation of the castes. This is slight in the primitive species, but not noticiable for the evolved species. In this respect *E. ruidum* should be considered to be a highly advanced Ponerine. It would be useful, in the future, to extend this analysis to a broader sample of species in order to more completely test the value of this relationship. We know that caste polymorphism is a good indicator of the level of socialization and this feature can be generalized to all the social Hymenoptera (Michener, 1974 ; Lin and Michener, 1972). Thus, social evolution tends to radically separate the queen caste, which is concerned with reproduction, from the worker caste which deals only with the trophic function of reproductive assistance. This process is at work in the ants, and appears very early in their evolution, although we must admit that it is not spread in a homogenous way accross all the sub-families (Wilson, 1953). This evolutive process of separation, which can be objectively judged at the morphological level, can be correlatively observed at the behavioural level and by the degree of integration of the queen into the social roles.

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References

BARONI URBANI C., 1968. – Domination et monogynie fonctionnelle dans une société digynique de *Myrmecina graminicola* Latr. *Ins. Soc., 15*, 407-411.

BENZECRI J.P. et al., 1973. – L'analyse des données. *Dunod*, Paris, *T.II*, 630 p.

BONAVITA A., POVEDA A., 1970. – Mise en évidence d'une division du travail chez une Fourmi primitive. *C.R. Acad. Sc. Paris, 270*, 515-518.

BROTHERS D., MICHENER C.D., 1974. – Interactions in colonies of primitively social bees III. Ethometry of division of labor in *Lasioglossum zephyrum*. *Journ. Comp. Physiol., 90*, 129-168.

BROWN W.L. jr., 1954. – Remarks on the internal phylogeny and subfamily classification of the family Formicidae. *Ins. Soc., 1*, 21-31.

BROWN W.L. jr., 1960. – Contribution toward a reclassification of the Formicidae. III. Tribe *Amblyoponini* (Hymenoptera). *Bull. Mus. Comp. Zool. Harvard, 122*, 145-230.

BROWN W.L. jr., GOTWALD W.H., LEVIEUX J., 1970. – A new genus of Ponerine ants from west Africa (Hymenoptera Formicidae) with ecological notes. *Psyche, 77*, 259-275.

BUCKINGHAM E.N., 1911. – Division of labor among ants. *Proc. Amer. Acad. Sc., 46*, 425-507.

DOBRZANSKA J., 1959. – Studies on the division of labour in ants genus *Formica. Act. Biol. Exp., 19*, 57-81.

FRESNEAU D., CHARPIN A., 1977. – Une solution photographique au problème du marquage des insectes de petite taille. *Ann. Soc. Entomol. F., 13*, 423-426.

FRESNEAU D., DUPUY P. – A study of polyethism in a primitive ant : *Neoponera apicalis* (Hymenoptera : Formicidae), in preparation.

GOETSCH W., EISNER H., 1930. – Beiträge zur biologie köznersammelnder Ameisen, II. Teil. *Z. Morph. Okol. Der Tiere., 16*, 371-452.

GOTWALD W.H., LEVIEUX J., 1972. – Taxonomy and biology of a new west african ant belonging to the genus *Amblyopone* (Hymenoptera Formicidae). *Ann. Ent. Soc. Amer., 65*, 383-396.

HEYDE K., 1924. – Die Entwiccklung der psychischen Fähigkeiten bei Ameisen und ihr Ver halten bei abgeänderten biologischen bedingungen. *Biol. Zbl., 44*, 623-654.

KIIL V., 1934. – Untersuchungen über Arbeitsteilung bei Ameisen. *Biol. Zbl., 54*, 114-146.

LE MASNE G., 1953. – Observations sur les relations entre le couvain et les adultes chez les fourmis. *Ann. Sc. Nat., 15*, 1-56.

LENOIR A., MARDON J.C., 1978. – Note sur l'application de l'analyse des correspondances à la division du travail chez les Fourmis. *C.R. Acad. Sc. Paris, 287*, 555-558.

LEVIEUX J., 1972. – Comportement d'alimentation et relations entre les individus chez une Fourmi primitive, *Amblyopone pluto. C.R. Acad. Sc. Paris, 275*, 483-485.

LIN N., MICHENER C.D., 1972. – Evolution of sociality in Insects. *Quart. Rev. Biol., 47*, 131-159.

MICHENER C.D., 1977. – Aspects of the evolution of castes in primitively social Insects. *Proc. VIIIth Int. Congr. I.U.S.S.I., Wageningen, the Netherlands*, 2-6.

OKLAND F., 1930. – Studien über die Arbeitsteilung und die teilung des Arbeitsgebietes bei der Roten Waldameise. (*Formica rufa* L.). *Z. Morph. Okol. der Tiere, 20*, 63-81.

OSTER G.F., WILSON E.O., 1978. – Caste and Ecology in the social Insects. *Princeton University Press*, Princeton, New Jersey, 352 p.

OTTO D., 1958. – Uber die Arbeitsteilung im Staate von *Formica rufa rufo-pratensis minor* Gössw. und ihre verhaltensphysiologischen Grunlagen : ein Beitrag zur Biologie der Roten Waldameisen. *Wiss. Abh. Dtsch. Akad. Landwirt., 30*, 1-169.

TAYLOR R.W., 1978. – *Nothomyrmecia macrops* : a living-fossil ant rediscovered. *Science, 201*, 979-985.

TRANIELLO J.F.A., 1978. – Caste in a primitive ant : absence of age polyethism in *Amblyopone. Science, 202*, 770-772.

WEBER N.A., 1972. – Gardening ants, the Attines. *Mem. Ann. Phil., 96*, 146 p.

WEIR J.S., 1958. – Polyethism in workers of the ant *Myrmica. Ins. Soc., 5*, 97-128.

WILSON E.O., 1953. – The origin and evolution of polymorphism in ants. *Quar. Rev. Biol., 28*, 136-156.

WILSON E.O., 1968. – The ergonomics of caste in the social insects. *Amer. Nat., 102*, 41-46.
WILSON E.O., 1971. – The Insect Societies. *Belknap Press of Havard University Press*, Cambridge, 548 pp.
WILSON E.O., 1976. – Behavioral discretization and the number of castes in an ant species. *Behav. Ecol. Sociobiol., 1*, 141-153.
WILSON E.O., CARPENTER F.M., BROWN W.L. jr., 1967. – The first mesozoique ants, with the description of a new subfamily. *Psyche, 74*, 1-19.