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Classification of Ant Nest Complexes

A. A. Zakharov

Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119071 Russia
e-mail: ferda@bk.ru

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Abstract—The nest complex is an intrinsic form of spatial and functional organization of ants, a real structural level of an intrapopulation rank. The proposed classification of ant nest complexes is based on the properties of the elements composing the complexes and on scenarios of settlement development. The stages of life of an ant settlement and the stages of development of the corresponding complex are described (the proto-, meso-, and hypercomplex). The following main species-specific features are used in the classification: the basic level of intracolonial structures (clan, column, pleiad); the nest type (sectional, capsule-like); the mode of colony founding (solitary queen, pleometrosis, temporary social parasitism); the mode of sociotomy (binary division, budding, fragmentation); the definitive colony size (N_c); the presence of a defended territory; the form of polycaly (simple polycaly: PC_1, polycaly with breeding nests: PC_2, polysectional nests: *PSN*), etc. Based on the data on 120 ant species (including all the well-studied ones) showing clear differentiation into gynes and workers, eight basic social types are distinguished, which are named by their most specific traits: (1) recurrent sociotomy based on a clan; (2) diffuse polycaly; (3) recurrent sociotomy based on a single colony (column); (4) closed (ordinary) polycaly; (5) open (obligate) polycaly; (6) linear settlements; (7) dissipated pleiads; (8) unitary pleiads. The general description of an ant nest complex includes its social type, development stage, and current state. The classification of nest complexes forms the basis for systemic study, use, and protection of ants.

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Ants, as eusocial insects, possess specific ways of development of population structures related to their ability for sociotomy and formation of temporary and permanent structures above the colony level. The self-development of ant settlements leads to establishment of vast territorial systems, namely, complexes of ant nests consisting of tens and hundreds of interacting colonies. The ***ant nest complex*** *is a system of conspecific ant nests whose adjacent foraging areas form a territorial continuum*.

The complex is the principal biochorological phenomenon at the population level in ants. Its size, structure, and configuration reflect the results of historical development of the ant settlement in its interaction with the topical, geographic, and synecological factors. The complex is the main scene of intrapopulation events in ants, since within it the main migration events take place, the processes of self-organization (establishment and optimization of the functional and chorological structures) are realized, the main exchange of genetic material occurs, the population density is optimized, and the settlement is restored and restructured under critical conditions. Under favorable conditions, dispersal of ants over the available habitats leads to structuring of the complex, with formation of subcomplexes within it or with separation of a part of the settlement as a secondary complex. In fact, the spatially isolated complex (or a group of nest complexes of the same species) is the local population, or metacomplex.

The ant nest complex is a self-developing system of conspecific nests interacting in certain ways, which may exist for decades and has a history of its own. Its life, similar to the life of an individual ant nest, includes the stages of growth, stabilization, depopulation, and degradation. The potential life span of the complex considerably exceeds that of an individual nest, and is mostly determined by its size and level of structuring. Complexes may vary in the total number of ants and the size, age, state, density, and the level of organization of the nests included in them. A complex may consist only of single young nests, of nest coalitions, or only of old, declining nests.

Many problems of the study, monitoring, protection of ants and their use in biological control of forest pests are somehow connected with the ant nest complexes (Zakharov et al., 2003). Such complexes, as

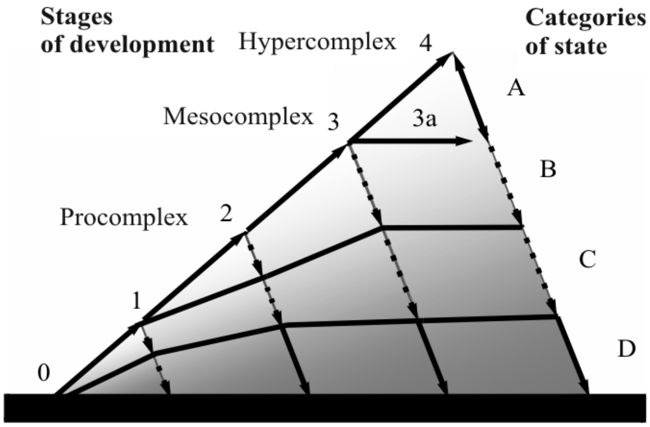

Fig. 1. Stages of development (0–4) and categories of state (A–D) of ant settlements. For explanation, see text.

real objects, have long been used as units of study, conservation, and exploitation.

At the same time, researchers often tend to overlook the complex itself as a distinct form of spatial and functional organization of ants and as an actual structural level reflecting, on the one hand, the features and abilities of individual ant nests, and on the other hand, all the evolutionary and ecological potentials of the species. Therefore, a special study of this level of organization of ant populations would be of obvious theoretical and applied significance.

There has been much progress in the studies of the structure of ant settlements, and a considerable amount of material has been accumulated. This is indicated by the regular appearance of the original research papers by the Russian authors (Gilev, 2003, Goryunov, 2007; Seima, 2008; Burgov, 2011, etc.) and the international reviews (Debout et al., 2007; Ellis and Robinson, 2014).

Each ant settlement has certain size and functional parameters and a history of its own, and is in a certain phase of its development. This should be taken into account if an adequate assessment of an ant settlement is to be produced.

This communication is devoted to the development of a classification of ant nest complexes, based on the properties of their elements and the scenarios of settlement formation.

This work uses the author's own and published data, including those summarized earlier (Dlussky, 1981; Zakharov, 1991) as well as the recent findings (Silverman and Liang, 2001; Mäki-Petäys et al., 2005; Zakharov, 2005; Debout et al., 2007; Goryunov, 2007; Seima, 2008, etc.). It is based on the structural historical approach to the study of social insects which has been developed by the author for many years (Zakharov, 1991, 2005). This approach presumes a systemic study of the insect communities and their social structures in the process of their self-development.

However, the classification of ant settlements and the nest complexes formed within them is fundamentally different from the classification of social structures as such (Zakharov, 2005), in the same way as the description of an economic region is different from its functional layout. The ant nest complex includes, among other elements, a system of material objects, such as nests, trails, etc., which appear and change in certain ways within the given territory. The classification should be logically related to the essential characteristics of the different types of communities and levels of their organization, which are needed for an adequate and comparable description of complexes of different ant species. Therefore, it is based on the principal characters of the species themselves and the modal scenarios of development of species-specific settlements.

The Modal Scenario of Formation and Staged Development of an Ant Settlement

The development of each settlement includes up to 5–6 distinct stages that differ in the characteristics of the elements (ant nests) composing the settlement, the level of integrity and the system of connections between them, the specific traits of territory use, and other aspects (Goryunov, 2007; Zakharov, 2013). They include the consecutive modal stages of the life of the ant settlement and the development of the complex established in it: *procomplex*, *mesocomplex*, and *hypercomplex* (Fig. 1).

The zero point should always correspond to the time of foundation of the primary nest. This nest can be founded in three ways: (1) founding of the new colony by a single queen (the foundress); (2) pleometrosis, which herein means only the joint founding of the new nest by several young mated queens; (3) temporary social parasitism. Only the complexes formed in these ways may be considered as primary ones. All the other settlements formed by sociotomy, migrations or recolonization from refugia should be regarded as secondary; their stages of development can still be assessed in the framework of the general system, but the approaches related to the colony cycle theory

(Starr, 2006) cannot be fully applied to secondary settlements.

Ideally, we would consider an even-aged monocentric complex developing from a single center (from one primary nest). However, this situation is very rare, and in reality we nearly always deal with settlements formed from several centers. In addition, as the result of many years of dispersal, the advanced center of a monocentric settlement becomes surrounded with concentric zones showing some earlier stages of development of the given complex (e.g., see Stukalyuk, 2013). In the polycentric variant, the complex acquires a mosaic structure due to the formation of subcomplexes within it, which may be at different stages of development (Zakharov and Kalinin, 2007).

Stage 0. The primary settlement in a new place is started with the founding of the primary nest, either by a single queen, several queens, or via temporary social parasitism. The primary nest grows and becomes ready to produce secondary nests.

Stage 1. Polycalic systems and/or temporary supracolonial structures appear; the number of nests grows but the nests remain dissociated and do not yet form a territorial continuum.

At the first two stages, there is still no complex, because not any group of ant nests but only a group with a high level of internal relations may be regarded as a complex (Alaev, 1983). Unification of the elements of ant settlements within a single territorial continuum may be considered an indicator of establishment of real and stable interrelations between them. In ecosystem morphometry, these events may be described in terms of consolidation and compartmentalization (Vinogradov, 1998).

Stage 2. Protocomplex: the stage of extensive development. The density of the settlement increases, and the territorial continuum is established, still at a low level of territory structuring and a relatively small size of the nests.

Stage 3. Mesocomplex: the stage of intensive development and structuring of the settlement. The degree of differentiation of the elements by size and function increases, as does the integrity of the complex. The territories of ant colonies become structured and able to support high population density and large nests. Permanent supracolonial structures start to appear.

Stage 3a. Stabilization of the mesocomplex: the stage of leveling of the nests by size and gradual decline of the dispersal activity. Large complexes may experience depression-restoration waves at this stage.

Stage 4. Hypercomplex: polymerization (Zakharov, 1991), i.e., integration of ant nests into a secondary federation or the formation of several interconnected nest aggregations in case of a primary federation. The hypercomplex is characterized by the highest levels of abundance, population density, integrity, self-regulation, and stability possible for the given species.

The ant settlement may stop at any of the intermediate stages (0–3) of its development and try to stabilize itself. The new community has no chance of being preserved at stage 0; however, this chance appears at a certain level of settlement development and increases from stage 1 to stage 3 (Zakharov, 2011).

The Key Features of an Ant Species

In this work, the key species-specific features refer to those traits which are of crucial significance for the existence and development of the ant community. Such features include:

the basic level of intracolonial structures (clan, column, pleiad);

the nest type (sectional or capsule-like);

the modes of nest founding (haplometrosis, pleometrosis, temporary social parasitism);

the modes of dispersal sociotomy (binary division, budding, fragmentation);

the definitive colony size (N_c);

the presence of a defended territory;

the form of polycaly (PC_0, PC_1, PC_2, PSN);

the spatial configuration of the settlement;

the type of permanent supracolonial structures (the metastable states possible for the given species: MSS-0 – MSS-3).

The number of queens and the key events in the life of an ant nest. It is essential for development of the settlement infrastructure that realization of specific structural variants may be blocked by some features or their combinations. One of the most important features is the number of egg-producing queens.

The number of queens in the colony is a crucial factor in the life of ant communities. Its changes considerably affect the organization of each individual nest and the local populations to which these nests belong. This problem has different aspects. Indeed, on the one hand, the number of queens is believed to determine the main traits of the social organization of ants (Bourke and Franks, 1995; Keller, 1995). On the other hand, the number of queens in nests of the same ant species may change within a broad range (from one to several hundreds), depending both on the stage of the colony development (Pisarski, 1982) and on the phase of its annual cycle, as this was demonstrated, for example, in *Linepithema humile*. In addition, the number of queens varies depending on the living conditions of ants in different parts of their range (Bourke and Franks, 1995; Bondar and Rusina, 2003) and in different biotopes (McGlynn, 2010). Transition from monogyny to polygyny may accompany the northward expansion of a species (Henze and Hölldobler, 1994) or its introduction into new regions (Tsutsui and Suarez, 2003).

The above examples show that the number of queens is as variable as most other parameters of the ant community. It may change depending on the size and age of the colony, climatic and topical conditions, nest design, population density, ecological factors, etc.

There are some parameters of the ant nest which are undoubtedly related to the number of queens. Polygyny increases the total reproductive potential of the colony and reduces its vulnerability (Starr, 2006). It also stimulates the development of subordination systems, thus removing the restrictions on the size of individual structures (Zakharov, 1991). Besides, polygyny ensures a higher level of heterogeneity, phenotypic diversity, and tolerance of ants, opening the way to formation of vast interrelated settlements (Crozier and Pamilo, 1996).

At the same time, the number of queens by itself does not limit any of the key functions of the ant community (Bourke and Franks, 1995; Zakharov, 2011). Both variants (monogyny and polygyny) permit the following events: (a) formation of new colonies by young mated queens (on their own or using the mechanism of temporary social parasitism); (b) the use of auxiliary nests, with transition to polycaly; (c) sociotomy; (d) formation of permanent supracolonial structures. However, each of these events follows considerably different scenarios in the monogynous and polygynous species.

(a) Polygynous species of the temperate zone more often pass through the phase of temporary social parasitism during colony founding, whereas independent founding is more typical of monogynous species. However, independent founding is often pleometrotic in both variants.

(b) Auxiliary nests can be built by all the ant species which have colonies so large as to make the use of such nests expedient. The threshold colony size is species-specific and related to other parameters of the ant communities and their living conditions (Zakharov, 2005).

(c) Colony budding in polygynous species involves the queens already present in the nest, whereas the new nests of monogynous species adopt queens from the original nest prior to budding or even after it (Schneirla, 1971; Dlussky, 1981; Bourke and Franks, 1995).

(d) During the establishment of secondary federations, polygynous species inhabiting large nests usually build special buffer nests between them, whereas in monogynous species the buffer function is performed by the auxiliary nests of polycalic systems.

Similar to the above, the mode of colony founding (haplometrosis, pleometrosis or temporary social parasitism) does not place any limitations, either (Zakharov, 2011). However, this mode determines the behavior of ants at the bifurcation points, namely, their choice between monogyny and polygyny (Batz and Hölldobler, 1982; Pisarski, 1982; Rissing and Pollock, 1988; Zakharov, 2011).

The Social Types

The form of organization of the ant settlement results from interaction of many features characterizing a particular species or population. Despite the great number of possible combinations of features, they can be realized in a fairly limited set of forms of settlement organization, which are common to different taxa of ants and even other eusocial insects. The limited number of these variants is largely determined by the limited number of variants of social structures (Zakharov, 1991, 2013).

Based on the key features and scenarios of development of settlements of 120 ant species, it was possible to distinguish eight principal social types, which were named by their essential traits (Table 1): (1) recurrent sociotomy based on a clan; (2) diffuse poly-

Table 1. General characteristics of the social types of conspecific ant settlements

Social type	Subtype	Basic level of colony	Colony founding	Number of queens	Type of community	Main mode of sociotomy	Dispersal sociotomy	Main type of connections	Type of nest	Type of polycaly	MSS-3
1. *Recurrent sociotomy, clan based*		Clan	Haplo-metrosis	MG, ephemeral OG	Intermediate	Extra-binary division	Binary division	–	Shallow	–	–
2. *Diffuse polycaly*		Clan	Haplo-metrosis	PG, gamergates	Coordination	Budding	Budding	Netlike	Shallow	Diffuse	Diffuse
3. *Recurrent sociotomy, colony based*		Single colony	Haplo-metrosis	MG–OG	Intermediate	Extra-binary division	Binary division, ephemeral coalition	Absent or netlike	Sectional	PC_1	–
4. *Closed polycaly*		Single colony	Haplo-metrosis	MG–OG	Subordination	Budding + fragmentation	?	Radial	Sectional	PC_1	*PC*
5. *Obligate polycaly*	5A	Single colony	Pleo-metrosis	Primary PG, physogastry	Subordination	Budding + fragmentation	Budding + adopting	Radial-netlike	Sectional, capsule-like	PC_2	SF_1
	5B	Single colony	TSP	Secondary PG, physogastry	Subordination	Budding + fragmentation	Budding + adopting	Radial-netlike	Sectional, capsule-like	PC_2	SF_1
6. *Linear settlements*	6A	Single colony	Pleo-metrosis	Primary PG	Subordination	Budding + fragmentation	Budding	Relay-netlike	Sectional, capsule-like	PC_2	*PF*
	6B	Single colony	TSP	Secondary PG	Subordination	Budding + fragmentation	Budding	Relay-netlike	Capsule-like	PC_2	*PF*
7. *Dissipated pleiads*		Pleiad	Haplo- or pleo-metrosis	Primary PG	Coordination	Intra-binary division	Fragmentation	Netlike	Sectional, capsule-like	*PSN*	*PSN*
8. *Unitary pleiads*	8A	Pleiad	Pleo-metrosis	Primary PG	Coordination	Intra-binary division	Budding, true coalition	Radial-netlike	Capsule-like	*PSN*	SF_2
	8B	Pleiad	TSP	Secondary PG	Coordination	Intra-binary division	Budding, true coalition	Radial-netlike	Capsule-like	*PSN*	SF_2

TSP, temporary social parasitism; MG, monogyny; OG, oligogyny; PG, polygyny; PC_1, simple polycaly; PC_2, polycaly with breeding nests; *PSN*, polysectional nest; *PF*, primary federation; SF_1, secondary federation based on a single colony; SF_2, secondary federation based on a pleiad; MSS-3, metastable state.

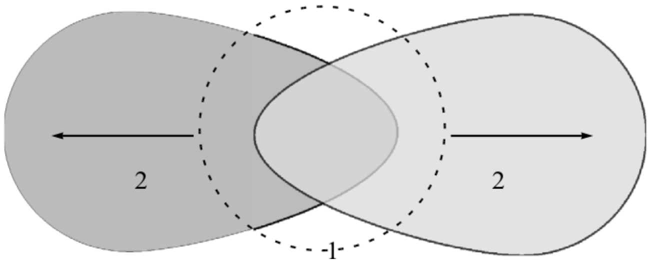

Fig. 2. Recurrent sociotomy in ants (social types 1 and 2); 1, the initial community at the beginning of division; 2, secondary (derived) communities. Arrows show the divergence and subsequent separation of the secondary communities.

caly; (3) recurrent sociotomy based on a single colony; (4) closed (ordinary) polycaly; (5) open (obligate) polycaly; (6) linear settlements; (7) dissipated pleiads; (8) unitary pleiads. The definitions of these social types and their model species are given below.

Social type 1. Recurrent sociotomy based on a clan (Fig. 2): a simple, spontaneously developing settlement. A *simple complex of solitary nests* is formed within a small optimal area. The structural level of the colony is that of a clan. The definitive colony size is $N_c = 3 \times 10^2$–1×10^3. The colonies are monogynous, founded independently by single queens. The mode of sociotomy is *binary division* with fast separation of the secondary nests, by which *the colonies return to their basic structural level* (Soans and Soans, 1971). The nests are sectional and shallow. The colony has no defended territory.

Model species: *Alloformica aberrans*, *Proformica epinotalis*, and *Myrmica lacustris* (= *deplanata*).

Social type 2. Diffuse polycaly (Fig. 3), at which the colony preserves its integrity but occupies several temporary nests without permanent residents. Ants move constantly from one nest to another, nests are often replaced with new ones, and the total number of nests in the system varies (Creighton, 1963; Zakharov, 1991). However, such a system is stable, and its internal flexibility allows the total colony to include as many as 2 thousand individuals. Sociotomy proceeds by fragmentation. The colony has no defended territory.

Model species: *Pachycondyla stigma*, *Rhytidoponera metallica*, *Rytidoponera terros*, *Anochetus* sp., and *Cryptocerus texanus*.

Social type 3. Recurrent sociotomy based on a single colony (Fig. 2): a simple, spontaneously developing settlement. Under optimum conditions, complexes of solitary nests are formed in small areas, with simple polycaly (PC_1) at the utmost. The structural level is that of a single colony. $N_c = 3 \times 10^3$–5×10^4. Monogyny → polygyny. Colonies are founded independently by single queens. Sociotomy proceeds by binary division leading to the formation of an ephemeral coalition (Wehner and Lutz, 1969; Zakharov, 1991), after which separation of the secondary nests returns the secondary colonies to the basic structural level. The nests are sectional and capsule-like. The defended territory is absent or partial.

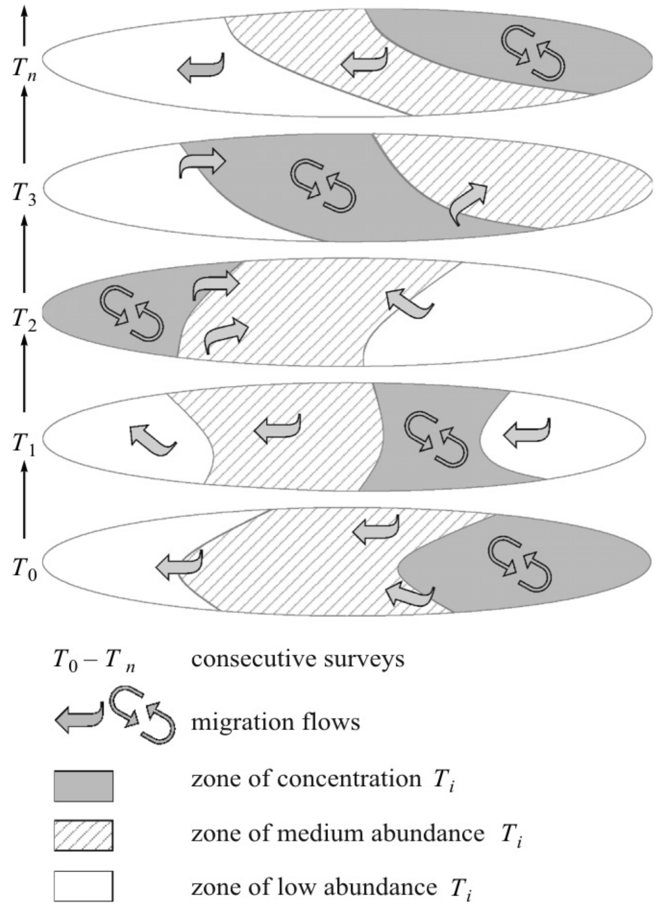

Fig. 3. Diffuse polycaly (social type 2), by the example of *Rhytydoponera metallica*, NSW, Australia, 1978. The zones of high concentration of individuals and the migration flows constantly shift within the foraging territory of a single diffuse colony (after Zakharov, 1991).

Model species: *Cataglyphis setipes*, *C. bicolor*, and *Messor intermedius*.

Social type 4. Closed (ordinary) polycaly: a compound complex of small monocalic and polycalic (PC_2) nests practically not reaching the level of supra-

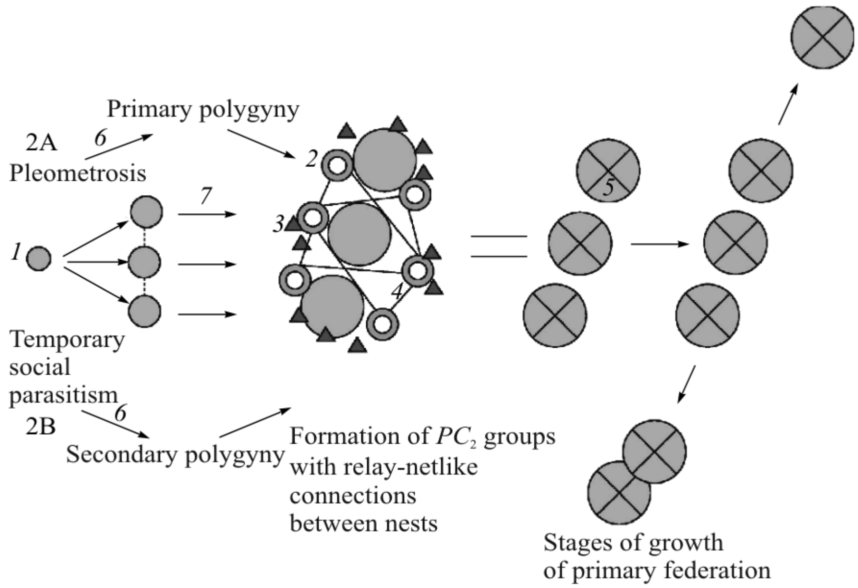

Fig. 4. Development of linear structures into a primary federation (social type 6): *1*, main (permanent, living) nests; *2*, breeding nests; *3*, foraging nests; *4*, connections between nests; *5*, a single PC_2 system; *6*, trends of development; *7*, directions of dispersal of the nest aggregation.

colonial structures. The structural level is that of a single colony. $N_c = 1 \times 10^3$–5×10^4. The colonies are monogynous, less frequently polygynous; they are founded independently by single queens and exist for a time comparable to the queen's life span (Bourke and Franks, 1995). The development of polycaly is largely determined by external (topical) conditions. The nests are sectional and capsule-like. The defended territory is absent or partial.

Model species: *Formica rufibarbis*, *Dolichoderus quadripunctatus*, *Messor aralocaspius*, *M. variabilis*, *Monomorium kusnezowi*, and *Manica rubida*. Some model species are temporary social parasites: *F. forsslundi* (on *F. picea*), *Lasius mixtus* (on *Lasius* s. str.).

Social type 5. Open (obligate) polycaly PC_2; adopters: a compound complex consistently passing through several (4) stages of development with increasing integrity and differentiation of elements by size and functions. The main system of connections is radial or (in case of PF_1) netlike. The structural level is that of a single colony, developing into PC_2; coalitions of columns are possible. $N_c = 5 \times 10^4$–5×10^5. Variants: (***5A***) pleometrosis with facultative transition to primary polygyny; (***5B***) temporary social parasitism with obligatory transition from monogyny (with a tendency for physogastry) to secondary polygyny. The development of polycaly is largely determined by endogenous conditions. Sociotomy proceeds by budding with adopting of gynes (Reznikova, 1983). In case of overpopulation, PC_2 form a secondary federation SF_1 (Zakharov, 1991). The nests are sectional and capsule-like. The colony has a defended territory.

Model species: (***5A***) *Liometopum microcephalum*, *Camponotus herculeanus*, *Lasius flavus*, *L. niger*, *Crematogaster sorokiny*, and *Cr. subdentata*; (***5B***) *Formica pratensis* and *Lasius fuliginosus*.

Social type 6. Linear settlements (Fig. 4): a compound complex consistently passing through the following stages: monocaly → simple polycaly (PC_1) → polycaly with breeding nests (PC_2) → primary federation (PF). The prevalent configuration is linear; PF has a relay-netlike system of connections. The territory is typically subdivided into the nesting zones, containing nest aggregations, and the foraging zones. The structural level is that of a single colony, developing through polycaly with breeding nests (PC_2) into a primary federation (Goryunov, 2007). $N_c = 3 \times 10^4$–1×10^6. Variants: (***6A***) pleometrosis with facultative transition to primary polygyny; (***6B***) temporary social parasitism with obligatory transition from monogyny to secondary polygyny. Sociotomy proceeds by budding and by regular (coordinated with the annual cycle) fragmentation and reintegration. The nests are sectional and capsule-like. The entire territory of large nests and federations is defended.

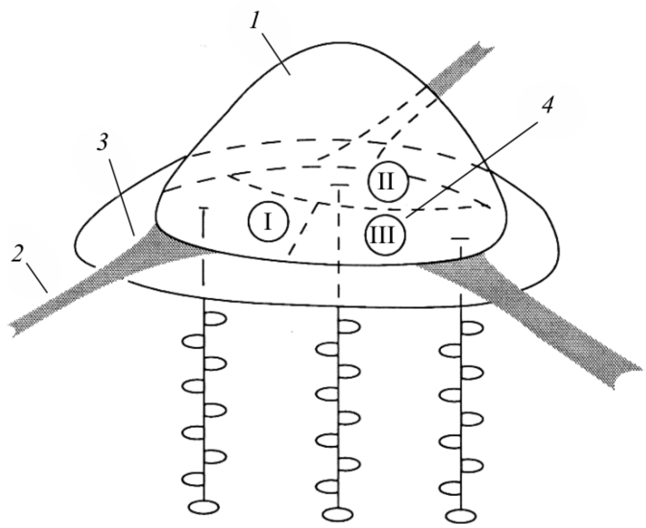

Fig. 5. The unitary pleiad: *1*, mound of a capsule-like nest; *2*, first-order epigeic trails; *3*, nest bank; *4*, sectors occupied by the columns composing the colony.

Model species: (***6A***) *Formica imitans*, *F. cinerea*, and *Iridomyrmex purpureus*; (***6B***) *Formica exsecta* and *F. pressilabris*.

Social type 7. Dissipated pleiads: a compound complex developing in stages with increasing integrity of the stereotyped elements. The main system of connections is radial or (in SF_2) netlike. The basic structural level is that of a pleiad inhabiting a polysectional nest. $N_c = 5 \times 10^3–1 \times 10^5$. Pleometrosis with transition to primary polygyny and dispersal of queens over the section of one nest. Sociotomy proceeds by binary division inside the polysectional nest. Fragmentation of large colonies is possible. Overpopulation may lead to the development of a secondary federation SF_2 (Mizutani, 1981; Zakharov and Fedoseeva, 2005). The nests are either sectional or of two types: sectional and capsule-like. The defended territory may be common or partial.

Model species: *Tetramorium caespitum*, *T. schneideri*, *Pheidole pallidula*, *Messor denticulatus*, *Myrmica rubra*, *Tapinoma karavaevi*, *Formica fusca*, *F. cunicularia*, and *Cataglyphis aenescens*.

Social type 8. Unitary pleiads (Fig. 5): a compound complex developing in stages with increasing integrity and complexity of its elements. The main system of connections is radial or (in SF_2) netlike. The basic structural level is that of a pleiad inhabiting a polysectional nest. $N_c = 1 \times 10^5–1 \times 10^7$. Variants: (***8A***) pleometrosis with transition to primary polygyny; (***8B***) temporary social parasitism with transition from monogyny to secondary polygyny. Sociotomy proceeds by binary division (inside the colony) and budding. Overpopulation leads to SF_2 (Zakharov, 1994). The nests are capsule-like. The colony has a common defended territory.

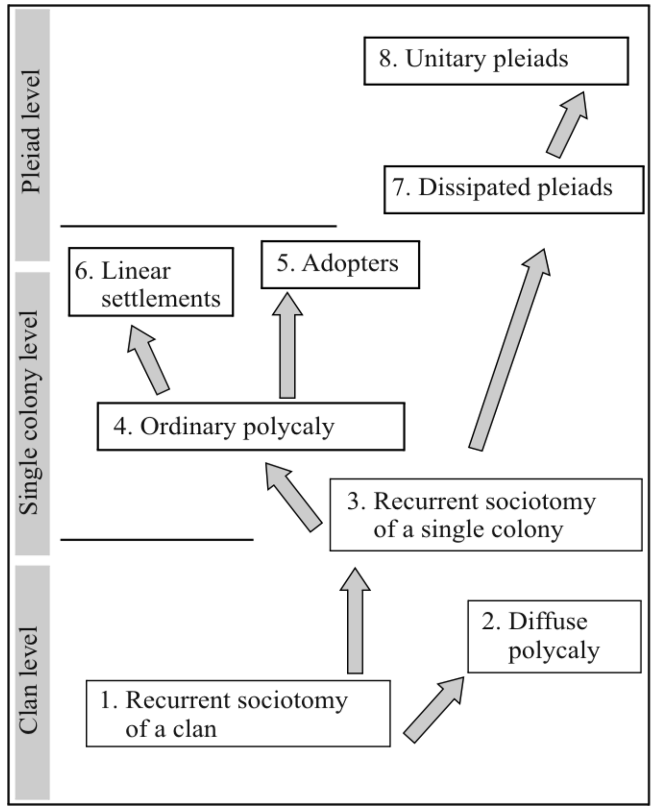

Fig. 6. The basic levels of intracolonial structures and the social types realized on their basis. For explanations, see text.

Model species: (***8A***) *Solenopsis invicta*; (***8B***) the Formica rufa group, *F. truncorum*.

The Properties of Species and the Forms of Community Organization

The ant community is a multilevel system with alternating subordination and coordination structures. This organization allows the potentials for growth and development of the community to be combined with its stability in time (Zakharov, 1991). The interaction of elements at different structural levels is realized according to different schemes, hierarchical (subordination-based) in some cases, and coordination-based, in others. Such differences are manifested in the presence of two essentially different trends in the development of the colony-level ant settlements at their transition to polycaly (Fig. 6):

(1) In the first variant, the nest develops along the path of classical polycaly (PC_1, PC_2), i.e., as a subordination system with nest differentiation by size and function and with obligatory domination of the central nest. The netlike (coordination) systems appear in this variant only during the formation of permanent supracolonial structures, namely primary (PF) and secondary federations (SF_1).

(2) In the second variant, the dominant position at the colony level belongs to the pleiads, or coordination-based systems of columns inhabiting the polysectional nests. The subordination structures are realized only at the level of temporary supracolonial structures, such as coalitions. The permanent supracolonial structures, namely secondary federations SF_2, again act as coordination systems.

These variants are related to a number of important principles which determine the specific traits in the formation of ant settlements.

The classical polycaly is characterized by the following traits: differentiation of nests according to their size, design, and function into the main (permanent) and auxiliary (breeding and foraging) nests; the radial scheme of connections; spatial and functional unity of the population of all the nests within one system. One more typical characteristic of this variant is the tendency for physogastry in queens.

The polysectional nest is characterized by the equality of the columns inhabiting individual sections; such columns form coordination-based systems and are interconnected by the "each-to-each" principle. The columns are multifunctional, spatially and trophically separated from one another, and capable of independent existence.

In the proposed scheme, social types **4–6** correspond to the vector of development of subordination structures, and social types **7** and **8**, to that of coordination structures. Social types **1–3** combine the traits of both variants.

All the properties considered above are related to the size and level of organization of the ant settlement. However, these properties or parameters change quite consistently during the development of the ant community from the primary colony founded by the queen (or from the offshoot, in case of sociotomy) to the nest in its definitive state (Chudzicka, 1982: Korzuchin and Porter, 1994). It is therefore obvious that adequate comparison of settlements of different ant species can be possible only if the nests to be compared are at the same stages of their life history. To meet this condition, we have to determine what constitutes the definitive state of an ant nest.

During the development of an ant nest, not only the number of its inhabitants grows but the nest becomes more structurally complex and acquires new properties related to its normal and stable functioning (Wilson, 1971; Zakharov, 1994). In the process, the ant colony also acquires essentially new abilities: stable rearing of workers and reproductives, maintenance of the temperature regime in the nest (in species with active thermoregulation), formation of new colonies by sociotomy, etc.

The possible ways of participation of the nest inhabitants in production of new colonies correspond to two qualitative levels of development of the ant community, or levels of its maturity (Zakharov, 1991). The criterion of reaching the *first, basic level of development* is the appearance of alate reproductives. In species with polymorphic workers, the full species-specific set of worker castes or size groups usually appears at this level. At the second level of maturity, the community becomes ready for sociotomy. This is the *level of complete development* of the ant nest which, strictly speaking, should be regarded as the true definitive level. The first level can be reached with any number of queens in the nest, whereas advancement to the second level is related to polygyny or to appearance of additional gynes. Close relationship between the colony organization and the nest design can be observed at both levels (Dlussky, 1981; Zakharov, 1991).

Analysis of the spatial structure of complexes in species with different life strategies and in different landscape and cenotic situations has revealed the presence of several modal variants: uniform, radial, netlike, dispersed, and linear (Stammer, 1938; Zakharov, 1991; Tschinkel, 1993; Seima, 2008, etc.). In most cases, the settlement assumes the external configuration of the optimal habitat. Exceptions to this rule are species with the characteristic linear configuration of settlements that is preserved under different topical and synecological conditions (Goryunov, 2007). The linearity of structures in such species is connected with clear subdivision of their territories into the nesting zones (nest aggregations) and foraging zones, and with some other properties due to which a separate social type can be distinguished for such species.

Table 2. Stages of formation and development of an ant nest complex and the possibility of their realization in species of different social types

Social type	Initial stages of settlement development			Stages of development of an established complex		
	0	**1**	**2**	**3**	**3a**	**4**
	development of the first nest(s)	formation of units of the complex	extensive growth; formation of territorial continuum	structuring of the complex	stabilization of the complex	superstability; formation of federations
1	—	—	•			
2	—	—	•			
3	—	—	•			
4	—	—	—	•		
5	—	—	—	—	—	•
6	—	—	—	—	—	—
7	—	—	—	•	•	•
8	—	—	—	—	—	•
Level of complexity			**Procomplex (P-complex)**	**Mesocomplex (M-complex)**		**Hypercomplex (F-complex)**

Realization of this stage: — invariable; • situation based.

The individual features characterizing social types have different weights. Such characteristics as the mode of the primary nest founding (by independent queens or via temporary social parasitism) determine only some very special differences in the settlement development; therefore they can be reduced to variants A and B within social types **5**, **6**, and **8**. By contrast, social types **1** and **3** are united by a common feature, namely the fact that sociotomy invariably returns the colony to its basic structural level. However, the difference between the basic levels of a clan and a single colony leads to essential differences in the duration and complexity of binary division, due to which these variants should be considered as separate social types.

The Categories of State and the Possibility of Realization of Different Stages of Development

The possibility of realization of individual stages is different for different social types (Table 2) and generally increases with the complexity of the settlement. The development of a particular complex may be arrested at any stage (Fig. 1) due to insufficient resources or negative external influences. Invariable development from the founding of the primary colony to the federation level takes place only in social type 6 (linear settlements). This is why the permanent supracolonial structures formed in this variant were called the primary federation. However, successful realization of this variant in a given settlement would also require a favorable topical and synecological situation as well as some time of development under "sparing" conditions (Goryunov, 2007). The general scheme of the "life cycle" of an ant complex is shown in Fig. 1.

It may be assumed that a colony of any species can potentially reach the definitive level, i.e., such a size and structure at which sociotomy becomes possible. However, this would require favorable living conditions and sufficient time. The importance of prolonged existence under stable and favorable conditions for the development of nest complexes was demonstrated in *Myrmica* ants (Mizutani, 1981; Zakharov and Fedoseeva, 2005). In *F. exsecta*, large complexes were found to be formed only by polygynous nests (Pisarski, 1982). However, polygyny in this species is always preceded by the monogynous stage; therefore, the primary nest has to develop under highly favorable conditions for several years before it can give rise to a well-developed nest complex.

The life of the nest complex, similar to that of an individual nest, passes through the stages of foundation, growth and development, stabilization, and decline (depression, degradation, and disintegration). Sufficiently strict criteria for assessing the state of nest

Table 3. Criteria of the state of nest complexes of ants of the Formica rufa group

Criteria	States of the complex				
	A active growth	**A**[1] stabilization	**B** depression	**C** degradation	**D** disintegration
Fraction of nests with conical mounds	≥ 0.8	≥ 0.6	≤ 0.5	≤ 0.2	0
Breeding nests and offsets	Regularly occurring	Usually on periphery	Occasional	Absent	Absent
Upper to basal mound diameter ratio	≥ 0.35	≈ 0.30	0.25–0.30	≤ 0.20	≤ 0.20
Mound overgrowing, fraction of *h*	0–0.2	≤ 0.4	0.3–0.5	≥ 0.6	≥ 0.6
Calculated *d* of nest with one column (d_{1c}), cm	≥ 50	≥ 50	49–45	44–41	~40
Fraction of connected nests	0.9–0.8	0.8–0.7	0.6–0.3	0.2–0	0

complexes of ants of the Formica rufa group were proposed (Zakharov, 2003; Table 3).

The categories of development and decline should always be included in the description of an ant complex, because without them it would be impossible to estimate its level of development, further dynamics, and cenotic significance.

Correspondingly, the general description of a complex should include the name of the ant species, the social type to which the complex belongs, the stage of settlement development, and its current state (the stage of its decline). An example is: *Formica truncorum*; ***unitary pleiads 3a-A***, which means the third stage in state A, i.e., an active, stabilized mesocomplex of the wood ant *Formica truncorum*.

The Specificity And Scope of the Proposed Classification

In view of the specific goals of this work, it would be reasonable to start with limiting the number of the settlement variants to be considered. The scope of the proposed classification is restricted to non-migratory ant species with differentiation of diploid individuals into the castes of gynes and workers. The settlements of nomadic ants should probably be considered within some special classification system. This is true, first of all, of the army ants (Schneirla, 1971; Zakharov, 1989; Gotwald, 1995). It must be admitted that, in spite of the extensive literature devoted to this ecological group of ants, too many aspects of their biology remain obscure. It also appears that a separate scheme should be developed for the so-called queenless ants, which lack morphofunctional differentiation of the diploid caste; such a scheme would probably include diffuse polycaly as one of the social types.

One more variant not covered by the proposed classification, whose specificity fully manifests itself only at the population level, is that of unicolonial ants. However, the very existence of unicolonial species, with uniformly loyal individuals in all the settlements within the entire population, is highly doubtful. First, all such ants are introduced species, which are certainly affected by the "bottleneck" related phenomena and the general deregulation of their settlements as biological systems. Second, the methods of assessment of mutual loyalty in ants still need to be tested.

The distinction between multicolonial and unicolonial ants (Hölldobler and Wilson, 1977) appears theoretically feasible if these variants are regarded not as species-specific stereotypes but as certain trends or vectors manifested under specific conditions and/or at specific stages of settlement development. In particular, unification of rudimentary colonies or the formation of secondary federations as the result of raids may be considered as stepwise manifestation of unicolonial trends, and disintegration of ephemeral coalitions, as manifestation of multicolonial trends. However, the idea of the actual existence of truly unicolonial species appears unconvincing, since it contradicts the results of laboratory experiments with groups of individuals taken from one colony of the supposedly unicolonial Argentine ant *Linepithema humile*: these groups became mutually hostile after only two months of isolated rearing on different diets (Silverman and Liang, 2001). These results demonstrate once more that the only mechanism maintaining the integrity of social structures (colony, federation, unicolonial community, etc.) and loyal interactions in ants is exchange of individuals between the subsystems (Semenov and Zakharov, 1987).

This work is the first attempt at creating a unified classification of ant settlements with consideration of their development. The two main goals achieved, namely the model of development and the classification of nest complexes, already open the way for making comparable descriptions of the ant settlements with different basic structures, levels of development, and states. They provide the basis for adequate assessment of the interaction of the genetic and social aspects in the life of insect societies. Besides, they allow the researcher to re-evaluate the role of some important traits and factors in the life of ant communities (such as the number of queens) and to consider new spheres of their interaction. Such a classification provides additional instruments for a detailed study of the world of social insects and, hopefully, further improvement of the classification itself.

The classification studies of ant nest complexes also have an obvious applied value, since they create the basis for describing and monitoring ant settlements, effective control of dangerous introduced ants, protection and use of beneficial ants, and conservation of rare and endangered species.

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