===================== **REVIEW** =====================

Phenoptosis in Arthropods and Immortality of Social Insects

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Abstract—In general, there are no drastic differences in phenoptosis patterns in plant and animal organisms. However, there are some specific features characteristic for insects and other arthropods: 1) their development includes metamorphosis with different biochemical laws at consecutive developmental stages; 2) arthropods can reduce or stop development and aging when in a state of diapause or temporal cold immobility; 3) their life cycle often correlates with seasonal changes of surroundings; 4) polymorphism is widespread — conspecifics differ by their lifespans and phenoptosis features; 5) lifespan-related sexual dimorphism is common; 6) significant situational plasticity of life cycle organization is an important feature; for example, the German wasp (*Paravespula germanica*) is obligatorily univoltine in the temperate zone, while in tropical regions its lifespan increases and leads to repeated reproduction; 7) life cycles of closely related species may differ significantly, for example, in contrast to German wasp, some tropical hornets (*Vespa*) have only one reproduction period. Surprisingly, many insect species have been shown to be subjected to gradual aging and phenoptosis, like the highest mammals. However, queens of social insects and some long-lived arachnids can apparently be considered non-aging organisms. In some species, lifespan is limited to one season, while others live much longer or shorter. Cases of one-time reproduction are rather rare. Aphagia is common in insects (over 10,000 species). Cannibalism is an important mortality factor in insects as well as in spiders. In social insects, which exist only in colonies (families), the lifetime of a colony can be virtually unlimited. However, in case of some species the developmental cycle and death of a colony after its completion are predetermined. Most likely, natural selection in insects does not lengthen individual lifespan, but favors increase in reproduction efficiency based on fast succession of generations leading to increased evolvability.

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Whoever dies having reached the ultimate life limit
has no advantages compared to the one dying prematurely.
Marcus Aurelius

The one who has failed to provide for grandchildren is a parasite.
Joke

From the perspective of the evolutionary biologist, death is necessary for the development of life. Evolution is about selecting the fittest and eliminating the less fit, including parents who are bad primarily because of their gene combinations being obsolete. Furthermore, the living space has to be emptied. Of course, we can assume that death happens accidentally. But it is far more likely that such an important biological process follows certain laws. By now, many quite diverse examples supporting the latter option have appeared [1]. However, until recently, the process of programmed aging and death had no scientific term of its own. It was only in 1997 that V. P.

Skulachev re-introduced the term originally suggested by A. Weisman, "phenoptosis" (programmed death of an organism), that has was formed similarly to the term "apoptosis" (programmed cell death) [2, 3]. The author of this review, an entomologist and naturalist working with bees and wasps, encountered the problems of phenoptosis when justifying the concept of potential immortality of social insect colonies as a special form of life [4].

The purpose of this review is to examine the patterns of phenoptosis in insects, spiders, and some other arthropods with special emphasis on social insects. In the vast

army of insects, lifestyle differences are so immense that it is practically impossible to provide a comprehensive review of the diversity of phenoptosis processes in this group. This article is but the first and most difficult step in this direction.

Understanding the genetic basis of inheriting is undoubtedly one of the greatest achievements of biology. However, the discovery of genes immediately gave rise to a number of new, more complex questions. First, it is the problem of embryogenesis. How can a single fertilized (and in the case of insects − sometimes unfertilized) cell, the egg, be the basis for the development of an entire organism with differentiated but genetically identical organs? What is the mechanism of the precise apoptotic program destroying provisory and atavistic organs in the process of embryogenesis? Second, it is the problem of managing the development cycle. It is particularly acute in insects and other invertebrates that undergo a number of transformations (metamorphoses) in the course of development.

Metamorphosis can be identified as the most specific feature of insects. Larvae and adult insects are so different that they were often described as separate species while being genetically identical. How does the dragonfly larvae, a crawling under the water monster with a so-called grasping mask near the mouth, know how and when to transform into an adult insect, imago, the four-winged dragonfly? And dragonflies do not even have pupae − they are among the insects with incomplete metamorphosis (hemimetabola). Obviously, the programs of an organism's development and destruction can be recorded in the same place. Undoubtedly, the strategies of organization of phenoptosis in insects should be considered in light of the entire life cycle, which can last for decades. In this case such concepts as aging and phenoptosis cannot be applied to pre-imago stages − eggs, larvae, and pupae. However, there are exceptions. For example, some eggs and larvae can die naturally due to cannibalism or competition; this is phenoptosis resulting from the actions of other organisms. Examples of neoteny can be found among acariform and some other mites and insects [5-7]. Propagating larvae are as susceptible to phenoptosis as imago.

All invertebrates are cold-blooded (poikilothermic) organisms. It is difficult to call it a specific feature since these organisms comprise a majority in terms of both species composition and biomass. For arthropods it means that, being rather warm-blooded during the active period (the temperature of a flying hawk moth is about 39°C), during periods of rest they can − within certain limits − cool down to ambient temperature and "provide no heat for the world". A prolonged cold snap causes them to fall into a stupor (saving energy and slowing down development or aging) or into a special physiological state, diapause, when metabolism and aging slow down significantly (in case of adult organisms) [8]. Thus,

the program of phenoptosis (of course, if it does exist) can be significantly slowed by simply changing the temperature (usually combined with the shortening of daylight hours). All entomologists dealing with live insects know that many organisms that do not fall into diapause can still be kept for a long time in the refrigerator. Is cold stupor just a deceleration of the processes of development and aging? Or perhaps temperature (and other factors) cause qualitative changes in the scenario of aging (and phenoptosis)?

Animals live in adverse conditions, when it is impossible to survive in an active state, in a state of diapause. Some species of insects have a distinctive feature − superdiapause − that can last for 2-3 years. It is tempting to suggest that insects in a state of diapause are rather preserved and do not come closer to death. This is indirectly evidenced by the inhibition of enzymes responsible for aerobic oxidation of energy substrates and activation of enzymes involved in anaerobic breakup of carbohydrates. However, there are cases when one cannot speak of any preservation. For example, in case of southern butterflies *Philosamia cynthia* and cotton bollworm *Helicoverpa armigera*, diapause can start, proceed, and end in rather high temperatures, but very high mortality rate is observed [8]. Apparently, this phenomenon should be studied case by case for each species.

Diapause might be related not only to temperature decrease, but also to its increase, reduction of humidity, and other conditions incompatible with active lifestyle. Something similar can be observed also in other representatives of the animal and plant kingdoms. We should also mention the ability to wait for a long time (sometimes for years) for meeting with the host (the object of parasitism) in parasitic insects and mites [9].

Seasonality, characteristic of insects and other invertebrates, is of particular interest in context of the discussed themes. This seasonality is mostly expressed in moderate climate with cold winter, but it is also manifested in the tropics. In annual (univoltine) species, the developmental cycle is completed in one season (we will discuss them below). It would seem that in this case nature itself serves as an instrument of phenoptosis, replacing a genetic program. If insects in any case cannot survive the winter (live to an old age), then what is the reason for having such a program? However, potentially the majority of species can change from being univoltine to polyvoltine or even lose seasonality depending on circumstances.

Insects are characterized by extensive polymorphism. Depending on the circumstances, development of different individual organisms of the same species can follow alternative paths. For example, the decision on falling into winter diapause is often taken not based on a rigid genetic program (obligatory diapause), but depending on the circumstances (facultative diapause). Summer female aphids (representatives of the order Homoptera)

with their parthenogenetic reproduction and autumn sexual individuals are actually different organisms with different types of reproduction. Phenoptotic programs should also act differently for them, but as far as we know, nobody has ever studied it. Casts of social insects present even greater variety. The genome of representatives of genetically identical different casts miraculously triggers completely different life programs.

Concluding the talk about the main specific features of insects, we should reiterate that these organisms are characterized by extreme variability, and it is practically impossible to find a rule without exceptions (perhaps we can only state that there are no insects the size of a dog). Yet, it should be admitted that compared to vertebrates, and in particular to "higher" animals (birds and mammals, including humans), most insects and other invertebrates have many orders of magnitude higher fertility, and alternation of generations also occurs many times faster. Thus, they are the champions of evolvability [10]. This is always recalled in connection with the fruit fly *Drosophila*, which, due to its fast development, proved to be of such help for genetics. However, in the wild such an ability should be compensated by rather high mortality.

Insects and similar organisms, due to their high fecundity and rapid development, are particularly badly in need of well-functioning mechanisms of limiting the population size. All of us know the consequences of outbreaks of the populations of some species, such as locusts or silkworms. They can also be regarded as particular examples of phenoptosis resulting in death of a large part of the population [11]. However, the percentage of species capable of such outbreaks is extremely small. The vast majority of insects maintain the number of their populations due to various regulatory mechanisms including high mortality caused by parasites, predators, or adverse weather. However, relatively low life expectancy, namely, phenoptosis, seems to play a special role in it. It is quite frightening to imagine what would have happened if the majority of insects lived and reproduced not for weeks or months, but for years. Usually, insect parents never meet their adult offspring, do not care for them, but also do not compete with them. In the case of social insects, parents and progeny obligatorily live together, but in this case the progeny are not directly involved in reproduction. It is for insects and other rapidly reproducing animals that phenoptosis becomes particularly important.

AGING

Aging is a balanced weakening of an organism's vital functions with age leading to a gradual increase in the risk of death [12]. Ceasing of reproduction is an important stage. If death is unavoidable for each organism, then gradual aging may be not compulsory, but optional; so it is important to distinguish between the problems of phenoptosis and aging. Many arthropods age in the same manner as other animals. It has been noted that the shape of the animal survival curves presented in dimensionless variables is practically the same for all studied forms, indicating the universality of the fundamental aging mechanism [13]. We can assume that it is *reactive oxygen species* that serve as the universal agent gradually leading to the organism's death. At least, SkQ1, the antioxidant that slows aging in vertebrates, also affects *Drosophila* [12].

We have much data on the aging of insects because they are often used as a convenient laboratory object [14, 15]. For example, the large cockroach *Blaberus* can live in the laboratory for almost two years (80 weeks), but 50% of them die at the age of about one year and three months (61 weeks). By this age, most of them developed a pathology that might be called tarsal catch. The tarsus loses its mobility and sticks out at an angle to the leg. This leads to the situation when the anterior and middle pairs of legs cling to each other when the cockroach starts moving, and the insect falls [16]. Such individuals could hardly survive in the wild. This is a rather rare case, when aging leads to clear morphological changes.

Usually, senile changes are manifested in general decrease in activity and mobility. Cockroaches have a very well-developed reaction of avoidance in response to tactile stimuli. For example, in the case of young American cockroaches *Periplaneta americana*, touching the dorsal part of the abdomen always causes an escape reaction, while with age this response is lost [17, 18]. However, the cockroach's decapitation restores the response in 73% of cases. Hence, this conduct disorder was related to some age disturbances in the subesophageal ganglion or other parts of the brain affecting other functional systems [19]. Interestingly, wasp-stunners preying on cockroaches strike with their sting in the area of subesophageal ganglion to immobilize the victim [20].

Spontaneous locomotor activity seems to decrease with age in all insects. This has been repeatedly tested on *Drosophila* [21-25]. The trajectory of the fly's movement (walking) from the center of the experimental arena to its edge is usually straight in young individuals, but becomes like a sine wave with age [22]. Thus, although drosophila were observed for about a month (from the 7th to the 35th day of imago life), they demonstrated all the signs of the notoriously famous aging and senility. It is also worth noting that the basic number of eggs (usually several hundred) are laid during the first two weeks of life, although reproduction may continue for a long time (probably almost till death). Fertility and lifespan greatly depend on temperature. Usually, the female does not live longer than two months, but under certain conditions this period may be extended more than twice (according to an internet source – up to 153 days).

Drosophila also serves as a model object for studying genetic aspects of aging and longevity. Generally speak-

ing, any changes in metabolism affect the entire functioning of the organism, including life expectancy and aging. In each case, one needs to consider the mechanism of a gene's effect on the specific phenoptotic mechanism. This task goes far beyond our competence. But we can still provide several examples. There are genetically different lines of drosophila with different lifespans and different specific features of aging. It has been shown that the rate of attenuation of spontaneous locomotion changes in some transgenic flies. A mutation has been found that can slow the development of behavioral signs of aging and affects the lifespan [25]. It was shown recently that GADD45 gene overexpression in response to DNA damage in the drosophila nervous system leads to a significant increase (up to 75%) of the lifespan [26, 27].

Thus, there is no doubt that most insects age gradually, and at least externally this process is not principally different from that observed in other animals. The fact that usually different groups of organisms are considered together in gerontological studies is an indirect confirmation of this preliminary conclusion. Gradual extinction is the most complex case in the problem of phenoptosis. It can result from both a balanced evolutional program and from random events (patterns of a higher order that do not fit into our understanding of cause–effect relationships in the existence of living matter).

When do insects, spiders, and other invertebrates live to old age in the wild? What is the role of non-reproducing individuals in a population? These are fundamental questions. Depending on the answers, we will have either to assume that the aging process is not affected by natural selection or to accept that some qualities increasing the success of the offspring are selected (it is clear that ultimately it is not the number of the offspring, but their success in reproduction that is important, and the latter, for example, can be provided by the cost of life of the individual who has already ceased to lay eggs). In temperate latitudes, one can meet a multitude of tattered insects (butterflies, grasshoppers, dragonflies, etc.) with reduced mobility. These are representatives of the species in which imago cannot live through winter under any circumstances. Many of them will die in the cold stupor, "will go under the snow". It looks like they are the old individuals that are of no interest for natural selection. If such an insect (or a spider) is taken into the warmth and fed, in any case its lifespan will increase only slightly. This fact indicates the existence of the program of slow phenoptosis or, conversely, the absence of a program of life maintenance after a certain point. Then there should be no fundamental differences between the inhabitants of the temperate latitudes and the tropics. At some point, we could observe the female jumping spider (5 mm in size) caught in November in Tunis. She was kept in a cage at room temperature. Soon she built a cocoon, laid eggs and for some time was protecting the cocoon and the offspring, which for some reason died by January (cannibalism

might be one of the reasons although we have no proofs). Usually spiders do not eat when protecting offspring [28]. Nevertheless, in February our jumping spider undoubtedly was catching fruit flies and had normal motor activity. However, she stopped eating in the beginning of March, stopped moving about a week later, and died in three days. Perhaps, this general picture of gradual extinction might fit many animals.

Are there any insects that do not grow old? In English, this phenomenon is called "negligible senescence" [29]. Non-aging animals have no significant correlation between their age and death probability, or, to be more precise, this probability is negligible. Non-aging animals live long (sometimes for hundreds of years), reproduce, and grow for their entire lifetime (perhaps, it is becoming unusually large for their ecological niche size that ultimately leads them to death). These animals are few, but they are of fundamental importance as they provide an example of alternative ways of phenoptosis without gradual aging of an organism [1, 30]. So, if an organism can create itself out of a single cell in the course of embryogenesis, it can also sustain itself for at least several hundred years in ontogenesis. Of invertebrates, certain clams, urchins, and some other organisms are non-aging animals but not arthropods. Formation of the final list belongs to the future as information on the concrete non-aging species is scattered across different sources. However, we need to note two important moments. First, most known to us today non-aging long-lived organisms (both vertebrates and invertebrates) live in the water or are closely connected to it (Galapagos tortoise is an indubitable exception). Apparently, in the water habitat conditions are more stable than on the land. Secondly, taxonomically related species differ radically in the specifics of aging and life expectancy [1]. The problem of conservatism and variability of the paths of development of living organisms (in terms of not only phenoptosis, but also other key organizational principles) could be the subject of a separate study.

Social insects (which will be discussed below) occupy a special place among insects and in general in the animal world. Social insects live in colonies, which have one or several queens laying eggs and many so-called workers. In most species, the queens live for many years (in case of some termites up to 30 years, and leaf-cutting ants *Atta* — for about 20 years) and lay eggs during their entire lifetime [31, 32]. Their metabolism is fundamentally different from the workers, although they are genetically identical (except for higher termites). Apparently, the queens should be classified as non-aging. The queens of the honeybee *Apis mellifera* (which live for 5-6 years in contrast to worker bees living for about a month) were shown to manifest very high activity of the gene of vitellogenin, the yolk glycoprotein synthesized in the cells of the fat body. When allocated into the hemolymph, the vitellogenin protein is absorbed by the developing

oocytes. The fact that vitellogenin protects the bee queens against paraquat treatment causing the formation of reactive oxygen species indicates that this protein takes the brunt of oxidative stress, acting as an antioxidant and contributing to the increase in lifespan [15, 33, 34].

How do queens die? In the colony of honeybees, the worker bees do not allow the queen to grow decrepit; they kill her and replace her by a new one as soon as the old queen starts laying fewer eggs and her secretion of pheromones changes (possibly because of running out of sperm). This is an example of indirect behavior-caused phenoptosis [35]. In the case of leaf-cutting ants, the queen lives in a colony until its natural death, which is followed by the death of the entire family. We have no data on the specifics of the queen's aging (including its duration).

We would hardly find non-aging species among single insects. Adult insects in their chitinous shells do not really grow (although some increase in size is possible), while non-aging animals usually grow through their entire lifetime. Adult insects (with the exception of silverfish and some mayflies) do not molt, but the junction of sclerites has some webbed parts that can be stretched (as the abdomen of the queen of social insects). However, it does not protect against age-related accumulation of damages of skeleton, limbs, and especially wings. This is probably not even related to the problems of growth, but to the evolutionary strategy of insects characterized by high fertility combined with high mortality rate, as well as distinct seasonality of life cycles in most habitats. Here, natural selection favored not the increase in lifespan, but the increase in the efficiency of reproduction during the limited favorable time.

However, there are numerous examples of adult insects living for several years while repeatedly reproducing and successfully living through winters (e.g. large ground beetles, *Carabus*, *Calosoma*). It can happen that within the same genus, imago forms of some representatives live for one season, while others — for several seasons. Quite astonishingly, the lifespan can vary depending on the situation. For example, in the case of the tundra-dwelling ground beetle *Carabus nitens*, the lifespan of the beetle increases in the northern populations — it gains the ability for multiple reproduction during several seasons after winter. As a result, the number of individuals in the northern populations remains high [36]. There are no data on the specifics of these beetles' aging and dying.

To some degree, insect larvae that sometimes develop for many years and even decades can be considered non-aging organisms. The case of 17-year-old cicadas (*Magicicada septendecim*) is rather well known, and a closely related species develops for 13 years. Development of the larvae of longhorn beetles that feed on wood (usually affected by fungus) can last for decades under adverse conditions. Cases have been described when adult beetles suddenly came out of dry wood furni-

ture or out of the walls of log houses. They were dwarf-like due to poor nutrition [37]. Larvae (with the exception of neoteny cases) do not reproduce and cannot be programmed to die. However, the conditions of larval development affect the subsequent life and death of the imago. In addition, larvae can affect the reproduction of genes in their "kinsmen". Long-living larvae are worth studying from the biochemical perspective, since they are not exposed to reactive oxygen species for decades, i.e. they have some protective mechanisms. It would be interesting to try to artificially trigger these mechanisms in an adult insect.

Non-aging species can also be found among spiders and mites. Tarantulas (Theraphosidae of mygalomorph spiders) can live more than 10 years; the females periodically molt during their entire lifetime, keeping the ability to restore lost limbs; they reproduce up to old age. Molting occurs once or twice a year after each mating period. A *Eurypelma californica* female lived in captivity for 20 years, and a male for 13 years [38]. All the molting imago of arthropods — at least until the last molting — can be called non-aging. Other spiders, having reached sexual maturity, do not molt; many of them do not live for more than a year, and some live for several years.

Bloodsucking argasids (Argasidae ticks) can fast for more than 10 years, and in the laboratory their lifespan can reach 25 years. The females repeatedly feed on blood and repeatedly lay eggs in relatively small portions. These are the signs of non-aging animals. It is not entirely clear whether argasids can be considered non-aging organisms. However, there is no doubt that they slow aging when fasting. Imago forms of the infamous Ixodidae, close relatives of argasids, eat and lay eggs only once [9]. This is a typical example of phenoptosis associated with reproduction.

Let us now consider some examples of different types of phenoptosis in insects and spiders.

APHAGIA

Aphagia of imago forms is characteristic of many species of insects [35]. In these cases, the "energy center of gravity" of the life cycle is shifted to the larval stages. Fasting allows in some cases accelerated reproduction and increase in its efficiency, reducing the risk of the imago dying while leaving no offspring. It is clear that lack of food inevitably leads to death. Thus, aphagia (inability to replenish energy reserves) can be considered as a special type of phenoptosis (according to the classification by Libertini [35], obligatory and fast phenoptosis). Is it starvation that always causes death of aphags? What biochemical processes accompany individual death in each case? We have no data on these issues. Undoubtedly, death of aphags comes after the completion of the period (albeit short) of reproduction. It is possible that the adult

insects possess some stock of nutrients/energy to complete this vital task, and their death results not from starvation *per se*, but is determined by some additional phenoptotic mechanisms. There are cases of similar dying at the end of the life cycle — these animals, being quite capable of eating, give up food some time before death.

Mayflies (order Ephemeroptera with more than 2600 species) are the most popular example of aphags. In general, they cannot be considered short-lived insects as their larvae develop in water for 2-3 years. This is what I. I. Metchnikow writes about mayflies: "We cannot doubt the existence of natural death in the animal world, but it is certainly a rather rare case. Wonderful insects known as mayflies, are the best example of it... The entire life and organization of adult mayflies indicates that here we are dealing with natural death. And it comes not because of lack of food for these insects or because they cannot find something necessary for their existence, but because they are born unviable, devoid of organs absolutely crucial for life". Having completed a thorough microscopic examination of dead mayflies, he concludes: "Brain, nerve centers, muscles and other organs show no signs of phagocyte-mediated destruction, which is believed to be a general rule of senile degeneration" [39]. So what is the exact reason of mayflies' death? Is it really starvation? Note, however, that some mayflies do not live for several hours, but longer — for a day or two; when the weather does not favor flying, they sit still and can live up to 10 days [40], and according to some sources perhaps even longer. Apparently, it is participation in the mating flight, which happens synchronously in each mayfly species (it is an essential feature of their biology), that serves as the main signal for the completion of the life program (and acute phenoptosis). For males, it does not matter, whether they managed to mate, all of them in any case die. With regard to females, we have no data, but there can hardly be remaining celibate females as mayflies usually have a large excess of males.

Aphags also include many stoneflies (order Plecoptera, ~2000 species), many caddisflies (order Trichoptera, ~10,000 species), representatives of the small order Megaloptera, horntails (Siricidae of Symphyta: Hymenoptera), some beetles and butterflies of different families, and gadflies (a group embracing four families of parasitic flies). In some species we observe facultative aphagia, the ability to lay eggs without eating, although it reduces fertility.

There are also cases of larval aphagia. For example, the first age larva of parasitic blister beetles (Meloidae) and alderflies (Sialidae) do not eat. Typically, spider nymphs molt for the next age without additional eating. Pre-imaginal aphagia has nothing to do with phenoptosis, since it is a stage of development, but not its completion. However, if there are general patterns of the organism's development including aphagia as part of a life cycle, then perhaps some biochemical features will be common for

both larval and imaginal aphagia. Or, on the contrary, we will discover fundamental differences, which is not less interesting.

Bagworm moths (Psychidae) provide the most striking example of phenoptosis associated with aphagia [41]. Caterpillars of bagworm moths live in small cases, very similar to those of caddis. In this case the caterpillar pupates, and it is here that the adult butterfly is born. Males have wings and actively search for females. Females have no wings; they do not leave their cases, just put out the tip of their abdomen for mating. Then the female lays all the eggs and quickly dies. Young caterpillars leave the maternal case and construct the cases of their own, completing the construction as they grow. Giving up mating presents the extreme degree of shortening of adult life. The bagworm moth (*Solenobia triquetrella = Dahlica triquetrella*) reproduces parthenogenetically. The female is born from a pupa, immediately lays eggs, and dies. Its life lasts only for several minutes. However, it is not that simple; there are some speculations that this moth also has a tetraploid parthenogenetic line [42]; then it is a case of obligate vegetative propagation combined with phenoptosis.

Thus, among insects we find thousands of examples of phenoptosis resulting from innate aphagia. This feature is characteristic of insects; it is combined with the presence of metamorphosis, since giving up food at imago stage is possible solely due to the supply of nutrients accumulated by larvae. Aphagia can also start at the end of life. These cases are associated with taking care of offspring (e.g. among spiders) and will be discussed below.

DEATH AFTER REPRODUCTION. COMPLETION OF THE LIFE CYCLE

There are many examples when the process of single reproduction triggers the program of obligatory phenoptosis, both in the plant (all annual flowering species) and animal kingdoms. The death of thale cress (*Arabidopsis*) after flowering and spawning of some salmonids connected to profound hormonal changes incompatible with life, are the most well-known and beautiful cases. Octopus provides an example of this phenomenon among the invertebrates [43, 44]. In all the given examples we know the biochemical mechanism of phenoptosis, and it can be controlled. For instance, the female *Octopus hummalincki* normally dies shortly after the birth of offspring, but if the so-called optical glands are removed, it turns from a single-mating into multiple-mating creature. We do not know of any cases of phenoptotic mechanism studied as thoroughly in arthropods. However, it is arthropods (in contrast to vertebrates) that often reproduce only once and live only for one season. We have already mentioned ticks (Ixodidae) [9]. Female ticks can wait for the provider for up to 2 years, but once she has satiated with

blood, increasing its weight 80-120 times, she lays eggs and dies. The engorged female practically loses mobility. She falls on the ground, lays the entire portion of mature eggs (up to 20,000!) and looks completely dead, although she continues to live for several days longer (at least, that was the case with *Dermacentor reticulatus*, which we studied). This monstrous increase in size does not cause death by itself. Nymphs, when eating, increase their weight 20-100 times, and it is required for their further development. However, the process of phenoptosis is probably switched on after laying eggs. Let us recall that other ticks (e.g. Argasidae) do not manifest this phenomenon.

The examples of phenoptosis when mother's death benefits the offspring (i.e. increases the reproductive success of the mother) seem to be the most logical, since they can be easily explained by natural selection. Females of some species of spiders build a rather perfect nest for their offspring and immure themselves in it (together with the eggs). In the case of *Diaea ergandros*, a spider from the family Thomisidae (they run sideways like crabs), the female lives in the nest together with its offspring for several months, catches prey for them, and then dies and serves as food for the offspring. The female can take other spiderlings into its own brood (up to ~44% of "foster children"), but it catches for them smaller prey and these spiderlings grow more slowly. Before the female's death, her ovaries once again start to grow and yolk-rich cells are formed. It serves one goal — for the mother's corpse to be more nutritious and tasty for small spiderlings: "all the best — to the children" [45].

And what about insects, the main subject of this review? Oddly enough, there are not so many clear examples of phenoptosis triggered by laying eggs. This happens in the group of aphags, but even here the laying of eggs often takes a long time. In case of the already mentioned 17-year-old cicada and its relatives, death happens after mating due to a sudden dehydration of the organism — in males shortly after swarming, and in females — some time after laying eggs. And phenoptosis is a prerequisite for the existence of the population [11].

We can speak about death after reproduction with respect to insects with strictly annual developmental cycle. They are usually characterized by multiple reproduction, which takes a period of time when the female lays eggs (it usually makes a few clutches, rarely lays eggs one at a time). We have already spoken about these types in the section "Aging". Phenoptosis after reproduction is in this case obligatory, but not acute. It is rather the completion of the life cycle (which includes reproduction) than specific phenoptosis following the single reproduction. The point is that the majority of species univoltine in the north of their areal, become bi- and polyvoltine in the south, where it is warmer. Hence, most cases can be attributed to slow aging ending in death. This is the most complex aspect of the problem of phenoptosis. Some bugs (order Hemiptera) are often used as an example of strict-

ly univoltine species. Let us consider the predatory bug *Picromerus bidens* of Pentatomidae, which became the subject of studies because it was used in the biomethod of fighting against leaf-eating pests. It lives from North Africa to 64° of north latitude in Europe and America. In case of this bug, it is eggs (and not imago as in other Pentatomidae) that overwinter. Adult individuals appear in June or August, but females start laying eggs in late August or September, waiting for the short daylight hours. However, if the bugs are kept with long-light days, they start laying eggs, but with a delay of 30-53 days. The eggs start to develop only when they are first cooled. However, individual eggs in the clutches develop without it. Moreover, there is evidence that adult bugs can be found in spring — sporadic individuals that had not mated in autumn could overwinter [46, 47]. These data, as well as the above-discussed information on ground beetles indicate that life cycles and the specifics of insects wintering are highly variable even within the same species and much more so among different, though closely related species of insects. Below we will provide more such examples when speaking about social insects. It is likely (although this assumption cannot be rigorously proved) that all adaptations to living in temperate climate with cold winter are secondary in invertebrates because they originally appeared in warm tropical areas. Hence such a variety of types of wintering. Accordingly, seasonality is not a constitutional parameter determining phenoptosis in insects and other invertebrates — natives of the tropics.

So, what is written in the genetic program of the development of picromerus? All the parameters of the life cycle vary. However, the period of mating and egg-laying is just one in all individuals. The only question is its duration. Can we assume that phenoptosis in bugs results from reproduction? This is partly true. However, the observed pattern is also similar in its time scale to slow phenoptosis of higher animals and humans. Having completed the reproduction period, male and female bedbugs live for about a month longer. It seems completely redundant from the perspective of natural selection. But, as our elders say, "you won't die without death". A similar picture of the completion of the life cycle can be observed in many insects. For example, a carpenter bee builds a nest (gnaws it in wood) during the summer season; this nest has a due number of cells, and the bee lays an egg in each cell. Having completed the last cell, the mother bee sits at the entrance and guards the nest. It lives until autumn, but can never overwinter.

It should be noted that the completion of the life cycle is not always linked to seasonality. The vast majority of insect species inhabit the tropics, and at least some of them could live and reproduce for years. However, it hardly ever happens. In temperate latitudes, many species produce several generations during one summer. Lifespan and reproductive potential are always balanced. Of course, generations can overlap, but usually parents die

by the time of the birth of offspring. The existence of elderly non-reproducing parents can be justified when they distract predators from their young offspring, often at the cost of their life.

In many species males live much shorter times than females. In some cases it is mating that leads to the male's death. Drones, being born in summer, can overwinter (worker bees do not always expel drones). However, a drone dies shortly after mating, especially if its genitals came off (it happens if the insect was the last one among the drones mating with the queen during its mating season). We have no information on the role of celibacy in extending the lifespan of males from different species. Clearly, in many cases males are physiologically incapable of prolonged life and die in their due time (of age?) regardless of mating. It was reported that non-mating males of black widow *Latrodectus hasselti* still die within a short time [48].

CANNIBALISM

Cannibalism is found in various animals. For example, the so-called cainism is rather common among predatory birds, when only one of two chicks survives. However, this is not a meaningless sacrifice, but a way to improve the reliability of reproduction. Cannibalism is perhaps more widespread among arthropods than among representatives of other taxa of the animal kingdom. Let us continue our talk about spiders. Journalists formed the opinion that the female spider necessarily eats her mate. This is obviously not true, but there is no smoke without a fire. When the female does not need the male, or when it became too old and cannot quickly retreat, the female can eat it – for that matter, as any other representative of the same or different species. But in case of one of the species of Australian black widow *Latrodectus hasselti*, the males literally "climb in the teeth" of their partner, opening their abdomen. While the female chews its abdomen, the male has enough time to fulfill its mission. Thus, the black widow justifies its name, although it is not entirely true, since the female only injures the male and does not eat it completely. Let us recall that spiders transmit the sperm via modified limbs (pedipalps) located on the caphalothorax, so they do not need the abdomen for mating. We have to say though that mating is possible also without cannibalism, which is observed in 65% of cases.

Male spiders have two pedipalps into which they place the sperm. If the spider dies after the first mating, the content of only one pedipalp is used. But those males that did not die of wound after the first mating are favored by the females. Males found a very interesting way to improve their reproductive success. A large percentage of males form a constriction in the middle of the abdomen (due to muscular efforts) during the courtship, which lasts for hours. By this they both attract females and increase their resistance to injuries, since the female chews the back of the abdomen, and the organs in the front part are left intact. This increases the chances to survive until the second mating. However, this does not change the essential type of phenoptosis. After mating, the male dies of wounds. However, the lifespan of males that failed to mate is also rather short. In another species of black widow, *L. hesperus*, sexual cannibalism is rare (about 2% of cases), and the males do not try to sacrifice themselves. Accordingly, there are no constrictions on the abdomen of the males of this species [48].

Mantises are often mentioned in connection with cannibalism among insects. Their males can complete copulation without a head; this is even better because the central nervous system contains restraining centers (think of cockroaches with their avoidance response restored by decapitation). However, the possibility does not mean the need. Usually there is no cannibalism, and only an old weakened male, who in any case would not be able to mate, allows to be eaten himself. In such a way the male pays alimony to its offspring by the substances of its own body, a beautiful example of harmony in nature [49]. By the way, a hungry female can eat its own ootheca – we had a chance to observe it in the laboratory. However, the programmed death of an individual does not always involve some direct utilization of the dead organism (the way it happens with the dead drone).

Sexual, as well as the usual fratricidal cannibalism, can be considered as an adaptive strategy. In these cases an excessive number of individuals are born; they will not be allowed to breed, but will benefit the species as a whole by being eaten by their blood relatives. That is why such a strategy can be supported by natural selection. Cannibalism takes place both among adult individuals and among larvae. This is a type of phenoptosis active in immature stages.

Normally, mantises of both sexes are scattered across the territory and do not eat each other, they meet only during mating. But if they are not given an opportunity to disperse (as it sometimes happens when they are kept in cages), brothers and sisters in the litter will start killing each other until the density of the population is reduced to an acceptable limit. As a result, the winners will receive the benefit in the form of food, but those eliminated from reproduction killed individuals will also pass their genes to offspring – their nephews and nieces. This is far more beneficial than everybody's death from overcrowding. Similar events can also take place among other predatory insects and spiders.

Caterpillars of cotton bollworm *Helicoverpa armigera* provide another example of terrible cannibals. If two individuals happen to be within each other's reach, one will surely eat another, even with excess of food. This helps to reduce the density of the population and to improve the efficiency of nutrition at the population level. Herbivorous caterpillars do not have enough protein, and

due to cannibalism, they get it "off the shelf". In this case, fertility is clearly excessive. Females lay far more eggs than the allowable number of butterflies that could survive in the given conditions.

In case of parasitoid riders (parasitic wasps), one host can provide the development of a limited number of individual riders. The excessive numbers of parasitoid larvae die at early stages in the course of re-infestation so as to provide the development of the remaining larvae. This is surely an adaptive mechanism of phenoptosis acquired in the course of evolution.

Social insects perfected the idea of planned non-breeding. They have specific features that cannot be found in any other group of organisms. Potential immortality has become a "free app" to the social lifestyle (definition will be given below).

So far we have talked about organisms programmed for mortality, and only the mechanism of phenoptosis presented the problem to be solved. But is it possible to imagine biological immortality? Let us assume that the conditions are stable enough and the resources are excessive. Is it possible to somehow cancel elimination of the unfit, reduce reproduction to the size of accidental death, and live until death not from some internal cause, but from an accident/disaster? Changes in the habitat conditions (which cannot remain eternally constant) can also be viewed as a disaster. It is clear that absolute immortality is unattainable. However, the issues of infinity of spirit and matter are far beyond biology and, according to the personal opinion of the author, go well beyond the limits of the human mind. As for biological immortality, this is the mechanism of life that does not include transition to death as an inevitable stage.

Perhaps prokaryotic bacteria are the closest to immortality in its biological understanding (they have no clearly formed nucleus and some organelles characteristic for multicellular eukaryotes); bacteria divide into identical halves, and one cannot tell which one is the successor of the original organism — in fact, it is the original organism, only in two copies. Errors in reproduction, though very important as the only mechanism of variability required for evolution, are not inherent for the process (this is not the case in eukaryotes, the holders of real nuclei in the cells). Theoretically, a bacterial cell can divide forever. In this case, there is no fundamental difference between individual and species immortality. Other vegetatively propagating organisms, primarily plants, can also be considered immortal. However, they pay for this immortality with the reduction (or absence) of genetic diversity [1].

Other examples of immortality can be found on a qualitatively different level of life, among social (or eusocial) animals. Here the developmental cycle includes sexual reproduction, and immortality is combined with the increase in genetic diversity without catastrophic increase in population density.

SOCIAL INSECTS

Eusociality (or true social lifestyle) is found almost exclusively among insects, a rather clearly defined group (according to modern concepts, superclass) of arthropods. Nothing similar was found in other invertebrates. Oddly enough, another example can be found in mammals, perhaps the most remote from insects group of the animal kingdom. We are talking about the naked mole rat (*Heterocephalus glaber*). But this is rather a surprising deviation than the main path of the development of mammals.

Eusociality is a special form of life in which individual organisms cannot exist separately, but only in a common nest in a physiologically coordinated group united by kinship ties, in the family. Following English-speaking authors, a family is called a colony. This is a prime example of an unacceptable use of the term as it is already taken and is used when referring to joint living of equal individuals (sea birds, aphids, solitary bees digging burrows near each other). However, it is difficult to argue with the established practice, even if it is illogical.

Only one or several females is involved in reproduction in a colony, and other organisms, the so-called workers, are unable to reproduce. It is a colony (sometimes called a "superorganism"), and not an individual that is the unit of life. In contrast to the colony of independent animals, individuals in a colony of social insects are not equal: in this case, there is separation of functions. Here are the main characteristics of eusociality clearly formulated by Edward Wilson: 1) a group of individuals living together and cooperating for various vital functions; 2) overlapping of at least two generations; 3) separation of reproductive functions — the presence of reproducing and non-reproducing individuals (the so-called workers) in the colony [50]. From a biological perspective, this is the highest level of sociality (read: development of living matter), surpassing even the one observed in human society. We still do not have asexual workers; however, one should not confuse biological and cultural aspects of social organization. What do we mean by cultural aspect? Let us take ants as an example (they can only be social). One family of ants can remain unchanged for hundreds of years, theoretically — for an unlimited time. However, during this time, all the inhabitants, including egg-laying females (the queens), are repeatedly replaced. That is, the family becomes genetically different. However, structurally and functionally it remains the same. Such a state we will also regard as a continuation of life. Similar patterns are observed in human society: individuals are replaced, but the cultural and material basis of the system needed for survival and production of offspring remains. It is no secret that we have long been evolving differently than animals in the wild. There is no need to repeat the truism that without a special education among other people, a person will not be able to use the achievements of

civilization, and humans as a species will dramatically reduce their number and habitat, and possibly altogether die out.

Adaptability of the existence of non-breeding individuals is the main feature of eusociality. This happens also in species without eusociality when an individual cares for offspring in the post-reproductive period, contributing to the maintenance of its own genes due to already produced offspring. Preservation of cultural traditions can be the second, less obvious function. Nobody, of course, prevents the animals in the prime of life from performing this function, but it is important that non-breeding individuals are also fit for this role. In the majority of animals, it is senile individuals who have already produced offspring that are involved in it. Here comes the natural selection of the second order. The genes of the individuals who could become the bearers of cultural traditions or increase their adaptability due to "clever" behavior are favored. Perhaps we should even recognize that evolution of culture, though not contrary to the laws of genetic evolution, cannot be described by these laws, and there are specific laws of cultural evolution. For example, we can assume that in the same gene pool, different conditions (which are accidental) can lead to different social structures in a colony or population, which will later evolve independently. "Skulachev hares" present here an intermediate option (forgive me an involuntary pun, an allusion to Skulachev ions). If in the case of young animals selection primarily favors fertility (other physiological parameters do not affect survival rate), then in old, but still capable of reproduction individuals, selection favors "cleverness", ability to survive in spite of decreasing vital functions [1].

Giving up direct reproduction throughout the entire life cycle is the next stage. This idea was evolutionarily implemented by eusocial animals, insects. Here we already speak not about the secondary specialization of senile individuals − bearers of culture in post-reproductive period, but about the creation of a separate caste of wise and skillful "elders" from birth, who would be incapable of reproduction, but useful for gene reproduction due to their other qualities. Such a division into castes is only possible with a special mechanism of gene transfer, the one characteristic for social animals. This mechanism can be compared to activation energy in chemical reactions.

Some time ago, we witnessed hot discussions on the mechanism of natural selection favoring the existence of non-breeding individuals. Workers do not mate, do not lay eggs, but take care of the offspring of others. How could such an "altruism" develop? Actually, there is no more altruism in such a behavior than in the situation when the male allows being eaten by its female partner when it can no longer mate, or when a person bequeaths his corpse for research in the anatomical theater. The fact is that workers raise their blood relatives, often sisters,

with whom they share many genes. Thus, the workers transmit their genes to offspring and − from an evolutionary perspective − reproduce, although "by proxy". The same type of questions arose repeatedly also when discussing evolutionary mechanisms of the formation of phenoptosis. How does natural selection select those who no longer propagate, but, on the contrary, die? However, these problems can be easily solved if we extend the evaluation of individual fitness from only its own life to the life of its relatives, at least its offspring, and better − the entire population [51]. We risk assuming that the concepts of individual and group selection as the models of our ideas can easily convert into each other (if we evaluate individual fitness taking into account other individuals bearing common genes). For example, how can we translate a geocentric system of planetary motion into a heliocentric one (although it is obvious that the geocentric system is extremely inconvenient). However, the principles of evolution leading to increased evolvability are described in a completely different way [51]. Here natural selection makes a step back so that later to make two steps forward. It is impossible to explain this phenomenon within the traditional concepts. Increase in evolvability seems to play an important role in the development of insects, also social, as we will see below. Apparently, this is the reason for giving up potential immortality in many species of social insects.

The life of a worker has less value for social insects than that of a queen. The bees sting when protecting the nest. The sting usually gets stuck in the skin of vertebrates and comes off together with the poison gland; as a result, the bee quickly dies. The same happens with stinging harvester ants of the genus *Pogonomyrmex*. Other stinging insects, wasps (Vespidae) and bumblebees (*Bombus*, Apidae) do not leave their stings, but attacking the enemy, especially the vertebrates, is always connected with increased risk of death. In the case of bumblebees, the insects sometimes die not because they cannot pull the sting out of the vertebrate skin, but because the attacking bumblebee grabs the enemy with its jaws so hard, that it can be shaken off only if its head is torn off. This is the example of individual phenoptosis associated with behavior. Phenoptosis of workers can be compared to apoptosis in a multicellular organism. However, workers possess complex behavior and some free will. Aggressiveness of the colony defenders directly depends on its size. One can approach the paper nest of wasps and even touch it at the initial stages of development, while the colony has only two-three workers (which perform the functions of builders, foragers, and nurses rather than guards). But when the nest reaches the size of a soccer ball, it is better not to approach it closer than 2 m. The life of each worker is more valuable in a small colony than in a large one, and the attack of a pair of workers is far less effective than that of dozens or hundreds. Defenders adaptively change their behavior depending on the condi-

tions. But even in the case of a large colony, wasp guards first hover around the potential enemy, swoop at him, hit with their heads, and only then sting. So, even when being ready to sacrifice their lives in case of need, wasps still try to survive. The same is true for other insects − bumble-bees and bees. Aggressiveness of a bee colony also strongly depends on race; here we can talk about genetic determination of the specifics of phenoptosis.

Termites have a special morphologically different caste of soldiers. They can neither reproduce nor eat. Their only function is to protect the nest, even at the cost of their lives. Sometimes a caste of large workers with powerful jaws typical for some species of ants is also called soldiers, but their specialization is not as narrow: they can eat and care for the brood. In the case of termites, situations happen when the nest is broken, and then the construction workers repair the nest while the soldiers protect the nest from the outside. When the work is completed, the soldiers remain outside and inevitably die. This is a rather peculiar case of phenoptosis associated with behavior. Soldiers of many Rhinotermitidae and higher termites (Termitidae) have a huge frontal gland secreting a sticky substance that helps to glue enemies comparable in size with the soldiers. The soldiers also are glued to it and die, having fulfilled their mission. Representatives of nose termites (Nasutitermitinae) have a long rostrum on their heads, which allows spraying the enemy with a protective secretion without suffering from it themselves [52]. But it is bomb-soldiers that are perhaps the most spectacular kamikaze in the animal world. Soldiers of *Globitermes sulphureus*, Termitidae, have both powerful jaws and a gland with sticky secretion. The soldier first grips into the enemy with its jaws, and then, because of excessive efforts, the soldier's body is torn, it seems to explode. As a result, the enemy is effectively glued. These protective mechanisms are primarily directed against ants [53]. Oster and Wilson [54] called the globitermes soldiers "walking chemical bombs". Defensive behavior of *Neocapritermes taracua* termites from higher termites is even more fascinating (this case is discussed in the book by Skulachev et al. [1]). In this species, old workers with blunt jaws start functioning as soldiers. Generally speaking, this problem could be resolved if representatives of this species repeatedly molted, as happens with many termites. However, the life of *Neocapritermes* is different. The enzyme phenol oxidase of hemocyanin type is accumulated in the worker's body with age; it shines through the abdomen as two blue spots. When the enemy cracks the termite, the enzyme combined with the secretion of the salivary glands forms a poisonous explosive compound. As a result, both the termite and the enemy die [55]. We cannot but quote the book [1]: "Lonely or extremely poor people often save money for their own funeral. The termite-worker saves the blue enzyme throughout its entire life so that to die as a hero for its termitary". Similar "explosive" behavior was previously dis-

covered also in ant runners *Camponotus saundersi* [56]. Thus, workers and soldiers, which, in a way, have already sacrificed their lives by giving up reproduction, sacrifice it for the second time.

A viable colony is needed for the mechanism of reproduction of asexual individuals to work; and it is colony that is the unit of species existence in the case of eusocial organisms. In the simplest case, a colony consists of one fertilized female and her offspring, and the problems of colony development can be compared to the problems of embryogenesis. What is the reason of some offspring developing into workers (sometimes belonging to several casts) comparable to somatic cells in the organs of a multicellular organism, while others − into reproducing individuals analogous to sexual cells? Conditions of individual development play an important role in this process. The queen excretes pheromones that suppress ovarian development in workers. In the absence of the queen, workers start laying unfertilized eggs. In the case of primitive species, direct contacts between individuals leading to the establishment of dominant−submissive relationships play an important role. For example, in the case of polistine wasps, several queens, usually sisters, can work together when building a nest. However, later only one of them gets into dominating position and lays eggs, while the others start functioning as workers. Basically it is equivalent to the situation when some individuals sacrifice their lives in cannibalism so as to increase the number of their blood relatives. However, there is an important difference: a subordinate female can get into a dominating position when the situation changes. Workers are divided into specialized groups according to the needs of the colony; individual specialization can change depending on age and situation. This is an example of a far more flexible organization than that of a multicellular organism with differentiated organs.

Let us repeat that even though the types of social organization of a colony are extremely diverse, it always develops, lives, and reproduces as one unit. All the colony queens and workers can be repeatedly replaced, but the nest, some traditions, and the territory protected against representatives of other colonies will remain; in the case of terrestrial insects (e.g. ants), roads leading to the local areas of food supplies remain for many years. In general, this can be compared to the life of an organism, whose reproductive cells undergo genetic changes with time. Geneticist will consider it as a different (though related) organism (the old one is, in a way, dead), but zoologists and historians will see it as basically the same individual: it looks the same, exists in the same space. In terms of structure, the insect colony can be compared to an organism, and from genetic perspective − to a population. Thus, a colony is a superorganism with certain features of a population. That is why, when considering colonies of social insects, we will discuss not genetic, but rather morphological and functional as well as cultural immortality.

However, it is important to remember that queens are replaced not in all species of social insects, whose colonies do not change genetically during their lifetime. In this case, a colony can be compared to a usual organism that dies at its due time.

In contrast to a multicellular organism, a colony has no single coordination center similar to the brain (if, of course, brain can be considered as such a center). Sometimes people say that the queen controls the colony. This is not true. The queen and the workers affect each other, and each element is essential, but not sufficient — similar to cooperation of organs in our body. Perhaps, the working bees have even greater freedom of choice than the queen does, who can only lay eggs and eat throughout her entire lifetime. We have already discussed that in a colony of honeybees, it is working bees that hatch a new queen and kill the old one when she gets old (or runs out of sperm reserve while not being able to re-mate). It would be wrong to say that it is a "deliberate" decision: the smell of the aging queen gradually changes, more and more working bees become aggressive toward her for physiological reasons, and the program of production of a new queens is triggered. As a result, the old queen is killed, and a new queen is hatched from her laid egg due to special care of nanny-workers (in another situation a usual working bee would develop from this egg). It is nothing personal.

Social insects are extremely diverse (tens of thousands of species), and transition to the social way of life arose repeatedly in different groups [52, 57, 58]. Termites and representatives of the order of Hymenoptera (wasps, bees, and ants) present fundamental differences. It is absolutely impossible to discuss all the details in this review, so we would like to note the most important point: in case of some species, colonies reproduce only once and inevitably die after hatching reproductive individuals, while other species are potentially immortal, i.e. they repeatedly reproduce and are not programmed for dying. In the first case, we observe a phenomenon similar to post-reproductive phenoptosis, only at the level of a colony.

In addition to production of sexual individuals released from the nest, colonies can multiply by division, creating new families; this happens when the parental colony has several queens, some of them moving to the new colony. If, due to some unknown genetic reasons, the species can have only one queen (e.g. in honeybees), a new queen develops in the part of the colony left without the queen. This is somewhat similar to endless vegetative reproduction, although there is an important difference: young queens can be either taken from other colonies or they mate with males from other colonies, increasing genetic diversity of a new colony. However, one cannot talk about social insects as a whole without the risk of averaging very diverse data. Here are some examples illustrating both the concept of immortality and programmed

death. Let us start from the very beginning, from the most ancient insects.

Termites belong to the group of insects with the so-called incomplete metamorphosis; moving larvae hatch from eggs, they generally looks like adult insects, only small and without wings. Larvae grow and molt, shedding the integument that has become too tight (insects have exoskeleton, and their growth is related to the change of integument). Some larvae undergo a planned development into full-fledged males and females and leave their nest so as to establish a new one. Other larvae turn into soldiers who will guard the nest and their relatives (bearers of common genes) until the end of their lives. But the majority of larvae stop in their development; these are underdeveloped individuals without external signs of sex; they serve as workers. Thus, in the case of termites it is underdeveloped males and females that become workers [31, 52].

Termites are the most ancient order consisting entirely of species with high level of sociality, without any transitional forms. It seems that at a certain level of development they discovered the way of living as immortal (under stable conditions) colonies. Here is the scheme. In the colony there is a royal couple. The female lays eggs (laboratory record is 86,000 per day); the male periodically fertilizes the female; some workers die, while others hatch from the eggs. If one partner from the royal couple dies, it is not a problem. In contrast to Hymenoptera, which will be discussed below, the termites never take in young males and females that had left the same or other nests during the breeding season. The losses are replenished out of internal resources. Several males (in case of the king's death) or females (in case of the queen's death) will develop out of nymphs (workers). With the growth of the colony, there appear several males and females (polygyny develops). There seem to be no programmed limitations of the family lifespan, although we do not know how many times the royal pair can be replaced. We could not find any data on the record (over 30 years) lifespan of a termite colony; perhaps, there are no such data (consultations with specialists were ineffective).

According to some reports, some species of higher termites (Termitidae) for some reason lost the ability to grow males and females that could replace a dead king or queen. The death of the royal couple results if gradual death of the colony. It is tempting to assume that over the millions of years of their existence, termites secondarily developed a new type of phenoptosis on the colony level to increase their evolvability. This would prove that natural selection eliminates immortality when it is associated with stagnation — reproduction without a sufficient increase in genetic diversity [4]. However, data on inability (or limited ability) of some termite species to produce male and female substituents require further verification. Nevertheless, we present our arguments hoping that in time there will appear indisputable factual material con-

firming our hypotheses (or perhaps it exists already, but is unknown to us).

Theoretically, termites would benefit from taking young sexual individuals into a queen-less family — it would increase genetic diversity of the family and could justify its immortality. However, apart from theoretical assumptions, there is a need for a concrete mechanism that would determine a particular event ("activation energy"). And termites did not develop such a mechanism.

Hymenoptera are insects with so-called complete metamorphosis. A worm-like larvae (completely different from the adult winged individual) hatches from an egg; it goes through the pupal stage before turning into imago. In the case of social species, adult females with undeveloped ovaries play the role of workers, and males are hardly involved in the family social life [52, 58]. Speculative scientific assumptions sometimes turn out rather illogical! In Hymenoptera, only females can be workers, and males are not involved in social life because they lack maternal instinct that would enable them to care for offspring. And underdeveloped termites of both sexes have this instinct?

Hymenoptera comprise a relatively young order of insects, and most species are solitary. We can observe all the transitions from the solitary to social way of life. It is among Hymenoptera that many species of the temperate latitudes live for only one season and then die — a typical example of programmed death. These species have not yet "learned" wintering as a colony; only fertilized females survive the unfavorable period similar to solitary insects. Another example seems to be more interesting. The development cycle of a relatively small and modestly colored bee, *Evylaeus marginatus* or *Halictus marginatus* (Halictidae), lasts for 5-6 years. This time is equal to the lifespan of the female founder. In the first years, its offspring consists only of females that become workers. They live for one season and each year overwinter in the nest. In the last year, some males also appear in the offspring, the female founder dies, and her daughters become full-fledged females, mate, overwinter in the nest, and in spring fly away to establish new separate families [59]. It would seem that a new female could be adopted and live in the colony nest. However, the colony breakdown is genetically predetermined. Even after overcoming a one-year development cycle, the *Halictus* colony remained programmed for mortality. We can assume that in the case of species with a rather primitive level of the development of sociality, a family has not yet acquired the ability to be independent of the lifespan of a single female, while higher termites (according to not fully validated data) and higher ants (such as leaf-cutting ants) have already "given up" such an ability. However, it is hardly possible to verify such assumptions.

Well-known black-and-yellow (yellow jacket) wasps (Vespidae) and bumblebees (*Bombus*, Apidae) also live for one season in the temperate latitudes. Fertilized females overwinter singly in various shelters, and in spring each of them separately establishes a new family. Males die in autumn. This is one of the typical examples of phenoptosis differences in males and females.

There is usually only one queen in a colony: in the temperate latitudes wasps and bumblebees are strictly monogynous. At the beginning of the season only female workers with underdeveloped ovaries hatch of the eggs laid by the queen, while by the end of season fully developed males and females appear that leave the nest and mate. Usually, tens, sometimes hundreds, and rarely even thousands of individuals are in the nest by the end of the season. Young females overwinter, and all the others die. The cycle repeats. It seems to be a usual programmed phenoptosis at the family level. There are many such examples. What was the reason of speaking about wasps and bumblebees? The point is that these insects happened to be involved in an unplanned experiment.

A usual European inhabitant German wasp (*Paravespula germanica*) and earth bumblebee (*Bombus terrestris*) were accidentally brought to Tasmania and New Zealand; wasps also mastered Africa and South America [52, 60]. It is not so easy to accidentally bring somewhere a social insect — one needs to bring a fertilized female. Yet it did happen. It had fantastic impact. In a mild climate without cold winter the lifespan of wasp colonies increased to at least two years, and their number increased many-fold to reach up to a million individuals! A black and white picture of a wasp's nest of human height was repeatedly published. Periodically families produced young queens and males that flew away; however, it did not lead to the completion of the family development cycle. Strictly monoginic in the temperate climate, wasps became polygynous in the tropics. It is assumed that the colony took in additional queens while the female founder was still alive. In polygynous colonies, several eggs were laid in each cell, which is rare in temperate latitudes. The first hatched larvae ate all the excess eggs [61] — an interesting example of cainism. Hence, the death of a family is not genetically determined in German wasps. In the case of the common wasp (*P. vulgaris*), a close relative of the German wasp, large colonies can also be polygynous, but Spradberry [61] reports of only one case when the wasp colony overwinters (California, USA). Several species of tropical hornets (*Vespa*), also rather close relatives of mentioned wasps, have strictly one-year development cycle, although they can build nests throughout the entire year [62].

Ground bumblebees, when in the tropics, become similar to hornets in terms of organization of their life cycles. Bumblebees also lose seasonality and females start building nests even in winter. However, by starting the production of sexual individuals, the colony was signing itself the death sentence — it could not repeat this procedure for a second time. This situation was similar to that of thale cress: the end of flowering means death. Hence,

the death of a colony is genetically determined in bumblebees. This is especially surprising because of the fact that replacement of queens was observed in bumblebees living in temperate latitudes. Some overwintered queens do not establish nests of their own, but fly searching for other nests during the season and try to infiltrate those nests. If the female founder for whatever reason becomes weakened, it is expelled by the replacing female. Sometimes this new female can even belong to another species. However, no replacements were observed in the warm climate. Why? Theoretically, bumblebees can reproduce many times, there is a well-known example: colonies of *Bombus atratus* inhabiting the Amazon basin live for several years and repeatedly reproduce. Moreover, some young fertilized females return to the nest and lay eggs until they kill each other in the course of fights using the sting. Thus, monogynous periods alternate with polygynous ones [52]. Apparently, immortality is an unstable state that is not supported by natural selection. That is why we observe such differences between rather closely related species.

Honeybee (*Apis mellifera*) occupies a special place in the animal kingdom. Undoubtedly, this species represents one of the evolutionary peaks. This bee, a native of the areas with warm climate (scientists argue whether they come from South-East Asia or Africa), adapted to life in harsh conditions almost as well as in their historic homeland. Perhaps it is the only invertebrate capable of maintaining body temperature of about 35°C all year-round [58]. The colony of honeybees can be considered immortal similarly to prokaryotic bacteria dividing into equal parts. Bees reproduce by swarming, when the colony divides into two. Unlike wasps and bumblebees, the bee queen absolutely cannot survive without workers, she cannot feed on flowers and collect pollen, and she does not even have specials tools for it, the so-called baskets (corbicula) on the hind legs. The old queen flies away with the swarm, and a new queen, the daughter of the old one, hatches in the remaining half. This daughter is sent to the mating flight, mates with drones from other colonies, and for several years becomes a full-fledged queen procreator. We have already discussed that the decrepit queen is killed by her own daughters-workers (in the old or new nest, where she flies with the swarm); she is then replaced with a new one. This phenoptosis is associated with two processes — physiological changes in the queen, and the worker bees' reaction to these changes. What is exactly happening with the aging queen? Can she be rejuvenated? Does she age gradually? As far as we know, nobody has studied these particular questions.

The bee colony can consist of 100,000 worker bees (usually tens of thousands), but there is always only one queen. This is the bottleneck in bee biology. Death of the queen can lead to the death of the entire colony. But usually the colony — like an organism healing a wound — tries to prevent it. Bees can take another queen into the family (from the genetic perspective it is completely disadvantageous for the workers, but social insects, similar to human society, are characterized by special rules of conduct) or hatch a new queen from a young larvae. The queen and the workers are identical genetically, and individual destiny depends only on the care received at the larval stage — the quality of food and the size of the cell in which the larva develops. Let us recall that metabolism and the ability to resist aging are very different in the queen and workers. The queen usually lives for 5-6 years, while the workers — only for about a month in the warm season. The laws of phenoptosis are completely different in these two cases.

Thus, we can say that honeybees achieve immortality by dividing the colony superorganism at the next turn of the evolutionary spiral after bacteria. Unlike bacteria, swarming bees increase their genetic diversity. Natural selection should favor such division. Similar to bacteria, in this case there is also no clear distinction between the existence of the concrete individual (colony) and the species as a whole.

Asiatic honey bees or Eastern honey bees or Indian bees (*Apis cerana cerana* = *Apis indica*) are very similar to honeybees. However, there are several differences: in this case it is the young, and not the old queen that flies away with the swarm; besides that, Asiatic bees cannot hatch a new queen in the family instead of the lost old queen [63]. But these are the key points related to the organization of the life cycle and phenoptosis! Here we once again meet the amazing variability of the life cycles in closely related insect species (though it is typical also for other organisms, perhaps to a lesser degree).

Colonies of many ant species are also practically immortal [52]. Ants constitute a huge group consisting only of social species, which significantly differ in the level of the development of sociality. Ant workers secondarily lost wings. Let us consider the well-known red wood ant (*Formica rufa*). Their anthills built of twigs and needles are a familiar part of the forest landscape. The maximum size of the anthill dome can reach 10 m in diameter [52]. Such a nest grows for many years, gradually increasing in size, just as non-aging animals grow through their entire life. Large colonies include millions of workers and many queens. Family size is an important indicator of the level of development of sociality; complex social structures can be stably maintained only with large colony size. There are data on anthills existing at the same location for one hundred years. It is clear that not only workers, but also queens were repeatedly replaced during this time (although queens live for many years). The registered in laboratory record for the lifespan of the ant *Formica fusca* queen was 18 years. Interestingly, workers can also live for 5-6 years, but in the wild they usually die within 1-1.5 years before reaching old age. Old workers are the guardians of traditions, in the spring they rebuild the sys-

tem of roads surrounding the anthill. Ants reproduce repeatedly. Most of us have had an occasion to see winged males and females simultaneously flying out of different families. A female of red wood ants cannot establish a colony of its own; she searches for a ready nest, sometimes seizing the nest of another species (so-called social parasitism) and sometimes, if there is a "vacancy", she returns to her parental family.

Usually the ants guard the territory around the nest against enemies and especially against strangers of their own species; the larger the colony, the larger is the guarded territory. However, under stable conditions colonies may give up the protection of their territory and unite in a so-called federation − commonwealth of colonies connected by a network of roads and mutually beneficial exchanges [64, 65]. Ants of some other genera also form such federations [52]. It was estimated that in the case of the Northern wood ant (*Formica aquilonia*) the number of ants living as single colonies is about 7 million per hectare, and when the colonies are united into a federation, this parameter rises to 15 million. The record in the size of an ant federation was registered for *Formica yessensis* ants living on Hokkaido Island in Japan. It consisted of 45 thousand nests located in an area of almost 3 km^2. It embraced about 300 million workers and over a million queens. In fact, such a system presents a single multinest pan-anthill. A federation is much more stable than an isolated colony. Anthills and roads remain at the same place for decades. If an anthill is destroyed, ants immediately rebuild it. The federation jealously guards its structure.

Undoubtedly, from a biological perspective the federation is the highest form of social organization. A federation is by nature immortal and far more stable than an individual colony. However, its potential immortality can be realized only if one essential condition is met: stability of the habitat. There are fewer and fewer areas not affected by human activities. Perhaps, immortality should be considered as a very narrow specialization often disadvantageous under real conditions. Not only a federation, but even an individual colony of red wood ants can hardly be found in the parks of a large city; in Moscow the last of the Mohicans can still be met in Moose Island Park. However, in the city, even on the pavement, one can notice black garden ants (*Lasius niger*) or ants from the *Myrmica* genus, with much more primitive social organization [58].

In the entire animal kingdom, eusociality is widespread only among insects. Apparently, only this group has biological prerequisites essential for the development of eusociality. However, there is one example when nature tried to create this phenomenon in mammals. The naked mole rat (*Heterocephalus glaber*), a rodent from the family of Bathyergidae, inhabiting arid areas of Ethiopia, Somalia, and Kenya, lives in burrows in rather large (for mammals) colonies (families) (30-80 individuals); only

one female and 2-3 males in a colony are involved in reproduction. Other individuals of both sexes do not breed in the presence of that dominating female (affected by its smell and direct physical impact). They play the role of worker bees, and most of them die in this capacity at the age of about 3 years. However, in case of death of a reproducing animal, it is replaced by one of the workers, male or female, depending on the gender of the dead animal (like in termites). Here we see all the signs of eusociality, and the colonies of the naked mole rat are apparently potentially immortal. As in insects, the dominating female lives much longer than workers do. The limit of her lifespan is unknown; now there is a 32-year-old female living in the laboratory. This is an absolute record for a rodent of this size.

Naked mole rats are interesting not only because of their eusociality, but also due to their unique physiological characteristics. They belong to non-aging animals, and that 32-year-old female is as vigorous as during her first year of life. Naked mole rats do not maintain constant body temperature and do not suffer from cancer [1, 66].

Compared to termites, bees, and wasps, the level of sociality in naked mole rats is rather low: the colonies are relatively small, there are no morphological differences between castes, and the function of workers is temporary − all of them can mate and reproduce in the absence of the queen. From the example of the naked mole rats, we are likely to witness the early stages of the development of sociality. For example, termites appeared on Earth about 150 million years ago, and the earliest rodents (not naked mole rats) − about 60 million years ago. What will happen to naked mole rats in the next millions of years?

In conclusion, let us note that compared to the lifetime of arthropods (spiders and insects appeared about 400 million years ago), the history of the development of many other groups of animals is much shorter (e.g. the age of humankind is about 300 thousand years, i.e. three orders of magnitude shorter). One also needs to remember that in the case of arthropods, generations are replaced more often − they evolve faster. Accordingly, their range of various biological adaptations is also incomparably higher than in vertebrates. The material discussed above also suggests that the role of environmental signals in realization of various versions of genetic programs of aging and phenoptosis [67] in insects and ticks is higher than in most other animals.

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