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Wilhelm Goetsch (1887 - 1960): pioneering studies on the development and evolution of the soldier caste in social insects

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Abstract

The eco-evo-devo of social insects addresses long-unanswered questions in Myrmecology, especially how novel castes originate and evolve. While this is an emerging field of broad interest to myrmecologists, German scientists prior to 1960 were quite active in studying such questions, but their attempts have largely been forgotten. The collective amnesia is partly because these papers are written in German and therefore inaccessible to the non-German speaking myrmecologists and partly because individual-level mechanistic approaches to studying social insects were eclipsed by population genetic approaches with the publication of Hamilton's classic papers in 1964. Here, we present the first of a series of commentaries and translations of insightful papers written by German scientists before 1964 on the development of social insect castes as it related to colony function and social evolution. The goal of these translations and commentaries is to reveal findings and ideas that remain understudied to this day. Our first translation and commentary is of two papers by Goetsch from 1937 and 1939 on caste determination and evolution in *Pheidole* ants and *Anoplotermes* termites.

Key words: *Pheidole*, caste determination, origin of novel castes, social insects, eco-evo-devo, ants, history of evo-devo, phenotypic plasticity, adaptive demography, soldier caste, ancestral developmental potential.

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Commentary

With the current pace of scientific progress being so rapid, more dedication and focus is needed for us to make new contributions, and even more so for us to keep up with the stream of relevant literature. This tempts us to cite reviews rather than primary literature when writing our own papers, which unfortunately adds to the fading of past findings and concepts from our collective memory. Another way that contributions fade from active memory is through impediments to the exchange of information, a requirement for steady progress. If exchange of findings by researchers in different countries is hampered by war and ideology, the opportunity to bring fertile ideas together can be lost. This was the case in parts of Europe and Russia in the 1930s - 1950s. The vast literature on social insects provides good examples of ideas lost from collective memory.

References to social insects have a rich and complex history, dating back as far as ancient Egypt (WHEELER 1928, WILSON 1971, KRITSKY 2015). Yet, the historical "pre-Hamilton" literature, that is, papers published before W.D. Hamilton's insights into the role of relatedness in the evolution of insect societies (HAMILTON 1964a, b), have in general

received little attention from social insect researchers. This is especially the case for the literature in the German and French languages, which declined as primary languages of science after World War II, thereby cutting off non-native speakers from the trove of work published by researchers in those countries. Here, we focus on the German literature on social insects from the late 1800s to the mid 1900s – a period of immense scientific activity where Germans made many observations and discoveries worthy of our appreciation today. The activity of German scientists is made clear by skimming through the references section of *The ants* (HÖLDOBLER & WILSON 1990). This retrospective article is a collaboration between Christian Metzl, a talented young Austrian biologist with his own translation company (www.oldgermanpapers.com), and Diana Wheeler and Ehab Abouheif, who wrote the commentary. By translating papers written in the late 1800s to the mid 1900s, we aim to highlight the significance of the eco-evo-devo research program on social insects, especially ants, which drifted off the stage on which developmental and evolutionary biology were being integrated during the consolidation of the modern synthesis of evolutionary biology. Integrating



Fig. 1: *Pheidole pallidula*. Minor worker (left) and soldier (right). Photo by Hugo Durras.

past findings and insights into a “re-emerging” field of eco-evo-devo will bolster the ongoing reconfiguration of the framework in which we study social insects (WHEELER 2003, TOTH & ROBINSON 2007, ABOUHEIF & al. 2014).

We selected two papers published in 1937 and 1939 by Wilhelm Goetsch to highlight his pioneering work on the development and evolution of the soldier caste in ants and termites. ZAUNICK (1964) summed up Goetsch’s biography as follows: Johann Heinrich Wilhelm Goetsch was born in 1887 in Gotha, Germany. He habilitated at the University of Strasbourg in 1917 before moving to Munich in 1921. From 1929 - 1931, he was full professor at the University of Santiago de Chile. In 1934, he became professor of Zoology at the University of Breslau, Germany and assumed directorship of the Institute of Zoology and its Museum. After 1945, he worked in his own laboratories in Krumpendorf and Salzburg, Austria, as well as in Barcelona, Spain. In 1947, he became honorary professor of the University of Graz, Austria. Goetsch died in 1960 in Säckingen on the Rhine, Germany. He did his first experimental work on hydra, but during his travels to Chile from 1921 - 1958, he became interested in social insects and did many studies on the ants and termites of South America (GOETSCH 1932, 1935). He received worldwide recognition for his books: Tierkonstruktionen or Animal constructions (GOETSCH 1925); Die Staaten der Ameisen or The colonies of ants (GOETSCH 1937b); Termiten-Staaten or Termite colonies (GOETSCH 1939b); and finally Vergleichende Biologie der Insekten-Staaten or Comparative biology of insect colonies (GOETSCH 1940, 1953).

In the first paper, The generation of “soldiers” in ant colonies (GOETSCH 1937a), Goetsch presents the first known experimental evidence for environmental influence on caste determination in social insects. In the second paper, Novel termite soldiers out of artificial nests (GOETSCH 1939a), he describes his discovery of soldiers in a “soldierless” termite genus called *Anoplotermes*. To the best of our knowledge, GOETSCH (1939a) is the first formal observation and discussion of the existence of ancestral developmental potentials in social insects.

Soldier determination

The genus *Pheidole*, also known as the “big-headed ants”, is a hyperdiverse ant genus with ~1000 described species

(ANTWEB 2017). Almost all species in *Pheidole* have two discrete worker castes called “minor workers” and “soldiers” (WILSON 2003) (Fig. 1). The soldiers are a distinguishing feature of this genus and are defined by their head to body size allometry, in which soldiers have disproportionately large heads relative to their body size (WILSON 1953). The heads of the soldiers are much larger than those of minor workers and are generally specialized for defense and food processing, while the minor workers perform most of the tasks in the colony, such as foraging and brood rearing (WILSON 2003). GOETSCH (1937a) is an overview of caste polymorphism in the worker caste of ants and a report of his experimental results on the effect of nutrition on soldier determination in *Pheidole pallidula* (Fig. 1). GOETSCH (1937a) used incipient *P. pallidula* colonies raised from mated queens collected in southern Italy. As colonies developed, he saw that soldiers generally appeared in the second set of workers produced. When the colonies were larger, he began to experiment with different types of food. For example, he fed one group only sugar and honey and the other insect carcasses. Soldiers developed only in colonies that were fed the dead insects. This demonstrates that protein induces soldier development, a finding that was confirmed later by PASSERA (1974), but Passera’s work was also obscured because it was published in French.

By switching the diet that colonies received and keeping track of larval sizes, GOETSCH (1937a) deduced that larvae must receive the protein at some point during the first five days of larval life to trigger soldier development. GOETSCH (1937a) narrowed the timing of the critical feeding period down to days four and five by following the development of individual larvae with known nutritional history. In so doing, he identified timing of an environmental cue as a key factor in determining a caste polyphenism. The timing of the nutritional period fits well with results obtained 50 years later in WHEELER & NIJHOUT’s (1983) classic work on *Pheidole bicarinata*, which reported that soldiers are produced only when fed a high protein diet and that a critical period for juvenile hormone (JH) sensitivity occurred on days four to six of the last larval instar. Larvae which were reared at 27 °C would reach Goetsch’s days four and five at about the beginning of the last instar. Therefore, GOETSCH’s (1937a) and WHEELER & NIJHOUT’s (1983) studies together show that a nutritional sensitive period is followed immediately by a hormonal sensitive period, and in the absence of a positive signal by the close of the hormonal sensitive period, minor worker larvae pupate, but larvae that do receive such a signal continue to grow and become soldiers (WHEELER & NIJHOUT 1983). The sensitive period has not been studied further and should be an important focus for future study.

Caste demography

GOETSCH (1937a) also considered the distinction and relationship between continuous polymorphism and complete dimorphism, as well as the effects of ecological variation and natural selection on worker demography. He noted that variation in the amount of “meat” he gave larvae is associated with size variation within minor worker and soldier subcastes. Ants with continuously polymorphic workers present an unbroken series of workers over a broad size range, as he illustrated with *Solenopsis gayi* and *Messor structor* (see Figs. 1 and 2 in GOETSCH 1937a translation). In contrast, ants with a dimorphic worker caste have two distinct size

classes and shapes, as he illustrated with *Pheidole pallidula* (see Fig. 3 in GOETSCH 1937a translation). Furthermore, by manipulating diet, GOETSCH (1937a) produced a wider range of sizes for both minor workers and soldiers than was normally observed. Most of the ants could be assigned to one or the other caste, but he eventually found a single individual that he designated a “true intermediate,” where “its head could serve as the end of a worker series or as the beginning of a soldier series” (see Fig. 5c in GOETSCH 1937a translation). He concluded that by forcing the expression of worker sizes that were not normally expressed he could produce individuals that linked the normal minor worker and soldier sections of the size frequency distribution. GOETSCH (1937a) then inferred that artificial forms are intermediate in dimorphic ants, and suggested that continuous polymorphism may have been the ancestral state for dimorphism.

However, there is more to caste than just size. WILSON (1953) added a second metric, allometry. In the 1930s, HUXLEY (1932) and THOMPSON (1942) had published on allometry and shape, but GOETSCH (1937a) was apparently unaware of their work. Critical size, the weight at which metamorphosis is set to begin, is also a key player in the evolution of caste systems (WHEELER 1991). Taking allometry into consideration, soldiers and minor workers in *Pheidole* are clearly distinct castes. Measurements of thousands of ants, combined from both control and experimental treatments, show that large workers and small soldiers can overlap in pupal size (WHEELER & NIJHOUT 1983). One striking example is the experimental induction of minor workers as large as normal soldiers after application of a JH mimic (methoprene) to larvae raised in a colony made up of 100% soldiers (WHEELER & NIJHOUT 1983, 1984) (Fig. 2). The aberrantly large minor worker and small soldier each, particularly their head and thorax, show the distinct coloration, sculpture and shape of normally sized members of their respective castes. In Fig. 2, the large minor worker head appears identical in shape, coloration, and lack of sculpture to the normally-sized minor worker head on the far right (Fig. 2). So, the specific morphology of a soldier caste goes beyond simple size; it includes other traits such as cuticle sculpture, color and shape. Size and caste specific morphology can be decoupled. GOETSCH’s (1937a) drawing of heads of small and large workers and soldiers also shows an individual identified as a “transitional form” (see Fig. 5c in translation). However, the drawing looks just like a small soldier and is not sufficiently detailed to persuade us that this ant is truly an intercaste that is a mix of minor worker and soldier traits. Nonetheless, GOETSCH’s (1937a) ideas about the evolution of colonies with complete dimorphism from colonies with continuous polymorphism have been discussed by WILSON (1953) and are certainly worthy of further investigation.

The production of minims: blastogenic versus trophogenic

For social insects, the nature vs. nurture question has been framed in terms of whether caste is determined by blastogenic (in the egg) or trophogenic (external / nutritional) factors. This dichotomy has been considered as a variant of the more general nature vs. nurture question (ENGELMANN 1970). GOETSCH (1937a) used his founding *Pheidole pallidula* colonies to test whether the small stature of workers emerging from the first eggs could be altered by the source of larval nutrition received after hatching. The first eggs laid and reared by the queen became typical minims, smaller than the workers that would be produced later. GOETSCH (1937a) then

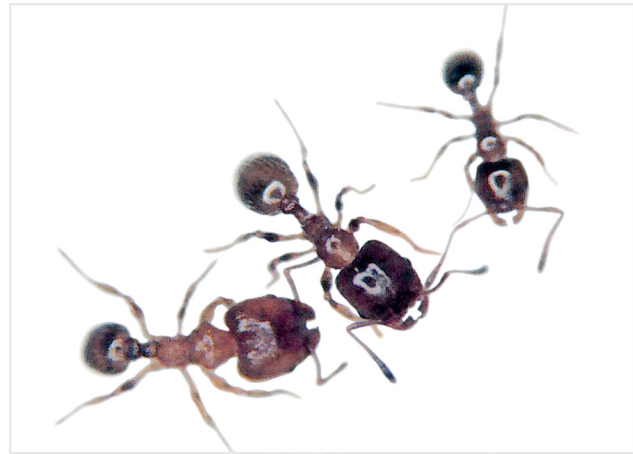


Fig. 2: *Pheidole bicarinata*. A minor worker the same size as a soldier. Normal soldier (left), normal minor worker (right), large minor worker (center). Photo by Diana Wheeler.

placed founding queen-laid eggs in older colonies where they received nutrition from workers, which normally produced workers significantly larger than minims. Nevertheless, eggs laid by founding queens still yielded minim-sized workers. GOETSCH (1937a) concluded that the basis of their small size was blastogenic, in the “germ or egg.” Remember that in the 1930s the nature of genetic material was not yet known. Several years later, GREGG (1942) correctly pointed out that eggs, including ant eggs, contain nutrition in addition to whatever form genes took. It was then clear that the term blastogenic was ambiguous. During foundation and incipient colony development, eggs can vary in the amount of yolk they are supplied by the queen. Reduced yolk in eggs laid by founding queens could be the mechanism that increases the number of first workers produced at the expense of worker size, which is reduced, as suggested by WHEELER (1986). Reduced yolk content (nurture) shifts the outcome of gene x environment interactions within the egg itself.

Historically, the nature vs. nurture controversy heated up with the burgeoning of *Drosophila* genetics in the early twentieth century, and later intensified with the rise of population genetics and early molecular biology (WEST-EBERHARD 2003, KELLER 2010, TABERY 2014). In this context, the determination of *Pheidole* soldiers could not be accommodated in a framework that required either one or the other (WHEELER 2003), because the environment of developing *Pheidole* soldiers and other polyphenic organisms is central to developmental outcomes (WHEELER & NIJHOUT 1981, GILBERT 2001, WEST-EBERHARD 2003, GILBERT & EPEL 2009). Evelyn Fox Keller argues that, in retrospect, the intensity of the nature-nurture debate was fueled by a vocabulary problem, where terms as central as “gene” and “environment” were used with little consensus of their meanings (KELLER 2010). Lack of consensus on terms is an important factor indicating a need for a paradigm shift (KUHN 1996). In this commentary, we assert that phenotypes result from gene x environment interactions and that a new phenotype can arise by initiating a change in either factor. Therefore, an important contribution was made by GOETSCH (1937a), who demonstrated that the soldier phenotype was induced entirely by nutritional experience (environment) with no apparent contribution of soldier-specific genes.

Effect of different diets on soldier determination

GOETSCH (1937a) fed his *Pheidole* colonies different types of food and observed how they were distributed and whether soldiers were produced. Chunks of flies or mealworms, which he called “meat,” were the only diet that enabled soldier determination in *Pheidole* colonies or colony fragments. He stressed that workers gave meat to a few individual larvae that fed on it for extended periods. In contrast, liquid food, such as sugar water, honey, frog or rabbit blood or meat juice, was distributed by workers by giving many larvae small amounts, which did not induce soldiers. The finding that liquid protein is not associated with soldier development is intriguing. Were the liquids high enough in protein? Does the type of handling by workers make the difference? His observation that liquids are dispensed to many larvae in small amounts is similar to the process described in fire ants (CASSILL & TSCHINKEL 1995). In contrast, he reported that solid food is distributed unevenly to larvae, with preference given to those of larger size. In *Pheidole spadonia*, CASSILL & al. (2005) described in detail the process by which minor worker larvae feed on cut up fruit flies – they found that minor worker larvae received roughly equal amounts, but unfortunately, no soldier larvae were included in their study. Therefore, whether some larvae receive preferential feeding still requires future confirmation.

The results of GOETSCH’S (1937a) diet treatments remind us that we still know so little about how the different elements of diet affect caste determination. “Diet” encompasses more than the simple nutrient tetrad of protein, carbohydrates, fats and vitamins. In honey bees, for example, KAMAKURA (2011) showed that one of the component proteins of royal jelly acts to induce queen development through the epidermal growth factor pathway independently of the insulin-TOR pathway, which had been the major focus of researchers (WHEELER & al. 2006, MUTTI & al. 2011). Furthermore, ZHU & al. (2017) discovered that regulatory microRNAs derived from plants, which are major components of the bee bread fed to worker larvae, suppress queen development. ZHU & al.’s (2017) contribution points out the interconnectedness of consumer and consumed, even to the level of meta-epigenomics. Finally, in ants, LEBŒUF & al. (2016) discovered JH and microRNAs in the liquid food that is trophalaxed between workers in *Camponotus floridanus* colonies. The results suggest that not only nutrition, but also signaling molecules flow through the colony, including to larvae, creating ample means of generating differential nutritional and physiological environments in different developmental stages and castes. Together, GOETSCH’S (1937a) and more recent studies highlight the importance of understanding how different elements of diet are processed and distributed, and how they affect caste determination.

Geographic variation: immediate effects on and evolutionary tuning of demography

The finding that soldiers required meat in their diet led GOETSCH (1937a) to consider how caste demography would be affected by different ecological environments. In his discussion, he outlined the importance of geographic variation as an important factor driving evolution of size and shape within ant castes (GOETSCH 1937a). In the case of *Pheidole pallidula*, different geographic locations show micro-differences in size and shape constituting what he called “micro-races,” and he proposed that micro-races are

produced by an interaction between genes and environment. He also proposed that presence and absence of the soldier subcaste in *Solenopsis gayi* across Chile may be caused by presence of seeds in their diet in the North and absence of seeds in the South (GOETSCH 1937a). This would mean that external conditions can induce the presence or absence of subcastes within a species’ geographic range.

Before we comment on these observations, we owe GOETSCH (1937a) credit for his prescient, though rudimentary, discussion of what modern social insect researchers now call “adaptive demography,” the idea that colonies optimize their performance in response to new environments. In recent times, YANG & al. (2004) produced evidence in the field for adaptive demography – that is quantitative, microevolutionary divergence in caste ratios and body size of minor workers and soldiers in *Pheidole morrisi* across a geographic range that spans from New York to Florida. These differences are thought to be colony-level adaptations to climate as well as to competition from fire ants. GOETSCH’S (1937a) work with *P. pallidula* fits well with the findings of YANG & al. (2004). However, it remains unclear whether the differences between micro-races that GOETSCH (1937a) observed had been environmentally induced or were evolved responses that had been genetically assimilated over many generations. Furthermore, in light of YANG & al.’s (2004) findings of quantitative differences, GOETSCH’S (1937a) report of qualitative differences – the presence or absence of the soldier caste over a similar geographic range within *Solenopsis gayi* – is questionable. One possibility is that GOETSCH (1937a) had been observing populations of different species of *Solenopsis* over the same range. This highlights the need for good field studies to generate further evidence for adaptive demography within the majority of ant species, making this another important future direction for study.

Origin of novel castes

Of the ~1000 described *Pheidole* species, there are at least eight that have evolved a third discrete worker caste called “supersoldiers,” with heads that are disproportionately larger than those of soldiers, minor workers, and even the queen (WILSON 2003, RAJAKUMAR & al. 2012). Field observations show that the supersoldier caste in *Pheidole obtusospinosa* use their large heads to defend against army ants (HUANG 2010). In 2012, RAJAKUMAR & al. (2012) reported the discovery of a “supersoldier-like” anomaly in a field colony of *Pheidole morrisi*, a species with only a minor worker and soldier caste (WILSON 2003). This anomaly is strikingly similar to the evolved supersoldier caste in *P. obtusospinosa* (RAJAKUMAR & al. 2012). To understand the developmental processes that triggered the appearance of this anomaly, RAJAKUMAR & al. (2012) applied high doses of JH to developing larvae during the critical period just prior to when minor workers and soldiers are determined. This JH treatment induced the development of supersoldiers in *P. morrisi*, a species that has not evolved a supersoldier caste (RAJAKUMAR & al. 2012), revealing the existence of a hidden developmental potential to produce supersoldiers in *P. morrisi*. Furthermore, RAJAKUMAR & al. (2012) also induced the development of supersoldiers in several, phylogenetically distant, *Pheidole* species that do not have a supersoldier caste, revealing that this hidden potential likely exists across the whole genus. Finally, phylogenetic analyses consistently show *Pheidole rhea*, a species with an evolved supersoldier caste, is one of the most basal lineages within *Pheidole* (MOREAU 2008,

RAJAKUMAR & al. 2012). Collectively, these findings allowed RAJAKUMAR & al. (2012) to infer that an early ancestor within *Pheidole* evolved a supersoldier caste and that it was phenotypically lost early in the evolution of the genus. However, despite this phenotypic loss of the supersoldier caste in the majority of *Pheidole* species, the potential to induce the development of supersoldiers was retained throughout the genus for approximately 25 - 47 million years (MOREAU 2008, RAJAKUMAR & al. 2012, WARD & al. 2015). Therefore, the potential to produce supersoldier-like anomalies is ancestral, widespread, and can be recurrently induced in natural populations, and if these anomalies provide any fitness advantage to their colonies, then natural selection can fix them through an evolutionary process called “genetic accommodation” (WEST-EBERHARD 2003). RAJAKUMAR & al. (2012) provide evidence that genetic accommodation of induced supersoldier-like anomalies led to the re-evolution of a supersoldier caste in *P. obtusopspinosa*. In general, this suggests that one evolutionary pathway to the origin of novel ant castes is through the induction and fixation of ancestral developmental potentials.

In his article on *Pheidole pallidula*, GOETSCH (1937a) observed that under “exceptionally favorable food conditions” his nutritional manipulations produced “unnaturally large soldiers,” with heads larger than that of the queen. He called these anomalous soldiers a “pathological hypertrophy,” acknowledging that they are exceptions and not a normal part of *P. pallidula* colonies. We propose that these unnaturally large soldiers that GOETSCH (1937a) observed while doing his nutrition experiments are equivalent to the supersoldier-like anomalies discovered in *Pheidole morrissi* on Long Island, New York, USA. GOETSCH’S (1937a) supersoldier-like anomaly in *P. pallidula* further supports the existence of an ancestral developmental potential to produce supersoldiers across *Pheidole*, and suggests that variation in nutrition is a critical factor in environmentally inducing ancestral supersoldier potential.

Our translation of GOETSCH (1939a) reveals that he was far ahead of his time in thinking about the significance of ancestral developmental potentials to the evolutionary process, and in 1939 extended his observations and discussions to other social insects. He reported the environmental induction of “nose-soldiers” in the termite genus *Anoplotermes*, which evolutionarily lost the nasute soldier caste (see Figs. 1, 2, and 3 in GOETSCH 1939a translation). *Anoplotermes* is in the family Termitidae and so its ancestors had soldiers (BOURGUIGNON & al. 2015). Therefore, GOETSCH’S (1939a) discovery of an anomalous *Anoplotermes* soldier represents the reactivation of an ancestral potential in a termite colony. This finding triggered broad discussions of ancestral developmental potentials in the social insect literature in the 1940s (GREGG 1942, LIGHT 1943). GREGG’S (1942) discussion of GOETSCH’S (1939a) discovery is particularly insightful: “It would mean that although soldiers do not appear in normal wild colonies and are supposed to have dropped out phylogenetically, their genes are in reality still retained by the species. This can be reinterpreted in favor of environmental control by assuming that, while genes are admittedly present, some change in the physiological thresholds in the particular colony has in part enabled them to come to expression. The anomaly might also be interpreted as the result of phylogenetically suppressed genes which cause the degeneration of certain characters (in this case the soldier caste), but which have not been entirely lost because of other vital influences in the termite colony.”

GOETSCH (1939a) also explored the environmental conditions which may have induced the ancestral developmental potential to produce nose-soldiers in this soldierless genus. He recounts, in an engaging style, his homeward journey from the Iguazú river and the environmental conditions the colonies in his baggage were being subjected to. He suggests that in his experimental colonies the nasute soldier program may have been reactivated by feeding on solid protein (their own brood) or by the lack of an inhibitory pheromone that normally suppresses the nasute soldier development. To summarize, GOETSCH (1939a) provides evidence for the existence of ancestral developmental potentials in two independently evolved social insects – ants in the genus *Pheidole* and termites in the genus *Anoplotermes* – and suggests that nutrition plays a key role in activating them.

Unfortunately, GOETSCH’S (1937a, 1939a) ideas on the role of ancestral developmental potentials in the origin of novel ant castes have generally been underappreciated in the recent social insect literature. GOETSCH (1939a) asked whether all “unrealized forms,” including the production of small and large soldiers and what he thought were “intermediate” or “transitional” forms, play a role in the origin of novel castes. GOETSCH (1939a) proposed that these unrealized forms provide the bridge to explaining how species evolved discrete worker castes. He proposed two alternative possibilities for the role of unrealized forms or ancestral developmental potentials, which he could not distinguish given the evidence available to him. The first possibility he proposes is that unrealized intermediate forms existed in the worker caste of an ancestral colony but that they were gradually removed through natural selection (without a trace in the fossil record), eventually giving rise to discrete castes. He argued that if this first possibility is correct then the phylogenies of social insects, such as *Pheidole*, must be revised to make species with continuous worker castes closely related to species with discrete castes. Alternatively, the second possibility is that discrete castes evolved by induction and without gradual loss of unrealized intermediate forms. He argued that unrealized intermediate forms may have never existed in the first place because of “certain developmental processes,” but that they can be induced by the right environmental factors, especially nutrition in the case of *P. pallidula* soldiers. We now know that these “certain developmental processes” are hormonal thresholds and epigenetic processes that regulate developmental plasticity (GREGG 1942, WHEELER & NIJHOUT 1981, NIJHOUT 1994, WEST-EBERHARD 2003, RAJAKUMAR & al. 2012, ALVARADO & al. 2015). RAJAKUMAR & al. (2012) show that it is possible to evolve a novel worker caste (supersoldiers) through the induction of discrete phenotypes without the gradual loss of intermediate forms. However, it is almost 80 years after publication of GOETSCH’S (1939a) article, and we still lack sufficient data to distinguish between GOETSCH’S (1939a) two alternative possibilities for the origin of new castes. This remains an exciting area for further research.

Conclusion

In addition to the more practical reasons we laid out at the beginning of this commentary, historical and cultural factors can also lead to the functional loss of work by past researchers through the episodic nature of science itself. As proposed by Thomas Kuhn with his view of scientific revolutions and paradigm shifts, when new findings cannot be accommodated by a current paradigm, its framework collapses, and knowledge is then re-assembled into a new,

presumably more inclusive overarching framework (KUHNS 1996). As the scientific endeavor lurches through this process, some findings and points of view can fall away and be lost, swept out of the mainstream of the new, accepted dogma. By revisiting older literature, we find overlooked and underappreciated contributions that remind us of questions and findings that remain as loose ends after the re-assembly of current knowledge into new frameworks. These orphaned contributions can be thought of as a cryptic literature that has been obscured by the evolution of scientific ideas but that can still be accessed today through deliberate excavations.

In the case of social insects and GOETSCH (1937a), (1939a) – although his findings were included by WILSON (1971) in his book *The insect societies – they were eclipsed* by HAMILTON'S (1964a, b) publications on inclusive fitness. Hamilton's work signaled an era where population genetic approaches to studying social insects over-took mechanistic individual-level approaches. It is clear Goetsch deserves credit for laying part of the foundation of eco-evo-devo in social insects, long before modern studies on the subject. Some of his observations add to the current knowledge base, while others raise important questions for future study. They also serve as a reminder of the importance of basic natural history, and the wealth of such information languishing in older non-English European literature.

In summary, one way to develop a more inclusive framework for organizing our understanding of insect sociality is to explore older literature and revisit earlier findings and points of view that have been buried by our copious more recent contributions. We will continue digging into the literature from the first half of the last century when colonies were assumed to have their own emergent properties and integration (WHEELER 1911, 1926). As a first step, we hope these translations have shown that eco-evo-devo of social insects was as active and exciting in the first part of the twentieth century as it is today (ABOUHEIF & al. 2014).

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The generation of "soldiers" in ant colonies

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In some species of ants, the workers are so varied in shape and size that, when viewed individually, they could be thought of as distinct species. The largest of workers play a special role: These animals often attain the length of queens, and in any case share the size or shape of their heads. They can also resemble queens with regard to their brain structure (PANDAZIS 1930) and eye formation (EIDMANN 1935). In the hitherto most well-studied seed-harvesting ants of the genera *Messor* and *Solenopsis*, I have termed such animals "giants" (Fig. 1 - 2). From those "giants," all sorts of transitions lead to the smallest of workers, which appear quite dwarfish. This is seen most vividly in, for instance, the fungus-growing *Atta* species. In addition to genera such as these, which exhibit a sliding polymorphism, there are species with a merely dimorphic worker caste, where small forms are faced by "giants" without any transition forms. In these cases the "giants" are traditionally called "soldiers." How big the differences can be is exemplified by *Pheidole pallidula* NYL., a small Mediterranean ant, in Fig. 3.

The development of such a polymorphism or dimorphism has already been a matter of much dispute. Two viewpoints are pitted against each other: Some assume that the prerequisites that lead to a certain size or form are to be found in the germ or egg (= blastogenic development), while others view particularly rich or special nourishment as the cause (= trophogenic development).

In order to get closer to answering this question, I conducted experiments on *Pheidole pallidula*. On Capri, in mid- and end-July 1936, I captured around 100 *P. pallidula* queens, immediately after they had flown out. In some cases, it was possible to watch the animals fly off from the nest and become fertilized in the air, and to capture them afterwards. In this way, I could track every phase of the nest's foundation in detail.

In my cultures, it took only about four weeks for the first small workers to arise (Tab. 1). These minute workers only lived for a short while, one month at the most (Tab. 2), whereas the workers generated later stayed alive for many months. Because the next, generally slightly larger series of workers had already grown up when the first small workers died out, the young colony as a whole suffered no harm.

To find out whether the smallness of the first workers is caused blastogenically or trophogenically, I transplanted eggs laid by very young queens into nests which had already brought up normal workers. Contrary to all expectations, the emerging young were again short-lived small workers (Tab. 2, no. 9 and 10). Only occasionally they were a little larger than those brought up by young queens alone. Thus, they developed according to their origin rather than their location, i.e., their smallness was determined in a largely blastogenic way.

In a number of cultures, the first soldiers developed already out of the second series of larvae, being tended and raised by the first small workers (Tab. 3). In one case, this happened so rapidly that a blastogenic cause was conceivable. However, continued examination showed that, although

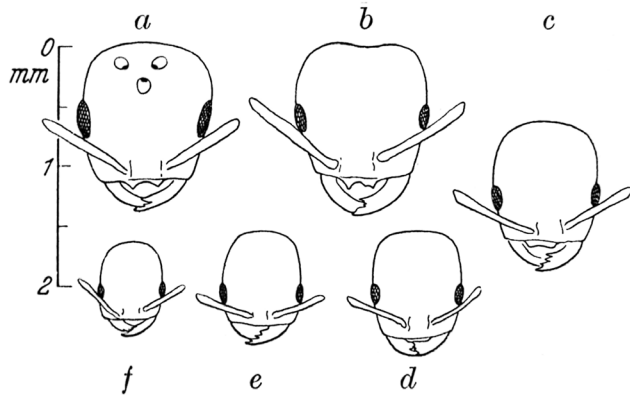


Fig. 1: Chilean ant *Solenopsis gayi* (SPIN.). Santiago. Heads (without antenna end segments). (a) Queen (with 3 ocelli), (b) "giant" (= worker attaining the size of queen), (c - e) transition forms, (f) smallest worker (= polymorphism of the worker caste). Left: scale in millimeters.

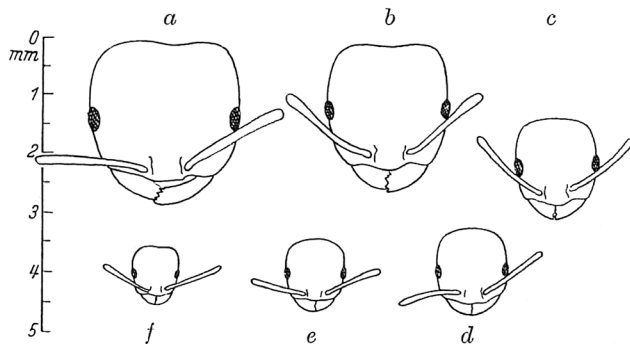


Fig. 2: Seed-harvesting ant *Messor structor* (LATR.). Mallorca. Heads. (a) Giant, (b) large worker, (c - e) middle-sized workers, (f) smallest worker (= polymorphism of the worker caste).

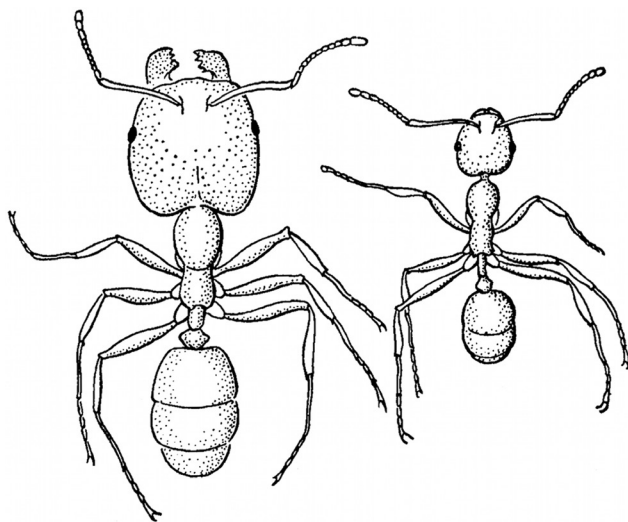


Fig. 3: "Soldier" and worker of *Pheidole pallidula* NYL. Capri (= dimorphism of the worker caste).

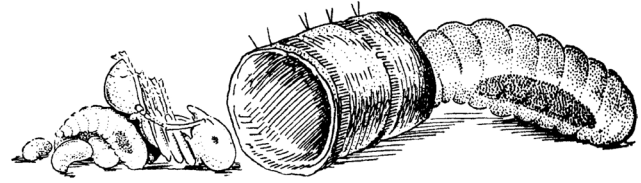


Fig. 4: *Pheidole pallidula* NYL. Capri. Left: middle-aged and older worker larvae and worker pupa. Right: soldier larva sitting at a food chunk, later turning into a soldier. **Comment:** A puzzling feature of this figure is that it does not depict *Pheidole* larvae (WHEELER & WHEELER 1976). The drawing is more reminiscent of poneroid larvae, which have flexible necks. *Pheidole* soldier larvae have heads closely held against stocky bodies, with little freedom of movement. Also, they are not motile. They have never been observed performing the feeding behavior described by Goetsch (S. Aron, M. Huang, pers. comm.).

only eggs from later series can give rise to soldiers, the actual expression of their form is determined trophogenically.

The first fact that caught my eye was that better nourished colonies delivered a higher number of soldiers. This observation prompted me to conduct a series of feeding experiments, the detailed description of which would go beyond the scope of this article. Generally, I divided the cultures into two groups, so that two cultures each had a comparable population strength and brood size. For ten days, one group was fed solely sugar water and honey, while the other group received chunks of flies or mealworms. After ten days, I switched the feeding regimen for fear of losses due to a too unbalanced diet. The duration of each developmental stage was known to be around ten days at 25 - 27°C (Tab. 1). Therefore, as soldiers arose in the colony, it was possible to calculate whether their egg, larval or pupal stage coincided with meat or sugar feeding.

These preliminary experiments showed that soldiers only arose when their larval stage coincided with meat feeding. This result was confirmed later in experiments lasting one month: Again, soldiers were raised only where meat was available.

To narrow down the period of time in which the determination to soldiers may take place, further experiments were undertaken, starting with a food switch (Tab. 4a). The cultures which, until then, had been fed meat and delivered soldiers, were now fed sugar, and vice versa. After a short while, soldier larvae, exceeding the normal size, developed in the nests which now received meat. All these soldier larvae developed into soldier pupae which eventually eclosed. Another result was that this happened only in colonies containing young larvae, aged five days or less. Larvae older than that developed only into workers, even when fed meat.

It was a more difficult task to narrow down these five days even further. I proceeded by putting together some small colonies without brood, in which the emerging larvae remained clearly visible. This is easier said than done, since young queens often kill their brood or even workers when disturbed. In two cases, I eventually managed to raise particular, previously chosen larvae into soldier pupae. In doing so, it became apparent that commencing meat-feeding on day four or five was sufficient for the determination to soldiers (Tab. 4b, no. 10).

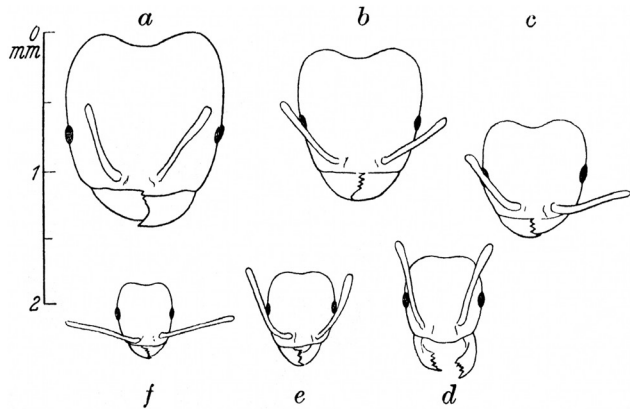


Fig. 5: Breeding results in *Pheidole pallidula* NYL. Culture Windsor C15. Capri and Breslau. (a) Normal soldier, (b) small soldier, (c) transition form, (d) large worker, (e) normal worker, (f) small worker (small soldier and transition forms are artificially produced).

Thus, the fate of the larvae is determined in a time span of – at most – two days. If they receive chunks of flies or mealworms during that time span, they develop into soldier larvae and then soldiers; if not, they remain workers.

In the experiments so far, the animals were fed solid food in one case, and liquid or semi-liquid food in the other case. Therefore, chemical composition as well as texture could be the decisive factor. The last experiments, carried out under constant control, revealed with particular clarity that those larvae which later grew into soldier pupae remained sitting at food chunks tossed in front of them and kept feeding on them all by themselves.

It is a peculiarity of *Pheidole* to carry pieces of captured insects into the nest as a whole and throw them to the brood, most often favoring larvae which have a certain head start. Thus, a few larvae remain seated at the chunks for days and obtain lots of nourishment. Liquid food, on the other hand, is distributed by the workers in a different way: They fill their crop and pass the liquid on drop by drop, sometimes here, sometimes there. In these cases, many larvae are getting fed, but each receiving only a little food. Therefore, I commenced feeding liquid meat and solid sugar, i.e., frog or rabbit blood, meat juice and raw egg white on one side, and hard bread crumbs soaked in sugar water on the other side. Again, I began with a food switch, after which the blood was consumed eagerly and distributed to the brood, drop by drop, in the manner described above. Thereby, it could clearly be seen that many, almost all larvae were getting fed: After a short while they exhibited red stomach content. At the same time, I carried out control experiments, in which I fed frog or rabbit meat: The chunks were thrown to only two or three larvae, which remained sitting at them.

After four weeks, soldiers developed only in cultures that had been fed meat chunks, whereas all larvae raised with liquid protein became workers. Later experiments, carried out for half a year, showed again that it is always the solid texture of the meat which is to be made responsible for the generation of soldiers (Tab. 5). This, in turn, is caused by the peculiarity of *Pheidole* to throw meat chunks directly to the larvae and let them eat constantly and without disturbance.

The fact that experiments with solid sugar did not yield similar results also has to be attributed to certain characteristics of *Pheidole*: Most often, they did not carry the sweet

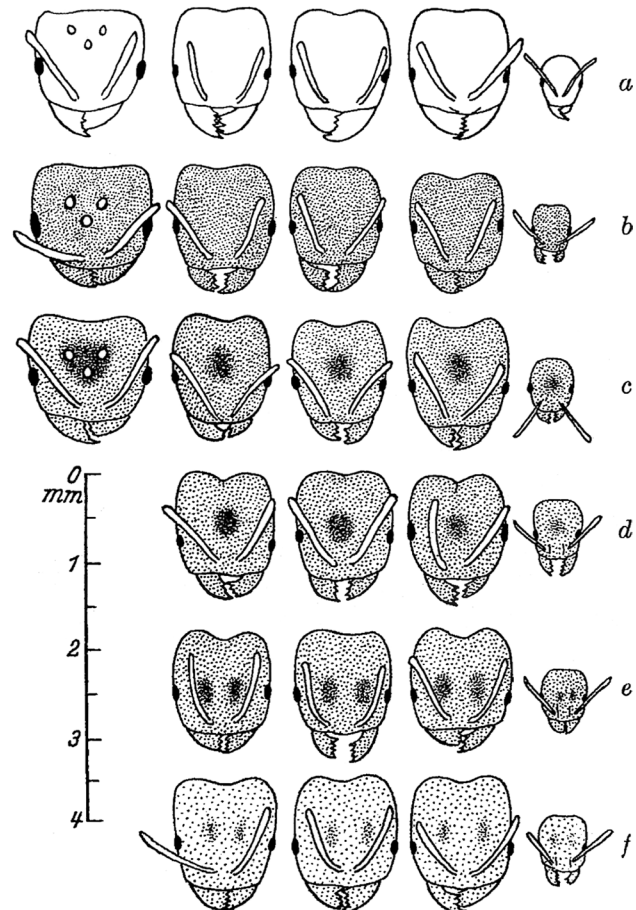


Fig. 6: Generation of races in *Pheidole pallidula* NYL. Left: queen (with ocelli), middle: 3 soldiers, right: 1 worker. (a) S. Alessandro B 29, Ischia; base color yellow; head without spots. (b) Tragara G8, Capri; base color dark brown; head without spots. (c) Windsor C15, Capri; base color brown; head with one spot. (d) Windsor F1, Capri; base color brown; head with one spot. (The animals in this colony are the “siblings” of the queen of the colony Windsor C15; remarkable similarity of color and pattern of the two generations.) (e) Tiberio B25, Capri; base color brown; head with 2 spots. (f) S. Romualdo B 44, Rovigno; base color light brown. (Among the workers, differences in color and pattern are less clear. The outline of the heads has been recorded using a Seibert-Promar apparatus, provided by the Deutsche Forschungsgesellschaft. They have subsequently been drawn by university illustrator Rose.)

Tab. 1: Duration of developmental stages in *Pheidole pallidula*. Column 3: mean of 30 queens.

Breeding conditions	28 - 30 °C Ischia	25 - 27 °C Naples	25 - 27 °C Capri
Egg stage	7 days	12 days	7 - 10 days
Larval stage	5 days	10 days	11 - 12 days
Pupal stage	13 days	11 days	8 - 13 days
Total duration	25 days	33 days	28 - 33 days

Tab. 2: *Pheidole pallidula*. First deaths.

Notes: 1. The number of dead ants is often higher in cultures raising the brood of several queens than in those with the brood of just a single queen (B24, G13). It should be noted that only some of the dead ants can be seen.
2. Even when transferred into other nests, the first eggs of young queens develop only into small, short-lived workers (D5, E4, E8).

Consecutive number	Culture	Notes	Workers eclosed	First dead	No. of dead	Age of dead (days)
1	B 1	1 queen	19 th Aug.	16 th Sep.	2	28
2	Na 3	1 queen	10 th Aug.	2 nd Sep.	1	18
3	G 15	1 queen	23 rd Aug.	20 th Sep.	2	28
4	B24	Originally 2 queens	20 th Aug.	4 th - 14 th Sep.	5	15 - 25
5	C 5/6	Originally 2 queens	18 th Aug.	2 nd Sep.	2	15
6	G 10	Brood of 4 queens	20 th Aug.	2 nd Sep.	2	15
7	G 13	Brood of 4 queens	20 th Aug.	11 th - 18 th Sep.	13	22 - 29
8	D5	Fert. eggs with unfert. queens	24 th Aug.	6 th Sep.	2	13
9	E4	First eggs with older queens	26 th Aug.	13 th Sep.	2	18
10	E8	First eggs with older queens	26 th Aug.	22 nd Sep.	2	27

Tab. 3: *Pheidole pallidula*. Emergence of first soldiers.

Notes: 1. In a number of cultures which later contained many soldiers (e.g., C15, B25), no soldiers arose in this second series of offspring. Also, the workers of this series were again small and short-lived.
2. Although in C 5/6, G8, G10 and G13, the brood of several queens was present, only one soldier each arose.
3. In G10, the first soldier pupa developed on day 17, i.e., 12 days after the first workers brought food chunks back into the nest for the first time. The egg which later became a soldier must have already been developed at that time.

Consecutive number	Culture	Notes	First workers eclosed, days after mating	Soldier pupa, days after workers	First soldier eclosed, days after workers
1	B 1	1 queen	31	25	42
2	B 3	1 queen	31	?	41
3	B 24	1 queen	32	25	40
4	Na 3	1 queen	35	25	36
5	C 5/6	originally 2 queens	35	25	36
6	G 8	1 queen + brood B7	33	27	-
7	G 10	1 queen + 3× brood	32	17	33
8	G 13	1 queen + 2× brood	32	24	?

crumbs into the nest, but licked them outside the nest until their crop was filled. In those cases where they did carry the crumbs into the nest, they did not throw them directly to the brood. Apart from that, sugar is certainly not suitable as the sole nutrient for *Pheidole*, as was observed repeatedly: They quickly become oversaturated with it and remain, when fed sugar exclusively, in a constant hunger-like state.

Thus, the result of these feeding experiments is as follows: If, during a particular, brief period of time, the larvae receive an abundance of concentrated, solid food, so that they can rapidly grow much larger, they develop into soldiers. If not, they become workers.

Now, it has been known for a long time that the size of soldiers can vary slightly.

Does this fact fit in with their now clearly ascertained trophogenic generation? I certainly believe so, because the larvae continue feeding even after their ultimate determination to the soldier type. If they continue to be well nourished, they grow large; if not, they remain small. It is the same with workers, once their fate has been determined.

At any rate, it was possible to experimentally generate large workers (Fig. 5d), in addition to the first small workers arising out of the first eggs (Fig. 5f) and the bulk of normal workers (Fig. 5e). Similarly, one can obtain small soldiers (Fig. 5b) in addition to normal soldiers (Fig. 5a). Finally, it is possible to obtain large soldiers, though these are an exception in *Pheidole*. Such large soldiers, with heads bigger than that of the queen, need to be considered a somewhat pathologic hypertrophy, only arising under certain conditions. Maybe a blastogenic factor also plays a role, one that induces the generation of a few particularly large eggs in older queens. Under exceptionally favorable food conditions, these eggs may develop into such unnaturally large soldiers. Incidentally, they are handicapped, rather than aided, by their giant heads.

The forms described so far could still be attributed to one caste or the other, and I strived to obtain true transition forms between workers and soldiers. By feeding colonies sugar and giving them a few meat chunks just once, and by disturbing the feeding larvae in various ways, I obtained two pupae which were actually in the middle. One of them eclosed: The 3 mm long imago was exactly in the middle between a normal worker and a normal soldier (2.50 mm and 3.75 mm), and its head could serve as the end of a worker series or as the beginning of a soldier series (Fig. 5c).

This artificial creation of intermediate forms and small soldiers in *Pheidole* successfully bridges the gap between species with dimorphic and those with polymorphic worker castes. Hence, it may be necessary to slightly revise the systematics, as it is precisely the lack of intermediate forms in the genus *Pheidole* that is adduced as a hallmark when compared to the subgenera *Allophidole* and *Cardiophidole* and the genus *Ceratophidole*. The reason why intermediate forms arise naturally in the genera and subgenera mentioned above, but can only be "constructed" artificially in *Pheidole*, is, of course, as yet uncertain. In *Messor* species, one can at

Tab. 4: (a) Generation of soldiers when fed meat or sugar. (b) Generation of soldiers when fed liquid or solid protein. SL = soldier larva, developing into soldier pupa (SP) and then soldier. Soldiers were only raised when young larvae received solid meat (insects, frog meat), never when they received sugar water (Tab. 4a) or liquid protein such as blood or meat juice (Tab. 4b). In culture G24, the meat-eating larva, which turned into a soldier pupa, was watched daily.

Tab. 4a:

No.	Culture	Notes	Food	Result after 5 days	Result after 10 days	Result after 20 days
1	Na 3	Old larvae	Meat	–	–	–
2	G 13	Old larvae	Meat	–	–	–
3	B 3	Old larvae	Meat	–	–	–
4	C 15	Young larvae	Meat	1 SL	3 SL	2 SL, 2 SP
5	G 8	Young larvae	Meat	2 SL	6 SL	3 SL, 4 SP
6	D 1	Old larvae	Sugar	–	–	–
7	B 27	Old larvae	Sugar	–	–	–
8	B 25	Young larvae	Sugar	–	–	–
9	G 15	Young larvae	Sugar	–	–	–
10	K 1	Young larvae	Sugar	–	–	–

Tab. 4b:

No.	Culture	Notes	Food	Result after 5 days	Result after 10 days	Result after 20 days
1	Na 3	Old larvae	Liquid	–	–	–
2	G 15	Young larvae	Liquid	–	–	–
3	B 1	Young larvae	Liquid	–	–	–
4	B 25	Young larvae	Liquid	–	–	–
5	K 1	Young larvae	Liquid	–	–	–
6	B 3	Young larvae	Solid	–	–	–
7	C 15	Young larvae	Solid	2 SL	6 SL	6 soldiers
8	G 13	Young larvae	Solid	1 SL	1 SP	1 soldier
9	G 8	Young larvae	Solid	3 SL	3 SP	3 soldiers
10	G 24	3 young larvae	Solid	1 SL	1 SL	1 SP

Tab. 5: Generation of soldiers in *Pheidole pallidula* as a result of varied feeding. Experiments from 22nd Aug. 1936 to 22nd Feb. 1937.

SL = soldier larva, developing into soldier pupa (SP) and later soldier (Sold.) Soldiers were raised only when larvae were fed meat chunks (MC); feeding sugar juice (SJ), sugar chunks (SC) or meat juice (MJ) only led to workers. In culture Windsor C15, intermediate forms (IF) were successfully generated by a short, single dose of meat in a period of sugar feeding (Fig. 5c).

Time	Culture Solaro G8		Culture Tiberio B 35		Culture Tragara B3		Culture Windsor C15	
	Food	Result	Food	Result	Food	Result	Food	Result
- 2 nd Sep.	MC + SJ	SL	MC + SJ	–	MC + SJ	SL	MC + SJ	–
- 1 st Oct.	MC + SJ	Sold.	MC + SJ	Sold.	MC + SJ	Sold.	MC + SJ	Sold.
- 16 th Oct.	MC	SL	MC	SL	SJ	–	SJ + 1 MC	IF
- 9 th Nov.	MC	SP	SJ	–	MC	SP	MC	SL
- 23 rd Nov.	MC	SL	MJ	–	MC	SL	MC	SL
- 28 th Nov.	Hunger	–	MJ	–	Hunger	–	MC	SL
- 6 th Dec.	SC	–	Hunger	–	SC	–	Hunger	–
- 17 th Dec.	SC	–	MC	SP	SC	–	SC	–
- 6 th Jan.	MC	SP	MC	SP	MC	SP	MC	SL
- 15 th Jan.	Hunger	–	Hunger	–	Hunger	–	Hunger	–
- 27 th Jan.	MC	SL	SC	–	MC	SL	SC	–
- 2 nd Feb.	MC	SP	MC	SP	MC	SL	MC	SL

least speculate. According to our examinations, development is much slower in *Messor* than it is in *Pheidole*. It takes 24 - 29 days until the eggs hatch, 16 - 23 days until larvae turn into pupae, and 17 - 28 days until workers emerge from them. The larvae are often fed solid food, such as insect parts, bitten grains and ant bread, which is made out of masticated seeds. The slower development increases the likelihood of a disturbance or a change of food type, and optimal conditions are seldom realized. Thus, only a few giants arise, but a multitude of intermediate forms.

The situation is probably the same in *Atta* species; the durations of developmental stages elucidated so far are similar to those of *Messor*.

These results of experiments on *Pheidole pallidula* are in accordance with observations I had made earlier in Chile. There, *Pogonomyrmex bispinosus* only had workers of the giant type, while closely related Mexican and Argentinian species exhibited polymorphism. In artificial nests I could see that the Chilean form gives solid food to the larvae; I also observed that "the larvae mostly remained in one spot and did not get carried around, as they are in *Messor*" (GOETSCH 1932). Thereby, they can feed undisturbed and turn into soldier larvae in the critical time period.

In *Solenopsis gayi* SPIN. it was observed that animals living in the north of Chile carry grains into the nest and give the chewed seeds to the larvae as ant bread. Only in those regions giants could be found (GOETSCH 1935), albeit not in each and every nest. The polymorphism was most pronounced in those nests that had access to various foods, and almost completely vanished in the South, where *Solenopsis gayi* fill their crops and feed their larvae from it, similarly to our *Lasius* species.

Thus, different diet can easily lead to forms so different from one another that they appear as geographic races, maybe even as distinct species or genera. A naive collector, without knowledge of the real situation, would not consider a *Pheidole* worker and a *Pheidole* soldier conspecifics, let alone siblings!

It is also noteworthy that ants, in addition to such externally caused forms, also establish real micro-races (mutations). This tendency is particularly strong in *Pheidole*, as exemplified in Fig. 6. Cross-breedings between such micro-races (which have been observed directly), in conjunction with the influence of external conditions, give rise to a great abundance of forms, which in ants often leads to the introduction of five-fold names.

The ability to transform dimorphic species into polymorphic ones by appropriate means is apt to end discussions that have been going on for some time. It stood to reason that polymorphism and dimorphism somehow belong together, and it also seemed natural to assume that the gap between workers and soldiers could be explained by extinction of the intermediate forms.

In doing so, it was implicitly assumed that such intermediate forms did exist at some point in time and vanished only because of certain causes, perhaps selection. These are prerequisites derived from the theory of evolution, where they play a role in the assembly of incomplete morphoclines. Yet, the observations in *Pheidole* show that such intermediate forms are not extinct, but are simply not realized because of certain developmental processes, which in turn are influenced by external conditions. Conversely, we may even be able to apply these experimentally demonstrable processes to incomplete morphoclines, i.e., we can speculate

that intermediate forms, which have been assumed to have been real, have never been alive, because they have not been realized in the first place.

Inspired by the *Pheidole* experiments, thus, it is quite conceivable that presumably extinct forms have actually never existed. On the other side, the similarity of some ant or termite soldiers to extreme forms of fossil animals can hardly be ignored. Especially when one has to realize that those exaggerations, outfitted with giant heads and mighty mandibles, can only stay alive as long as the circumstances allow it. Whenever there is a change for the worse in an ant or termite colony, the soldiers are the first to die. In *Pheidole pallidula*, MENOZZI (1936) has recently demonstrated once more the disappearance of soldiers in winter, and I could demonstrate the same in *Calotermes flavicollis* in an artificial nest (GOETSCH 1937).

Now that we know a little more about the generation of soldiers, we need to examine the generation of the other castes of ant colonies in more detail. After the present observations, which are expanded on in a recently published work (GOETSCH & KÄTHNER 1937), there can be no doubt that males, as in bees, arise out of unfertilized eggs, and are therefore determined genetically. Size and shape, on the other hand, can be influenced by external conditions such as nutrition, but also by the differently developed ovaries of queens or egg-laying workers. In order to answer the question why, in one case, the progenitress of a colony arises, and in other cases vestigial females, i.e., workers and soldiers, a multitude of experiments have already been performed, with remarkable results in *Pheidole*, *Leptothorax* and *Lasius*. It seems that the formation of queens is governed by an interaction between internal and external conditions, just as in the generation of soldiers, maybe as in any developmental process. Certain prerequisites of a more blastogenic kind need to be present, which allow external factors to intervene in order to form the ultimate shape, and intervene only in a specific, transient phase of readiness. If we manage to approximate these conditions, it may be possible to "construct" true ant queens in a similar way as it has already been successfully done with ant "soldiers."

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Novel termite soldiers out of artificial nests

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In termites, there are generally two types of soldiers, namely the normal soldiers or “jaw-soldiers” (mandibulates) with greatly enlarged heads and mandibles, and the “nose-soldiers” (nasutes), with a giant frontal gland that has its opening at the end of a long, nose-like cone. In nose-soldiers, the jaws are generally completely reduced. Exceptions to this are the “fork-nasutes” of *Rhinotermes*, which are organized in a completely different way, and also some species in the genus *Armitermes*. The latter termites have long, slender, serrated jaws, which intersect under the “nose” (*Armitermes neotenicus* HOLMGR.).

These so-called “jaw-nasutes” resemble the soldier form described and depicted here, following a detailed examination by K. Offhaus (Figs. 1 - 3).

The upper part of the head is covered by golden chitin, has a semi-circular contour at its backside and sits on the head like a cap. Inside of it, several muscle bundles - which move the mandibles - can be seen (Fig. 1). The “nose” is slightly curved; the pore of the gland is at its tip. No trace of the labrum can be found; it seems to be incorporated into the formation of the nose, as evidenced by developmental stages.

At the head capsule, the antennal fossa is clearly visible. When observed superficially, the antennae appear to have twelve segments. A microscopic examination, however, reveals a short, spherical scape, followed by a second, regularly shaped segment. The third segment, which is about as long as the second one, carries a small indentation. The fourth segment is half as long as the second one, while the fifth segment has about the same length. Nine other segments of equal length follow (Fig. 1); the soldier thus possesses 14 antenna segments.

When viewed from below, the head shows a well-formed labium with submentum and mentum, at which the labial palps are attached (Fig. 2). Glossae and paraglossae are present and hardly less developed than in workers. The labial palps have three segments, the first segment being half as long as the second one and the third one just as big as the second one. The mandibles of the soldier are not serrated (Fig. 3), but smooth and dagger-like. The tips do not cross. The maxillary palps have four segments, the first segment being half as long as the following three (Fig. 2).

For comparison, let us briefly describe the head of a worker of the same nest. Viewed from below, it exhibits an oval head with a big labium. The antennae are made up of 14 segments; the dark-colored mandibles are armed with four strong teeth. The maxilla carries a four-segmented maxillary palp. The lacinia is strongly chitinized. The labium is slightly broader and longer than in the soldier

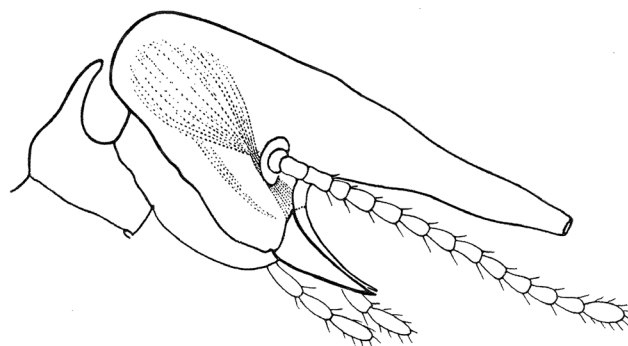


Fig. 1: Head of a soldier of *Anoplotermes cingulatus* (n. var.?), attained in an artificial nest. (In the wild, all *Anoplotermes* species are invariably devoid of soldiers.)

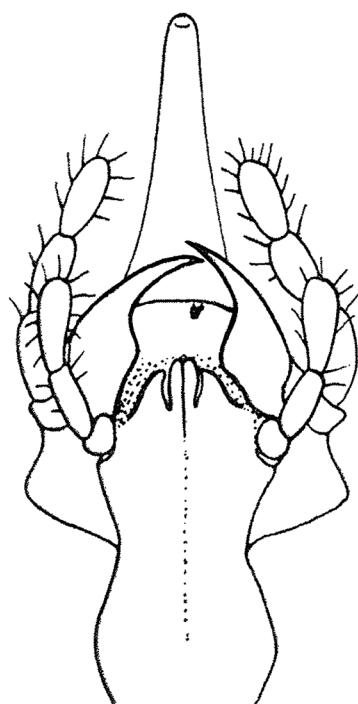


Fig. 2: Head of the same soldier as in Figure 1, ventral view.

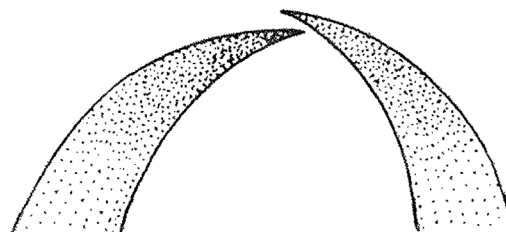


Fig. 3: Tips of the jaws under higher magnification; without any teeth.

and resembles that of Blattidae; a three-segmented labial palp can be seen at the mentum, along with well-developed glossae and paraglossae.

As of yet, we have not said anything about the species which the soldier described here belongs to. This happened on purpose, because it originated in an artificial nest, whose winged founders are of the genus *Anoplotermes*. Dr. C. von Rosen, to whom I owe a more accurate classification, placed

Tab. 1: *Anoplotermes cingulatus* (n. sp?). Foundation of colonies. (Only colonies which raised several young are represented here.)

No.	Culture	Nuptial flight	First eggs	First workers	Worker development finished	Enlargement of founding chamber	Highest no. of workers	Nest content as culture was killed
1	T.16	28 th Sep. 1937	7 th Oct. 1937	3 rd Dec. 1937	13 th Jan. 1938	21 st Jan. 1938	at least 13	Queen, king (23 rd Feb. 1939)
2	T.3	27 th Sep.	7 th Oct.	28 th Dec.	29 th Jan.	–	at least 7	Queen, king (3 rd Mar. 1939) 3 adult workers 1 adolescent worker 1 adult soldier
3	T.18	28 th Sep.	7 th Oct.	3 rd Dec.	3 rd Jan.	29 th Jan.	at least 15	Queen, king (25 th Feb. 1939) 5 adult workers 5 adolescent workers 3 soldier larvae 1 egg
4	T.17	28 th Sep.	7 th Oct.	14 th Dec.	10 th Jan.	–	at least 14	Queen, king (11 th Feb. 1939) 3 adult workers 1 adolescent worker 1 adolescent soldier 1 egg
5	T.19	28 th Sep.	18 th Oct.	7 th Dec.	1 st Jan.	–	at least 8	Queen, king (5 th Feb. 1939) 4 adult workers 1 worker larva 1 indetermined larva

Tab. 2: Overview of antennae and mandibles in termites with jaw-nasutes, and comparison to some *Eutermes* and *Anoplotermes* species.

No.	Species	Antenna segments	Mandibles
1	<i>Eutermes arborum</i> worker ... soldier ...	14 13	serrated –
2	<i>Eutermes laticeps</i> worker ... soldier ...	14 13	serrated –
3	<i>Eutermes latifrons</i> worker ... soldier ...	14 13	serrated –
4	<i>Eutermes chaquimayensis</i> worker ... soldier ...	14 14	with 4 teeth rudimentary
5	<i>Armitermes odontognathus</i> worker ... soldier ...	? ?	? serrated
6	<i>Armitermes peruanus</i> worker ... soldier ...	14 14	with 3 teeth toothed, saber-like
7	<i>Armitermes neotenicus</i> worker ... soldier ...	14 14	with 3 teeth toothed, heavily curved
8	<i>Anoplotermes cingulatus</i> var. worker ... soldier (only in artificial nest)	14 14	with 4 teeth toothless, dagger-like
9	<i>Anoplotermes</i> sp. worker... no soldiers	14 –	? –
10	<i>Anoplotermes iheringi</i> worker ... no soldiers	14 –	? –

them in the vicinity of *Anoplotermes cingulatus* (BURM.) SILV. And yet, the genus *Anoplotermes*, as the name suggests, is devoid of weapons and soldiers. For example, S. T. Light in KOFOID (1934) says: “The species of this genus are the only

termites lacking soldiers.” HEGH (1922) comments on this genus: “Special trait: absence of soldiers,” and HOLMGREN (1912/13) notes: “Soldier completely absent.”

There are thus no soldiers in *Anoplotermes* under natural conditions, and the question arises as to whether the unnatural upbringing in a glass tube can be made responsible for the generation of soldiers. Therefore, a brief account of the history of the colony in question, as well as its parallel breeds, is to be given.

The founders originate from a swarm which was observed at the Iguazú river, the eastern tributary of the Paraná. After their capture they were put into a glass tube with a cork pad and soil (on 27th Sep. 1937), and they immediately began with the “love walk.” Afterwards, a chamber was constructed, and on 7th Oct. the first eggs were to be seen, being carried around in the mandibles. The number of eggs increased: On 28th Oct., six; on 13th Nov., eight; on 7th Dec., ten eggs were found, whose size varied slightly. Eggs also vanished sometimes, and in this culture as well as in the parallel ones the couple was observed eating its own eggs on several occasions.

It was not until 28th Dec. 1937 that the first larva hatched, later than in the other glasses. In those other cultures, incidentally, the number of eggs was generally higher and the first young arose already between 3rd and 10th Dec. 1937.

One by one, more animals hatched: On 4th Jan. 1938, I could already count four larvae of different sizes.

At this time, I almost considered my termite cultures lost. The expedition had led me into the high Cordillera, and the cold of a snowstorm petrified the termites, which, after all, originate from the subtropics. I could only keep them alive by carrying them beneath my clothes, and so they survived this hazard.

Later on, they had to endure even more perils! I remember the shaking during the marches, which they eventually got used to, and the rocking and tossing of the ship and the train. Furthermore, they even experienced a foray by ants, which had escaped from a neighboring tube and actually destroyed two cultures before I could intervene. Thus, only a few of the young termite colonies arrived in Breslau unscathed, where the last one (T.3) lived until 3rd Mar. 1938.

The other colonies began to die out a little earlier, after many larvae had hatched and grown into fully developed workers (Tab. 1). Apparently, proper nourishment was lacking. In order to find out whether winged termites, just like *Atta* ants, bring along fungi for their manure beds, I had placed the termites not into soil from Brazil, which may have already contained the fungi in question, but into soil from Breslau. It was only a matter of chance that I had this soil at my disposal at the Iguazú, as my students had presented me with a small bag of "home soil" as a talisman upon my departure. As I determined later, this soil contained all sorts of organic substances, and the young growing workers, devouring the soil, certainly obtained nutrients from it. According to HOLMGREN (1906), whose statements I can confirm, *Anoplotermes* termites in the wild live in corridors in the soil, without building large constructions. In any case, the termites in my artificial nests refused to accept duff, decayed leaves or other things which are normally to termites' taste. Instead, they kept eating the soil time and again, which thereby passed their intestines several times. Presumably, they were missing something which is present in the wild, i.e., probably a fungal flora which may be growing in the soil or in the dung of the nest. Eventually, the only food left was that which the small colony itself produced: The eggs and the carcasses of the workers, which died off one by one. Hence, from a certain moment on, the termites only had this food, and it is noteworthy that the generation of soldiers commenced at this moment. Before that, all growing larvae developed into young workers, a fact which was observed not only in living animals, but also in the killed ones: With hindsight, it was fortunate that two cultures had been extinguished by ants, otherwise I would not have preserved this material at its level of development (Tab. 1, culture T.17 and T.19). The termites which had almost or fully completed their development while the good times lasted were true workers.

Not so those which grew up later. They, too, emerged from the egg as normal, small-headed larvae. Also, one indetermined larva was excised from an available egg (Tab. 1, culture T.18). However, when a period of unnatural conditions set in during their development, they altered their shape: All middle-aged larvae present in the older cultures as they died out already represented transition stages to soldiers. As shown in the table, one young worker larva was still to be found in culture T.19, which was the first to die off (5th Feb. 1938). In the older cultures, which were already deep in the period of altered conditions, no more worker larvae were present. In particular, three larvae of culture T.18 were profoundly altered: They exhibited a longer head and a labrum which was elongated to form a large cone, rooted far back at the head. This cone bore the gland at its base and was certainly the foundation for the future "nose". A somewhat older stage of the same culture did not exhibit this extreme shape, and even less so did the larvae of culture T.17, but even in those specimens a marked reshaping towards the soldier morphology was noticeable.

The longer the cultures stayed alive and the longer, therefore, the unnatural conditions stayed in effect, the more pronounced the tendency towards generation of soldiers was (Tab. 1). Finally, the question arises as to what may be responsible for this.

In ants, it has been demonstrated that feeding solid protein causes the generation of soldiers. This result was

subsequently confirmed by a multitude of examinations in Breslau and South America (GOETSCH 1937, 1939a, b). It is possible that this is also the case in termites, i.e., that forced feeding on their own brood is to be made responsible. It is also possible, however, that the lack of certain substances, which are always available under natural conditions, induces the generation of soldiers. After all, the observed phenomenon is certainly an induction of an already existing tendency, i.e., a developmental capability which in *Anoplotermes* remains without effect only because certain prerequisites, which do not occur in nature, are lacking.

Certainty about this can only be established through further experimentation. Yet one fact is already to be emphasized: In *Anoplotermes*, the generation of soldiers is induced by specific external influences, i.e., by so-called trophogenic or somatogenic conditions. This can be concluded with certainty from the experiments, since there wasn't merely a single soldier arising by chance, but all larvae of a certain age began to develop in this direction in various cultures, whereas nothing like this was noticeable earlier.

This novel soldier form, which so far only appeared in artificial nests, is important not only from a viewpoint of developmental physiology, but also gives us clues about systematics and phylogeny. First of all, it divests the genus *Anoplotermes* of its distinctiveness, which it still possesses in, among others, Escherich's systematic compendiums (ESCHERICH 1909). Because of its latently present but not naturally realized soldiers, it joins sides with *Armitermes*. Those termites, in turn, are close to the *Eutermes* species (as defined by Wasmann), i.e., close to the species with true nasutes (Tab. 2). Their detailed analysis (also of the workers) shows this most clearly. What Holmgren says about *Armitermes odontognathus* thus applies especially to our *Anoplotermes* soldier: It assumes a perfectly median position between true mandibulates and true nasutes, since it features both traits.

As for the mode of generation of soldiers, we can thus conclude the following: In termites, we have the possibilities of an exaggerated expression of the mandibles as well as the frontal glands, which are normally realized only separately. These possibilities are rooted in the genetically determined reaction norm. If any of them is realized at all, and how the morphology is ultimately formed, is determined, according to the present observations, by environmental influences.

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