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THE ORIGIN OF THE CASTES IN TERMITES.

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Of great interest to the biologist are the two views of the origin of termite castes, both based upon observation and experiment. According to the first view, held by the Italian entomologists, Dr. B. Grassi (15), Dr. Carlo Jucci (18) and (19), and others, the young are all alike and undifferentiated at the time of hatching, but differentiate into the various adult castes through the influence of external factors of immediate environment, such as food, the presence of protozoan parasites, the care received from the older workers, etc.

According to the second view, held by Thompson and Snyder (24, 25, 26, 27) and others, the young are not all alike at the time of hatching, but the castes are hereditary; some, if not all of the different castes are distinguishable from the beginning, and the castes are therefore predetermined in the egg or embryo by intrinsic factors.

The late Dr. C. B. Thompson (25 to 29) has proved that the ontogenetic origin of the castes of the termite *Reticulitermes flavipes* Kol. is due to intrinsic causes or germinal origin, and not to the extrinsic stimuli, which have long been credited with formative, indeed, almost creative powers. The fertile and sterile types as nymphs are internally differentiated at the time of hatching and very early in their post-embryonic development all the adult castes may be distinguished, disproving the hypothesis of determining or changing the castes by external means. Dr. Thompson believed (29) that the castes originated by segregation from a heterozygous parent form!

Dr. Carlo Jucci, in (18) and (19), in papers supporting the views of Grassi on the creative power of immediate environment, reopened the discussion of the differentiation of the castes

0673

in termites. Jucci not only disagrees with the results of Thompson's careful work, which proved the embryonic differentiation of the castes and that the "complementary" or "substitute" reproductive forms represent distinct hereditary castes, but also with the support given to this theory by Snyder's biological work (22 to 24).

Among termites, aside from the deälated reproductive adult which develops from the winged, colonizing, first form adult, there are both brachypterous and apterous reproductive adults. (Plate I, figs. 6, 7 and 8.) These adults develop, respectively, from nymphs of the second form, with short wing pads, and from apterous nymphs of the third form. In addition there are several abnormal or "intermediate" reproductive adults.

Jucci claims that the deälated reproductive form is the only *true adult* and that these other reproductive forms are merely "complementary" or "substitute neoteinic" forms. His proof is the peculiar, characteristic pigmentation of these forms, which only can be explained by him as an arrested development, i. e. this is not a *specific* character of a caste but the morphological expression, through the accumulation of catabolic products in the skin, of a physiological state to be attributed to a special diet.

Jucci states that he has proven that there is a definite correlation between the food and the peculiar pigmentation of these "neoteinic" forms. However, this theory may be disproved by merely following the development of the nymph of the first form (winged, colonizing adult) through to the post-adult stage. During this development of a *single individual* there is a wide range in the food, but no abnormal pigmentation occurs.

TABLE I.

*Development of the first form adult of Reticulitermes flavipes Kollar correlated with Food, Intestinal Protozoa, and Pigmentation.*

Nymph with long wing pads.	Young winged adult before flight.	Young winged adult after flight.	Post-adult, jaw muscles degenerate.
Food wood, protozoa present in intestine.	Food little or no wood, most of protozoa have been lost.	Food wood, protozoa present.	Food special diet from workers, no wood eaten, no protozoa.
Pigment lacking.	Pigment mature, dark.	Pigment mature, dark.	Pigment mature, but lighter, less dark.

While there is a definite correlation between the pigmentation of all of the reproductive adults and their exposure to sunlight, there is no correlation between this pigmentation and their food. The post-adults, although fed by the workers on a special diet, do not attain any of the pigmentation characteristic of the neoteinic forms, although there is a marked post-adult growth; the new tissue remains colorless, as in the nymphs from which they develop.

Furthermore, Snyder has shown (22, 23, 24) that the second form (brachypterous) nymphs develop in large numbers in certain colonies every spring; they occur in association with nymphs of the first form (with long wing pads) in the outer layers of the wood in which the colony is located; here conditions of temperature and humidity are most favorable for rapid development. Finally, these nymphs of the second form pass through a quiescent stage, similar to that through which the nymphs of the first form pass in developing to the winged adult, and develop to adults of the second form. Nymphs of the third form (apterous) have a similar development from apterous nymphs, but owing to the strong superficial resemblance between these nymphs and young adults and the worker caste, while they occur, they are difficult to detect in colonies.

If these brachypterous and apterous types of reproductive forms are not *true adult castes*, why do they normally develop in large numbers each year in colonies? Also why is there such variation in the composition of colonies each spring, with regard to the relative abundance of nymphs of these three forms? There is no need for them in the parent colony and hence it must be assumed that they are a colonizing form. These unnecessary reproductive adults then must either migrate to form new colonies, die, or be killed by the workers. If taken and placed with workers in artificial colonies, these forms will reproduce and live for years, establishing large colonies and breeding true to type. Unless workers are present to feed them, however, they will die, since they contain (as adults) no intestinal protozoa to digest the cellulose of wood for them.

However, how are new colonies founded in nature by brachypterous (second form) adults? What becomes of the large numbers present each year in parent colonies at the time of the swarm? They disappear at this time. While these brachyp-

terous adults appear to be able to endure full sunlight (as in the "pseudoflight"), it is quite probable that with workers and soldiers they normally have a subterranean colonizing migration. The workers and soldiers are attracted to the reproductive forms by their exudate.

With these facts, showing the normal progeny of colonies of *R. flavipes*, why should there be any need for the workers to "manufacture" complementary or substitute reproductive forms by arresting or checking by means of special feeding the development of nymphs of the first form to the normal winged adult. When or how this development is checked, neither Grassi nor Jucci elucidate.

Again, adults of the first, second and third forms display marked structural differences in head, eyes, and thorax (and legs in *Termopsis*)! It has never yet been proven that qualitative feeding can produce *marked structural changes*; such is not the case even in the case of the honeybee.

While Dr. W. M. Wheeler states (31) that qualitative feeding can not produce morphological differences in the worker, he also states that quantitative feeding may produce diminution of stature and some of the atypical phases found in ants. This is also true in the case of the termites. Wheeler (33) also grants that even if the caste of an ant be determined in the egg, special feeding of the larva may be necessary to bring it to maturity.

But since the work of Dr. J. Feytaud (13), Thompson, etc., shows that the castes of termites are already determined at the time of hatching, food can not determine the castes.

In the case of the "orphaned" colonies, where the parent reproductive forms have been lost, young forms, capable of reproduction, are already present in the colony, as nymphs in various stages of development to the typical adult, winged, brachypterous or apterous. These forms are utilized, but not created. Doubtless, however, their development is hastened by special care and feeding. If young nymphs are lacking at this time, older forms in various stages of development may be utilized—even partially developed winged adults.

Furthermore, if food could determine the castes, and at a late stage in the development of individuals to maturity, why are not fertile workers and soldiers "produced"?

Of course the care of and feeding of the young and repro-

ductive forms of termites by the workers is explained by "trophallaxis" (Wheeler (32)), or an exchange of nourishment, a purely selfish relationship. Snyder (23).

While the sex organs of soldiers of species in certain genera are well-developed none has been found that actually has laid eggs. Although soldiers with wing pads occur in species of several genera of the Kalotermitidae, this is not an indication of the maturity or functioning of the sexual organs. Heath's data (16) on fertile "soldiers" in *Termopsis* may admit of another interpretation when further studies of these forms have been conducted. Dr. Heath in a statement to the writer in December, 1924, stated that he has seen soldier-like forms laying eggs. These individuals have shorter heads than the normal soldier and the hairs on the abdomens are as in the reproductive form. This form is probably an "intermediate" reproductive form.

In the case of the non-social insects, various brachypterous and apterous reproductive forms occur within the species in the Zoraptera, Orthoptera and Hemiptera; notably among the aphids, where, according to Dr. A. C. Baker, there are "intermediates" with a loss of eyes and wings or loss in the length of the wings. The factors influencing the origin of these forms are apparently different than in termites; these non-social insects are not comparable to the social insects.

Dr. E. D. Ball (1) states:

"Migration is an adaptation that enables species to occupy regions which would otherwise be uninhabitable. \* \* \*

"There is another type of migration in which only certain specially modified individuals take part. Many modifications of this kind are found in the arid regions of the western country. Most of the leafhoppers that feed on the short grasses have abbreviated wings, an adaptation which enables them to move about freely in these tangles. The areas they inhabit are subject to periodic droughts in which animal life, including even the insects, may be destroyed. These insects have a special migratory form with slender body and long wings that is capable of flying long distances. These migratory forms always appear very early in the season from the first nymphs that mature. Within a few days of emergence they fly away to other regions and thus distribute the species, leaving only the normal short-winged forms in the original location.

"The Rocky Mountain Locust which was so destructive in the western regions from 1872 to 1876, was considered to be a distinct migratory species of grasshopper (*Melanoplus spretus*). Studies made during the recent

outbreak have shown that this grasshopper is not a true species but only a specially modified long-winged migratory form of the common injurious grasshopper of the northern part of the United States (*Melanoplus allanis*). Production of excessive numbers of the migratory form is probably correlated with periodic droughts. It is probable that migratory forms are present in many species in which they have not as yet been recognized."

In Italy, Grassi and Jucci find that the sexes swarm at different times from the same colony, and that no "true kings or queens" (developing from winged, migratory, first form adults) heading termite colonies (*Reticulitermes lucifugus* Rossi) occur in nature; the parent reproductive forms are those with short wing pads (developing from nymphs of the second form), and in case of these forms, the males do not live long after mating. These abnormal conditions in the biology of this termite seem to be unique and are peculiar to Italy.

It may indeed be, as Silvestri states (21), that climate determines which reproductive form can survive—but each type develops yearly, even in Italy, and even if conditions are unsuitable for the establishment of new colonies. Jucci explains that "true queens" are unnecessary in Italy because of the presence of "neoteinic" forms. However, the latter forms are present in the United States and elsewhere, where "true queens" (first form) also occur. It is peculiar that, if the climate is a factor of such importance, while "true queens" do not occur in nature in colonies of *Reticulitermes* (according to Grassi and Jucci), they do occur in colonies of *Kalotermes* in Italy. Of course there is some difference in the habitat.

The careful work of Dr. L. R. Cleveland (11) and (12) has proved that the intestinal protozoa have nothing to do with sterility or caste production in any of the three families (*Kalotermitidae*, *Rhinotermitidae* and *Termitidae*) of termites. For when wood is eaten by an individual of any caste, except normally in the *Termitidae*, protozoa are present and in the more highly specialized family *Termitidae*, many species of which do not feed on wood and which do not harbor protozoa in the intestines, sterility and caste differentiation occur as in the other termites. Protozoa occur in the intestines in a symbiotic, not in a commensal or parasitic, relationship and digest the cellulose which is the principal food of most termites. When the post-adult reproductive adults of certain species of the

Kalotermitidae feed on wood, protozoa are present. Grassi, in his hypothesis, did not correlate wood diet and the presence of protozoa!

With regard to the role of nutrition, Prof. E. Bugnion's (3 to 9) careful studies of certain termites (Termitidae) of Ceylon prove that there is no evidence of special feeding, since all the young forms receive the same food and the same care or lack of care. Dr. H. Heath's work (16) in California led him to conclude that food was not a factor in caste determination.

Dr. C. B. Thompson's work with *thirteen* species, in *nine* genera, of American termites has proven that although newly hatched young are exactly alike externally, there are marked internal differences; all the fertile forms can be recognized from the sterile ones especially by the larger brains, eyes and sex organs. In a very short time all of the castes can be distinguished. (Plate I, figs. 3, 4 and 5.) Thus we may say that the castes of termites are due to heredity and not to their immediate environment, as is claimed by Grassi and Jucci, working with two species of termites. Dr. Thompson's work has since been confirmed by Claude Fuller (14) working on South African termites and Dr. A. D. Imms (17) working on a termite from Thibet.

Another aspect of the question of the castes of termites, of vital interest to biologists ever since Darwin, is the problem of how they have arisen in the evolutionary process. To-day it is most logical to consider the termite castes, not as mutants, but rather as "segregants," which arise generation after generation by the splitting and recombination of the genes of a heterozygous parent form.

A caste, like sex, may depend upon one factor and since the second and third reproductive forms apparently breed true to type (Snyder, 23), lethal factors must be considered. Caste may also depend upon the quality or quantity of egg material. In either case, determination of the caste is made before the hatching of the young, or predetermined in the egg.

The writer believes that the development of castes can best be explained by genetics and believes that the hereditary material (germ plasm) of the whole complex of the first-form termite queen is very heterogeneous in nature. The eggs are formed by the division of the complex so that each egg received a

different set of hereditary units, some eggs developing into first, second or third-form fertile individuals, others into the sterile workers and soldiers. The first-form queen produces five to seven kinds (varying with the species) of offspring, one to three fertile and two to five sterile types—only one type being like itself (the parent), the others all different in structure and behavior. Various less common, abnormal or “intermediate” reproductive adults are merely other segregants.

There is a parallelism between termites and Mendelian segregants, where there is a splitting up of a complex parental hereditary material into many simpler types of offspring or segregants.

To summarize, in conclusion, it would seem that, since it has been proved that the fertile and sterile castes are differentiated at the time of hatching and since there is no positive proof that special qualitative feeding can determine the castes—(and indeed there is much evidence to disprove this)—and that intestinal protozoa do not cause sterility in the neuters, the burden of proof of the origin of the castes due to immediate environment still lies with those advocating this hypothesis! The castes in termites are undoubtedly blastogenic in origin! To regard them as segregants appears to be the most inclusive and plausible explanation!

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EXPLANATION OF PLATE III.

The Development of Termites (*Reticulitermes* spp.) from Parent Adults to Post Adults.

Fig. 1.—*Reticulitermes tibialis* Banks.

Sexual, winged, colonizing adult.

Fig. 2.—*Reticulitermes flavipes* Kollar.

(a) The egg. After Marlatt;

(b) Newly hatched young (nymphs).

Fig. 3.—*Reticulitermes flavipes* Kollar.

Newly hatched nymphs.

a, reproductive type, male;

b, worker-soldier type, female;

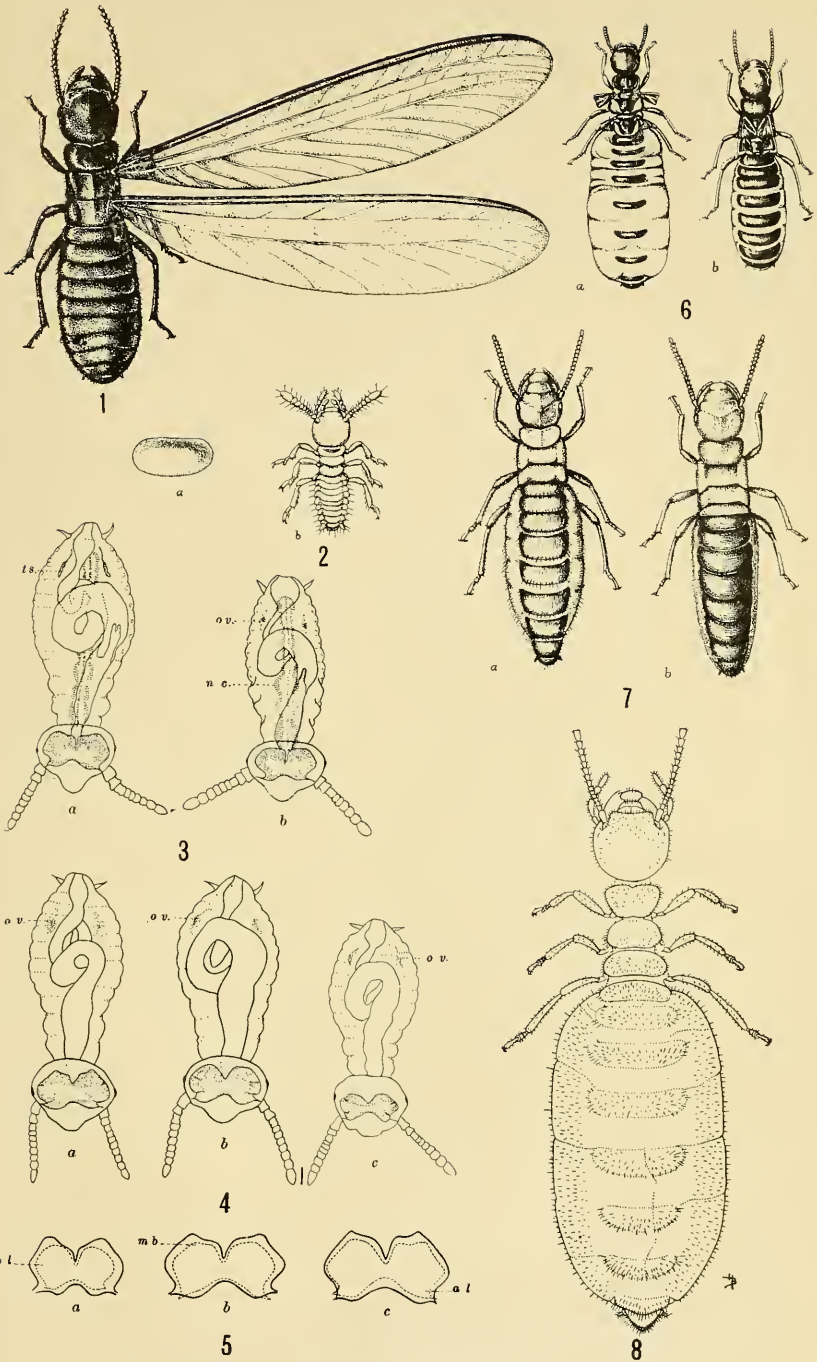
ts, testis; ov, ovary; nc, nerve cord.

After Thompson.

Fig. 4.—*Reticulitermes flavipes* Kollar.

Female nymphs, with ten antennary segments, body length 1.3 mm.

a, reproductive type of the first form, with large brain and large ovaries;



Development of Termites.