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REMARKS ON THE INTERNAL PHYLOGENY
AND SUBFAMILY CLASSIFICATION OF THE FAMILY
FORMICIDAE

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INTRODUCTION

At present, the most widely accepted subfamily classification of the *Formicidae* is that gradually evolved over many years by MAYR, FOREL and EMERY and refined most recently by W. M. WHEELER (1920, 1923). Eight subfamilies are distinguished: *Ponerinae*, *Cerapachyinae*, *Dorylinae*, *Leptanillinae*, *Pseudomyrmecinae*, *Myrmecinae*, *Dolichoderinae* and *Formicinae*. Clark has raised anew or resurrected seven additional subfamilies in his work of 1952: *Myrmeciinae*, *Nothomyrmeciinae*, *Eusphinctinae*, *Amblyoponinae*, *Discothyrinae* (1), *Odontomachinae* and *Aneuretinae*. Of these, I am willing, to accept as a valid and useful subfamily only the *Myrmeciinae*. The present incomplete state of our morphological knowledge renders the remainder of his judgments premature. Actually, CLARK'S 15-subfamily classification is founded almost entirely upon Australian representatives, although the Australian fauna, rich and varied as it is, can be only a poor fractional basis for a classification aiming to cover the whole world fauna. Several of CLARK'S subfamilies have enjoyed supratribal rank in the past, and such rank might be argued for them even now, but there seems to be scant excuse even for tribal rank in the case of the *Eusphinctinae* or the *Discothyrinae*, let alone elevation of these groups as subfamilies. Furthermore, both names appear to violate nomenclatorial custom, which demands that tribes take their names from the oldest included genera.

Such immoderate and arbitrary subfamily revisions as CLARK'S are not likely to gain the support of many myrmecologists, but they may be fairly taken as overdue signs of revolt against the inadequacy of the present classification as an expression of phylogenetic relationships and as a useful foundation for practical keys. It is my purpose here to offer some opinions concerning the relationships of the ant subfamilies. These opinions are based on more than fifteen years' work with ants in museum and library as well as in the field, and on new and old morphological evidence, habits of the insects, and many less tangible impressions gained through correspondence and conversations with colleagues and in my own studies. It

will no doubt be felt by some myrmecologists that the evidence presented with these opinions is sometimes too slight for the purposes to which it is put. Nevertheless, I feel that an informal statement at this time may afford other workers the chance to stack more or less new ideas against impressions gained from their own independent studies. Any discrepancies will, it is hoped, soon lead to fruitful discussion and investigation that should eventually bring the classification closer into line with phylogenetic reality.

The *Myrmeciinae*.

I consider the genera *Myrmecia* Fabricius, *Prionomyrmex* MAYR and *Nothomyrmecia* CLARK to constitute a single subfamily, the *Myrmeciinae*. These ants, living and fossil, are the most generalized forms we know today in both their anatomy and their habits. They possess a strong, well developed sting and have the maximum number of clearly differentiated alitruncal sclerites, separated by strong sutures in the worker as well as the female. All possess the maximum numbers of palpal segments found in ants (6 maxillary, 4 labial) and the primitive number for antennal segments (12 in female and worker, 13 in male) in common with many related aculeate groups. The middle and posterior tibiae each bear a pair of apical calcariae, and each tarsal claw has a strong median tooth. The known wings possess a full complement of veins, except that the first radial crossvein is lost in some species. The crossvein *cu-a* is lined up with or very close to the point of divergence of the first free abscissa of *M*. No other ants have a more complete constant venation. The males have notaulices and parapsidal furrows on the mesonotum, and their genitalia include all the characteristic formicid elements as well-developed structures. All castes are usually large in size, with large eyes, and all have moderately heavy integument, distinctly sculptured over the head and alitrunk and usually over the petiolar node, while the gaster is characteristically smooth and shining.

In habits, the known myrmeciines are probably primitive for ants, and the method of nest foundation forces the founding queen to leave the nest in search of food for herself and for the first brood. Apparently the adults feed largely on nectar, while the larvae are given dead insects as their chief food. Communication between individuals appears to be limited when compared to the relations observed in the colonies of some other subfamilies of ants, and the foraging activities are carried out by individuals, not by groups [HASKINS (C. P.) and HASKINS, (E. P.) 1951]. The female and worker castes are often connected by a series of intermediate forms, and the workers may vary considerably in size and slightly in allometric characters, so that worker polymorphism is often more or less evident (WILSON, 1953).

The *Myrmeciinae* are divided into three tribes, each to its single nominate genus. The Baltic Amber *Prionomyrmecini* include a single species, *Prionomyrmex longiceps* MAYR, in which the postpetiole is constricted behind,

the eyes are placed near the middle of the sides of the head, and the mandibles are elongate-triangular, with serially dentate opposable apical (masticatory) borders. The *Nothomyrmeciini* (equal to subfamily *Nothomyrmecinae* and tribe *Nothomyrmecii* of CLARK) also include only a single known species, *Nothomyrmecia macrops* CLARK, of which the two reported specimens were collected at an unknown locality somewhere between Eucla and Esperance, just inland from the southern coast of Western Australia. This remarkable ant, described in 1934, remains known only from these two type workers despite attempts by several interested collectors, including myself, to recover it in the vicinity of Esperance and to the east of that town. The head of this species is essentially like that of *Prionomyrmex*, but the postpetiole is fully incorporated into the gastric tagma without a trace of a constriction. This condition is like that seen in the *Formicinae* and *Dolichoderinae*, and may or may not be the primitive one for ants as a family. At any rate, *Nothomyrmecia macrops* appears to satisfy nearly all conditions demanded of an ancestral stock leading to the *Dolichoderinae* and *Formicinae*, and there is reason to believe that a form with ocellate workers, but otherwise very much like *Nothomyrmecia* and closely related to it, gave rise to the two important higher families.

The third tribe in the *Myrmeciinae* includes the well-known Australian bull-ants of the genus *Myrmecia* (various other genera or subgenera seem to be no more than vague species-groups within *Myrmecia*). The tribe *Myrmeciini* is characterized in the female-worker castes by the very large eyes, occupying approximately the anterior half of the sides of the head, and by the long, slender mandibles, variously dentate on their inner margins, which are not squarely opposable but are usually crossed over one another at full closure. The postpetiole is as in *Prionomyrmex*, constricted behind and therefore separate from the gastric tagma. The three tribes form a relational series, with *Prionomyrmex* intermediate and combining characters of the two extremes. It seems probable, but not certain, that the triangular, serially dentate mandibles and medially placed eyes are more primitive than the condition seen in *Myrmecia*. The *Myrmeciini* may represent a relatively late offshoot of the line, but there is no solid evidence for this one way or the other.

The *Pseudomyrmicinae*.

The constriction of the postpetiole posteriorly leads to the formation of an abdominal pedicel with two segmental elements (nodes), characteristic of the *Myrmicinae* and the *Pseudomyrmicinae* as well as the *Myrmeciini*, *Prionomyrmex* and some other groups. On the basis of this structure of the pedicel, as a matter of fact, the *Myrmicinae* and *Pseudomyrmicinae* have always been related. There seems no other reason why these two subfamilies should be considered close, and if one grants that the

binodal pedice may have arisen convergently, then the way is cleared to considering other relationships for the pseudomyrmecines and myrmecines. I believe that there is no close connection between the two, and feel instead that the pseudomyrmecine ancestors were binodally pedicellate myrmeciines of the same stock which gave rise to *Myrmecia* and *Prionomyrmex*. An examination of a primitive *Pseudomyrmex*, such as *P. mutilloides* EMERY, in conjunction with any *Myrmecia* species, and considering all castes of both sexes, reveals very striking correspondences in structural details. I invite my colleagues to make this comparison, since it is far more convincing than any amount of verbal description. See also EMERY'S discussion of 1877, which he later (1911) modified after criticism from MAYR.

« The MYRMECIOID COMPLEX ».

If my conclusions are correct, we shall have to assume that three important subfamilies, *Dolichoderinæ*, *Formicinæ*, and *Pseudomyrmecinæ*, are descended from myrmeciine ancestors. Anatomical divergence at the base of the *Myrmeciinæ* involved mainly the postpetiole, which became modified as a node of the pedicel on one side, and became or remained an undifferentiated part of the gaster on the other. The line from the first side led to *Myrmecia*, *Prionomyrmex* and the *Pseudomyrmecinæ*, while that from the second gave rise to *Nothomyrmecia*, to the *Dolichoderinæ* through the tribe *Aneuretini*, and, either directly or through the *Aneuretini*, to the *Formicinæ*.

In spite of the rather fundamental split based on the character of the postpetiole, I believe that the *Nothomyrmecini* should be regarded as an element within the *Myrmeciinæ*. *Nothomyrmecia* is very conservative in other respects, and is so like the other myrmeciines that one feels the postpetiolar differences had slight biological significance in themselves, so long as other modifications had not been imposed like those fundamental internal ones characterizing the dolichoderines and formicines. I regard the subfamilies *Myrmeciinæ*, *Dolichoderinæ*, *Formicinæ* and *Pseudomyrmecinæ* as composing one phylogenetic unit, which may be called the "Myrmecioid Complex" for convenience. The common characters of the primitive members of each of the subfamilies in this complex are surprisingly numerous and obvious, even under superficial consideration. T. EISNER is now investigating the structure of the proventriculus in representatives of the complex, and his work is shedding light on the origin of this organ, so well developed in the three higher subfamilies.

The *Ponerinæ*.

I understand the subfamily *Ponerinæ* to include the elements so placed by WHEELER (1922), with the exception of the *Myrmecini* and the *Cylin-*

dromyrmicini. The groups making up the *Ponerinæ* are extremely heterogenous, but I feel nevertheless that CLARK's subfamilies *Amblyoponinæ*, *Discothyrinæ*, *Odontomachinæ* and *Ponerinæ* should be considered as tribes within one subfamily, at least until more information concerning their morphology is available. The tribe *Amblyoponini* contains some species with very primitive characters in the wing venation and particularly in the structure of the petiole. The shape and both anterior and posterior attachments of the typical amblyoponine petiole may be more primitive even than those of the *Myrmeciini*, especially when the striking resemblance of this segment to those of primitive tiphiid wasps (*Anthobosca*, *Diamma*) is considered. In other characters, the amblyoponines show basic specialization for hypogaecic existence as wholly carnivorous foragers, and in one genus, *Onychomyrmex*, development of legionary habits has brought about structural modifications of larvae and adult workers and females ("dichthadiiforms") showing a remarkable convergence with corresponding doryline phases.

While at first sight the *Amblyoponini* may appear sufficiently distinct as a group to deserve subfamily rank, widened survey soon discloses that the tribe *Typhlomyrmicini* (BROWN, 1953) has characters intermediate between those of the *Amblyoponini* on one hand and of the remainder of the ponerines on the other. The enigmatic genus *Dorylozelus* FOREL, inadequately described, also has features that might be taken as intermediate, and in this connection, the *Prionopelta*-like mandibles so sketchily drawn by INEZ FOREL (FOREL, 1915) are intriguing. The wing venation of the genus *Typhlomyrmex* is also interesting in that the first free abscissa of *M* arises distinctly basad of cross-vein *eu-a*, unlike that of normal ponerines, but suggestive of the condition characterizing the doryline wing. Mann's brief field note of 1922, in which he mentions *T. robustus* foraging under the bark of a rotten log "in files," may or may not indicate that this species follows a legionary mode of life. It is not impossible that *Typhlomyrmex* is the relict of a group derived from the amblyoponines, and from which were derived in turn other large and important groups. Too little is known about the anatomy and biology of *Typhlomyrmex* at present to allow anything more than the most rarified speculation concerning its phylogenetic significance, but the genus is certainly worthy of detailed study.

Other ponerine tribes seem to be more or less closely inter-related, but not all the details are clear. I have recently altered the composition of the *Platythyreini*, an undoubtedly archaic tribe, to include genera formerly placed in other tribes (BROWN, 1952), and I believe that the platythyreines show relationships to both the *Ponerini* and the *Ectatommini*, particularly to the latter. The *Ponerini* and *Leptogenyini* are also close together, and both show distant affinities with primitive *Odontomachini*. The *Ectatommini* should include *Paraponera* (see also WEBER, 1946), a genus customarily placed in a separate tribe, and the *Proceratiini* are so close that they may eventually have to be considered as mere specialized ecta-

tommines. The *Ectatommini* appear to be the stock from which the *Myrmicinæ* developed at an early stage (BROWN, 1950), since many characters link them, and the fossil genus *Agroecomyrmex* seems to provide a transitional form.

« The PONEROID COMPLEX ».

The relationships of the *Ponerinæ* to the Myrmecioid complex are not very clear, but numerous characters, including the wing venation and the metapleural glands, show that they had a common ancestry. All ants seem to be related either to the Myrmecioid Complex or to the *Ponerinæ*. There seems to be no doubt that the family *Formicidæ* is a monophylectic one in the sense that the individuals composing the single ancestral population carried the formicid characters and were social in habits, and would therefore, if living today, be recognized as true ants. The Poneroid Complex is here considered to include *Ponerinæ*, *Cerapachyinæ*, *Myrmiciniæ*, *Dorylinæ* and *Leptanillinæ*.

The *Cerapachyinæ*.

In the past, I have considered the curious Cerapachyine group to be just another tribe among the *Ponerinæ* (BROWN and NUTTING, 1950). I still feel that such a placement for the group is arguable, and we may ultimately return permanently to the position of EMERY (1911) in considering the cerapachyines as aberrant ponerines. KUSNEZOV (1952) has disagreed with my opinion on the cerapachyine placement, but his argument is largely irrelevant because it is based almost entirely on the characters of the single aberrant genus *Acanthostichus*, with particular emphasis on the dichthadiiform females among the few known species. It is now known that several cerapachyine genera, like *Phyracaces*, produce normal winged or ergatoid females according to species, and that many (if not all) cerapachyines follow a nomadic or legionary existence. As in the widely separated legionary species in the ponerine genera *Onychomyrmex* (see above) and *Simopelta* (BORGMEIER, 1950), the cerapachyines show adaptive structural modifications in the worker, female and larva, and to a lesser extent in the male where this caste is known, that can easily be defended as convergent and correlated with convergent modes of life. Similarities in structure and behavior have been emphasized by students of adult and larval morphology who have believed at one time or another that the cerapachyines represent a stock transitional between the *Ponerinæ* and the *Dorylinæ* (EMERY, 1901; W. M. WHEELER, 1920; G. C. WHEELER, 1950). Granting numerous similarities between some dorylines and some cerapachyines, I have nevertheless refused to accept the hypothesized cerapachyine origin for the dorylines (BROWN and NUTTING, 1950; BROWN,

1950), and I am still refusing to accept it. Not only do the cerapachyines show divergent and more advanced reduction in the wing venation and in the elements of the alitruncal wall, but even the larvae of certain genera show fundamental reduction in the vestigial legs and gonopods that have been found well developed in doryline genera (G. C. WHEELER, 1938, 1950). Proponents of the cerapachyine origin for the army ants must overcome these and other serious morphological objections.

It is possible, however, to support the cerapachyines as a weak subfamily on an entirely different basis, and in view of the fact that myrmecologists have acquired the habit of considering them distinct from the ponerines as a subfamily, I am glad to do so if only to maintain reasonable stability in the classification. I refer to the pygidium of the worker, which is more or less flattened or impressed toward its apex, and is bordered apically, at least on the sides, by serially arranged small to minute spinules. During 1950 and 1951, I canvassed several myrmecologists privately in an attempt to determine just how universal the pygidial spinulation is among cerapachyines, but I received few satisfactory answers. Following discussion between us, CLARK (1952) used the pygidial character in his subfamily key (*loc. cit.*), although at that time our knowledge concerning the universality of the character, and indications of its exclusiveness to the cerapachyines, were very incomplete. I have since been able to confirm the presence of the character over a much wider representation of the group, including members of all genera and subgenera of cerapachyines. In the genus *Simopone*, the pygidial spinules may be reduced to two very small units on each side (*S. baxeri* Menozzi or a nearly allied species from the Philippines), but even this reduction does not alter the value of the character. *Paraponera* possesses a fringe of stout spinules around the edges of the pygidium, but close inspection shows that these arise, not from the pygidium, but from the sternal plate beneath. Certain species of *Pachycondyla* are convergently similar in pygidial structure to the cerapachyines, but are otherwise quite different. I have not yet been able to examine all cerapachyine species, so there may yet prove to be one or more exceptions to this character. Furthermore, some few non-cerapachyines not yet studied may show structures of a similar nature that would make difficult the use of the character in a key. Reports on the rarer craepachyine and ponerine species by specialists who have access to them will eventually clear this matter up, but meanwhile employment of the pygidial spinulation as a group character seems to be justified. It will be noticed that under this arrangement the *Cylindromyrmicini*, placed by WHEELER in the *Ponerinae* in 1922, will revert to the *Cerapachyinae*, and thereby the complaints of WHEELER (*loc. cit.*) and CREIGHTON (1950) concerning identification of the cerapachyines as a distinct group appear to be met satisfactorily.

The *Dorylinæ*.

At present the precise affinities of the *Dorylinæ* are unknown, and even the relationships among the tribes within the subfamily are uncertain. It is not beyond possibility that the dorylines are diphyletic. If a relationship has to be guessed, I should prefer to derive the subfamily either as one or two phyletic groups from the Poneroid Complex, although a Myrmecoid origin is not wholly impossible. As has already been mentioned, the genus *Typhlomyrmex* shows doryline tendencies in its wing venation and other characters, but these may be merely convergent. *Aenictogiton* EMERY does not appear to be a doryline group, as has long been maintained; it may represent the males of a cerapachyine or ponerine genus.

There should appear within a short time important papers from BORGMEIER and from RAIGNIER and VAN BOVEN on the principal doryline groups. It is hoped that these works will offer a survey of morphological features that have not hitherto received proper attention, especially the male genitalia, internal structures, and mouthparts. Without more such information, the relationships of the dorylines will remain largely problematic.

The *Leptanillinæ*.

This little subfamily has suffered such drastic anatomical reduction in most of the usually valuable phylogenetic characters that it is doubtful whether we shall ever be certain of its true affinities. The habits of the species are such as to render their discovery highly fortuitous under present collecting methods, and it is possible that forms as yet unknown will reveal their ancestry more clearly. Until that time, however, subfamily rank for the *Leptanillinæ* may as well be maintained. Present opinion seems to favor relating this group to the *Dorylinæ*.

The *Myrmicinæ*.

As already mentioned, the *Myrmicinæ* appear to represent a line or lines derived from a primitive ectatommine stock, although the situation is confused by the inclusion in the subfamily of certain highly aberrant groups (such as *Melissotarsini* and *Metaponini*) whose affinities are very uncertain. More generalized myrmicines have retained some primitive characters of the ectatommines, such as the very similar male genitalia, deep notaulices in the male, heavy and deeply sculptured integument in all castes, tendency toward development of paired propodeal teeth and metapleural lobes or teeth, well developed sting in female castes, pectinate calcariae on middle and posterior tibiae, etc. An important biological

adaptation in many myrmicine groups is the ability to utilize the starch of seeds and other vegetable sources as a major portion of the diet. This adaptation may be correlated with the absence of a complex proventriculus such as is found in other higher groups of ants. The starch-eating habit appears most likely to be a primitive potentiality among myrmicines, though it is very unevenly developed among the genera and has apparently been lost entirely in tribes like the Dacetini. The internal classification of the *Myrmicinae*, from tribal levels right down to the subspecies, is almost hopelessly confused and is borne down by a tremendous weight of unrecognized synonymy. Specific synonyms frequently cross generic or even tribal limits as a reflection of the fact that these limits are often poorly marked or really nonexistent. Work now in progress will lead to the merging of several important tribes and genera that long have been artificially maintained to no useful purpose.

The *Dolichoderinae* and *Formicinae*.

The probable origins of these groups have been discussed earlier. I believe that the *Aneuretini* should be retained as a tribe within the *Dolichoderinae* until we know much more than we do at present about aneuretine morphology and biology. The *Formicinae* are quite distinct from the *Dolichoderinae* by widely differing characteristics of the apparatus connected with the production and ejection of venomous and repugnatorial substances, and by the nature of the substances themselves. While these differences are largely internal, the female-worker formicines possess a characteristic nozzle-like projection at the tip of the gaster, terminating in a circular orifice frequently rimmed by a coronula of guard hairs. It should be noted, after EMERY, 1922 and BUREN 1944, that this poison outlet is distinct from the cloacal orifice and is situated ventral to the latter. It is formed by the inrolling of the posterior portion of the hypopygium (sternum of abdominal segment VII) to form an open-ended cone. That some (possibly all) formicines can spray liquid poison through this nozzle to a considerable distance is well known. In spite of the fact that this structure has been accurately characterized in the literature at least twice since 1922, most writers persist in misidentifying it as the "cloacal orifice." Lack of attention to this detail has caused dolichoderines to be described as formicines, and *vice versa*, on several occasions within the last two decades, and it even accounts for the erection of synonymous genera such as the "formicine" *Aphantolepis* WHEELER, which is actually based on a clearcut *Technomyrmex* of the *sophix* group. The infracloacal nozzle is lacking among the *Dolichoderinae*, which apparently extrude their defensive fluid through the true cloacal orifice. As in most of the subfamilies, the tribes and genera of the *Formicinae* are in need of thorough revision, but that is another problem that cannot be discussed here.

The phylogenetic conclusions discussed above are schematized in a tentative tree (fig. 1); this diagram should be taken only as a suggestion of possible evolutionary lines, many of which are obviously of a highly speculative kind. While I realize fully that any part of this scheme may be overturned by a single morphological discovery in the future, I shall be

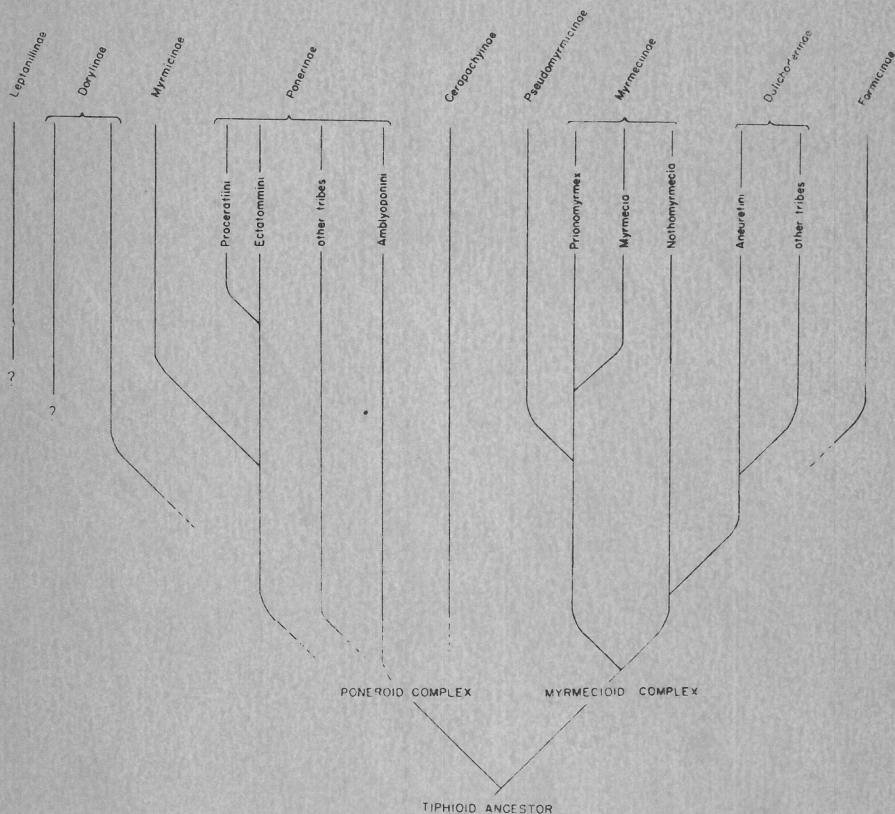


Fig. 1. — Tentative phylogenetic tree for the subfamilies of the *Formicidae*, including certain strategic tribes and genera. This diagram is based on the currently available information concerning all ant genera, both living and fossil, and from all adult phases and the known larvae. Wherever possible, statements in the literature have been checked against actual examples in the Museum of Comparative Zoology at Harvard University. Morphological criteria have been given the greatest weight.

satisfied if it serves only to shake the peculiarly fixed faith with which some myrmecographers regard the speculations of W. M. WHEELER and his predecessors.

In the body of this paper, I have not discussed the writings on ant phylogeny of MORLEY (1938, 1939) because I believe that they are not worth a serious lengthy critique. MORLEY bases his speculation chiefly on second-hand data, much of which is erroneous to begin with. This author's breath-taking chains of assumptions, beginning with the long-

discredited notion of a mutilloid origin for the ants (via *Mystrium!*), appear to have convinced few myrmecologists, and his notes constitute little more than just another of the many curiosities abounding in the myrmecological literature.

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