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Taxonomic Revision of the Nearctic Genus Acanthomyops (Hymenoptera : Formicidae)

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Contents

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Acanthomyops, an exclusively North American genus, is closely related to the common, dominant, holarctic genus *Lasius*, from which it may be unequivocally separated in all three castes on the basis of the number of segments in the maxillary palpi. *Acanthomyops* has short, 3-segmented maxillary palpi, while those of *Lasius* are 6-segmented and long. Another attribute of *Acanthomyops* that serves as a convenient diagnostic character for field collectors using a mouth-type aspirator is the presence of a characteristic odor produced by the mandibular glands of disturbed workers. This odor, a defense mechanism, is like that of oil of citronella or lemon verbena. As sensed by a collector with normal olfactory powers the odor is pronounced. A few species of *Lasius* possess a similar odor, but it is sensed, at most, as quite weak. *L. umbratus* probably has the strongest odor of any species of *Lasius*, yet it is decidedly weaker than that of all species of *Acanthomyops* I have collected.

For most of its history since the genus was erected by Mayr in 1862, *Acanthomyops* has been treated as a subgenus of *Lasius*, under which name most literature references are to be found. Much of our knowledge of these ants has been gained in this century; only 4 species were named before 1900. Three of these were named by European myrmecologists, while one was named by an American entomologist. Since 1900 a number of taxa have been discovered and named, mostly by Americans. Many of these taxa are still essentially unknown biologically, but a few have been investigated with varying degrees of thoroughness. The late William Morton Wheeler and William F. Buren figure prominently in both taxonomic and biological work on this genus since 1900.

[1] This publication is a modified version of a thesis presented to the Faculty of the Graduate School of the University of Minnesota, March 18, 1967, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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The present status of *Acanthomyops* is as follows: 15 named species, including 3 new, plus the recognition of 2 clear-cut and 3 putative hybrids. It is unfortunate that, despite all the work done to date on the genus, we are still quite ignorant about many aspects of the biologies of most of the included taxa. It is hoped that field and laboratory studies carried out in various parts of the North American continent will remedy this situation. In appropriate places throughout the text, attention will be drawn to specific points that are especially in need of investigation.

The limits of the geographical distribution of the presently known taxa of *Acanthomyops* are as follows: From the state of Hidalgo in southern Mexico to southern Canada, and coast to coast in the United States. All, or nearly all, of the 48 continental states and the southern provinces of Canada are inhabited by one or more species. The species in the southern parts of the range generally are to be found in mountains.

Nests are often difficult to locate because workers are exclusively subterranean in their habits, except for short periods of time just before and during nuptials. For this reason many collections are made by chance encounter. The nests are built in the soil, usually under the cover of objects such as stones or logs, but sometimes, especially in the Plains States, loosely compacted earthen mounds of varying size are made. Some taxa nest partially in rotted wood; these colonies are typically found in association with stumps and logs. Most taxa in the eastern states show a preference for fairly moist conditions, selecting fields, pastures, and woodlands as nesting sites. In the western states many taxa exhibit a greater tolerance for drier conditions in the selection of their nesting sites.

Many species of *Acanthomyops* are known to regularly attend subterranean aphids and coccids, which represent a wide variety of taxa. Probably the species whose biologies are unknown likewise subsist principally on the honeydew of these homopterous insects. Too few specimens of aphids and coccids were included in the samples of ants received for study to risk any generalizations on this interesting association. For up-to-date discussions on the relationship between ants and certain Homoptera, the reader is referred to Way (1963) and Nixon (1951). *Acanthomyops* is known to harbor some species of arthropods other than Homoptera. These include certain mites, bethylids, and pselaphid beetles; some of these species are probably true myrmecophiles. Again, however, the paucity of material received for study and the highly specialized nature of the subject make anything more than brief mention out of the question.

At the time of the nuptial flights, which are more or less characteristic as to season for a given species, the workers in mature colonies of *Acanthomyops* open up the nest entrance widely by excavation. Nests in this condition are found readily even before the actual flights begin to occur. Details of flight behavior vary with the species. Talbot (1963) has studied this behavior for several of our more common species and recorded it in some detail. Flights occurring in natural surroundings often involve the participation of an extremely large number of alate individuals. The queens and males congregate on the ground, and, when the conditions are right, fly up into the air in large numbers. Later, many descend from their flight, often giving rise to large aggregations of ants in restricted local areas; this frequently leads to concern on the part of persons residing in the area. Nuptial flights sometimes originate from the basements of homes and stores. Confronted with the evidence of flights of the latter type, which usually take place during the winter months, occupants often fear that their buildings are infested with termites.

From time to time, economic entomologists, county agents, and others receive specimens of several of the more common species of *Acanthomyops* for identification. Specimens are usually sent either because the alates are believed to be termites, or because the workers have been found tending homopterous insects on the roots of domestic plants.

Most myrmecologists believe that all species of *Acanthomyops* are temporary social parasites of *Lasius*. We have, however, very little evidence on the mode or modes of colony foundation in the genus — most of it being largely circumstantial. Work done by Tanquary (1911) represents the most determined effort to date to elucidate the nature of colony foundation in the genus. Methods of colony foundation in *Acanthomyops* are in critical need of solid evidence from field and laboratory studies. At appropriate places in the text, reference will be made to our present knowledge about colony foundation, the evidence on which the generalizations are based, and the specific lines of research that are urgently needed.

A revision of almost any large, common, and widespread ant genus will involve a number of difficulties, including the disposition of numerous synonyms. Opinions varied among myrmecologists before this revision on what difficulties might be encountered in revising *Acanthomyops*. Not as many tangles were encountered in the revision of this genus, as had been in its companion genus, *Lasius*. This was true because it is a smaller and geographically more restricted genus and also because there are fewer collections. Thus there was less exposure to the onslaught of irrepressible amateurs and other casual students, some of whom aggressively spend their energies clogging the literature with synonyms. This is perhaps what the late Professor William Morton Wheeler had in mind when he used the phrase, *mihi* itch.

Although at the time that this study was started, *Acanthomyops* was not beset with some of the complications encountered in many ant genera, it was nevertheless badly in need of revision. The literature was both scattered and scanty and, until recently, no papers were really comprehensive. It was difficult to gather information of almost any kind, but the taxonomic separation of species was especially troublesome. This problem was remedied partially when Buren (1950) published a paper on queens, which included a comprehensive key. Shortly thereafter, Creighton (1950) raised *Acanthomyops* to the status of a genus, briefly reviewed most of the known taxa, and included a key to the workers. These papers advanced the knowledge in this area by making identifications possible in 2 castes. Their keys were based on a relatively small number of specimens, however, which made it difficult for the authors to assess the relative reliability of diagnostic characters, their limits of variations, and their distributional behavior.

Genera long in need of revision tend both to discourage attempts to make determinations and to generate a higher proportion of errors of identification than when a recent revision, with detailed keys, illustrations, and distributional information, is available. Identification attempts, mostly by myrmecologists, had been made on about ⅓ of the 1414 samples that were received for study. Although many general entomologists appeared to recognize the genus *Acanthomyops,* few risked making specific identifications. Of the determinations made, about ¼ were either to "sp.", or in my opinion were incorrect. This made it imperative to establish strict rules for making generalizations based on published information. The restrictions imposed and some of the reasons for their inclusion are considered under the section on general methods and procedures.

Despite its shortcomings it is hoped that this revision will be useful to a wide group of users, and will stimulate further general collecting and biological field work on *Acanthomyops.* To a great extent its success will be measured by how quickly it becomes obsolete.

Reference Collections and Acknowledgments

The amount of material needed to revise most groups adequately involves fairly substantial numbers of specimens. Relatively fewer collections of *Acanthomyops* are made than of many better known and more easily collected genera. For this reason some persons wondered if it would be possible to amass a number of nest samples and individuals sufficient for adequately revising this genus.

In attempting to assemble material for study, 105 requests were made, mostly by letter, and a notice requesting specimens was inserted in *Entomological News.* Answers to 70 of the requests were received, but not all sent specimens. Material for study was sent by 44 persons and institutions; most of the shipments contained 1 or more series of *Acanthomyops.*

The present revision is based on 1414 nest samples. A conservative estimate of the total number of individual ants contained in these nest series is 30,900, with totals by caste as follows: workers, 24,600; queens, 4100; males, 2200. The samples originated from widely scattered points, with only 4 of the states of the continental United States and 2 of the provinces of Canada failing to yield specimens. The number of nest samples received from single political subdivisions ranged from 1 to 149.

A large proportion of the samples originated from east of a line joining the eastern boundaries of North Dakota and Texas. Thus inferences based on western specimens are relatively weaker than those based on eastern samples. The amount and distribution of this material made a revision at the alpha level possible.

To make available a comprehensive reference collection for future students of *Acanthomyops,* representative duplicates from many widely distributed nest series were segregated. This collection, which contains many types, was deposited in the Museum of Comparative Zoology of Harvard University.

In the list below, all institutions are followed by the name of the persons primarily responsible for making the loan. Where individuals contributed specimens from private collections, the person's name precedes that of the institution.

There is no coding of collections by letters because, except for the less frequently encountered species, only the distributional maps show all collection localities — 1 point to each county where 1 or more collections were made. In certain cases, collection data are incorporated into the text for the more common species. Space limitations have made it mandatory to omit long lists of localities. This should not cause any significant loss of essential information. If more detailed information is ever needed, a full statement of all collections, in typewritten form, is available in the MCZ at Harvard University and in the Department of Entomology at Cornell University.

University of Arkansas, Fayetteville (E. Phil Rouse and Lloyd Warren).

W. L. Brown, Jr., Cornell University, Ithaca, New York.

William F. Buren, U.S. Public Health Service, Bethesda, Md.

California Academy of Sciences, San Francisco (G. I. Stage and Hugh B. Leech).

University of California, Davis (A. T. McClay).

Canada Department of Agriculture, Ottawa (C. D. F. Miller).

Carnegie Museum, Pittsburgh, Pa. (George Wallace).

W. G. Carter, Davidson, North Carolina.

A. C. Cole, University of Tennessee, Knoxville.

Colorado State University, Fort Collins (T. O. Thatcher and James H. Shaw).

John G. Franclemont, Cornell University.

George M. Happ, Catholic University of America, Washington, D.C.

Museum of Comparative Zoology, Harvard University, Cambridge, Mass. (W. L. Brown, Jr.).

University of Idaho, Moscow (W. F. Barr).

Illinois Natural History Survey, Urbana (H. H. Ross and George Rotramel).

Iowa State University, Ames (Jean L. Laffoon and R. J. Gagne).

Paul B. Kannowski, University of North Dakota, Grand Forks.
University of Kansas, Lawrence (G. W. Byers).
Los Angeles County Museum (Roy R. Snelling).
University of Michigan, Ann Arbor (T. E. Moore and H. K. Townes).
University of Minnesota, St. Paul (Edwin F. Cook).
University of Nebraska, Lincoln (W. E. LaBerge).
North Carolina Department of Agriculture, Raleigh (D. L. Wray).
North Carolina State College, Raleigh (David Young).
Ohio State University, Columbus (Paul H. Freytag and Charles A. Triplehorn).
Oregon State University, Corvallis (J. D. Lattin and Paul O. Ritcher).
L. L. Pechuman, Cornell University.
Pennsylvania Department of Agriculture, Harrisburg (Larry D. Rhoads).
Robert W. Poole, Cornell University.
Purdue University, Lafayette, Indiana (Leland Chandler).
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Raymond Sanwald, Medford, New York.
San Diego Society of Natural History (Francis X. Williams).
Richard S. Soper, Jr., Insect Path. Res. Inst., Saulte Ste. Marie, Ontario, Canada.
Mary Talbot, Lindenwood College, St. Charles, Missouri.
United States National Museum, Washington, D.C. (M. R. Smith and D. R. Smith).
University of Utah, Salt Lake City (Albert W. Grundmann).
A. Van Pelt, Greensboro College, Greensboro, North Carolina.
Virginia Polytechnic Institute, Blacksburg (M. Kosztarab).
Washington State University, Pullman (Roger D. Akre).
Neal A. Weber, Swarthmore College, Swarthmore, Pennsylvania.
A. Richard Weisbrod, Cornell University.
George C. and Jeanette Wheeler, University of North Dakota, Grand Forks.
University of Wyoming, Laramie (W. Don Fronk).

Although a number of individuals might well have been singled out for special mention, I will call particular attention to only the collections made by Drs. George C. and Jeanette Wheeler and their students. These extensive collections made in all parts of North Dakota, over a period of about 30 years, provided me with nearly all of the material received for study from this state. If collections of comparable magnitude and variety had been available for study from other states, the revision could have been vastly improved. Whatever other uses may be made of such extensive local collections, their value in making better revisions possible seems to me to be of prime importance. It is unfortunate indeed that North Dakota is a state that stands essentially alone in the distinction of having had

specialists regularly and intensively collecting within its borders over such a long period of time.

A number of individuals have rendered assistance in a variety of ways other than sending specimens. Dr. William L. Brown, Jr., Cornell University, made office space available to me, assisted in many ways throughout the course of the study, and critically reviewed first drafts of the manuscript. Dr. Edwin F. Cook, University of Minnesota, assisted in various ways, and read the first draft of the manuscript. Dr. Byron W. Brown, Jr., Dr. A. C. Hodson, Dr. David J. Merrell, and Dr. F. G. Wallace, all of the University of Minnesota, read the manuscript and suggested improvements. Miss Julia W. Lowie, Ithaca, New York, prepared initial copies of various presentations, such as tabulations and regression plots, typed the first draft of the manuscript, and helped in other ways. Mrs. Patricia Quackenbush, Ithaca, New York, inked the illustrations. Mr. Allen Esserman, Mr. Eric Mintz, and Mrs. Mary Kozel, Cornell University, handled the details of programming and running the metric data through the computer (Control Data 1604). Dr. L. L. Pechuman, Cornell University, made his Wild M5 drawing attachment available for making illustrations. Dr. Lowell Uhler, Cornell University, let me use a compound microscope during the latter phases of the study. Dr. Bruce Wallace, Cornell University, discussed certain problems relating to hybrid taxa. Mr. William H. Gotwald, Cornell University, prepared habitus figures of the 3 castes of *A. interjectus*. Dr. Herbert W. Levi, Museum of Comparative Zoology of Harvard University, kindly provided me with a sample outline map, copies of which were reproduced and used to show species distribution. Dr. R. Dean Schick, State University College at Cortland, New York, made a binocular microscope available for my private use during the early stages of the study. To all of these individuals, and to a number of others, not mentioned, I express my thanks for their help.

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Definitions of Special Terms

In general, most terms used in this study are widely known. A few special terms, although known to many myrmecologists, may tend to cause difficulty for others. It is for this reason that the terms listed below have been defined to clarify their use in this paper. Several of the terms, mostly those dealing with measurements, are illustrated by figures at the end of this section.

Alitrunk: That part of the body of the higher Hymenoptera usually termed "thorax" by nonspecialists. It is embryologically derived from the true thorax and the first segment of the abdomen; they are fused into a single structure in the adult. A more recent term for alitrunk is mesosoma, but long-term usage of alitrunk in ant taxonomy has prompted its continued use in this study. For *alitrunk length,* see *Weber's length of alitrunk* (AL).

Alitrunk ratio (ALR). The size of queens relative to that of workers, which often has diagnostic value, is measured by ALR $= ALq/AL_w$. Values of ALR, cited for various taxa in the systematic part of the text, are always given in a standardized way: first, the average value computed from the total sample; second, the value or range of values, in parentheses, for *n* intranidal pairs of queens and workers. The figures for *plumopilosus* will serve to illustrate the general form of entry: ALR = 1.44 (1.39 — 1.48, n = 3).

Allometry. The use of constant differential growth rates, first expressed quantitatively by Huxley (1924), is often valuable in taxonomy. The relationship was originally expressed as $y = cx^k$, or its equivalent, $\log y = k \log x + \log c$. In this study an arithmetic linear variant to represent size allometry in a more limited way is deemed adequate to describe covariation in *Acanthomyops, viz.,* $y = mx + b$. It should be noted, however, that scatter diagrams are the sole means used to show sample regressions of y on x. Such regression plots imply the existence of a line of "best fit", even though such a line is not explicitly computed and drawn. It will be a simple matter for any reader to determine the position and slope of such a line approximately. It should further be noted that in 2 cases where sample regressions of 2 taxa are compared by plotting them in a single figure, a line is used that separates most of the points of one taxon from those of the other. These are not regression lines; the term coined for them is *critical dividing lines.* They were computed by the use of the following relationship:

$$y = (x - x_1)(y_1 - y_2)/(x_1 - x_2) + y_1.$$

Allopatric populations: Populations of taxa that are sufficiently remote from each other geographically so that any point on the range boundary of one is separated from any point on the range boundary of another by a distance greater than the sum of the natural cruising ranges of the reproductive castes of each. In the strict sense, allopatric species would be those fulfilling the above-cited criteria for all contained demes of each taxon. See *Sympatric populations.*

Angular inclination of hairs. Terminology relative to the inclination of both pilosity and pubescence is shown in figure 9, which was redrawn from Wilson (1955).

Appressed pilosity and pubescence. See figure 9.

Cephalic index (CI): 100(HW)/HL.

Critical dividing line. See definition under *Allometry.*

Cryptic species. See *Sibling species.*

Decumbent pilosity and pubescence. See figure 9.

Erect pilosity and pubescence. See figure 9.

Eye length: Maximum measurable length of compound eye.

Femur index (FI): 100(FW)/FL. Applicable to queen caste only in this study.

Femur length (FL) and **femur width** (FW): Maximum measurable length and width of the fore femur obtained from the dimensions of the smallest rectangle that just encloses it (fig. 3). In this study, applicable to the queen caste only.

Head length (HL): Maximum measurable length of head, as seen in perfect full-face view, from clypeal apex either to occipital border, or to an imaginary straight line connecting posterior corners of head (fig. 2).

Head width (HW): Maximum measurable width of head, including eyes, in all castes, taken through center of eyes with head in perfect full-face view (fig. 2).

Index. This term as employed in various scientific disciplines, has encompassed many widely divergent arithmetic combinations. In a more strict sense, index usually denotes the quotient of 2 minimal or maximal dimensions of a single anatomical structure, expressed as a percentage, and set up so as usually to make the resulting figure less than 100. Both femur and cephalic index are used in this study in conformity with this stricter definition. Scape index is, however, not an index, *sensu stricto.* Since its dimensions are taken from 2 separate structures, it is more properly called a ratio. There would seem to be little merit, however, in proposing to change its formal designation to *scape ratio* at this late date.

Parameres: Outermost pair of appendages of the genital armature of the male, which act as claspers. In reference to these structures some earlier myrmecologists used the term *stipites.*

Perfect full-face view: Orientation of head so as to maximize both HL and HW.

Pilosity: Longer, delicate to coarse hairs, often modified from a simple condition in at least some part of their length. They are generally distinguishable from pubescence hairs.

Propodeum: An equivalent of the term *epinotum* used by earlier myrmecologists. It is embryologically the first segment of the abdomen, which in the higher Hymenoptera, becomes fused with the posterior thorax to form the alitrunk of the adult.

Pubescence: Hairs, usually underlying pilosity, that are typically very short and delicate.

Pygostyles: A pair of small, delicate hairy appendages, which are attached to the posterior edge of the tenth abdominal tergite in the males of many ant species. The distal tips of these structures are generally more or less visible in dry specimens of *Acanthomyops.* Statements made about pygostyles by earlier myrmecologists often involved the use of the term *penicilli.*

Scape index (SI): 100(SL)/HW.

Scape length (SL): Maximum measurable length of scape, excluding its articular neck and condyle (fig. 2).

Sibling (= **cryptic**) **species:** Species so closely resembling each other in 1 or more castes, that they defy separation by usual taxonomic means. Applicable to more than 2 taxa, although siblings generally occur in pairs, either allopatrically or sympatrically.

Standing hairs: Pilosity that averages forming angles of 45 degrees or more with the cuticular surface, *i.e.*, subdecumbent, suberect, or erect.

Subdecumbent pilosity and pubescence. See figure 9.

Suberect pilosity and pubescence. See figure 9.

Sympatric populations: Populations of 2 or more taxa that overlap, or are so close geographically, that the maximum distance between the ranges is equal to or less than the sum of the natural cruising ranges of the reproductive castes. See *Allopatric populations.*

Weber's length of alitrunk (AL): Maximum measurable midline length of alitrunk from anterodorsal margin of pronotum to flange on posteroventral apex of propodeum. In practice, this measurement is often taken from the side (fig. 1).

General Methods and Procedures

Information provided in this section does not include the details of the techniques used in making measurements. Most comments on measurement data proper are to be found in the section entitled "Measurements".

As nest samples were received and processed, the following information was recorded on standardized data sheets in duplicate: (1) all data associated with sample; (2) estimate of number of individual ants by caste; (3) county where collected, if not covered under item (1); and (4) a tentative determination of the taxon. The originals went to make up a set of data sheets that were arranged by taxa, while the duplicates were arranged geographically by collection localities. These two sets of data sheets served as the basis for making a number of tabulations other than those involving standardized measurements.

In view of the goal of taking measurements of selected structures on approximately 1000 specimens, an attempt was made to choose specimens randomly. One specimen of each caste present in an alcoholic series was chosen at random and pointed for later measurement. This consisted of removing a specimen, without the aid of the microscope, from the watch glass into which the nest series had been emptied. In the case of already pinned or pointed material, the first specimen of each caste in the series as received, was designated for measurement. Specimens from essentially all nest series received in the earlier phases of the study were measured. Additional measurements were made later in the study from samples col-

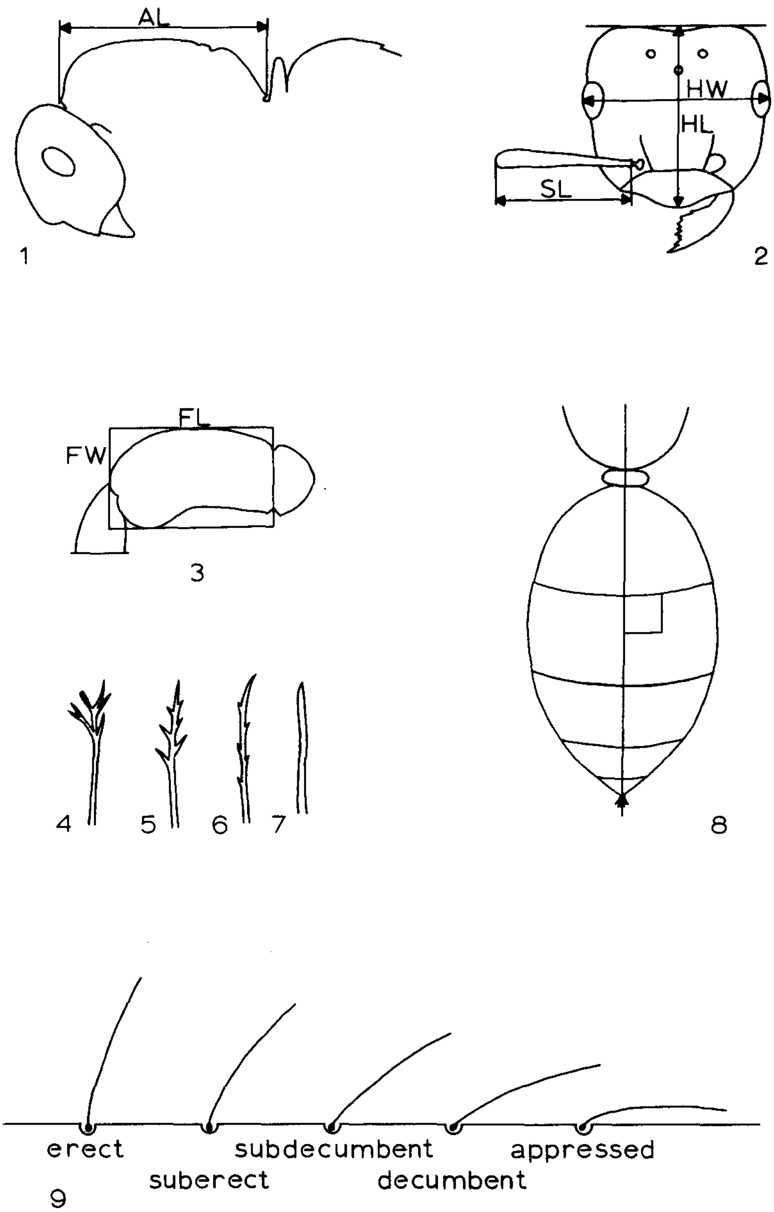


Fig. 1. Weber's length of alitrunk (AL).
Fig. 2. Scape length (SL), head width (HW) and head length (HL).
Fig. 3. Femur length (FL) and femur width (FW). *Fig. 4*. Plumose hair.
Fig. 5. Strongly barbulate hair. *Fig. 6*. Weakly or finely barbulate hair.
Fig. 7. Simple hair. *Fig. 8*. Location of standard square on gaster used in showing pubescence of workers and queens of all taxa.
Fig. 9. Angular inclination of hairs; terminology and illustrations after Wilson (1955).

lected in areas where few or no prior measurements had been taken. This gave fairly wide geographic coverage for metric data. Although the procedures indicated above do not assure randomness, they approach it, and hence are far better than the conscious selection of specimens possessing special attributes.

There remains another problem concerning randomness: How random was the selection of the nest series received for study? Only vague answers to this question can be given. However, collections of larger and more conspicuous solitary insects are usually less likely to be randomly drawn than are nest samples of ants. Specimens of many moths, butterflies, and beetles are often selected primarily on the basis of one or more unusual features not possessed by other available members of the taxon.

The subsample of specimens measured was in the approximate proportion of 1:30 of the overall sample received for study. It would be difficult to estimate the relationship between this overall sample of about 30,000 ants and the universe of *Acanthomyops* at any point in time. However, it must be on the order of 1 to many billions.

It was originally intended to measure not more than 1 specimen of a caste from a nest series, except for the very infrequently collected taxa. However, because of exchanges between lenders made before specimens were received for study, a few nest series were split on arrival. In some cases, measurements were made from 2 parts of a single colony before being aware of it, but none of these measurements of split colonies was discarded. Thus inferences drawn on metric data are largely, but not entirely, based on random singles for all of the more frequently encountered taxa. For those taxa so rare that only one or a few nest series were available for study, it was sometimes necessary to measure more than one specimen of a caste per colony. The basis on which the generalizations are made about each set of metric data is indicated in the text.

After selecting the specimens for measurement, each nest series was looked over in its entirety, and all apparently unusual features were noted for possible later use. Several teratological specimens and a male–female sex intergrade were encountered. Two worker specimens with 4-segmented maxillary palpi were found, one in *subglaber,* the other in sample 5 (= *claviger*).

A further result of this general review of nest series during the course of processing specimens was an initial evaluation of certain diagnostic characters. Notes made on these first impressions, together with the results of later study, led to the abandonment for general use of a number of characters. For example, wing venation in both sexes was variable and often tended to be erratic; the right and left wings of a single specimen were frequently quite different from each other. Dentition of the mandibles, especially in workers and males, was entirely too variable to be of value as a diagnostic character, as were relative proportions of the lengths of the segments of the labial and maxillary palpi, especially in the males.

Since some of the characters used extensively in this study display substantial variability, it is obvious that a fair amount of variability *per se* was not considered to be sufficient reason for rejecting a diagnostic character for general use. Several criteria were used for retaining a character with what appeared to be reasonable variability. A character had to lend itself to fairly simple verbal or symbolic manipulation to assure its being clear to the reader. Some characters fulfilling this criterion were quite variable, but lent themselves well to use in combinations of characters with which they often exhibited little concordance. Finally characters, where other factors were more or less equal, were sometimes chosen because long use had made them familiar to myrmecologists.

The petiolar scale, a fairly variable structure in *Acanthomyops,* fulfills the above-mentioned criteria for retention. On the other hand, the length of the scape in repose, as it has been used in the past, presents serious problems of interpretation. It involves a loosely defined relationship between scape length and a head dimension, which is roughly the equivalent of a partial head measurement, taken more or less diagonally. Creighton (1950) has suggested that scape length with respect to the head is less variable than the petiolar scale. Assuming this to be true, as it may be for some standard measurements that might be developed for the petiolar scale, there nevertheless remains a serious problem of communication. To avoid ambiguity in conveying useful information about scape length in relation to the head, the scape index has been used in this revision. It yields information which in a sense is approximately equivalent to that provided by the older approach sanctioned for so many years in myrmecology. The scape index has the virtue, however, of being made up of 2 clearly defined, easily taken measurements. Furthermore, it is amenable to concise expression as a single figure, samples of which can be analyzed statistically.

The generic term "index" has been used in such a wide variety of ways that its definition was included in the section defining special terms. Its use in this study is in conformity with the stricter definition of index in 2 of the 3 cases where it is used.

The use of generalizations from the literature was restricted to cases in which species identity could be verified and statements could be clearly associated with voucher specimens. The few exceptions to this rule are indicated at appropriate places in the text. It is doubtful that many will lament the attendant loss of words, as most workers are already struggling under a mass of published information, some of which is of dubious validity at best. That myrmecologists do not suffer this misfortune alone is attested by Professor Urey's now famous recommendation for handling scientific literature. The precautions that I have taken do not assure that the included material is free of error. It is, however, more likely to be valid and to have a higher degree of reliability than it might have had if all published statements had been used indiscriminately.

Loss of potentially useful information came about in a variety of ways. I seldom received extant biological notes associated with nest samples. Thus many generalizations were made possible only because the literature was analyzed to determine the status of the relationship between available nest samples and literature statements. The review of about 60 local lists was especially frustrating. The proportion of misidentifications, which varied with the writer and the castes available, was relatively high in these lists. In one case, data associated with 6 nest samples, which embraced 4 taxa, were welded into a notably general "generalization" under a single species name, not applicable to any one of the 4 taxa.

Many of the annotated lists used quotations, or their paraphrased equivalent, instead of presenting firsthand information. Some of W. M. Wheeler's species generalizations based on specimens observed in the Northeast, kept turning up with a monotonous regularity in papers dealing with areas far removed geographically from Wheeler's locale. Students collecting in geographically restricted areas over a period of time have an ideal opportunity to become intimately familiar with many aspects of the local fauna. Including significant parts of this information in their papers and retaining voucher specimens materially increases the value of their work. The faunal studies of W. G. Carter (1962a, 1962b) are notable in that these minimum requirements were largely met. Such papers offer subsequent workers who may be puzzled over some aspect of a species or complex a chance of finding clues that are important to the resolution of their problem.

Excluding firsthand information in favor of quotations often produces 2 problems. First, the statements used in the new context are often inappropriate and of doubtful validity. Second, the "lost information" can seldom be retrieved except by repeating the original work, which is rarely feasible. Workers attempting to use the papers of writers who have in effect "covered their tracks" suffer primarily from the loss of potentially useful information. Most experienced researchers can at least partially cope with the first problem, as they have had to learn how to maneuver their way through the literature, selectively discounting much of its content.

Another way in which published statements lose their value is by the disappearance of once extant voucher specimens. Instances of this situation in the MCZ may have resulted from a custom in vogue during Wheeler's day. His students took representatives of ant series with them when they left Harvard. The exodus of these *fragmenta umbilici* to the hinterlands may be the chief reason why some series are now completely exhausted. At another major institution, voucher specimens sent in to form the basis for certain published statements were thrown out by a staff member who decided that they were of no value!

If many of the situations discussed above had been handled differently, it would have enabled me to materially improve the scope and quality of the present revision.

A Wild M5 stereomicroscope with its companion drawing tube was used in making the illustrations of body parts. Drawings were prepared in a standardized way for the queens and workers of essentially all taxa included in the keys. For each worker, outline drawings were made as follows: (1) right half of head showing scape as seen in perfect full-face view, (2) profile of body dorsum showing pilosity, (3) crest and upper sides of petiolar scale in anterior or posterior view, and (4) pubescence enclosed by a standardized square located just to the right of the body midline, and immediately behind the posterior edge of the first tergite of the gaster (fig. 8). The side of the standardized square used to enclose pubescence measured slightly over 0.3 mm. As viewed when making a drawing, the area was delimited by 4 lines, each with a length equivalent to 4 successive unit squares of the reticle. The same series of illustrations were made for the queens, and in addition, an outline of the fore femur was drawn. All of the figures are in the same size proportion by caste, with the exception of those illustrating pubescence. After reduction, standardized squares showing pubescence in both castes had a magnification of approximately 50×. Other worker illustrations are 25×, while those for queens are 12.5×.

These illustrations should be useful in making various parts of the keys more understandable and in providing information that, though not included in the keys, may help make some otherwise difficult determinations possible.

The following alphabetic list of taxa, including synonyms and variants, provides a statement of the data associated with specimens used to make the illustrations:

arizonicus, worker, Miller Canyon, Huachuca Mts., Cochise Co., Arizona, Nov. 10, 1910, W. M. Wheeler; queen, "Parmerlee," Cochise Co., Arizona, June, Nathan Banks.

bureni, worker and female, Comstock, Barron Co., Wisconsin, August 16, 1941, William F. Buren.

californicus, worker, Palmer's Canyon, San Gabriel Mts., near Claremont, Los Angeles Co., California, Dec. 9, 1910, W. M. Wheeler; queen, San Gabriel Mts., Los Angeles Co., California, August 10, 1909, F. Grinnell, Jr.

claviger, "typical" form, worker and queen, Pipestone Lake, Berrien Co., Michigan, Sept. 7, 1952, W. C. Tyner, No. 517.

claviger, southeastern variant, worker, Siler City, Chatham Co., North Carolina, July 14, 1946, M. W. Wing, Col. No. 32–46; queen, Raleigh, Wake Co., North Carolina, Dec. 4, 1947, D. B. Anderson.

colei, worker, Cochise Stronghold, Dragoon Mts., Cochise Co., Arizona, July 29, 1954, A. C. Cole, AR-109.

coloradensis, worker, Morton Co., North Dakota, Sept. 5, 1951, Paul B. Kannowski, No. 309; queen, Manitou, El Paso Co., Colorado, Aug. 9, 1903, W. M. Wheeler.

creightoni, worker and queen, Warner Ranger Station, Moab, La Sal Mts., Grand Co., Utah, July 1933, W. S. Creighton.

interjectus, worker, Wharton State Forest, near Atsion, Burlington Co., New Jersey, July 30, 1962, M. W. Wing; queen, Ithaca, Tompkins Co., New York, Feb. 25, 1964, Dick Turner. The habitus figures of *Acanthomyops* prepared by Mr. William H. Gotwald, Jr. were based on a colony of *interjectus* which I collected in Wake Co., North Carolina.

latipes, worker, Edwin S. George Reserve, Livingston Co., Michigan, Sept. 2, 1961, Mary Talbot, No. 61–59; queen, Douglas Lake, Cheboygan Co., Michigan, August 21, 1944, C. H. Kennedy, No. 5024.

latipes* × *claviger, worker and queen, Selden, Suffolk Co., L.I., New York, July 1961, R. Sanwald.

mexicanus, worker and queen, Guerrero Mill, Hidalgo, Mexico, May 1913, W. M. Mann.

murphyi, worker, Edwin S. George Reserve, Livingston Co., Michigan, August 9, 1960, Mary Talbot, No. 60–50; queen, Morganton, Burke Co., North Carolina, July 16, A. Forel.

***murphyi* × *latipes* (= *pogonogynus*),** worker and queen, Red Feather Lakes, Larimer Co., Colorado, June 14, 1933, V. S. L. Pate and A. B. Klots.

murphyi* × *subglaber, worker and queen, Medford, Suffolk Co., L.I., New York, August 1961, R. Sanwald.

occidentalis, worker and queen, Broadmoor, south of Colorado Springs, El Paso Co., Colorado, July 14, 1903, W. M. Wheeler.

***parvulus* (= *claviger*),** worker, Herrin, Williamson Co., Illinois, T. H. Frison and H. H. Ross.

plumopilosus, worker and queen, Backbone State Park, Delaware Co., Iowa, Sept. 13, 1940, William F. Buren.

pubescens, worker and queen, Jenkins, Crow Wing Co., Minnesota, August 11, 1941, William F. Buren.

***Sample 5* (= *claviger*),** worker, near Buttermilk Falls State Park, Tompkins Co., New York, June 30, 1962, W. L. Brown, Jr.

subglaber, worker and queen, Selden, Suffolk Co., L. I., New York, July 1962, R. Sanwald.

subglaber* × *plumopilosus, worker and queen, Selden, Suffolk Co., L.I., New York, August 1961, R. Sanwald.

Measurements

The occasional use of metric data, other than rough, overall, specimen lengths, is not new in ant taxonomy. Wheeler and McClendon (1903), for example, list approximately 40 different measurements in micron units, which were used for the purpose of making comparisons among the queens of *claviger, latipes,* and the hybrid then called alpha-*latipes*. During the period from about 1925 to 1935 there was a substantial increase in the volume of such papers. The publications of this period, largely by European myrmecologists, often contained extensive metric data, both primary and secondary. The data of these papers was analyzed statistically with varying degrees of thoroughness. The enthusiasm of many of these writers over the new-found metric approach to taxonomy was evident, some intimating that older and more conventional methods were rapidly becoming outmoded. The paper by Palenitschko (1927) will serve as an example of this group.

Following 1935 there was a period of years during which the use of metric data was generally less extensive, and more or less sporadic. Publications in recent years, largely by W. L. Brown, Jr. and his students have included much data of this kind. These papers contain certain carefully defined measurements, and their derivatives, in the form of indices and ratios. There is, however, no evidence that this group views the use of metric data as a panacea, making it either desirable or possible to generally abandon the use of more conventional approaches to ant taxonomy. Rather, they consider certain kinds of metric data as a useful adjunct to the better elements of older approaches. This is the attitude toward the usefulness of metric data maintained throughout this study.

In selecting the structures to be measured and in deciding on the specific measurements to be taken, consideration was given to the probable value of a measurement in effecting separations among the taxa of *Acanthomyops*. Of importance, also, was the belief that a measurement should be simple to make and capable of clear definition. In so far as possible, I attempted to conform to conventions used in recent years in the making of similar measurements on ants. Wherever this goal was achieved, it is possible to make intergroup comparisons of the results of measurement among various ant taxa.

The amount of metric data accumulated in this study was so large that it could not all be included, although fairly substantial parts of the data are used. Univariate frequency tables of all standard measurements and their indices for all taxa in both the queen and worker caste are included. These tables, plus other statistical summaries that are presented in the diagnosis section for each taxon, should provide all the information ordinarily needed. However, to make available a complete record of the metric data in its original form, where measurements and their derivatives are associated, copies of the computer tape are deposited as follows: (1) Museum of Comparative Zoology of Harvard University, and (2) Department of Entomology, Cornell University. These original data sets will make it possible for interested future students to carry out analyses not undertaken in this revision.

On each of a series of randomly selected workers of all taxa, 4 linear measurements were made as follows: scape length, head width, head length, and alitrunk length. On each series of all taxa with queens, 6 measurements were made as follows: the 4 measurements indicated above for workers, plus femur length and width. All conventions observed in making these measurements are detailed in the section on the definition of special terms. The definitions include the letter code designations used for these measurements. These 2-letter codes are used for all measurements and indices extensively employed throughout the text and keys. Where measurements were taken for some special purpose, and hence were of limited use, such as the separation of two closely related taxa, no special name or code was assigned. They are defined fully at the point where they are used. The absence of tables of measurements for the male should not be taken to indicate that no measurements were made. On the contrary, a number of measurements were taken on males, mostly on extremes, and indices were computed for them. This metric data served as an aid in preparing a more usable key to this caste.

A Wild M5 stereomicroscope fitted with an ocular reticle consisting of a square, a side of which gave a specimen measurement of 2 mm at a magnification of 50×, was used in making measurements. Each side of this square was subdivided into 20 equal parts; thus the side of a unit square had a value of 0.1 mm. For the measurement of a structure over 2 mm, but under 4 mm, the value obtained with a magnification of 25× was doubled. Calibration against a standard stage micrometer slide substantiated the high accuracy of the above-mentioned specifications claimed for the reticle by the manufacturer.

The use of a specially mounted mechanical stage and an adjustable holder designed for use with pinned insect specimens facilitated rapid orientation of specimens and generally eased the exacting task of making the measurements. A pair of Spencer A/O microscope illuminators provided the variations of lighting needed.

Taking a measurement involved 2 separate and distinct processes, a count of unit squares followed by an estimate to the nearest tenth in the next square. Thus the last digit of numbers recorded for measurements is different from, and less certain than, the digits preceeding it, because it involved the estimation of a proportional part of the side of the unruled terminal square. As measurements were taken, they were recorded in units of 10^{-2} mm to avoid the use of decimal points.

Several hundred initial measurements were made to develop consistency in technique, and to pinpoint any problems that might warrant special attention before or during the process of recording formal measurements. This procedure involved measuring several series of 15 to 20 workers and queens repeatedly at intervals of 2 or 3 days. These preliminary measurements were continued over a period of several weeks, before agreement between successive measurements was deemed close enough for the purpose at hand. As an added precaution, Dr. W. L. Brown, Jr. checked several of the series of measurements which I had made. As agreement between our results was very close, it appeared that both accuracy and precision were sufficient to warrant beginning the process of taking formal measurements.

During the period of making formal measurements, continuing rechecks were made on approximately 10 percent of the specimens processed. This involved remeasuring some structures a second time, and where there was lack of agreement, taking further measurements until a decision could be reached as to the proper value to record. Although this added much extra work to an already long and tedious task, it was felt to be needed to approximate the true value of the variates more closely.

The chief problem during the early stages of taking measurements, and one that required constant attention thereafter, was the "undermeasurement" of a structure because of faulty alignment. In coping with this difficulty, it was found to be convenient to focus simultaneously on the endpoints delimiting the structure to be measured; this gave a first approximation to proper alignment. Next, it was necessary to make trial measurements while slightly altering the alignment. In this way it was possible to closely approach the true, maximal value.

The number of formal measurements recorded and the indices derived from them are as follows: 731 workers and 270 queens produced 4544 primary measurements and 2272 indices. The 6816 items of metric data were used in the production of the statistical tables presented in the treatment of each taxon. These metric data also formed the basis of the set of 15 univariate frequency tables, which follow the main body of the text. In these tables all primary measurements are grouped, while the indices are ungrouped, except for femur index. Groupings of roughly 20 to 30 classes seemed to be the most convenient arrangement of this data. Examination of the frequency distribution of measurements and their indices for the workers and queens of several taxa where sample size was about 50 or more indicates approximate normality. A number of these distributions exhibit slight skew, mostly to the right.

The computer (Control Data 1604) program used to generate certain statistics, uniformly assumed normality of distribution. Computer results, listed under each taxon in the section on diagnosis, include: (1) arithmetic mean, (2) standard deviation, and (3) three standard deviation limits for mean. Both primary measurements and their derived indices were treated in the same manner in the computer run. Sample size is very small in some taxa, consequently statistical statements about these samples are weak. Only the collection of a number of additional nest series of these taxa, preferably over widely separated geographic areas, will correct this situation. In the meantime it seemed better to include all information at hand, however small the sample size, than to exclude certain taxa from statistical treatment. Thus metric data were processed and presented in a uniform way, despite the obvious limitations inherent in some of the included samples.

An error analysis on a sample of metric data was carried out during the summer of 1965. The purpose of this analysis was to assess the range and distribution of the random errors of measurements and indices. The results obtained should make for a more enlightened use of the keys, and of other parts of this paper where metric data is used.

Recorded were 558 remeasurements from 314 specimens drawn randomly from shuffled data cards. Indices were computed from 488 of the measurements. The series of specimens that formed the basis for measurement was composed of about ⅔ workers and ⅓ queens, and ranged over most of the taxa. One, 2, or 3 measurements of pairs of dimensions were made, with average values being recorded in the latter cases.

To facilitate comparisons and groupings of errors derived from structures of varying absolute size, percentage errors were used. They were computed by means of the following relationship, with original measurement denoted by *m*, and remeasurement by *r*: $100(m-r)/m$. An equivalent relationship was used to compute index errors.

Table 1 shows that errors associated with indices generally have a greater spread than those of primary measurements. By viewing the errors of the combined numerators (N), the combined denominators (D), and, in the last column, the combined indices (I), it is evident that the spread of index errors in this sample is about twice that of the measurement errors. The number of measurement errors exceeding the 2 percent class mid-points is slightly over 5.5 percent, while that of the indices is nearly 14 percent. The number of measurement errors exceeding the 3 percent class mid-points is a little over 0.6 percent, while that of the indices is a little over 3.5 percent. It is evident from these figures that if errors in the range of –3.50 to 3.49 . . . percent are acceptable, then a measurement or index drawn at random would be just acceptable or better about 96.5 percent of the time. This is generally a true statement if the error introduced by the rounding process is not taken into account.

Exactly how any given reader may wish to handle the details of error analysis is a matter of personal preference. The figures in table 1 provide the basis for computations and interpretations of various kinds. It may be noted, however, that percentage errors are few outside the –3 and 3 class mid-points, whether rounding error is or is not deemed sufficiently important to be considered formally. It should be evident also that index figures will tend to be less reliable than primary measurements, irrespective of whether rounding error is formally taken into account.

The data of table 1 and the few generalizations cited above may be helpful in those places where comparisons between individual measurements or indices need to be interpreted. Wherever statistics, such as the mean or standard deviation, are generated by operations on groups of these data, however, precision tends to be increased, since the errors are distributed in an approximately normal manner.

Detection and elimination of blunders, although not related to error analysis, is essential to rid data of careless mistakes. Although care was exercised in all stages of the present study, some blunders did creep in. Certain procedures were routinely used to ferret out these mistakes. All sets of figures were proofread. Squares of the reticle were counted twice. Unusual results were questioned and rechecked, including all extreme

Table 1. **Frequency distribution of a sample of 802 percentage errors of measurements and indices, shown by category ***

Percentage error, class mid-points	(1) AL	(2) SL	(3) HW	(4) SI	(5) HW	(6) HL	(7) CI	(8) FW	(9) FL	(10) FI	(2+5+8) N	(3+6+9) D	(4+7+10) I
6										1			1
5										0			0
4	1		1	1			1			1		1	3
3	0	4	2	5	1	2	2	3	1	3	8	5	10
2	2	6	5	8	4	5	5	4	5	3	14	15	16
1	11	13	16	18	10	13	20	3	5	3	26	34	41
0	39	58	61	42	51	50	29	34	30	26	143	141	97
−1	9	12	13	13	12	11	21	2	8	4	26	32	38
−2	6	7	4	10	5	4	4	6	4	4	18	12	18
−3	2	3	2	6	2	1	3	2	1	7	7	4	16
−4		1		0	1		1			1	2		2
−5				1						0			1
−6										1			1
Totals	70	104	104	104	86	86	86	54	54	54	244	244	244

* Errors of individual measurements and indices, shown in the first 10 columns, are followed by: the sum of the errors of the numerators of the 3 indices (N); the sum of the errors of their denominators (D); and the sum of the errors of the 3 indices proper (I).

values that turned up in any of the univariate or bivariate work sheets. With respect to taking measurements, the fact that the value of the unit square of the reticle did not require conversion was fortunate, since this is a frequent source of error. Because of the various precautions taken, it is believed that the present study is relatively free of blunders.

Colony Foundation

Since it is generally believed that all or most species of *Acanthomyops* are temporary social parasites, a survey of available field collections and of the literature was made in order to assemble as much data on mixed colonies as possible. This involved checking several hundred vials of *Lasius* and *Acanthomyops* in my personal collection, as well as all *Acanthomyops* samples received. I checked all literature references that seemed likely to contain information on colony founding, including some 60 local lists. About 4/5 of these lists mentioned *Acanthomyops*. The results of the survey are listed below for both field collections and laboratory studies. Whenever I have seen the specimens, the name of the host is followed by "(det. Wing)."

Field studies

A. latipes mixed colonies

1. Freeport, Cumberland Co., Maine, September 3, 1946, M. W. Wing. This moderate-sized colony consisted of a single dealated *latipes* queen plus workers of *Lasius neoniger* (det. Wing). The colony was collected in the area known as the "Desert of Maine", a few acres of sand with scattered clumps of grass surrounded by a mixed growth of bushes and trees. The nest was in pure sand, dry on top, but quite moist just below the surface. It had a small crater-type entrance, with galleries leading well down into wet, compact sand. The *latipes* queen was located about 10 inches below the surface. The collection included the queen and a few of the associated *neoniger* workers.

2. Tanquary (1911) reported that Wheeler collected a mixed colony of *latipes* and *Lasius americanus* (= *alienus*?) at Ellisville, Mass., April 21, 1910. The colony was under a stone. Professor Wheeler noted that the workers of the two species were about equally numerous and that they were of about equal size. The nest contained many very small larvae (identity not determined). The workers of both species carried the larvae to safety when the nest was opened, but the *latipes* workers were more active in this pursuit than were those of *americanus*. The species were on friendly terms, occupying the same galleries. Examination of this MCZ series showed *latipes,* but no specimens of *Lasius*. A curious fact is that a single worker of *Pseudolasius* sp. was included on a pin along with 2 of the *latipes* workers. How a specimen of a genus known only from tropical

Africa, Asia, and Australia became mixed with this series of *latipes* is an enigma.

3. Colebrook, Conn., August 23, 1904, W. M. Wheeler. *A. latipes* plus *Lasius alienus* (det. Wing). The sample contained 4 pointed workers of each species; their nest proportions remain uncertain.

4–6. Colebrook, Conn., W. M. Wheeler. Three mixed colonies of *latipes* and *Lasius americanus* (= *alienus?*). These 3 mixed colonies plus the one cited above are reported by Wheeler (1910a, 1910b).

7. Cheboygan Co., Michigan, Sec. 27, Inverness Twp., June 27, 1952, P. B. Kannowski, No. 378. This sample was composed of about 30 workers of *latipes* and 6 workers of *Lasius neoniger* (det. Wing).

8. Pigeon River, Cheboygan Co., Michigan, July 11, 1947, C. H. Kennedy, jack pines at footbridge. This sample was composed of about 30 workers and a single pupal queen of *latipes*, and a few workers of *Lasius neoniger* (det. Wing).

9. Eight miles north of Keremeos, British Columbia, March 30, 1941, H. B. Leech. The note associated with these specimens stated that both species were "all mixed together in galleries under a stone". This sample was composed of about 25 workers of *latipes* and 5 workers of *Lasius crypticus* (det. Wing).

10. Gregg (1963) reported a mixed colony of *latipes* and *Lasius alienus* from Colorado.

11. On August 22, 1961, Mary Talbot located a mixed colony in the Edwin S. George Reserve, Livingston Co., Michigan. At her request, W. L. Brown, Jr. made an identification based on existing keys that was incorrect; the *Acanthomyops* species was *latipes*, not *murphyi*. I have not seen the *Lasius* workers associated with this sample. Talbot (1963) published a note on this mixed colony. With appropriate name changes, it may be briefly summarized as follows: A small mixed colony of *A. latipes* and *L. neoniger* was found under a stone on a hillside. It contained workers of both species, and worker pupae of *latipes*. The colony was kept in the laboratory for several days. Whenever the artificial nest was opened, the workers of both species cooperated in carrying pupae away from the lighted area.

The 11 field records cited above involve, so far as I know, only the true (or beta) *latipes*. This species has thus been taken in association with 3 of the 6 species assumed to represent potential hosts. My own data and that of Wilson (1955) show that throughout its known range, *latipes* has available one or more of the following species of the subgenus *Lasius*, which may serve as a host: *alienus* (= *americanus*), *crypticus*, *neoniger*, *niger*, *sitkaensis*, and *sitiens*.

A. murphyi mixed colonies

1–3. Sanwald (1964–65) reported finding 3 mixed colonies of *murphyi* and *Lasius neoniger* at Medford, Suffolk Co., New York. I have examined specimens from 2 of the 3 samples; the third sample was discarded. Dates of capture are given for the 2 samples as: August 25, 1962 (No. 29) and June 1, 1963 (No. 11).

4. Gregg (1963) reported seeing a dealated queen of *murphyi* enter a nest of *Lasius neoniger* near Falcon, Colorado.

A. claviger mixed colonies

1. Smith (1934) reported that the sample from which he described *A. parvulus* was associated with "*Lasius niger* var." His basis for the association was the statement of Frison and Ross, the collectors, that the ants came from soil beneath a rotten log in open woods. The *claviger* (= *parvulus*) specimens may actually have been associated with *Lasius*, or perhaps 2 totally separate nests may have existed under the log. It is impossible to make any definite assertion on the status of this sample.

2. Pollard, Escambia Co., Alabama, February 13, 1950, E. O. Wilson, F-226. A pin with 2 pointed worker specimens, one *claviger* and the other *Lasius umbratus*, is in the MCZ. There is no note to give any clue of possible nest association. The *L. umbratus* record was noted by Wilson (1955), but no mention was made of any relationship with *claviger*. The association is doubtful at best.

Laboratory studies

The only extensive experimental work published is that of Tanquary (1911). In his studies the only *Acanthomyops* species tested as a parasite was *latipes*, although several species were tried as hosts. Tanquary introduced artificially dealated queens into small colonies containing workers and brood of species assumed to be suitable hosts. He kept many colonies going simultaneously, and so was unable to make more than a few daily observations on any one. Whenever the queen died she was removed and replaced by a new one. He found that *latipes* queens did not do well under artificial conditions; many of them died in a few days, both those introduced into host colonies and those kept in reserve in their own colonies. The 8 host species that he listed were: *Lasius americanus, brevicornis, minutus, nearcticus, Acanthomyops claviger, interjectus, latipes,* and *subglaber*. *L. alienus* (= *americanus*) represented 14 of the 28 host colonies used. Since *L. neoniger* figures prominently in my listing of the mixed colonies of *latipes*, it is unfortunate that Tanquary did not test this species as a host. In 79 trials, he cited 2 clear-cut cases of adoption where the *latipes* queens lived, and estimated that at least 4 or 5 more would have been (or perhaps already were) adopted, had not the queen died. Examination of the *latipes* queens removed from his colonies showed no sign of bodily injury in the majority of cases, but a number had been dismembered and some eaten.

The 2 definitive cases of adoption are briefly summarized below. For additional information, the reader is referred to the original paper.

Exp. B-19/8. On August 9, a beta queen was placed in a petri dish with 12 workers and 150 cocoons of *L. americanus*. On August 10, she was found dead. On August 11, a second queen was introduced. On August 12, she was hovering over a pile of cocoons with a number of newly emerged workers. From August 13 to September 12, when experiments were terminated, she stayed with the brood and became covered more and more by workers. The many workers licked her body frequently. Tanquary commented that the increasing cluster of workers, which finally completely hid her from view, was much more pronounced than with the rightful queen in a pure *americanus* colony.

Exp. B-10/13. On August 10, a beta queen was placed in a petri dish with 30 workers and about 30 cocoons of *A. interjectus*. On August 11, the queen was dead; she was replaced by an alpha queen. From August 12 on, she hovered over the brood and was well received by the workers. Up until September 12, the host workers licked, crawled over, and touched the alien queen.

Observation of all artificial colonies showed that *latipes* queens always tried to hover over the brood of the host species. They were often attacked by the host workers, but did not attempt to escape. The callow workers emerging from a pile of cocoons over which a parasitic queen hovered, accepted her. Some of the older workers showed acceptance of the queen by crawling over and licking her body, while other workers were attacking her.

W. L. Brown, Jr. and E. O. Wilson (pers. commun.) separately undertook a series of experiments on dealate queens of *claviger*, which unlike those of other species overwinter above ground in considerable numbers, either singly or in aggregates. Their unpublished work involved many introduction experiments with both winter-conditioned and artificially chilled queens. Introductions were attempted with chilled and unchilled colonies of such possible host species as *L. alienus, neoniger, nearcticus,* and *flavus,* always without success.

Discussion

Wheeler (1910b) attempted to formulate a general statement on the colony-founding behavior of *Acanthomyops*. He stated that, on the basis of many field observations, he believed that *claviger* founded colonies independently. I have been unable to determine just what Wheeler's evidence was. It is probable, however, that he was referring to the well-known overwintering behavior of *claviger,* mentioned above and discussed in some detail in the next section on nuptial flights. If so, the fact that these queens are invariably without brood during the winter indicates that they are not then really in the act of founding colonies. He stated that *interjectus* probably founded their colonies independently, but gave no basis for this conjecture. He definitely considered *latipes* to be parasitic, as he had never seen this species founding a colony independently, and had direct evidence that it was a parasite. Because of their similarity to *latipes,* he considered both *murphyi* and *occidentalis* to be parasitic.

There may have been some change in his views on colony founding over the years; Wheeler (1933) commented on only one species, *latipes,* which he cited as an example of the conciliatory type of temporary social parasitism. Today many myrmecologists differ with Wheeler's early generalization. The majority believe that queens of all *Acanthomyops* species found their colonies as temporary social parasites, employing one *modus operandi.* The small amount of solid evidence makes any broad generalization hazardous at this time. Adherence to the current view, probably much oversimplified, may tend to seriously restrict the design of experiments that would offer the greatest promise of early results. The fact that general field collecting has come up with little more than clues over the last half-century points up its weakness as a means of elucidating specific problems of a specialized nature. Its inefficiency stems from the fact that too many goals are pursued simultaneously. One important contribution of general field collecting activity, however, is that it suggests the possibility of not one but several methods of colony foundation in *Acanthomyops.*

Although no one substantial generalization can now be formulated for the genus, mixed colony records do indicate that *latipes* and *murphyi* are parasites. Evidence, particularly from Tanquary's experiments, indicates the probable value of the long hairs and massive bulk of *latipes* queens in withstanding the attacks of host workers. The frequent licking of *latipes* queens by host workers suggests that secretions may also play an important role during adoption. Although there is less direct evidence of inquilinous habits in *murphyi,* its similarity to *latipes* in size, structure, and pilosity strongly suggests that these two species probably have similar methods of colony foundation. For the other species, however, the situation is far from clear, as evidence is either scanty and hard to interpret, or else entirely lacking. If one assumes that *claviger* and *interjectus* are similar to *latipes* in their habits, it is odd that no reliable records of mixed colonies are available. Both of these species are much more abundant and better-collected than *latipes,* for which 11 "mixed" records are cited above.

A few of the possible ways in which colonies may be established are given below in the form of a briefly annotated list:

1. Independent colony foundation by the claustral method appears to be a minor possibility because of the relatively small thoracic size of *Acanthomyops* queens. *Lasius* queens known to found colonies independently all have more massive thoracic dimensions.

2. Independent colony foundation during which the queen is intermittently claustral, foraging for herself and her brood during the initial stages of colony foundation as do some predaceous ponerines and myrmicines.

3. Parasitic colony foundation by early spring entry into a host colony. Especially likely for *claviger,* since its overwintered queens may have a

metabolic advantage over host workers. *Claviger* queens are active at lower temperatures than are the workers and queens of most ant species; during the warmer days of winter and early spring they are often seen walking about on the ground. The negative results of Brown and Wilson are suggestive, but do not entirely remove this method as a possibility.

4. Parasitic colony foundation in which the queen picks up a host worker and carries it about in her mandibles until she acquires the nest odor, making entry into the host nest less hazardous.

5. Essentially parasitic colony foundation where the queen lures a few workers away from a host colony, and moves with them to a new site to start her colony.

6. Colony foundation in which the queen burrows down to a root aphid colony of a suitable species and founds a colony claustrally in the presence of a steady energy source, thus releasing most of her scanty thoracic reserves for the synthesis of brood.

7. Essentially parasitic colony foundation in which the *Acanthomyops* queen cooperates with a *Lasius* queen. Tanquary (1911) stated that *latipes* and *L. americanus* queens remained on friendly terms when confined. Following the often simultaneous flights of *latipes* and *L. neoniger,* the queens of both species are frequently found together.

8. Independent or parasitic colony foundation by 2 or more queens of the same species, all of which continue on as nest queens. Wilson (1963) found that a number of rare parasitic species utilized polygyny as a means of increasing effective population size. Polygyny may be common in *Acanthomyops,* and not just confined to the rarer species. Evidence and theoretical considerations pertaining to polygyny are discussed later under the treatments of *claviger, latipes* × *claviger, plumopilosus,* and *subglaber* in the systematic section of the text.

Alates and Nuptial Flights

The alates of *Acanthomyops,* especially males, are known to be attracted to both regular and black lights. It is thus possible to increase sampling coverage of an area when this method is used in addition to the other commonly employed techniques. In an attempt to add to the number of samples for study, I checked some 15,000 to 20,000 miscellaneous winged ants collected at lights. This resulted in a modest increase of new specimens. The scarcity of *Acanthomyops* specimens collected at lights supported the fact that the genus is poorly represented in most collections, as the literature survey mentioned earlier had indicated. About 1/5 of the 60 local lists surveyed made no mention of the genus. Most of the lists that did include references to *Acanthomyops* listed 3 or fewer species, and 3 or fewer original collection records in total for all species.

Of the 1414 nest samples studied, nearly half contained alates or dealate queens, about 9/10 of which were dated at least to month. Nearly 500 such dated samples pertained to the 3 common species. The data for these samples, however, did not usually indicate clearly whether they represented nuptial flights or nest collections. The samples of *claviger, interjectus,* and *latipes* were analyzed to get a preliminary idea of the kinds of information that they would yield, and the degree of their reliability. All possible combinations of the castes represented in these samples were tabulated by week. The conclusions drawn from a study of these data were compared with those of the intensive study of Talbot (1963). This resulted in the simplified table shown below, and, in general, validated the assumptions made about the significance of the combinations of castes used in the work-table. Table 2 shows the frequencies by month for 3 categories: (1) Workers and alates: this includes any combination of alates associated with workers, and sometimes with dealate queens. (2) Alates: this includes any combination of alates not associated with workers, but sometimes with dealate queens. (3) Dealate queens: a category that occasionally includes workers, but never alates. This classification made it possible to place each sample definitively. Statements made about the significance of these categories are, of course, subject to error, but the following interpretations seem to fit in most cases. Category (1) indicates a nest collection, while (2) indicates collections made during or after a nuptial flight. Category (3) was introduced to cope with a peculiar feature of the seasonal history of *claviger,* not found in other species. Its usefulness will become apparent as the 3 common species are compared.

The 482 samples of the table originated from many and widely separated geographic areas, and represent a time span of many years. Thus average results and wide date ranges are to be expected because of the heterogeneous nature of the data. The results of intensive studies on a few species show that annual weather changes play an important role in the ecology of insects. Weather and other environmental factors interact in complex ways that may vary with the locale. Consequently, communities may vary not only from place to place, but may also undergo changes over time. The student of a particular group generally sees only one facet of the results of these many complex interactions in communities; he notes changes in one or more aspects of his own group. It is thus to be expected that any analysis of groups of *Acanthomyops* nest samples with alates, done either by year or by area, would give results differing from those of table 2. Sets of data restricted in space or time will, in general, show less variation than is evident in the heterogeneous data of the table, which have near-maximum date ranges.

Table 2 deals with the 3 common species only. The data on nuptial flights for the other taxa are discussed later in the text, each under its own taxon heading.

The discussions of *claviger, interjectus,* and *latipes* that follow will enable the reader to make ready comparisons between these common species. For each species, the main features of its cycle are followed by an

Table 2. **Frequency distribution by month for 3 categories of caste combinations in the 3 common species of *Acanthomyops*** *

Species and category	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Claviger												
Workers and alates				1		2	6	16	19	16	2	1
Alates	2	1		2	2	1	2	2	7	19	9	5
Dealate queens	6	2	14	13	1			1	7	16	11	18
Interjectus												
Workers and alates	3	10	13	15	8	10	8	2	3	1		6
Alates	2	4	11	9	16	11	15	1	2	2		5
Dealate queens	1			2		5	3	3	3			
Latipes												
Workers and alates						3	15	34	9			
Alates						2	2	13	4	2		
Dealate queens							4	9	4	2	1	

* See text for further discussion.

explanation of any that are unusual. At the end of each of the discussions based on tabular data, selected published information is summarized briefly. The papers reviewed include only those of writers making statements based on personal observations, the species identity of which were either reasonably sure, or known to be correct. These summary statements provide a means of comparing the results of the large heterogeneous data samples of the table with smaller samples restricted to single localities and generally covering only a few years.

Annual sexual cycle of *A. claviger*

June may be taken as a starting point for the cycle of this species. During June and July most records of sexual forms in nests are based on queen larvae and pupae. The immature stages of queens were investigated in *claviger* to determine their seasonal distribution as closely as possible. It is estimated that 6 weeks to 2 months elapse from the first appearance of queen larvae to the time when adult queens are found in the nest. The timing for males is probably similar to that of females. Investigation of the seasonal distribution of the sexual immatures of other taxa was done far less exhaustively than in *claviger*. It is likely, however, that the estimate for *claviger* will hold for other taxa producing alates during the warmer months of the year.

By August, mature *claviger* nests contain adult alates in sizable numbers. These nests remain relatively numerous on into October. Most nuptial flights begin in September and continue into November, with a few occurring earlier and later. This is indicated in the table by the concomitant increase in the number of "alates" and decrease in the number of "workers and alates". The table indicates that the greatest number of flights take place in October.

Associated with flights is the appearance of many dealate queens. In *claviger,* unlike other species, the dealate queens remain numerous until the end of the following April, when they suddenly disappear. *A. claviger* infests buildings infrequently, so most of these queens are collected out-of-doors, either singly or in groups. Occasionally they are associated with alate females, and more rarely with males. They are found in woods or fields under trash, stones, logs, or other cover. It is evident that large numbers of dealate queens of *claviger* regularly overwinter in all or most parts of the range. The reasons for their sudden disappearance in late April are unknown. Intensive field studies of this species during the spring months might well lead to an understanding of its method of colony foundation. At worst such field studies stand a chance of turning up clues that could help in designing experiments to test likely alternatives.

Some of the tabular data require further explanation, since they do not fit well with the interpretations given above. Under "workers and alates", the single April record (Illinois) is probably of alates overwintering in a parental nest. Under "alates", one of the January records (Virginia) represents a flight from an infested house, the other a single queen found walking on a sidewalk (North Carolina) in the early afternoon of a warm day. The February record is also for a single queen specimen (North Carolina). Some *claviger* nests in the South undergo swarm-outs during the warmer days of winter. Although flights do not result from these swarm-outs, occasional queens and males fail to return to the nest. Hence specimens are occasionally collected under normal circumstances that appear unusual to one unfamiliar with this species' habits. One of the April records is based on a mixed collection of alate and dealate queens (Pennsylvania), the other on a single alate queen (Illinois). The May records include a single alate queen (North Carolina), and a collection of 1 alate and 10 dealate queens (Virginia). The April and May records may represent overwintering queens. A late June record is for a single male (Iowa); it may also represent an overwintering individual. The 4 records for July and August probably indicate "leakage" of the current annual crop of alates from nests.

The relative drop in the population density of dealate queens seen in the table for January and February is almost certainly apparent and not real. Since this species infrequently infests houses, and few field collections are made in the dead of winter even in the South, it is surprising to find as many as 8 records for these months.

A claviger is one of the two species with a sexual cycle that spans most of the year. The chief reason for this extensive time-range is the continuing abundance of overwintering dealate queens, which occur long after normal flight activities are over.

Under *A. claviger,* later in the text, there is discussed a smaller, more hairy variant located in and around North Carolina and Virginia. The study of the 2 variants of *claviger* failed to reveal any significant differences in the time-distribution of their alates. Such variation as did occur was almost certainly associated with differences in the climate of the two areas involved.

Talbot (1963) reported that extreme *claviger* flight dates at Tiffin, Ohio were September 11 and 25 during the period from 1933 to 1944. Buren (1944) reported flights during late August, September, and October in Iowa. Groskin (1947) reported an unusually late flight of *claviger* on December 3, 1963 in Pennsylvania.

Talbot's observations at the Edwin S. George Reserve in Livingston Co., Michigan began in early June and ended in early September each year. The first date on which she found a *claviger* nest with adult alates was August 20. In commenting on her flight observations in Ohio, she stated that rains induced the workers to open the nests. Flights took place in mid-afternoon, and were favored by decreasing light, warmth, and high humidity. The nest observed during the flight of September 22 still contained males and females on October 21. Because of this observation, she surmised that the alates may have overwintered in the nest and flown during the next spring. Since flights are known to occur later than October 21, it does not necessarily follow that this colony failed to empty its nest of alates during that year. Even when a few alates do overwinter in parental nests, there is no reason to assume that this results in flights during the following spring. To my knowledge no spring flights have been observed for *claviger*. Evidently such alates are "leaked" from the nest ineffectually. Certainly, natural selection does not demand that each and every individual be utilized to maximum advantage; its operation is, rather, a probabilistic function of populations of individuals.

Annual sexual cycle of *A. interjectus*

One factor complicating the interpretation of the cycle of *interjectus* is that it frequently infests houses. The flights from houses come to official attention far more frequently than do normal flights. The samples of this species are thus strongly biased in this respect. Most naturally occurring flights take place in June and July, with a few earlier and later. The extreme flight dates are largely determined by conditions in a given locality and year.

Taking June as the starting point of the cycle, the number of nests with alates drops in July, while the number of flying alates rises. Flights have generally stopped by September, and by October no more dealate queens can be found. The nests of *interjectus* may, however, still contain a few sexual individuals. The beginning of winter brings on a number of nuptial flights, usually launched into the basements of heated buildings. These unseasonable flights continue through the winter and well into the spring. The few dealate queens collected during this period arise from these flights.

Close analysis of the data indicates that a sizable proportion of the records of workers and alates for March, April, and May are probably from field nests containing adult alates. In this species, it appears that the production of alates begins in the fall or winter of the previous year. Once a nest builds up a sufficient number of alates, the existence of the right combination of environmental factors may trigger a flight. This hypothesis would account for the unusually high number of *interjectus* flights associated with heated buildings during the winter and early spring.

A flight that I observed in Raleigh, North Carolina, on April 20, 1949 is the earliest natural flight known to me. The nest was located in grass near a sidewalk. Large numbers of males and females were swarming out of the nest at 5:30 p.m. Males, females, and workers were intermingled, and some females were breaking away and running up and down the sidewalk. Some males were attempting to copulate with females on grass blades as the flight progressed. In general, late May is the earliest time for natural flights even in the South. This species, however, like *claviger,* undergoes swarm-outs. Although these formicine warm-up drills occur frequently and involve large numbers of alates, they rarely result in unseasonably early flights. The swarm-outs may, however, give rise to some "leakage" of alates, which wander too far from the nest and fail to find their way back. *Interjectus* seems to be more strongly attracted to lights than do other species of *Acanthomyops*. Thus a number of the captures of this species in the period prior to regular flights occur at lights.

The sexual cycle of *interjectus* is atypical of the genus in that it nearly blankets the entire year. This is largely because the queens apparently prefer to found their colonies near buildings. The attractiveness of artificial lights may also influence their selection of nesting sites.

Talbot (1963) studied a single colony of *interjectus* in Livingston Co., Michigan during a 50-day period in 1960. Between June 16 and August 25, this colony, which produced only males that year, launched 22 flights. About 3 weeks of this period were unfavorable for flights; in a more favorable year the flight period might end earlier. Buren (1944) reported flights for July and early August in Iowa.

Talbot (1963) reported that June 11 was the earliest date on which she had found alates in nests. Since she normally arrived at the Reserve not much before June 11, this can only mean that some *interjectus* nests contained adult alates upon her arrival. Evidently adult alates occur in nests in the early spring, and perhaps in the winter.

Talbot observed 43 nests over a 10-year period; her data on this species are far more extensive than on the other 3 species studied. Rains provided the stimulus for workers to open up the nest by excavation. Flights occurred in the late afternoon, with temperatures between 67° and 80°F, relative humidity between 56 and 99 percent, and without wind. An estimate of the number of alates released during flights was made on several occasions. In 1960, when only males were produced in one colony studied, an estimated 40,000 individuals flew from the nest in 22 flights. In 1958, an estimated 63,600 males and females flew from a nest in 4 flights, and the nest still contained alates. The bulk of these alates, an estimated 55,200, were released during a 2-hour period on June 17. As flights from a given nest proceeded, fewer and fewer alates were released. In some nests alates were still left in the nest after the last flight had occurred. She noted that occasional matings took place on leaves and grass stems prior to flights.

Annual sexual cycle of *A. latipes*

The seasonal cycle of this species is typical of the other species of the genus except *claviger* and *interjectus*. It rarely nests near human buildings. The dealate queens disappear soon after nuptial flights cease. The cycle covers a relatively short, well-defined portion of the year.

During June and part of July, many of the nest records of sexual forms are based on immatures. Adult alates appear in nests from mid-July on into September. Most nuptial flights begin in late August and continue in September, with a few taking place in October.

Talbot (1963) cited August 2 as the first date for finding adult alates in nests. During a 10-year period, she observed 11 flights. They occurred in the late afternoon, often following rains. Before flights, workers opened up nests by excavation, but the time of digging out varied greatly from nest to nest. It ranged from a few days to several weeks before flight time. One colony was observed digging out on August 1, 1953, but had no real flight before September 8. However, a small number of males flew from this nest on 6 different occasions in abortive flight attempts. An estimate of the number of alates leaving a nest during a regular flight was made on September 4, 1961: the total was 2500 males and 4500 females.

Flights and inbreeding

Myrmecologists have known for some time that many colonies of higher ants produce only one sex or disproportionate sex ratios in any given season. But it was Marcus (1949, 1950) and Kusnezov (1953) who apparently first suggested that this is an important way of avoiding inbreeding. My own collecting in recent years in New York, and earlier in other areas indicates that atypical sex ratios are observed in several species belonging to the subfamilies Myrmicinae and Formicinae. Although colonies of these two types are frequently encountered, most nests produce sexual alates in approximately equal proportions in any one season. It thus appears that incest-avoidance is only partially accomplished by the scheme proposed by Marcus and Kusnezov.

The question arises whether a colony producing only one sex in a given season does so year after year. Talbot (1963) furnished some evidence to the contrary. She found that an *interjectus* colony that had been producing both sexes for several years produced only males in 1960. Only the study of a group of nests over a period of years will provide a general answer to this query.

Another observation of Talbot indicates how colonies with approximately equal numbers of both sexes may avoid close inbreeding. She found that, over a period of years, the females of one *interjectus* colony did not participate in the first flight of the season. Females began to fly from this colony on the second flight, and increased their participation in subsequent flights. The late flights of the season were often predominantly composed of females.

Incest-avoidance in *Acanthomyops* may be viewed as a function of several variables, the operation of any one of which would probably fail to hold close inbreeding to a low level. In addition, to the factors cited above, randomness of mate selection must certainly play an important role. Also, there may be important mechanisms not yet discovered. On purely qualitative grounds, it may be assumed that the existence of any 2 of the 3 following conditions would greatly reduce the amount of inbreeding: (1) random mating occurring at sufficiently high altitudes, or over prominent regional markers, to have assured considerable prior intermingling of the alates released from the many local nests; (2) many of the local nests releasing only 1 sex, or disproportionately large numbers of 1 sex, during a given flight; (3) many of the local nests containing 2 or more nest queens.

The proportion of mature *Acanthomyops* nests producing only males or females was estimated by analyzing 331 nest samples containing workers and one or both alates. These samples were classified into 3 categories: workers, queens, and males; workers and queens; and workers and males. The frequency of nests for each category is shown in table 3 for *claviger, interjectus, latipes,* and a category which lumps all other *Acanthomyops* taxa.

Table 3. **Sexual composition of nests of *Acanthomyops:* 3 common species, separately; single grouping of all other taxa.***

Taxa	Workers, queens and males	Workers and queens	Workers and males
Claviger	31	39	11
Interjectus	33	41	12
Latipes	21	23	19
Other taxa	44	40	17
Totals	129	143	59

* See text for further discussion.

Samples containing both sexes indicate beyond any doubt the caste composition of the nest from which they were derived. However, unless samples are large, they do not reliably indicate the relative proportions of the sexes in a nest. Collections containing a single sex, on the other hand, do not give clear-cut assurance of the caste composition of the nest. The size and complexity of many nests may lead to sampling errors. It is not uncommon to find males segregated from females before nuptial flights; the two sexes are often kept in widely separated chambers. Superficial collections from such nests will often contain workers and only one of the sexes. Given a series of nest samples collected by many individuals using varying techniques, any compensation made for sampling error can only be done in ignorance. I have arbitrarily halved the samples with a single sex. Rounding the totals figures of the tabulation, there are then 130 nests with both sexes, 70 with only females, and 30 with only males; this gives percentages of 57, 30, and 13, respectively. On the basis of this adjusted sample, 43 percent of *Acanthomyops* nests contain only one kind of alate. Although field work specifically designed to answer this question could provide more reliable estimates, this rough assessment indicates that unisexual nests occur fairly frequently in *Acanthomyops.* Thus nests with one sex may be an important way to avoid incest in this genus.

Interspecific Hybrids

Students of ants often wonder if certain of the intermediate variants encountered in the course of their taxonomic studies might not be interspecific hybrids. Wheeler (1909b) posed such a question about samples intermediate between *Lasius alienus* and *L. neoniger*. The possibility of the existence of hybrids in this case, and in some of those where formal hybrid designations have been given, cannot be entirely excluded. It seems more plausible, however, that they represent unrecognized siblings, or extreme variants of a single species. In other cases, suspected hybrids may, in fact, turn out to be hybrid in nature, as in the taxon known for years as alpha-*latipes*. In still other ant groups the situation remains uncertain, and only future study will enable a reliable assessment to be made; W. L. Brown, Jr. told me that his studies indicate the possibility of some interspecific hybrids in North American *Smithistruma*.

Some few taxa that are almost certain to be hybrids have been described as good species, as in *Acanthomyops pogonogynus* (Buren). Wheeler (1928) described *Lasius teranishii* as a new species. The data presented by Wilson (1955) show that the single known queen specimen of *L. teranishii* belongs to the subgenus *Dendrolasius*. It is intermediate in most of its characters between *L.* (*D.*) *fuliginosus* and *L.* (*D.*) *spathepus*. There is overlap in the geographic ranges of these species in Japan, where *L.* (*D.*) *teranishii* was found, and in the time of their nuptial flights. This strongly suggests that *L.* (*D.*) *teranishii* represents a rare interspecific hybrid.

Despite the fact that taxonomists dealing with ants and other insect groups have long suspected that reproductive isolation among some sympatric species in nature may not be perfect, little more than scattered opinions were voiced before the results of work on *Drosophila* were disseminated. As a result of these studies, it became apparent to taxonomists generally that it was something less than heresy to consider seriously the possibility of interspecific hybrids in their own groups. By analogy with *Drosophila*, the outcome of interspecific matings appeared to be a function of the degree of relationship of the parent species. It further seemed likely that if parental genomes were compatible, then offspring might be produced to become adults with varying degrees of fertility. The work on interspecific hybrids in *Drosophila* has thus had a far-reaching influence on contemporary insect taxonomy.

The work on *Drosophila* holds a special place in studies on insect hybrids because of the refined techniques that have been developed for their detection and study. The general review by Patterson and Stone (1952) reports 100 cases of interspecific hybridization since the first one was turned up in 1920. Hybrids in *Drosophila* are produced by parent species belonging to the same species-group, with some groups producing many, and others few, hybrids. In laboratory crosses, hybrids are produced reciprocally in about a half of the cases, the rest being one-way. Hybrid progeny have ranged from fertile in both sexes, through fertile in one sex only, to sterile in both sexes. The existence of interspecific hybrids in other insect groups is known from both laboratory breeding experiments and field studies. A few of the papers reporting or reviewing such cases are the following: Rozeboom (1954), Diptera, Culicidae; Sailer (1954), Hemiptera, Pentatomidae; Eyles and Blackith (1965), Hemiptera, Lygaeidae; Kettlewell (1965), Lepidoptera, Geometridae; and Clarke and Sheppard (1960), Lepidoptera, Papilionidae.

In all of the groups cited above, characters of hybrid progeny tended to be intermediate between those of the parent species, but a character was sometimes closer to one parent than the other. In some cases anomalous progeny were noted. Eyles and Blackith (1965) reported that certain crosses of lygaeids produced male progeny with incomplete genitalia, while in one, hybrid males lacked genitalia altogether. Fertility reported for hybrid taxa in the various groups ranged from complete sterility in both sexes to fertility sufficient to enable carrying hybrid crosses through the F5 generation.

Many of the hybrids produced by human intervention would not have occurred in nature for reasons that vary with the case. Thus the number of hybrid taxa with which a taxonomist is primarily concerned represents only a small fraction of the total number reported. The existence of occasional interspecific hybrids in nature represents a situation quite different from that of massive hybridization with introgression. No solid evidence for the latter situation has been turned up in the present study. However, it is entirely possible that some writers might have been inclined to view the situation encountered in *claviger* in the southeastern United States as representing a case of introgressive hybridization. The reasons why I have taken a different view of this case are detailed in the discussion of variation under *claviger*.

In this study, 5 cases considered to represent interspecific hybrids are reported; all but 1 must be considered rare. The 5 hybrid taxa, which are discussed in greater detail later in the text, are (1) *latipes* × *claviger*, (2) *latipes* × *coloradensis*, (3) *murphyi* × *latipes* (= *pogonogynus*), (4) *murphyi* × *subglaber*, and (5) *subglaber* × *plumopilosus*. Only *latipes* × *claviger* (= alpha-*latipes* of authors) approaches sporadic commonness.

Students of higher Hymenoptera lack the array of techniques that are available for the certain detection and study of interspecific hybrids in *Drosophila*. However, they have one distinct advantage over students of most other insect groups in that males are produced parthenogenetically. Thus where males are available and can be specifically diagnosed, it is possible to pinpoint the maternal parent of a hybrid sample. Males were present in samples of 2 of the 5 hybrid taxa. The identity of the maternal parents of these hybrids is as follows: the taxon known as alpha-*latipes* is produced by a *latipes* female and a *claviger* male, while *pogonogynus* (Buren) is produced by a *murphyi* female and a *latipes* male. The possibility that these two hybrid taxa may be produced by reciprocal crosses must await further study. Laboratory studies may settle this question if the necessary techniques are ever devised. On the basis of field collections alone, many more nest samples containing males are needed to answer the question with any degree of confidence.

The question of the fertility or sterility of these 5 hybrid taxa can not now be answered with much assurance. However, none of their queens are known to have been found as nest queens in nature. The great rarity of 4 of the hybrid taxa effectively assures this negative result, particularly since nest queens of *Acanthomyops* are very difficult to locate. A point

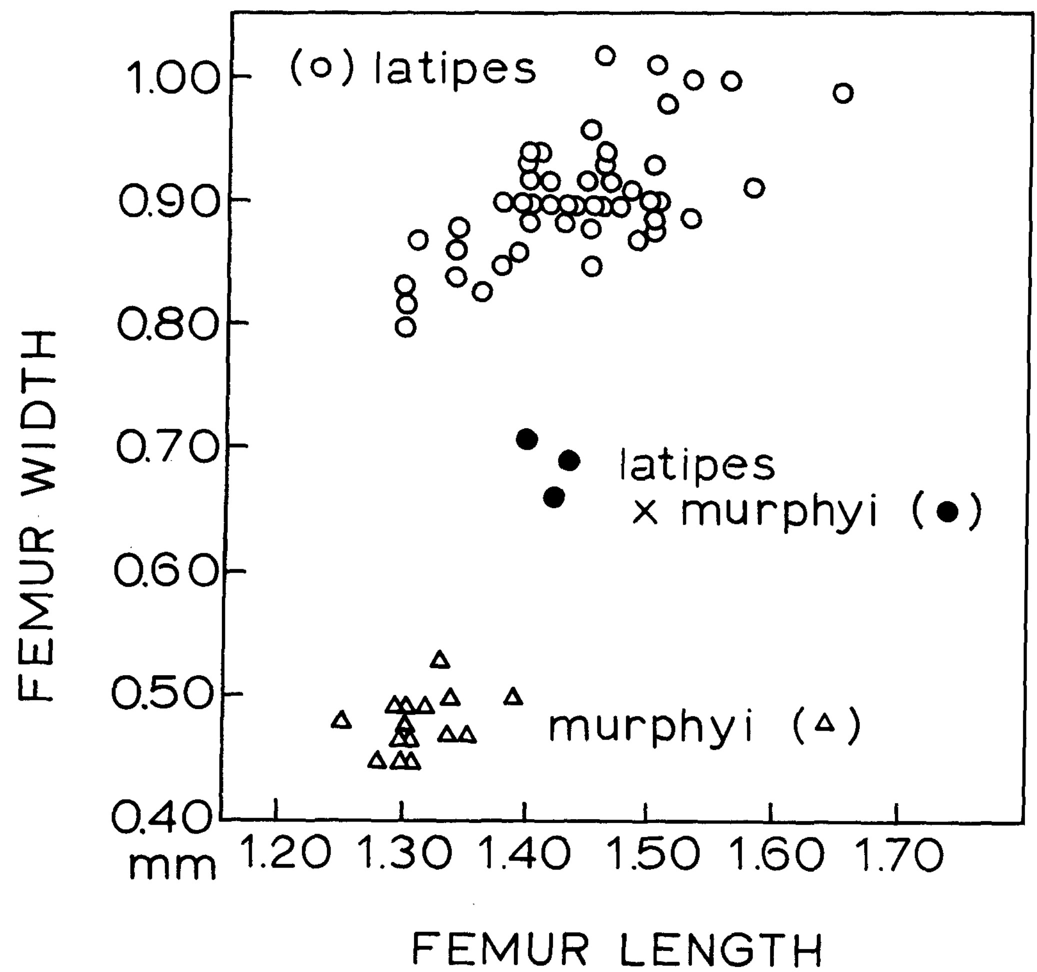


Fig. 10. Sample regressions of femur width on femur length in queen caste of *A. latipes* (N = 48), *murphyi* × *latipes* (N = 3), and *murphyi* (N = 15). Not over 2 queens measured per nest series, usually only 1. (See text for further discussion.)

suggesting the sterility of the sporadically common queens of *latipes* × *claviger* is the fact that the femur index has never failed to give clear separation among the queens of *latipes* × *claviger* and its parent species. If any significant amount of backcrossing or mating among hybrids took place, the femur index would be expected to break down as a clear-cut discriminant in proportion to the frequency of hybrid sexual activity. The laboratory experiment conducted by Tanquary (1911), in which a queen of *latipes* × *claviger* was adopted by an *A. interjectus* colony, was terminated before her fertility was ascertained.

It is evident that in rare sterile hybrids there can be no question of introgression. In the case of fertile hybrids that are produced in some numbers, it generally has been assumed that the gene pools of the parent species will progressively become more alike. Bigelow (1965) gives reasons why this may not necessarily be so. In studying large numbers of specimens

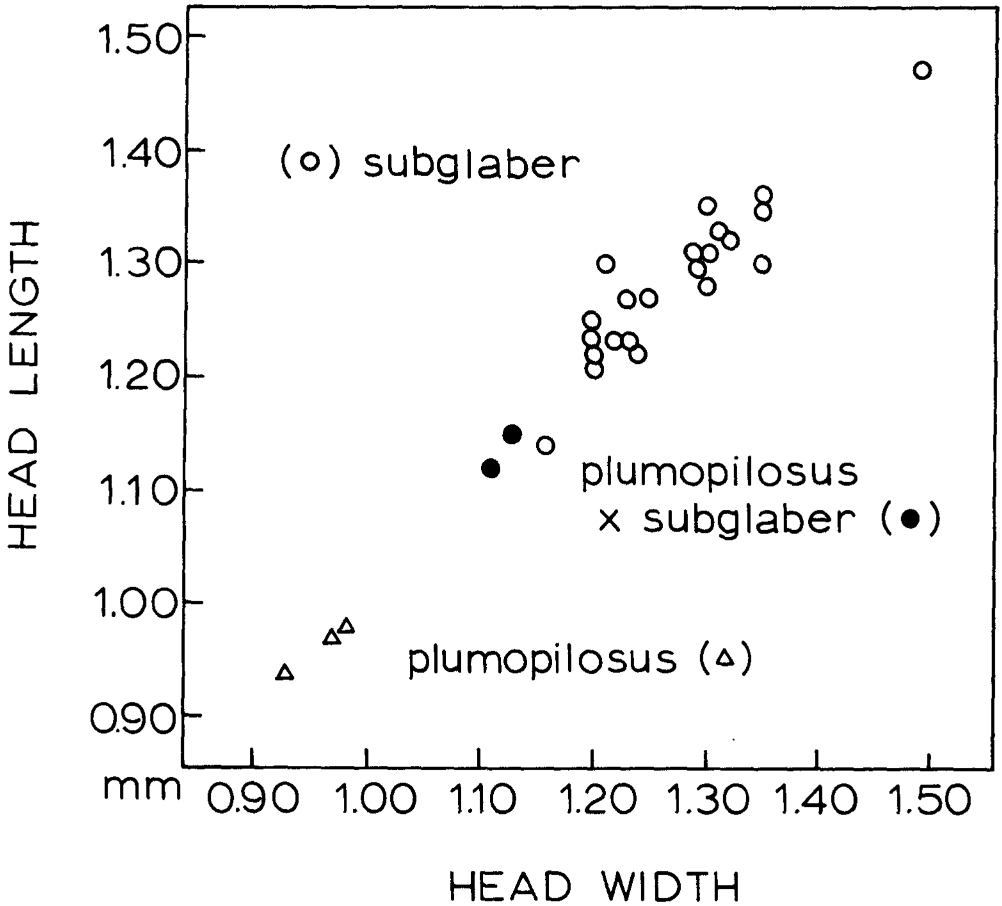


Fig. 11. Sample regressions of head length on head width in queen caste of *A. subglaber* (N = 22), *subglaber* × *plumopilosus* (N = 2), and *plumopilosus* (N = 3). Not over 2 queens measured per nest series, usually only 1. (See text for further discussion.)

of *claviger* and *latipes* in all castes, and going back about 100 years, I find no morphological evidence of any mixing of the gene pools of these two species. *Claviger* and *latipes* appear to be reproductively isolated in an effective way, despite the local production of moderate numbers of hybrids.

Another point of interest relating to the queens of *latipes* × *claviger*, and one that unfortunately cannot be evaluated on the basis of existing evidence, relates to possible variations in behavior patterns. There are grounds for supporting the hypothesis that *latipes* queens parasitize *Lasius* colonies. Entry into and adoption by the host colony is presumably made possible by complex instinctive patterns that have resulted from the action of natural selection over long periods of time. Despite these highly evolved patterns, no more than a very small proportion of queens can be successful as parasites. There is no reason to believe that a *latipes* queen fertilized by a *claviger* male would react differently from one fertilized by a male of her own species. Thus the number of colonies of *latipes* would be expected to bear a relationship to the number of *latipes* × *claviger* colonies solely as a function of the relative frequencies of these two types of matings. However, hybrid queens are presumably intermediate between the parents in a number of unknown behavioral ways, just as they are in many known morphological ways. Furthermore, there is evidence that the parental species may differ in the way in which they solve the problems of species perpetuation. The success of a dealated *latipes* × *claviger* queen, in the complex and risky business of getting adopted by a host colony, may well be somewhat decreased by inappropriate reactions. Thus, even if fertile, hybrid queens may stand little chance to produce offspring under natural conditions.

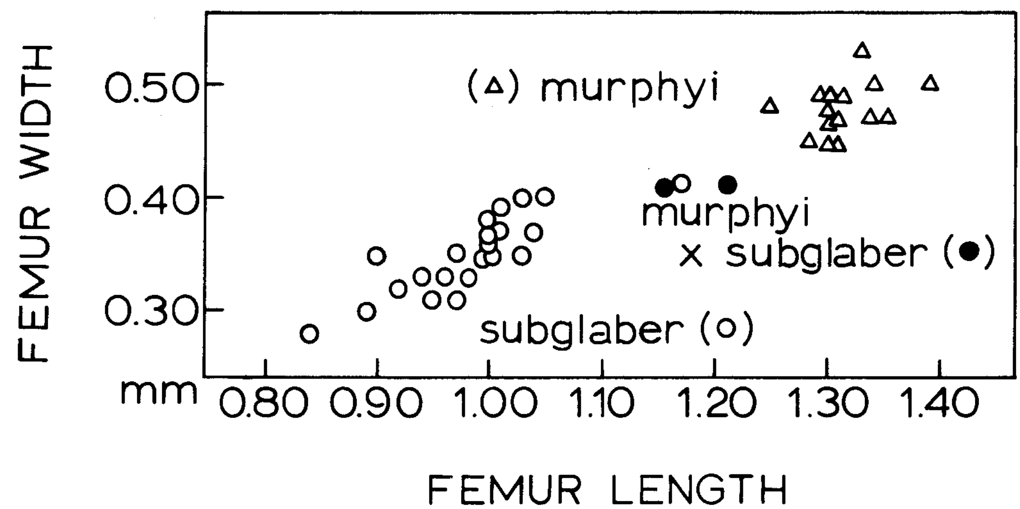


Fig. 12. Sample regressions of femur width on femur length in queen caste of *A. murphyi* (N = 15), *murphyi* × *subglaber* (N = 2), and *subglaber* (N = 22). Not over 2 queens measured per nest series, usually only 1. (See text for further discussion.)

Another area of investigation that may prove valuable was suggested by John and Lewis (1966). They urged that more studies of the endophenotype be made on insects. A detailed study of the karyomorphology of at least the known hybrid taxa of *Acanthomyops* and their parent species might shed light on some of the problems discussed above.

In the preliminary sorting of taxa for this study, although all hybrids were segregated as separate entities, not all were recognized as hybrids at first. Some were considered to be extreme variants of one of the parents, or of a closely related independent taxon. Only further study along several lines revealed their hybrid nature. There was, however, never too much question as to the identity of the parents, even when males were not

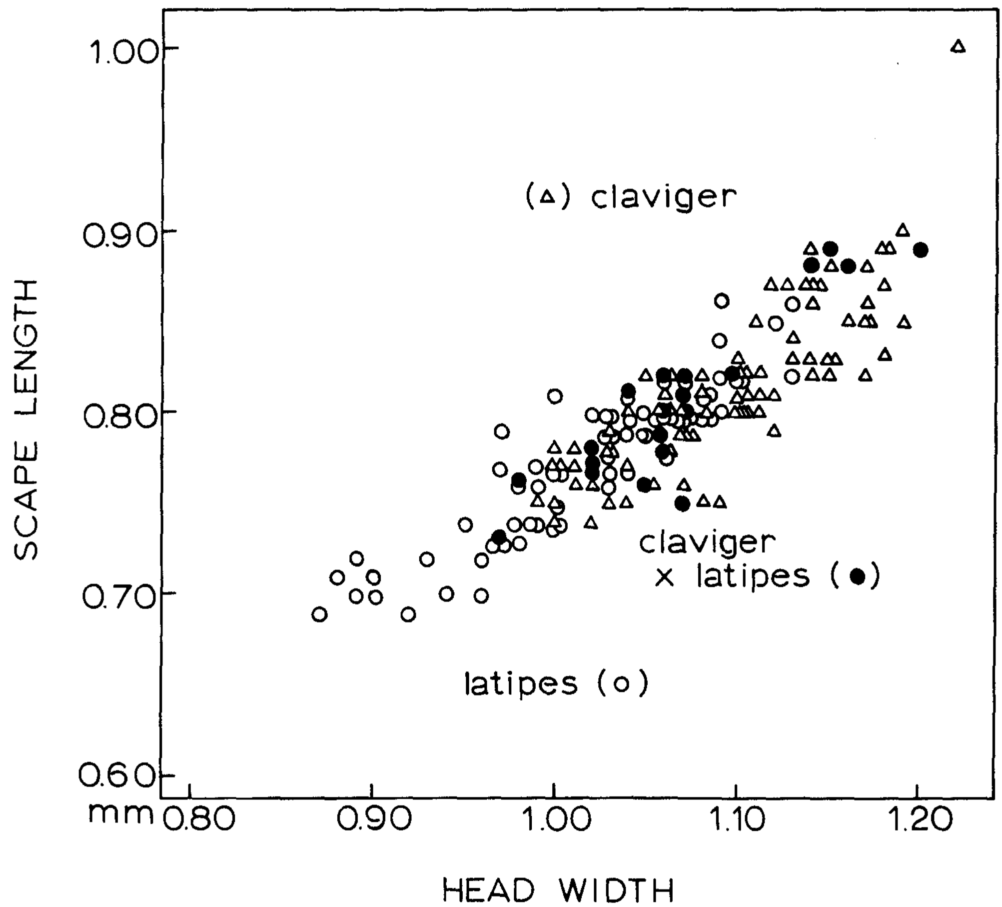


Fig. 13. Sample regressions of scape length on head width in worker caste of *A. claviger* (N = 78), *latipes* × *claviger* (N = 20), and *latipes* (N = 66). All workers measured from Illinois, Michigan, Minnesota, and New York are included in *claviger* and *latipes*. All measured workers are included in the hybrid taxon; they originated from the 4 states listed above plus Connecticut and Massachusetts. Not over 2 workers measured per nest series, usually only 1. (See text for further discussion.

present. To supplement the nonmetric characters used to compare hybrids with parents, regressions of metric characters were reviewed. As queens are interspecifically more distinct than workers, the regressions of queen characters were relied upon principally. Because of the great difficulty of assessing the status of a nest sample solely on the basis of the worker caste, those few cases where extreme variants were suspected of being hybrids are omitted from consideration here. The possible hybrid nature of each of these samples is discussed in the section on variation under the taxon to which they are referred.

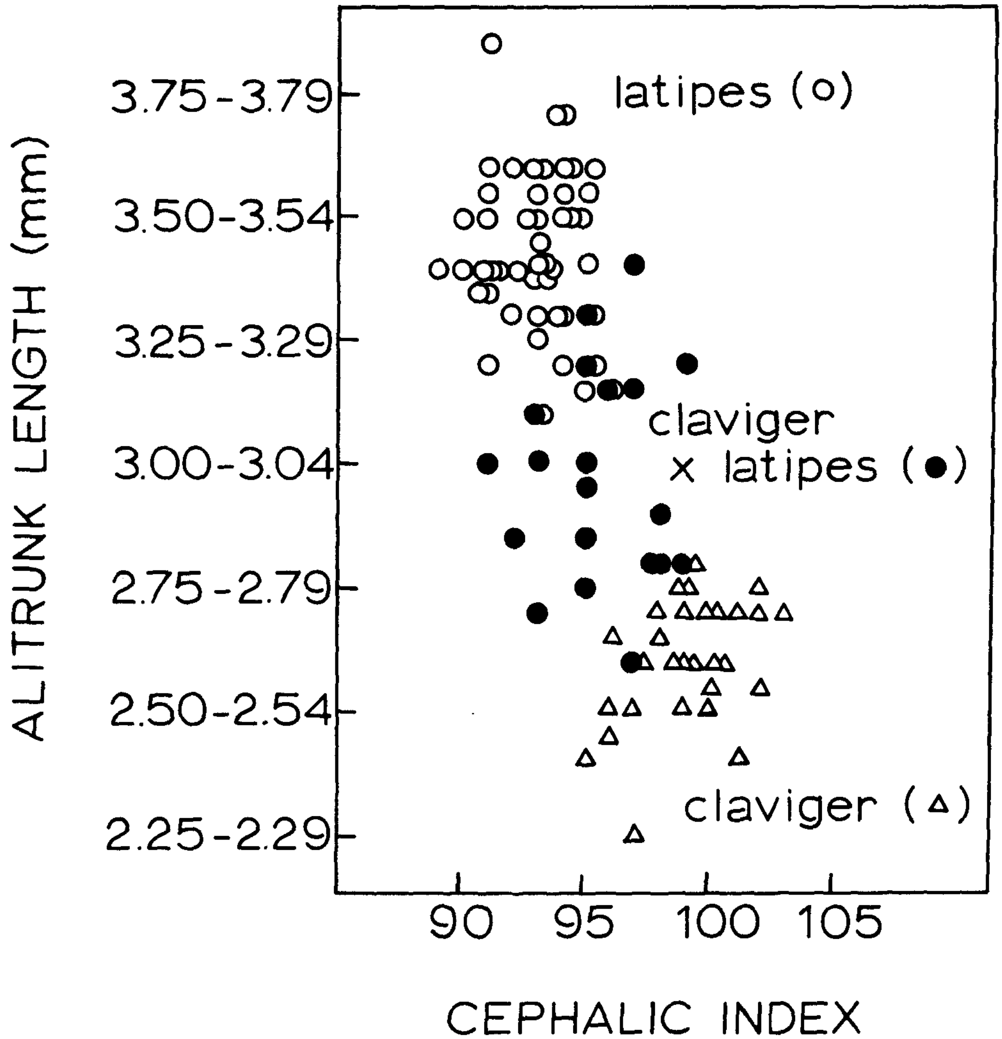


Fig. 14. Sample regressions of alitrunk length on cephalic index in queen caste of *A. latipes* (N = 48), *latipes* × *claviger* (N = 20), and "typical" *claviger* (N = 29). Not over 2 queens measured per nest series, usually only 1. (See text for further discussion.)

The procedures that enabled making a final decision on the hybrid status of certain nest series were facilitated by the use of regression plots that had been prepared for measured specimens of all taxa. The regressions had been plotted on sheets of semitransparent graph paper measuring 18 × 22 inches. Comparisons of the regressions of various taxa were made by superimposing combinations of these sheets over a strongly lighted tracing box. In these comparative studies the following standardized regressions were used: SL/HW, HW/HL, AL/SI, and AL/CI in both female castes, and FW/FL and AL/FI in queens. The 5 interspecific hybrid taxa reported in this study were intermediate between the parent species for all of these characters.

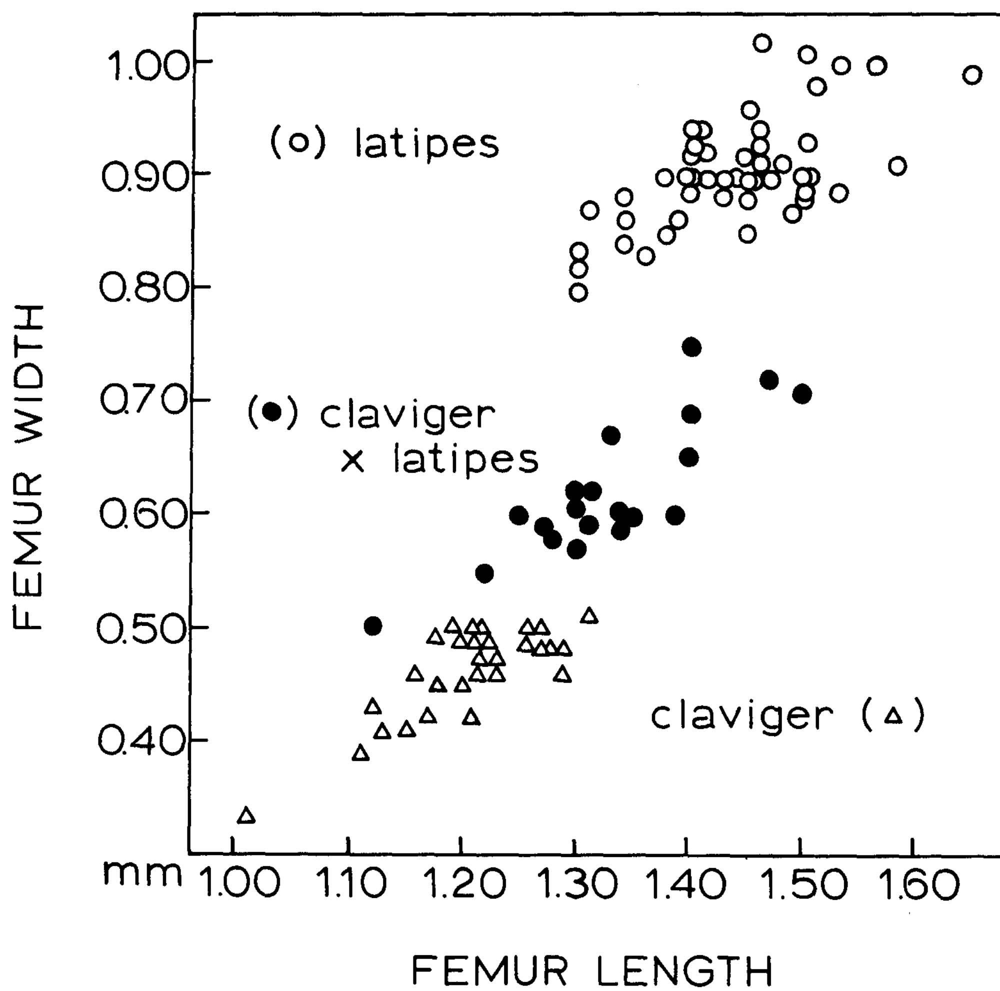


Fig. 15. Sample regressions of femur width on femur length in queen caste of *A. latipes* (N = 48), *latipes* × *claviger* (N = 20), and "typical" *claviger* (N = 29). Not over 2 queens measured per nest series, usually only 1. (See text for further discussion.)

In addition to the information provided by the presence of males and the regression comparisons of queens and workers, several other lines of evidence were considered. Geographic distribution of the supposed parent species was checked to see if their known ranges overlapped, or if it was likely that their ranges would have overlapped if more samples had been available. The time of nuptial flights was checked for both parent species to determine if they overlapped. And finally, where data were available, various ecological features were compared between the hybrid taxon and its parent species.

Space limitations make it impossible to publish more than a few of the regression comparisons; these are shown in this section (figs. 10–15). The other kinds of evidence used in arriving at a decision are presented in appropriate places throughout the text. For any student who desires to undertake a further study of hybrids in *Acanthomyops,* the reference collection is available in the MCZ, and copies of both the computer tape and the full statement of collection data, proving all of the raw data of this study, are available at Harvard and Cornell.

In selecting characters to be used in the published regressions, those that differed enough between parent species to provide reasonably good visual separation were chosen. But never did any of the unpublished regressions relating to these 5 hybrid taxa go counter to the assumption that the taxon in question was a hybrid of the stated parent species. A single figure showing regressions for queens is included for each of the following taxa: (1) *murphyi* × *latipes,* (2) *murphyi* × *subglaber,* and (3) *subglaber* × *plumopilosus.* In the case of the more frequently encountered *latipes* × *claviger,* 2 regressions for queens and 1 for the worker caste are included. The single sample that formed the basis for the decision on the status of *latipes* × *coloradensis* was received when the revision was virtually complete; no regression figure was included for this taxon. It may be noted that the univariate frequency tables provide further comparative data on the taxa. Even though these tables do not present the data in a form as suitable for the comparison of hybrids and parents as do the regressions, they are, nevertheless, useful for rough comparisons of characters not shown in the published regression figures.

The two regressions provided for the queens of *latipes* × *claviger* give examples of the separation of taxa by using 2 measurements as opposed to using a measurement and an index. The regression figure for the workers reveals the difficulty of establishing the hybrid nature of a taxon solely on the basis of this caste. *Latipes* males associated with *latipes* × *claviger* nest samples were compared with those from *latipes* colonies for a number of characters, both metric and nonmetric. The same procedure was followed for *murphyi* males. In both cases, no significant differences were found in any of the characters checked. For this reason no male regression figures are included.

Generic Status and Diagnosis

The genus *Acanthomyops* was erected by Mayr (1862, p. 699) to include a single species, *Formica clavigera* Roger, described from the queen caste. Mayr (1866) changed the status of his genus to that of a subgenus of *Lasius*. Creighton (1950) raised *Acanthomyops* to the rank of genus again. I concur with Creighton in this matter, as do most myrmecologists. Because of these changes, one would expect only to look under the names *Lasius* and *Acanthomyops* in a literature search. Unfortunately the situation is not that straightforward. Morice and Durrant (1914) called attention to the so-called Erlangen list of 1801, which was anonymously authored by Jurine. He had used the name *Lasius* for a genus of bees. If accepted, the Jurine paper would have necessitated sinking *Lasius* Fabricius, 1804. The Erlangen list was, however, ruled invalid by the International Commission of Zoological Nomenclature in 1935. Nevertheless, confusion existed for about 20 years following the publication of the paper by Morice and Durrant. During this period the name *Acanthomyops* was often applied in diverse ways. Nomenclatorial confusion continued after 1935 in the writings of Donisthorpe, who refused to accept the ruling; he used the name *Acanthomyops* to designate the species of *Lasius* (*sensu lato*). The historical details of this episode are discussed by Creighton (1950), Donisthorpe (1927), Wheeler (1916), and Wilson (1955).

The generic diagnosis of *Acanthomyops* is easily effected by comparison with the formicine genus *Lasius*, to which it is closely related. In many older keys the species of *Acanthomyops* run out to *Lasius*, from which they can be separated by their reduced number of palpal segments in all castes. *Acanthomyops* has 3-segmented maxillary and 4-segmented labial palpi. The members of the subgenus *Lasius* (*Chthonolasius*) are closely related to *Acanthomyops*. It is likely that these two groups are linked by a common ancestor (or perhaps ancestors). Reference to Wilson (1955) will provide detailed information on *Lasius*. Emery (1925) treated both *Acanthomyops* and *Lasius*. Figures 16 to 18 are habitus figures for the 3 castes of *Acanthomyops*. These illustrations, prepared by Mr. William H. Gotwald, Jr., were based on *interjectus*, a species typical of the genus.

The following comparative list gives some of the differences between *Acanthomyops* and *Lasius*. This set of diagnostic characters, which ranges from trends to distinct differences, should enable one to distinguish between these genera in both field and laboratory.

1. Maxillary palpus in all castes. *Acanthomyops*: 3-segmented and short. *Lasius*: 6-segmented and moderately to very long.

2. Mandibular gland of living worker. *Acanthomyops*: Chadha, *et al.* (1962) showed by photographs the relative size of the mandibular glands of *A. claviger* and *L. umbratus*. That of *claviger* is much larger, with an average linear measurement about 3 times that of *L. umbratus*. If *claviger*

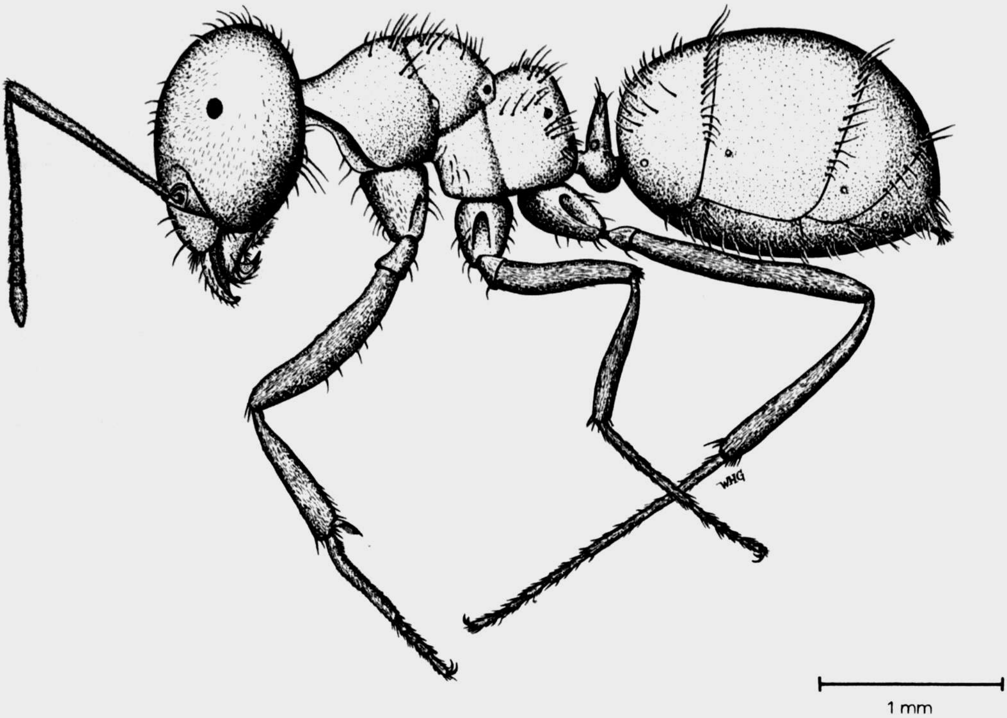


Fig. 16. Habitus figure of *Acanthomyops* worker, based on *interjectus*. Drawing by W. H. Gotwald, Jr.

is typical of its genus in this respect, a volume difference of about 27:1 is indicated. Although this character is one of degree, the difference is so great as to make it of diagnostic value where living workers are available. *Lasius*: It seems likely that *L. umbratus* has a mandibular gland approaching maximal size for *Lasius*. This is inferred from the fact that the most pronounced citronella odor of any *Lasius* sp. is produced by *umbratus*.

3. Products of the mandibular glands of workers. *Acanthomyops*: Chadha, *et al.* (1962) reported that the products of the mandibular glands of *claviger* are composed chiefly of citronellal and citral (both stereoisomers) in an approximate ratio of 9:1. The citronella oils, which subserve a defense function in *Acanthomyops,* also serve as an alarm mechanism, as they do in *Atta rubropilosa* (See Butenandt, *et al.,* 1959). The presence of tridecan-2-one, undecane, and "dendrolasin" are unknown in *Acanthomyops*. *Lasius*: Although the detailed composition of the contents of these glands are not now available for *Lasius,* field contacts with *umbratus* suggest the presence in smaller amounts of one or both of the substances present in *claviger*. The mandibular glands of *L. umbratus* and *bicornis* contain the nonterpenoids, tridecan-2-one and undecane (Cavill and Robertson, 1965). The mandibular glands of *L. fuliginosus* produce "dendrolasin", which may have an alarm function. (See Wilson, 1965.)

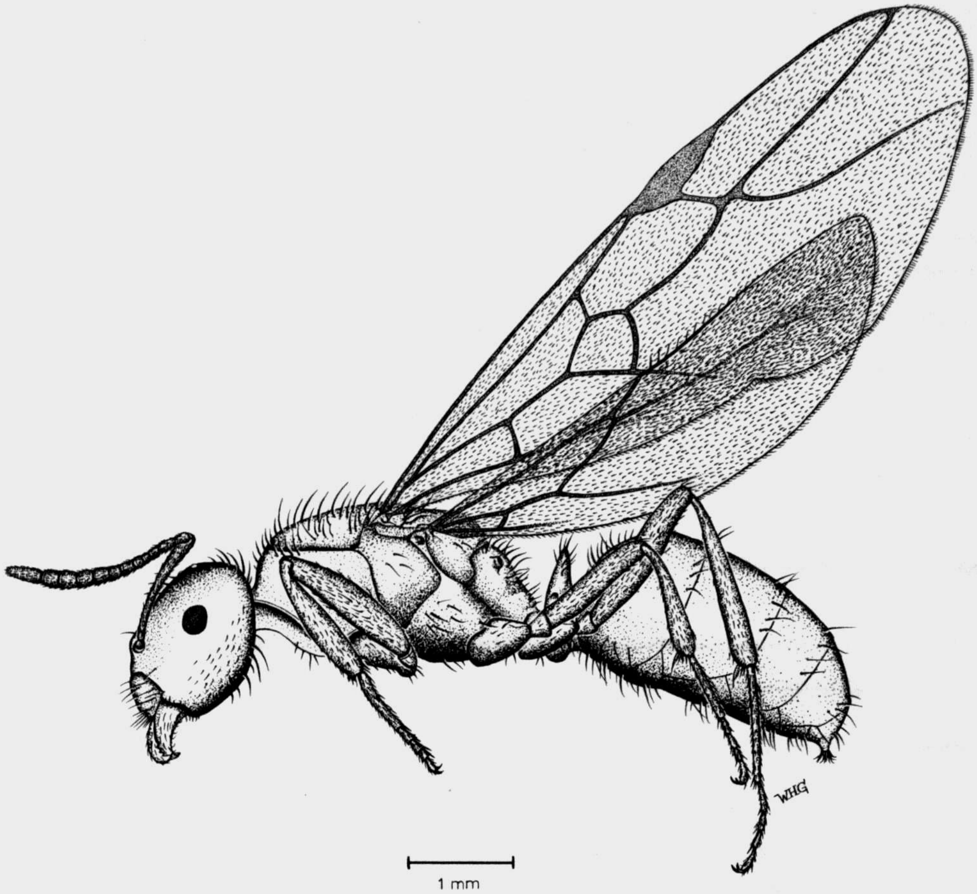


Fig. 17. Habitus figure of *Acanthomyops* queen, based on *interjectus.* Drawing by W. H. Gotwald, Jr.

4. Relative dimensions of eye and head width in workers. *Acanthomyops*: About 3 dozen workers ranging over most taxa were chosen to include many with minimal or maximal head width (HW). The maximum measurable length of the eye (EL) of each of these specimens was recorded, and 100(EL)/HW was computed. The resulting values ranged from 8.5 to 15.5. It appears that *Acanthomyops* averages and ranges lower in this respect than most subgenera of *Lasius*. *Lasius*: Comparable measurements and computations on about a dozen specimens gave the following values: *Lasius* (*L.*) 23–28; *L.* (*Chthonolasius*) 15–19; *L.* (*Cautolasius*) 12; and *L.* (*Dendrolasius*) 21.

5. Profile of propodeum in workers. *Acanthomyops*: Length of declivitous face of propodeum usually not much greater than that of dorsum, which is usually flat or more or less evenly rounded. *Lasius*: Declivitous face long relative to dorsum, which is often angular, showing abrupt changes of contour.

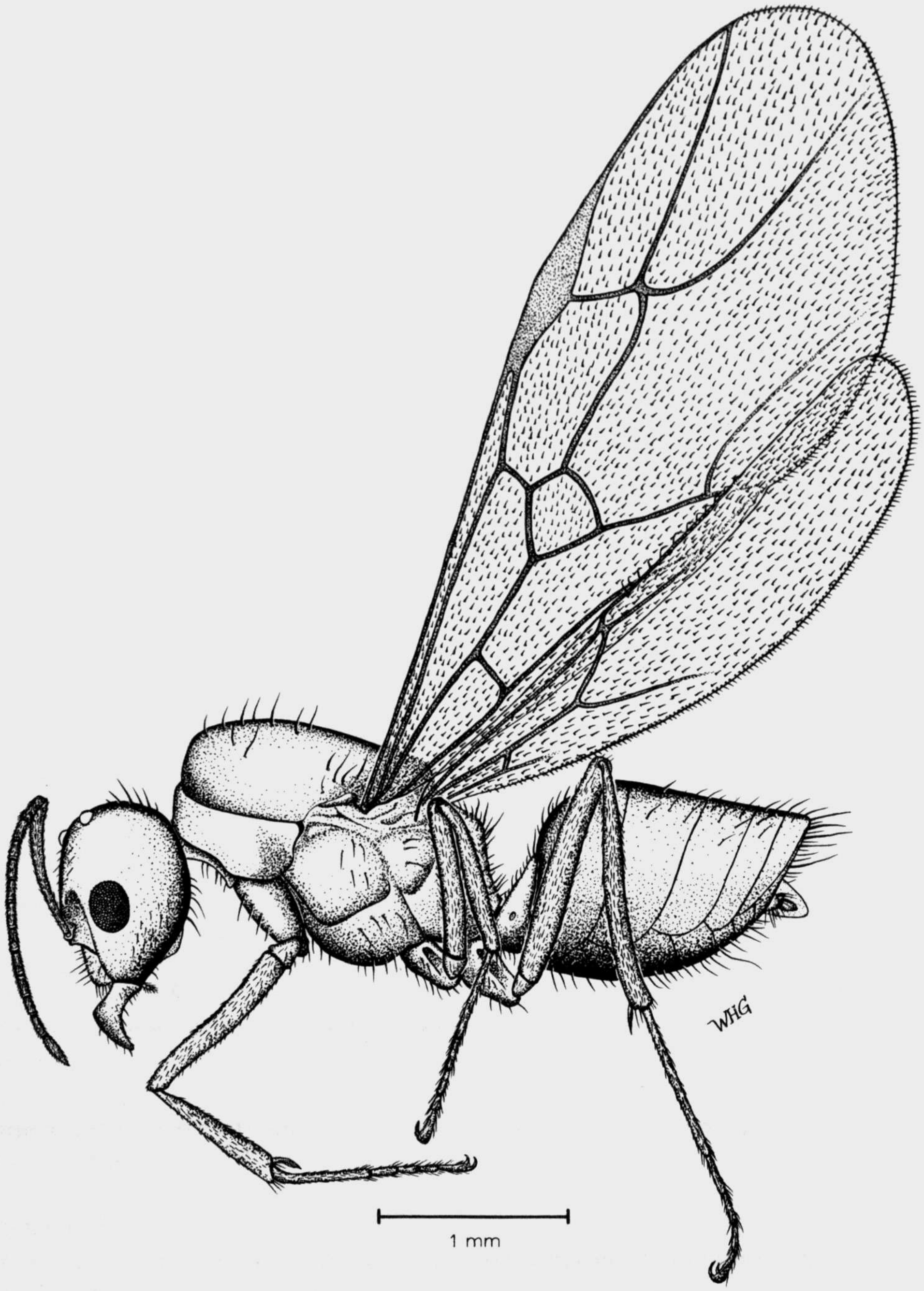


Fig. 18. Habitus figure of *Acanthomyops* male, based on *interjectus*. Drawing by W. H. Gotwald, Jr.

6. Shape of propodeal spiracle in all castes. *Acanthomyops*: More or less circular. *Lasius*: More or less elliptical in queens, with major axis often several times longer than minor axis. In males, shape similar to queens, but with less disparity in relative lengths of axes. In workers, shape ranges from circular to strongly elliptical.

7. Mesopropodeal spiracles of workers. *Acanthomyops*: Often prominent and conspicuous. *Lasius*: Usually less prominent.

8. Maximum dimension of metapleural gland opening (M) perpendicular to its long axis in relation to maximum dimension of propodeal spiracle (S) in all castes. *Acanthomyops*: In queens, ranging from M = 2S to M = S/2 in *latipes* in which M is greatly reduced in size. In males, M equal to or less than S. In workers, M approximately equal to S. *Lasius*: In queens, M greater than S in both *Lasius* (*L.*) and *L.* (*Cautolasius*), but M less than S in *L.* (*Dendrolasius*) and L. (*Chthonolasius*). In males, the same inequalities hold as for the queens. In workers, M greater than S for all subgenera except *L.* (*Chthonolasius*) where M is less than S.

9. Presence, relative number, and position of guard hairs with respect to opening of metapleural glands, in all castes. *Acanthomyops*: Always present, but usually less numerous and having their origin farther from the opening of the metapleural gland, which is often not covered. *Lasius*: If present, usually more numerous and arising close to a covered gland opening. Absent in queens and males of subgenus *L.* (*Dendrolasius*).

10. "Scale" impression of gaster in workers. *Acanthomyops*: Gaster usually without a distinct impression anterobasally. *Lasius*: Gaster usually with a distinct "scale-shaped" impression anterobasally.

Comments on Use of the Keys

Shorter key

This key was constructed for typical and near-typical specimens of 7 species in the worker and queen castes only. Males were excluded because they rarely need to be keyed out, and, furthermore, the limits of their variation are poorly known. The 7 included species are sporadic to very common, and are widespread in their distribution. In most areas, over 90 percent of the samples collected can be identified correctly by using the shorter key. However, there is a danger that the use of this key may occasionally result in the misidentification of a sample. Reference to the sets of illustrations, included in the treatment of each taxon, and to the 15 tables presenting frequency distributions of metric data, located at the end of the systematic section, will greatly reduce this risk. Should difficulty arise, it will probably be either because the species at hand is not 1 of the 7 included in the shorter key or because the specimens are atypical. In case of doubt, use the general key for the appropriate caste, always selecting the queen key rather than the one for workers whenever possible.

General keys

These keys were constructed to cover both typical and atypical specimens of all taxa. Various problems arise with respect to variation of characters. Some species and hybrid taxa are known only from 1 or a few collections; we are, therefore, ignorant of their limits of variation. In the very common species, there is little doubt about the limits of variation. However, the range of variation in some characters is so great as to make difficult the writing of a key that is at once workable and comprehensible. In constructing statements for the keys, extremes so infrequent in occurrence as to represent only a small percentage of the sample are usually included with appropriate qualifying statements.

Use of the keys assumes a familiarity with some special terms, all of which are defined, and some illustrated, in the section on definitions, beginning on page 9.

It is often essential in using the general keys to consider the set of separate descriptive statements as a group. This is especially true in the worker key.

Additional information, much of which is not in a given female key in any form, can be obtained from the figures illustrating outlines of body parts, pilosity, etc. These standardized illustrations have been done for each taxon except *latipes* × *coloradensis*. Other sources of useful information are the frequency distributions of metric data in the tables following the systematic section, and the statistical data accompanying the diagnosis of each taxon. These data are for queens and workers only.

Queen key

This key is the most reliable of the three. A large number of distinctive characters, representing several lines of specialization, are present in this caste. Also a fairly sizable collection of specimens was available for study. The key is thus relatively uncomplicated, even though some extreme variants were included.

The number of outcomes in the key is 18. This includes 14 species and 5 hybrid taxa, 2 of which are lumped together. Only *colei* remains unknown in the queen caste. In general the queen key should lead to correct identification of specimens about 99 percent of the time, often with only single specimens available.

Worker key

This key is less reliable than the queen key, but more reliable than the male key. A large number of specimens was available for study, but only minor differences of structure, pilosity, size, and color exist between the workers of many taxa. The closeness of some of the species in conventional taxonomic characters is often paralleled in metric characters. This made it difficult to construct a key that was both workable and comprehensible.

An attempt has been made to use as many relatively stable characters as possible in constructing the key. It is especially important that the various statements of a couplet be treated as a group in the worker key. Some of the characters used are not concordant, others are to a degree, but often are rather weak in their positive correlation. This makes it possible to use what amounts to a "majority vote" in deciding which route to take in the key. Extensive use of illustrations, frequency tables, and regression figures should supplement the worker key.

The number of outcomes in the key is 18. This includes 15 species, an atypical form of *claviger,* and 5 hybrid taxa, 3 of which are lumped with *latipes.* In general this key should enable the user to correctly identify at least 95 percent of his specimens, provided that a series of workers is available.

Male key

This key is less reliable than the other two, as relatively few of the nest samples studied contained males. Consequently the limits of variation of the diagnostic characters of this caste are poorly known. An attempt to circumvent the consequences of ignorance was made by running sevral species out twice. A serious study of males, including comparative data on genitalia, might result in a fairly reliable key. The work of Clausen (1938) strongly suggests that the subgenital plate may be the best single structure for separating the males of *Lasius.* Unfortunately he did not clearly indicate the degree of variability of this structure. Wilson (1955) found that the subgenital plate was fairly variable in some species of *Lasius.* The usefulness of the subgenital plate as a diagnostic character in *Acanthomyops* should be investigated.

There are 14 species included in the key; the male of *pubescens* is unknown. The male specimens included in a sample of *pogonogynus* are *murphyi.* The males included in samples of the taxon known as alpha-*latipes* are *latipes.* No males were associated with samples of the other 3 hybrid taxa.

Fortunately the male key will not be used much, since samples containing only males are not often sent in for identification or collected by entomologists. The reliability of this key is difficult to state, but may approach the 85 to 90 percent level, especially if series of specimens are available in the more variable species.

Shorter Key

1. Workers 2
   Queens 6
2. Standing hairs on dorsum of gaster confined to posterior edges of tergites beyond first. Pubescence on gaster dilute, that on head moderately dense. Crest of petiolar scale sharp in side

view, emarginate in anterior view. A large species ..6. *interjectus*

Standing hairs more or less uniformly distributed over dorsum of gaster, not confined to posterior edges of tergites. Pubescence, petiolar scale and size varying 3

3. In side view, crest of petiolar scale blunt (fig. 105); entire surface of gula covered by many standing hairs 4

In side view, crest of petiolar scale sharp (fig. 47) to moderate (fig. 133); gula either without hairs on with fewer standing hairs over the posterior ¾ to ½ of its surface 5

4. Standing hairs short, about twice as numerous on propodeum as elsewhere on dorsum of alitrunk .... 8. *murphyi*

Standing hairs longer, more or less evenly distributed over dorsum of alitrunk .... 7. *latipes* (= beta-*latipes* of authors)

5. Pubescence on first tergite of gaster dilute to moderate (2 larger species): 1. *claviger* (eastern) and 2. *coloradensis* (western). *Note*: For specimens collected between the ranges indicated by map 1, see text for details of separation.

Pubescence on first tergite of gaster dense to moderately dense (2 smaller species): 9. *subglaber* and 14. *occidentalis*. ***Note***: For specimens collected in the area of overlapping ranges as indicated by map 5, see text for details of separation.

6. In side view, crest of petiolar scale blunt and covered with 65 or more standing, or appressed and matted hairs 7

In side view, crest of petiolar scale sharp or moderate and covered with fewer standing hairs, none matted 8

7. Principal body hairs all standing, more or less evenly distributed. Fore femur very wide (FI 58 or more), with large, conspicuous genual plates. Antennal scape and funiculus short (SI 68 or less), very strongly clavate .... 7. *latipes* (= beta-*latipes* of authors)

Principal body hairs mostly appressed and matted to surface, unevenly distributed. Fore femur not as wide (FI 40 or less), with small and inconspicuous genual plates. Antennal scape and funiculus longer (SI 78 or more), more or less slender .... 8. *murphyi*

8. A smaller species with posterior border of head distinctly emarginate in perfect full-face view. Eyes large, eye length about equal to width of fore femur. Antennal scape short and slender, its apex reaching to about half way between eye and posterior corner of head .... 14. *occidentalis*

Species size varying, but posterior border of head not emarginate as seen in perfect full-face view. Eyes not appearing unusually large, eye length less than width of fore femur in at least the smaller species. Antennal scape and funiculus varying 9

9. A small species with standing body hairs very short and delicate. Pubescence on gaster dense in all specimens except those from East Coast below New England, where it is dilute . . . . 9. *subglaber*
   Larger species with standing body hairs long and not delicate. Pubescence on gaster dilute 10
10. CI 103 or more. Pubescence on most of head moderately dense. Basal margin of mandible with 1 or more denticles. Antennae long and slender. Body color variable, but mostly light brownish yellow to yellowish brown . . . . 6. *interjectus*
   CI 102 or less. Pubescence on most of head dilute. Basal margin of mandible without denticles. Antennae shorter, stout or slender. Body color medium to very dark brown 11
11. SI 66 or less. Antennal scape and funiculus moderately to fairly strongly clavate. Body color medium to dark brown, not appearing black to naked eye . . . . 1. *claviger*
   SI 67 or more. Antennal scape and funiculus at most very weakly clavate. Body color very dark brown, often appearing black or nearly black to naked eye . . . . 2. *coloradensis*

General Keys

A key to the queens of *Acanthomyops*

1. Principal body hairs standing, distally plumose (fig. 4), numerous, more or less evenly distributed over body . . 10. *plumopilosus*
   Principal body hairs either standing or appressed and matted to surface; simple or weakly to strongly barbulate (figs. 5–7), never distally plumose; varying in number and distribution 2
2. Body hairs either standing or appressed and matted to surface; numerous and unevenly distributed, especially numerous in frons, clypeus, genae, gula, pronotum, coxae meso- and metapleura, propodeum, and petiolar scale. Crest and sides of petiolar scale with 125 or more standing or matted hairs. Head noticeably distorted (fig. 111). SI 71 to 84, FI 35 to 51 . . . 3
   Body hairs standing, sparse to numerous, but if numerous then more or less evenly distributed over body. Crest and sides of petiolar scale with fewer than 125 standing hairs. Head not noticeably distorted (fig. 26). SI and FI varying. However, if petiolar scale has 125 or more standing hairs, then head is clearly distorted (fig. 93) and SI ranges from 59 to 68 and FI from 58 to 70 4
3. Hairs coarse, whitish-yellow, mostly blunt-ended, tightly appressed and matted to body. Petiolar livery so dense that it completely hides the underlying scale even when viewed from

the side with lighting from behind. SI 78 to 84, FI 35 to 40 .... 8. *murphyi*

Hairs finer, dirty yellow to reddish-brown, mostly with pointed tips, tangled and twisted, but not tightly appressed and matted to body. Petiolar livery dense above, but outline of scale is more or less visible when viewed from the side with lighting from behind. SI 71 to 74, FI 46 to 51 .... 8a. *murphyi* × *latipes* hybrid

4. In side view, standing hairs more or less evenly distributed over entire surface of gula, ranging in number from 16 to 80, and 0.20 to 0.40 mm long. SI 56 to 68, FI usually 35 to 70 5

In side view, gula either without any standing hairs, or with up to 36, these confined to posterior ¾ to ½ of its surface and ranging from 0.03 to 0.35 mm in length SI and FI varying. However, in the rare cases where hair distribution on gula is entire as described in the couplet above, than either (1) length of longer standing hairs on gula does not exceed 0.10 mm, or (2) SI greater than 70, FI less than 35, and antennal scapes often covered with prominent, delicate, suberect pubescence hairs 7

5. Fore femora with large conspicuous laminate genual plates, FW measuring 0.80 mm or greater, FI 58 or more. Crest of petiolar scale very blunt in side view; convex or straight in anterior view, without median emargination, or with an occasional small notch-like impression. Standing hairs on crest and sides of scale numbering 65 to 180. Antennal scape and funiculus extremely clavate, antepenultimate segment of funiculus at least 2.30 times wider than long. Length of standing hairs on gula 0.30 to 0.40 mm, ranging in number from 35 to 80. .... 7. *latipes* (= beta-*latipes* of authors)

Fore femora without or with only moderate genual plates, FW measuring 0.75 mm or less, FI 54 or less. Crest of petiolar scale sharp to very blunt in side view; convex, straight, or broadly emarginate in anterior view. Standing hairs on crest and sides of scale numbering 20 to 75. Antennal scape and funiculus weakly to quite clavate, antepenultimate segment of funiculus less than 2.30 times wider than long. Length of standing hairs on gula usually 0.30 mm or less, usually 35 or fewer in number 6

6. Fore femora without genual plates, FI 33 to 42. Crest of petiolar scale moderately sharp to sharp in side view; broadly emarginate, often distinctly so, in anterior view; not over 45 standing hairs on crest and sides of scale. Antennal scape and funiculus from weakly clavate to clavate, antepenulti-

mate segment of funiculus not over 1.55 times wider than long . . . . 1. *claviger*

Fore femora with moderate genual plates, FI 43 to 54. Crest of petiolar scale blunt to very blunt in side view; convex, straight, or more rarely with a slight median notch in anterior view; 50 to 75 standing hairs on crest and sides of scale. Antennal scape and funiculus quite clavate, antepenultimate segment of funiculus greater than 1.55 and less than 2.30 times wider than long . . . 7a. *latipes* × *claviger* hybrid (= alpha-*latipes* of authors) and 7b. *latipes* × *coloradensis* hybrid

7. Length of longer standing hairs on gula usually 0.20 mm or more, and posterior border of head not broadly and deeply emarginate as seen in perfect full-face view. In side view, number of standing hairs on gula usually 15 or more, but not less than 10. Longer standing hairs on posterior edge of first tergite of gaster usually more than 0.20 mm. Abundance of body pilosity and pubescence varying, but both never extremely sparse. Standing body hairs simple to weakly barbulate . . 8

Length of longer standing hairs on gula less than 0.20 mm (except for an occasional specimen of *occidentalis,* which has posterior border of head broadly and deeply emarginate as seen in perfect full-face view). In side view, standing hairs on gula 0 to 16, usually less than 10. Longer standing hairs on posterior edge of first tergite of gaster 0.20 mm or less, with 1 exception (*arizonicus,* southern Arizona, with pilosity on gaster about 0.4 mm; both body pilosity and pubescence extremely sparse). Standing body hairs simple to strongly barbulate 14

8. Longer standing hairs on dorsum of alitrunk 0.40 to 0.45 mm. SI usually 67 or greater, FI 34 or less 9

Longer standing hairs on dorsum of alitrunk less than 0.40 mm, usually 0.20 to 0.35 mm. SI and FI varying. However, if standing hairs on dorsum of alitrunk measure as much as 0.40 mm (a very few large *claviger* queens), then SI is 66 or less and FI 35 or greater 10

9. In anterior view, crest of petiolar scale usually narrowly but distinctly emarginate, or more rarely straight or convex; sides distinctly convex. Basal margin of mandible usually with 1 or more denticles. Penultimate and antepenultimate segments of funiculus at least as long as wide, usually longer than wide. In side view, gula with 10 to 18 standing hairs 0.25 to 0.35 mm long covering the posterior ¾ of its surface . . . . 6. *interjectus*

In anterior view, crest of petiolar scale broadly emarginate, usually deeply so; sides more or less straight and converging dorsally. Basal margin of mandible less commonly with a denticle. Penultimate and antepenultimate segments of funiculus a little wider than long. In side view, gula with about 14 to 16 standing hairs about 0.25 mm long located more or less centrally on its surface .... 3. *californicus*

10\. Crest of petiolar scale blunt as viewed from the side; as viewed anteriorly, crest straight and without emargination, or, at most, with a narrow median notch. Crest and sides of scale covered with 40 or more very coarse standing hairs ....8b. *murphyi* × *subglaber* hybrid

Crest of petiolar scale sharp to moderately sharp as viewed from the side; as viewed anteriorly, crest emarginate, either deeply or shallowly so. Crest and sides of scale usually with fewer than 40 delicate to moderately coarse standing hairs 11

11\. Antennal scapes uniformly and heavily covered with prominent, delicate, decumbent to suberect pubescence hairs about 0.07 mm long. In side view, entire surface of gula covered with 20 or more standing hairs, 0.20 mm or a little more in length. Pubescence hairs on gula numerous, decumbent, long (0.10 to 0.15 mm) and conspicuous. Entire dorsum of gaster evenly covered by standing hairs measuring 0.30 to 0.35 mm, and with pubescence moderate to dilute, long (many pubescence hairs measuring over 0.10 mm), and mostly inclined at angles of about 15 degrees with the surface. Crest of petiolar scale with longer standing hairs 0.12 mm or less. Sides of scale nearly straight and converging dorsally. Body color light brownish yellow .... 13. *creightoni*

Pubescence hairs on antennal scapes coarser, less numerous, and usually entirely appressed to surface, but some specimens have hairs decumbent to suberect, varying in length. In side view, only posterior ¾ to ½ of surface of gula covered with 10 to 20 standing hairs, and measuring 0.20 to 0.28 mm. Pubescence on gula shorter, usually appressed and not conspicuous. Distribution and length of standing hairs on dorsum of gaster varying. Pubescence on dorsum of gaster dilute to dense, but more or less appressed to its surface and shorter (most hairs well under 0.10 mm). Crest of petiolar scale with longer standing hairs 0.18 mm or more. Sides of scale varying, but often convex or straight and usually parallel to diverging dorsally. Body color of unfaded specimens darker, usually medium to piceous brown 12

12\. SI 66 or less. Scape and funiculus weakly to strongly clavate. Distribution of standing hairs on dorsum of gaster varying in the following manner: (1) confined to posterior edges of tergites except first, (2) more or less uniformly covering entire dorsum, or (3) intermediate between (1) and (2). Body color of unfaded specimens medium to dark brown, often with a slight reddish cast, rarely dark enough to appear black to the naked eye .... 1. *claviger*

SI 67 or greater. At most, scape very weakly clavate. Standing hairs on dorsum of gaster confined to posterior edges of tergites beyond first. Body color of unfaded specimens dark to piceous brown, often appearing black or nearly black to the naked eye 13

13. Dorsum of gaster densely pubescent. In side view, crest of erect petiolar scale approximately on level with propodeal spiracle. In anterior view, sides of petiolar scale straight and diverging dorsally, usually with 4 or fewer standing hairs per side, 0.10 mm or less in length. CI 100 or more, FI 31 or less. ... 11. *bureni*

Dorsum of gaster with dilute to very dilute pubescence. In side view, crest of erect petiolar scale above to well above level of propodeal spiracle. In anterior view, sides of scale moderately to strongly convex, usually with 10 or more standing hairs per side, 0.14 mm or more in length. CI usually 99 or less, FI usually 32 or more .... 2. *coloradensis*

14. Longer standing hairs on dorsum of alitrunk 0.35 mm or more; body pilosity sparse, posterior edge of first tergite of gaster with 0 to 6 standing hairs. Gula without standing hairs, or rarely with 1 or 2. Pubescence extremely dilute over whole body. SI 72 or more, FI 32 or less .... 5. *arizonicus*

Longer standing hairs on dorsum of alitrunk 0.30 mm or less; body pilosity denser, posterior edge of first tergite of gaster with 10 to 24 standing hairs. Gula usually with standing hairs. Pubescence varying from dilute to very dense. SI and FI varying 15

15. Dorsum of gaster very densely pubescent. In side view, crest of erect petiolar scale below level of propodeal spiracle, blunt to very blunt; crest with 2 or 3, and sides each with 0 to 2, standing hairs from 0.08 to 0.12 mm long. SI 75 or more, FI 30 or less .... 12. *pubescens*

Dorsum of gaster with pubescence varying from very dilute to moderately dense. In side view, crest of erect petiolar scale usually at, above, or well above level of propodeal spiracle, sharp to moderately blunt; crest with 4 or more, and sides each with 3 or more standing hairs, from 0.10 to 0.17 mm long. SI 70 or less, FI 32 or more 16

16. In anterior view, crest of petiolar scale with a distinct emargination, usually broad and fairly deep; sides more or less straight and usually diverging dorsally, but sometimes parallel. In side view, crest of scale sharp to moderately sharp. Mesoscutum moderately to densely pubescent. Body color light brown

to light yellowish brown 17

In anterior view, crest of petiolar scale convex or straight; sides more or less straight and parallel. In side view, crest of scale moderately blunt. Mesoscutum with dilute pubescence. Body color, except in badly faded specimens, darker brown, often with a reddish or piceous component 18

17. In perfect full-face view, head with posterior border broadly and distinctly emarginate, sides nearly straight and more or less parallel. In side view, standing hairs on gula numbering 8 or more, usually 0.15 mm or more in length. Width of scale at crest about equal to height above petiolar spiracle. Standing hairs on crest and sides of scale usually numbering 28 or more, often with as many as 60. CI 98 or less . . . . 14. *occidentalis*

In perfect full-face view, head with posterior border straight or nearly so, sides slightly convex. In side view, standing hairs on gula usually numbering 0 to 6, usually under 0.15 mm long. Width of scale at crest 1.2 to 1.4 times greater than height above petiolar spiracle. Standing hairs on crest and sides of scale usually numbering 26 or fewer. CI 100 or more . . . . 15. *mexicanus*

18. Standing body hairs simple, delicate; those on dorsum of alitrunk and gaster not more than 0.15 mm long; those on dorsum of gaster almost always confined to posterior edges of tergites beyond first. Crest of erect petiolar scale above level of propodeal spiracle . . . . 9. *subglaber*

Standing body hairs, especially those on occiput, dorsum of alitrunk, and crest of petiolar scale, strongly barbulate; many hairs on dorsum of alitrunk and gaster measuring up to 0.20 mm; those on dorsum of gaster unevenly distributed. Crest of erect petiolar scale at or just below level of propodeal spiracle. . . . . 9a. *subglaber* × *plumopilosus* hybrid

A key to the workers of *Acanthomyops*

1. Many standing body hairs with plumose tips (fig. 4) . . . . 10. *plumopilosus*

All standing body hairs simple, or weakly to strongly barbulate (figs. 5–7); never plumose distally 2

2. Gula without standing hairs, or rarely with, at most 1 or 2, which are much shorter than those on clypeus. Standing hairs on dorsum of gaster measuring 0.20 to 0.25 mm, almost invariably confined to posterior edges of tergites beyond first. Pubescence on gula and gaster extremely dilute . . . 5. *arizonicus*

Gula usually with standing hairs, length and distribution of those on gaster varying; in the few cases where hairs are absent on gula, then standing hairs on dorsum of gaster are not confined to posterior edges of tergites beyond first, and/ or pubescence on gula and gaster is from moderate to very dense 3

3. Length of longer standing hairs on dorsum of gaster 0.23 mm or more, on gula usually 0.20 mm or more. In side view, crest of petiolar scale sharp to moderately sharp; in anterior view, usually emarginate. Standing hairs on dorsum of gaster either strictly confined to posterior edges of tergites beyond first, or, if more or less widely distributed, then concentrated toward caudal margins 4

   Standing hairs on dorsum of gaster rarely more than 0.22 mm long, but if so, those on gula are less than 0.20 mm. Crest of petiolar scale varying as to sharpness and emargination. Standing hairs on dorsum of gaster varying, but usually more or less uniformly distributed over its surface, unless petiolar scale is moderate to blunt in side view, then there may be a relatively greater number of hairs on the caudal margins of tergites 5

4. HW 1.08 mm or greater, CI at least 98, usually 100 or more, SI usually 85 or less, and AL usually 1.40 mm or greater. Standing hairs on dorsum of gaster almost invariably confined to posterior edges of tergites beyond first, which has basal hairs. Pubescence on head moderate to dense. Mandible with 1 or more denticles on its basal margin . . . 6. *interjectus*

   HW 1.02 mm or less, CI usually 96 or less, SI 86 or more, and AL 1.30 mm or less. Standing hairs on dorsum of gaster more irregularly distributed over surface, but with majority of hairs on posterior edges of tergites beyond first. Pubescence on head dilute to very dilute. Mandible rarely with a denticle on its basal margin . . . . 4. *colei*

5. In side view, crest of erect petiolar scale well below level of propodeal spiracle, blunt; in anterior view, with a standing hair on each corner. Gaster very densely pubescent, body color brownish yellow. SI 83 or more . . . . 12. *pubescens*

   In side view, crest of erect petiolar scale either at or above level of propodeal spiracle, or not blunt; or, in anterior view, with at least a row of hairs. Pubescence on gaster, body color, and SI varying 6

6. In side view, crest of petiolar scale very to moderately blunt; in anterior view, convex, straight, or in rare cases with a slight median emargination. Standing hairs on gula almost always distributed over entire surface as viewed from the side . . . 7

   In side view, crest of petiolar scale moderately to very sharp; in anterior view, usually broadly emarginate. In a few cases crest may be straight or, more rarely, slightly convex. Standing hairs on gula almost always covering only the posterior ¾ or ½ of its surface, but in a few specimens, especially *claviger* from in or near North Carolina and Virginia, the entire gula may be covered with standing hairs 9

7. Standing hairs noticeably more numerous on propodeum than elsewhere on dorsum of alitrunk. Lateral surface and flexor edge of fore femur usually with 10 or fewer standing hairs, 0.05 mm or less in length. Length of standing hairs on gula, propodeum, and dorsum of gaster usually 0.10 mm or less. Antennal scapes with appressed pubescence . . . . 8. *murphyi*

   Standing hairs more or less evenly distributed over dorsum of alitrunk. Other characters varying 8

8. Number of standing hairs on gula 20 or more, often as many as 40, usually 0.12 mm or more in length. Lateral surface and flexor edge of fore femur usually with 12 or more standing hairs 0.06 mm or more in length. Longer standing hairs on dorsum of gaster 0.13 mm or more. Pubescence on antennal scapes varying from fully appressed to strongly suberect. . . . . 7. *latipes* (= beta-*latipes* of authors)

   NOTE: This couplet also receives 2 *latipes* hybrids: *pogonogynus* (Buren) and alpha-*latipes* of authors, and presumably the hybrid taxon *latipes* × *coloradensis*. An occasional aberrant specimen of *claviger* (eastern U.S.) or *coloradensis* (western U.S.) may fall here. See text under the appropriate species or hybrid for further details on the separation of these taxa.

   Number of standing hairs on gula 16 or fewer, not more than 0.10 mm long. Lateral surface and flexor edge of fore femur with 10 or fewer standing hairs, usually not more than 0.06 mm long. Longer standing hairs on dorsum of gaster usually 0.12 mm or less. Pubescence on antennal scapes decumbent to strongly suberect . . . . 8b. *murphyi* × *subglaber* hybrid

9. Standing body hairs either simple and delicate, or strongly barbulate. Standing hairs on fore femur varying, but if hairs delicate, then usually 5 or less, often only 2 or 3, and usually 0.05 mm or less in length, often only 0.03 or 0.04 mm. Longer standing hairs on gula usually less than 0.10 mm. In side view, crest of petiolar scale moderate; in anterior view, slightly convex, straight or shallowly emarginate. Pubescence on antennal scapes almost always suberect. SI 78 or less 10

   No standing body hairs strongly barbulate or unusually delicate, all simple or weakly barbulate. Standing hairs on fore femur somewhat variable, but usually either 6 or more, often as many as 15; or 0.06 mm or longer, often as long as 0.20 mm, or both. Longer standing hairs on gula usually 0.10 mm or more in length. In side view, crest of petiolar scale very to moderately sharp; in anterior view, usually emarginate, often deeply so. Pubescence on antennal scapes and SI varying... 11

10. Standing body hairs simple and usually delicate ..... 9. *subglaber*
Many standing body hairs strongly barbulate and coarse .... 9a. *subglaber* × *plumopilosus* hybrid

11. In side view, clypeus with a peculiar, deep indentation below the middle (fig. 42); otherwise characters agree reasonably well with a small worker of *claviger*. Sample 5(= *claviger* in part)
In side view, clypeus of normal conformation 12

12. Pubescence on sides of second tergite of gaster dense to very dense, distance between bases of pubescence hairs usually averaging well below ⅓ of their length, often contiguous. Most of body and appendages quite densely pubescent 13
Pubescence on sides of second tergite of gaster dilute to moderate, distance between bases of pubescence hairs usually averaging more than ½ of their length, often several times their length. Rest of body and appendages somewhat variable, but usually never more than moderately pubescent 14

13. In anterior view, crest of petiolar scale usually with a distinct median emargination; sides more or less straight. Longer standing hairs on gula usually less than 0.12 mm. As seen in perfect full-face view, 18 or more standing hairs on occiput, the border of which is medially emarginate in many specimens. Body and appendages yellow to brownish yellow... .... 14. *occidentalis*
In anterior view, crest of petiolar scale straight or shallowly emarginate; sides convex. Longer standing hairs on gula usually 0.12 mm or more in length. As seen in perfect full-face view, 16 or fewer standing hairs on occiput, the border of which is straight. Body and appendages yellowish brown to brown .... 11. *bureni*

14. Essentially all pubescence on antennal scapes conspicuously suberect. Pubescence hairs on gula and fore femur mostly suberect . 15
Pubescence hairs on antennal scapes either all appressed, a few decumbent to suberect, or many hairs decumbent. Pubescence on gula and fore femur appressed or decumbent 16

15. Length of standing hairs on gula 0.13 mm or more, on dorsum of gaster 0.18 mm or more. Pubescence delicate. Color yellow .... 13. *creightoni*
Length of standing hairs on gula usually 0.12 mm or less, on gaster usually 0.17 mm or less. Pubescence coarser. Color yellowish brown to brown .... 2. *coloradensis*

16. Length of longer standing hairs on the following structures

usually not over the stated amounts: clypeus, 0.11 mm; occiput, 0.10 mm; fore femur 0.06 mm; and dorsum of propodeum, 0.12 mm. Propodeum usually convex in profile. In side view, crest of erect petiolar scale above to well above level of propodeal spiracle .... 15. *mexicanus*

Length of longer standing hairs on clypeus, occiput, fore femur, and propodeum usually exceeds amounts stated above, often by nearly 100 percent. Propodeum rarely convex in profile. In side view, height of erect petiolar scale with respect to propodeal spiracle varying, but crest often at or below level of propodeal spiracle 17

17. Standing hairs on fore femur usually numbering 6 or fewer; on hind femur, none. Longer hairs on crest of petiolar scale usually 0.13 mm or more. A few standing hairs on dorsum of alitrunk moderately to strongly flexed. In many specimens standing hairs few or lacking in a central area of varying size on dorsum of gaster. Mandible sometimes with a denticle on its basal margin. SI 81 or more .... 3. *californicus*

Standing hairs on fore femur usually numbering 7 or more, on hind femur, 0 to 5. Longer hairs on crest of petiolar scale usually 0.12 mm or less. Standing hairs on alitrunk usually all more or less straight, those on dorsum of gaster more or less evenly distributed over its surface. Mandible without a denticle on its basal margin. SI 80 or less for most specimens ... 18

18. Most specimens falling above the critical dividing line, SL = 1.27 (HW) — 0.505. (A few small specimens of *claviger*, including its synonym *parvulus*, fall here). New Mexico to Manitoba and west. See text for further discussion ...2. *coloradensis*

Most specimens falling on or below the critical dividing line, SL = 1.27(HW) — 0.505. Kansas to Minnesota and east. See text for further discussion .... 1. *claviger*

A key to the males of *Acanthomyops*

1. At least a few standing hairs on dorsum of alitrunk distally plumose, others simple or barbulate .... 10. *plumopilosus*

No standing hairs distally plumose anywhere on body, all simple or barbulate 2

2. Crest of petiolar scale moderately to very blunt as viewed from the side 3

Crest of petiolar scale moderately to very sharp as viewed from the side 5

3. As seen from the side, 20 or more standing hairs cover entire gula. Body and appendages quite hairy, fore femur with 20 or more standing hairs with maximum length of nearly 0.10 mm. Antennal scapes stout, thickened towards apex, and

covered with prominent suberect pubescence. Apex of parameres usually distinctly truncate. AL usually 1.70 mm or more .... 7. *latipes*

As seen from the side, fewer than 20 standing hairs usually covering posterior ⅔ of gula, or centrally located. Body and appendages at most moderately hairy, on fore femur, usually 12 or fewer standing hairs with maximum length usually well under 0.10 mm. Antennal scapes slender, at most only very slightly thickened distally, usually covered with appressed to decumbent pubescence. Apex of parameres usually rounded. AL varying, usually 1.60 mm or less 4

4. In side view, crest of petiolar scale only moderately blunt; in anterior view, crest straight to slightly emarginate, sides more or less straight and usually converging dorsally. Located centrally on gula, 2 to 4 standing hairs ranging from 0.10 to 0.15 mm in length. Fore femur with 2 or 3 short standing hairs, 0.04 mm or less in length, middle and hind femora usually without standing hairs. Clypeus with 10 to 12 standing hairs, usually all straight. .... 3. *californicus*

In side view, crest of petiolar scale very blunt; in anterior view, crest and sides convex. Usually located on posterior ⅔ of gula, 6 or more standing hairs less than 0.10 mm long. Each femur with 10 to 12 standing hairs, usually 0.06 mm or more in length. Clypeus with 16 or more standing hairs, some flexed and twisted .... 8. *murphyi*

5. Longer hairs at posterior tip of gaster 0.27 mm or more. Gula without or with standing hairs, longest measuring 0.18 to 0.20 mm or more 6

Longer hairs at posterior tip of gaster less than 0.27 mm. Gula usually with standing hairs, the longest usually measuring well under 0.18 mm 9

6. Gula without standing hairs, those on rest of body sparse. Pubescence very dilute over entire body. AL 1.45 mm or less .. .. 5. *arizonicus*

Gula with at least a few standing hairs, those on rest of body fairly numerous. Body pubescence and size varying 7

7. A small species, AL 1.40 mm or less .... 4. *colei*

Larger species, AL 1.50 mm or more 8

8. Standing hairs on fore femur numbering 0 to 2. Pubescence on gaster very dilute, on most of head moderately dense. SI usually 70 or more .... 6. *interjectus*

Standing hairs on fore femur numbering 4 or more. Pubescence on gaster dilute to moderately dense, on most of head dilute. SI usually 68 or less .... 1. *claviger*

9. Longer hairs at tip of gaster less than 0.20 mm, and often less

than 0.15 mm 10
Longer hairs at tip of gaster 0.20 mm or more 11

10. A larger species, AL ranging from 1.35 to 1.60 mm. In anterior view, crest of petiolar scale slightly convex to straight, occasionally with a faint emargination. Standing body hairs delicate. Body color usually dark brown .... 9. *subglaber*
A smaller species, AL ranging from 1.05 to 1.30 mm. In anterior view, crest of petiolar scale usually distinctly emarginate, in a few cases only slightly emarginate; less commonly straight. Standing body hairs normal to moderately coarse. Body color usually light brown .... 14. *occidentalis*

11. Mesoscutum completely covered with pubescence 12
Mesoscutum with at least central area free of pubescence 14

12. Both mesoscutum and mesoscutellum completely covered with long pubescence hairs 0.10 mm or more in length .. 15. *mexicanus*
At least central area of mesoscutellum free of pubescence hairs, all of which are shorter, falling well under 0.10 mm 13

13. Pubescence on gaster dense. In side view, petiolar scale sharp at crest, very broad at base, and with sides straight; approximating an equilateral triangle. Body color dark castaneous brown .... 11. *bureni*
Pubescence on gaster dilute. In side view, petiolar scale moderate at crest, only moderately broad at base and with front side irregular; not triangular. Body color light to medium brown .... 3. *californicus*

14. HW 0.85 mm or less. Standing and pubescence hairs quite delicate. Body color light brown .... 13. *creightoni*
HW 0.90 mm or more. Hairs not especially delicate. Body color medium brown to dark brown 15

15. Standing hairs on fore femur 0 to 2. Pubescence on most of front of head moderately dense. SL usually 0.70 mm or more, SI 70 or more .... 6. *interjectus*
Standing hairs on fore femur 4 or more. Pubescence on most of front of head dilute to very dilute. SL usually 0.69 mm or less, SI 68 or less 16

16. Pubescence on sides of second tergite of gaster dilute to very dilute, pubescence hairs usually at least twice as far apart as long. Width of scale at level of petiolar spiracle usually not over 1.3 times height of scale above spiracle. Terminal width of pygostyles 0.03 mm or less. A smaller species, usually HW 0.99 mm or less and SL 0.63 mm or less. Body color dark to very dark brown, often appearing black or nearly black to the naked eye .... 2. *coloradensis*
Pubescence on sides of second tergite of gaster dilute to moderately dense, hairs rarely farther apart than long. Width of

scale at level of petiolar spiracle usually at least 1.5 times height of scale above spiracle. Terminal width of pygostyles 0.04 mm or more. A larger species, usually HW 1.00 mm or more and SL 0.64 mm or more. Body color medium to moderately dark brown, but rarely dark enough to appear black or nearly black to naked eye .... 1. *claviger*

Systematic Treatment by Taxa

1. *Acanthomyops claviger*

Formica clavigera Roger, 1862: queen, p. 241, pl. 1, fig. 13.
Acanthomyops claviger (Roger). Mayr, 1862: queen, p. 700.
Lasius claviger (Roger). Mayr, 1870: worker and male, p. 950.
Lasius (*Acanthomyops*) *parvula* M. R. Smith, 1934: worker, p. 213. *Syn. nov.*
Type locality: Pennsylvania.
Location of type: The type specimen, a queen bearing the locality data "Pennsylvanien", is in the collection of the Institut für spezielle Zoologie und Zoologisches Museum der Humboldt-Universität, Berlin. The type, probably collected by Schaum near Philadelphia, is more or less intermediate between the "typical" and "variant" forms. The distribution of standing hairs on the dorsum of the gaster is that of the "typical" form. The antennal scapes and funiculi are weakly clavate, as in the "variant" form. Most of the standardized measurements fall in the midrange of the "variant" form. The 2 other queens mailed to me for examination bear "Nordamerika" labels. They appear to represent samples from separate localities, both of which are probably different from that of the type. I wish to thank Dr. E. Königsmann for his kindness in lending me these specimens for study.

DIAGNOSIS. **Queen.** Head not deformed. Antennal scapes and funiculi weakly clavate to clavate, antepenultimate segment of funiculus not over 1.55 times wider than long. SI not over 66, usually 63 or less. Body size moderate; HW at least 1.22, and usually 1,38 mm or more; AL ranging from 2.08 to 2.82 mm, usually over 2.25 mm. FW 0.33 to 0.51 mm; fore femora without genual plates; FI 33 to 42. Crest of petiolar scale sharp to moderately sharp, usually distinctly emarginate. Scale covered with 45 or fewer standing hairs. Gula with standing hairs usually confined to its posterior ⅔, and usually numbering less than 24, their maximum length rarely over 0.30 mm. Pilosity on dorsum of gaster: (1) confined to rows on posterior edges of tergites beyond first, or (2) more or less evenly distributed over entire surface, or (3) exhibiting a pattern intermediate between these two. Pubescence on head and gaster usually dilute, occasionally moderate, usually more dilute on head than on gaster. Body color medium to dark brown, not appearing black to naked eye. **Worker.** Body size and pilosity moderate, pubescence dilute to moderate. Crest of petiolar scale sharp to moderate, usually distinctly to feebly emarginate. Separated from *interjectus* by the more or less uniform distribution of standing hairs over dorsum of gaster and by lower SL. Separated from *latipes* by the conformation of the petiolar scale, and standing hairs usually confined to posterior ⅔ of gula. Separated from *californicus* by SI usually 80 or less. Separation from *coloradensis* is difficult; it is discussed in the treatment of variation of that taxon. Comments on the synonym *parvulus* and on the atypical Sample 5 are discussed below in the section dealing with variation. **Male.** Scapes slender to somewhat clavate. AL usually 1.60 mm or more, HW often 1.00 mm or more, SL usually 0.65 mm or more. Terminal width of pygostyle 0.04 mm or more. Width of petiolar scale through spiracles at least 1.5 times its height above spiracles. Pubescence dilute to moderate. Body color brown to moderately dark brown, but rarely dark enough to appear black or nearly black to naked eye.

Table 4 gives selected sample statistics, lumping all measured workers: 179 *claviger,* 2 *parvulus,* and 2 Sample 5. It also lumps all measured queens: 29 "typical" *claviger* and 18 variants from the area in and around North Carolina and Virginia. Tables 27–41 give frequency, distributions for measurements, and indices. In these tables the workers of the two forms of *claviger* proper are lumped, but they are segregated from those of *parvulus* and Sample 5. Also the queens of "typical" *claviger* are kept separate from those of the variant form. By handling the two types of data in different ways, certain kinds of information are available that otherwise would be obscured. Figures 19–44 give standardized illustrations for typical *claviger* and for each of the variants. M. R.

Table 4. **Sample statistics for A. *claviger:* mean, standard deviation, and 3 standard deviation limits.***

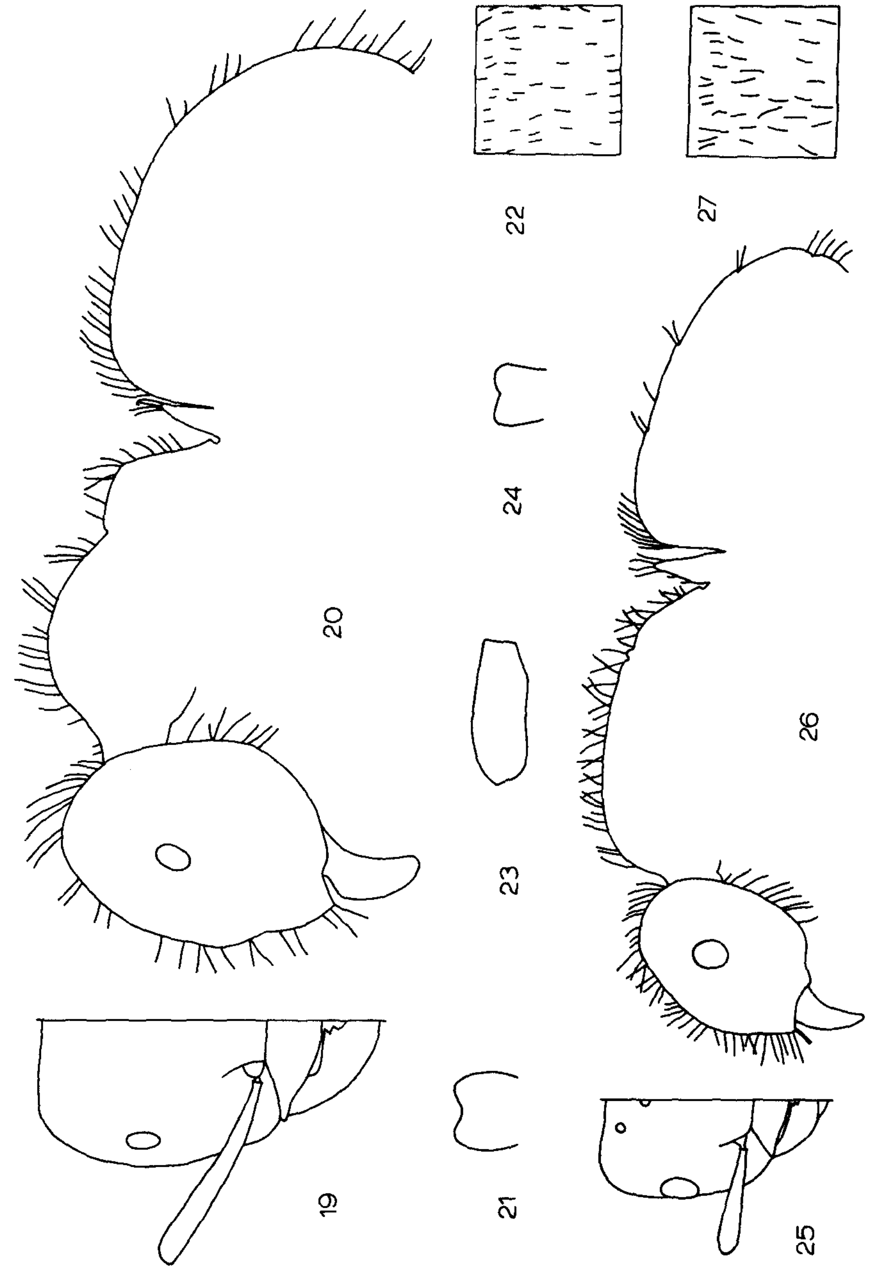
Variate	$\bar{X}$	S.D.	3 S.D. limits
	Workers (N = 183)		
SL	79.54	5.36	63.46– 95.62
HW	106.79	7.64	83.87–129.71
HL	109.54	7.38	87.40–131.68
AL	133.23	11.15	99.78–166.68
CI	97.41	1.68	92.37–102.45
SI	74.56	2.33	67.57– 81.55
	Queens (N = 47)		
SL	93.64	4.40	80.44–106.84
HW	152.68	10.06	122.50–182.86
HL	154.53	8.95	127.68–181.38
AL	255.89	16.80	205.49–306.29
FL	117.32	7.52	94.76–139.88
FW	44.60	4.27	31.79– 57.41
CI	98.77	2.07	92.56–104.98
SI	61.40	2.47	53.99– 68.81
FI	37.96	1.97	32.05– 43.87

* Unit of measurement is 10^{-2} mm. Not over 2 specimens of a caste (usually only 1) measured from any 1 nest.

Smith (1965, p. 86) gives a habitus figure of the worker. Wheeler and McClendon (1903, p. 150) give a habitus figure of the queen, and on page 155, figures of the antenna and mandible of the queen. A sample regression of SL on HW in the worker is given in the treatment of *coloradensis* (fig. 45). Figures 13–15, in the section on interspecific hybrids, give 3 regression plots involving *claviger*. ALR varies little between the typical and variant forms. ALR = 1.92(1.70 — 2.00, n = 10).

FURTHER DESCRIPTION. **Queen.** Standing body hairs simple to finely barbulate. Most standing femoral hairs on fore femora. Most of body surface shining, often strongly so. Appendages usually lighter in color than body. **Worker.** Standing body hairs simple to barbulate, moderate to numerous, of variable length, but most not extremely short. In most specimens, standing femoral hairs are largely confined to the fore femora. Pubescence variable, moderate at base of gaster, more dilute on its dorsum; that on front of head very dilute to moderate, but rarely more dense than at base of gaster. Body surface usually at least feebly shining. Body varying in appearance from robust to slender, the smaller specimens usually appearing at least fairly slender. Body and appendages pale yellow to brown. **Male.** Standing body hairs simple to minutely barbulate, usually moderate in number. Body surface usually shining. Color medium reddish brown to dark brown, head and alitrunk often darker than gaster, appendages lighter.

DISTRIBUTION. Most earlier records published as *claviger* from the West have turned out to be *coloradensis*. Of the 486 samples received for study, all but 2 came from the range of southern New England to Minnesota, south to Kansas and east to Florida. One MCZ sample bearing the label Papeete, Tahiti may be mislabelled. However, Wheeler (1911, 1932a, 1932b) considered it to be a recent and evanescent importation by commerce from the United States. The second sample, also in the MCZ, is labelled Broadmoor, Colorado, July 18, 1903, W. M. Wheeler; it consists of 2 alate queens. As indicated in the treatment of *coloradensis*, I believe that this sample is also mislabelled. The date is extraordinarily early for alate queens of *claviger* in nature. If they came from an infested house, the date is also unusual, as most flights associated with buildings occur in the winter. Furthermore, Wheeler (1917), after stating that he had seen only a few specimens of *claviger* from the West, listed only a worker from Old Pecos Pueblo, New Mexico, collected by Professor Cockerell, and several workers and females from Helena, Montana, collected by W. M. Mann. The 1 worker from New Mexico and 12 workers of the Montana series that are still in the MCZ are both *coloradensis*. The fact that Wheeler did not cite the collection from Colorado bearing his name as collector indicates that he considered this sample to be suspect. Because of the extreme doubt that surrounds this sample, I have not plotted it on the distribution map. The distribution points for most of the remaining 484 samples of *claviger* are

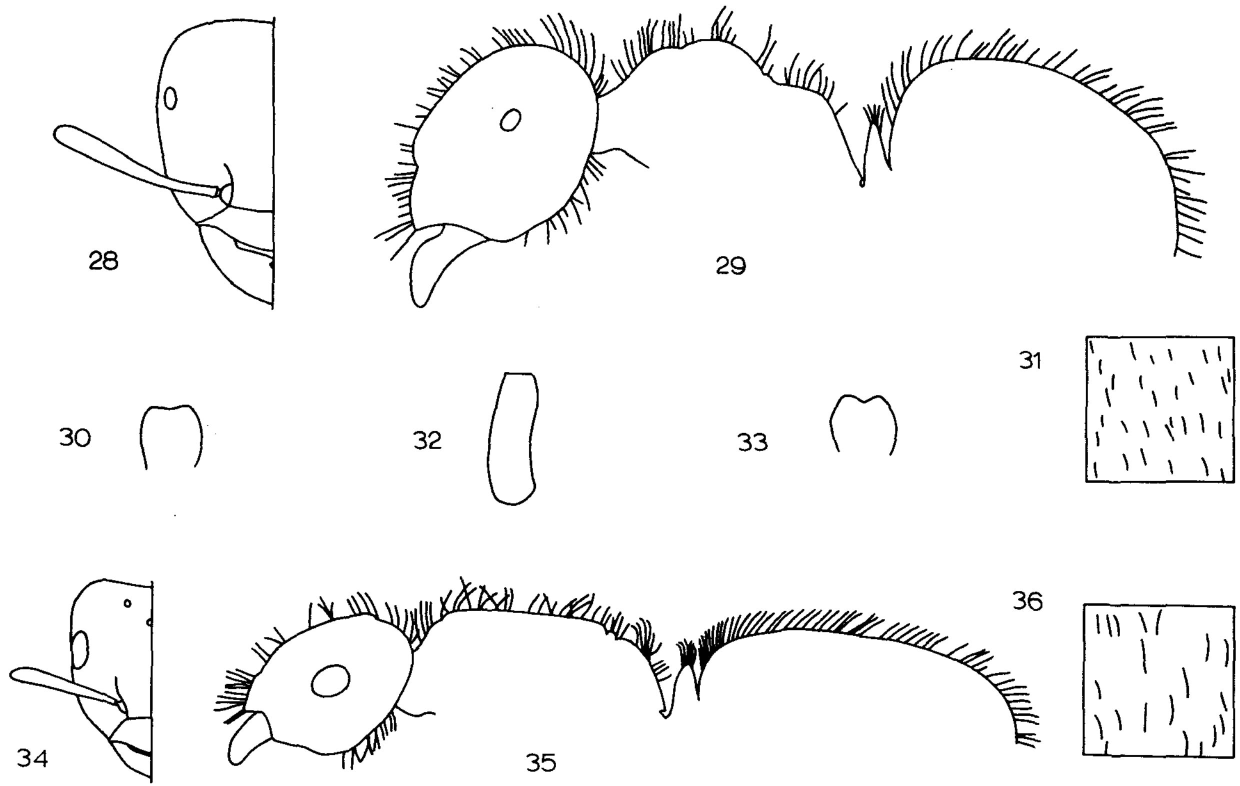


Figs. 19–27.· *A. claviger*, "typical" form. WORKERS (25×): 19, head; 20, body profile; 21, petiolar scale; 22, pubescence (50×). QUEENS (12.5×): 23, fore femur; 24, petiolar scale; 25, head; 26, body profile; 27, pubescence (50×). (For details, see p. 17 and fig. 8.)

plotted on map 1, which is included in the treatment of *coloradensis*. A few samples labelled only to state, but within the known range of *claviger*, are not included. The single known Florida sample of queens and workers collected by T. Pergande bore only a number to indicate its origin within the state. M. R. Smith has informed me that all data pertaining to the details of the Pergande ant collection were burned shortly after his death. A hollow triangle is plotted in northern Florida to indicate this record.

VARIATION. By reference to the map, measurement cards were selected for specimens originating in a band on the edge of the range. Of the 62 for workers and 29 for queens, nearly half in both castes showed one or more extreme values in about the upper or lower 5 percent of the metric range. Many of the extremely low values for workers occurred in the southeastern United States, where the smaller variant of *claviger* is found. As a further check, 20 worker measurement cards were drawn randomly, only 5 of which originated on or near the border of the range. One extreme value was included in this sample. Ten cards that included extreme values of worker HW at the upper and lower ends of the metric range were reviewed. Of these, 6 were on the edge, 2 near the edge, and 2 towards the center of the range. These data suggest that a more detailed study would show significantly more extreme values occurring at or near the periphery of the range than at its center.

Variation in some of the conventional characters is indicated in the treatment of the two variant forms below. The type series of the synonymic form *parvulus* (Herrin, Illinois) is within the range of variation for small *claviger* workers. The workers of Sample 5, in addition to the peculiar indentation of the clypeus mentioned in the key, are more aberrant forms than *parvulus*. Their standing body hairs are more strongly barbulate than is usually the case in *claviger*. Pubescence over the scapes is suberect in all specimens. The crest of the petiolar scale is less sharp than usual, and only very faintly emarginate in many specimens. One specimen examined exhibited 4-segmented maxillary palpi. Although an intensive study of this colony might help to explain some of its many unusual features, it is almost certain to be a variant of *claviger*. One peculiarity of this nest, observed in no other *Acanthomyops* colony, was an increase in average body size over a period of several months. When Brown first collected a sample of workers from this populous colony (near Buttermilk Falls State Park, Tompkins Co., New York) on June 30, 1962, he noted that they looked too small to be *claviger*. The nest was observed on a number of occasions thereafter. It became evident as the summer went on that the colony was becoming less populous. Examination of the several small series of workers collected on these visits showed that body size was increasing. Table 30 indicates this size increase for AL, as one of the measured workers was from the original collection, the other one was collected about 2 months later.

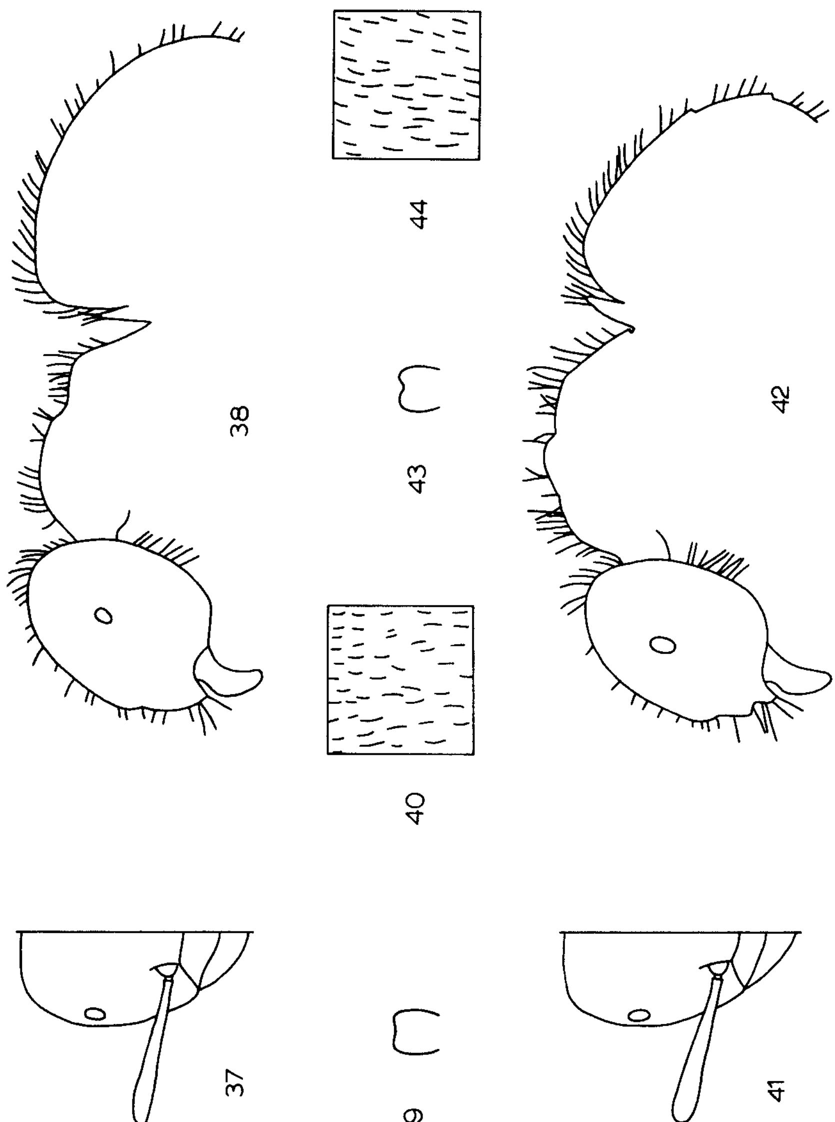


Figs. 28–36. *A. claviger*, "variant" form. WORKERS (25×): 28, head; 29, body profile; 30, petiolar scale; 31, pubescence (50×). QUEENS (12.5×): 32, fore femur; 33, petiolar scale; 34, head; 35, body profile; 36, pubescence (50×). (For details, see p. 17 and fig. 8.)

The difference in AL for these two specimens indicates the near-maximum average size increase that occurred over the summer.

DIFFERENCES BETWEEN THE TWO VARIANT FORMS OF CLAVIGER. Most of the samples originating from the area encompassed by all but the westernmost part of North Carolina and Virginia, most of Maryland, southeastern Pennsylvania, and southern New Jersey, are different from those from outside this area. In the discussion that follows, the form that predominates in and around North Carolina and Virginia will be called the "variant" form. The form that predominates outside of this area will be called the "typical" form. Differences between these two forms can be seen in all castes, but the queens show the most pronounced differences. This is perhaps why M. R. Smith (1951) listed the queens of *claviger* as dimorphic. In the worker caste, the variant form averages and ranges smaller and appears less robust. The standing body hairs are more numerous and shorter. The anterior surface of the gula is occasionally somewhat pilose. The metric data for *claviger* workers in the tables is not separated so as to show the differences between typical and variant forms. To make such a comparison available, a group of 21 variant workers from central North Carolina (Chatham and Wake Cos.) is compared below with a group of 18 typical workers from southeastern Michigan (Monroe and Washtenaw Cos.). AL is used in making this comparison; the unit of measurement is 10^{-2} mm. North Carolina group: mean, 124.81; standard deviation, 7.31; and observed range, 112–137. Michigan group: $\overline{X}$, 139.56; S.D., 8.08; and O.R., 129–157. In the males, the variant form usually has slender antennal scapes. The standing body hairs are more numerous and shorter. Body color is usually lighter, a medium reddish brown. Of the 15 intergrading characters of queens listed below, the first 7 are used in table 5.

1. Scape clavate in the typical form, weakly to moderately clavate in the variant.
2. Standing hairs on dorsum of gaster confined to rows along posterior edges of tergites beyond first in the typical form, evenly distributed over entire surface in the variant.
3. Longer standing hairs on dorsum of gaster mostly 0.32 mm or more in the typical form, 0.32 mm or less in the variant.
4. Standing hairs on gula almost always 20 or less in the typical form, 24 or more in the variant.
5. Longer standing hairs on gula usually 0.30 mm or more in the typical form, 0.30 mm or less in the variant.
6. Distribution of hairs on the gula: posterior ⅔ to ¾ in the typical form, sometimes over entire surface in the variant.
7. Longer standing hairs on the middle femora usually 0.15 mm or more in the typical form, 0.15 mm or less in the variant.
8. Pubescence over surface of scape appressed to strongly suberect in both forms, but a greater proportion of the typical form are partially



Figs. 37–44. Atypical *claviger* workers (25×). *A. parvulus*: 37, head; 38, body profile; 39, petiolar scale; 40, pubescence (50×). Sample 5: 41, head; 42, body profile; 43, petiolar scale; 44, pubescence (50×). (For details, see p. 17 and fig. 8.)

to strongly suberect.

9. Pubescence on gula appressed to more or less suberect, but most specimens of both forms have pubescence appressed or nearly so.

10. Number of standing hairs on the fore femora: typical form, 10 to 28; variant, 12 to 20.

11. Length of longer standing hairs on the fore femora: typical form, 0.20 to 0.33 mm; variant, 0.17 to 0.27 mm.

12. Distribution of standing hairs on the fore femora: typical form, usually basal ⅔; variant, usually basal ¾. Either form, may, however, have entire surface pilose.

13. Number of standing hairs on middle femora: typical form, 2 to 7; variant, 2 to 9.

14. Length of longer standing hairs on hind femora: typical form, 0.15 to 0.23 mm; variant, 0.12 to 0.20 mm.

15. Body color. Typical form variable, but usually fairly deep brown with only a few specimens showing a reddish cast. Variant less variable, lighter brown, may specimens with a reddish cast.

As the differences between the two forms of *claviger* have already given rise to some misconceptions about the species, it seems worthwhile to comment on them briefly. When queen specimens are sorted out by examination of a few of the more notable differences taken together, 2 principal forms appear. But in doing this, the fairly frequent exceptions to an assumed pattern are unconsciously ignored. If cognizance of the characters are taken separately, then a third group containing intermediates is segregated. Unless the characters are studied separately, it is easy to see how it would seem justifiable to speak of 2 species or 2 races. Once started on this course, it might be assumed that massive hybridization with introgression was taking place. If such an explanation were true, certain conditions would be expected to hold. First, the zone of introgression would be quite well defined and not very wide. Second, the characters of the progeny assumed to be hybrid would be largely intermediate between those of the parent species. Third, the characters of the progeny assumed to be hybrids would show considerable concordance. Fourth, the supposed hybrids would be confined to the zone of introgression, while each of the two parent forms would be confined to its own range. These conditions are in fact often not met. Within the area occupied mainly by the variant form, samples of typical and near-typical *claviger* occur. Not all intermediate samples are confined to the zone between the ranges of the two forms. Samples containing specimens with some of the characteristics of the variant form show up far outside North Carolina and Virginia. Concordance of characters is at best partial. It is evident that the hypothesis of massive hybridization with introgression does not account in a satisfactory way for the existence of these two forms.

The obvious need was to analyze the characters one at a time. In doing so, the differences between the two forms became less clear-cut than they had appeared to be at first. Table 5 shows the results of identifying 20 queen specimens by the use of the first 7 characters of the list above. These characters were used singly, yielding 140 determinations on the 20 specimens. By the usual means of identification, 10 of these queens would have been referred to the typical form and 10 to the variant. Three of the 10 variant forms were strikingly intermediate. Table 5 indicates the difficulty of effecting clear-cut separation among queen specimens when a number of characters are considered. Until detailed studies are undertaken on these two forms of *claviger*, it seems reasonable to assume that the variant form is responding, probably adaptively, to an unknown set of environmental factors that differ from those in the rest of the range. This is roughly the same area in which *subglaber* samples show considerable average change in pubescence and pilosity, and where *latipes* is seldom collected.

ECOLOGY. **Habitat.** The two forms of *claviger* discussed above do not appear to show any significant differences in their ecological responses. Habitat data in varying degrees of completeness were associated with 137 of the 486 samples of *claviger*. Samples collected in woods numbered 78, those in the open, 30, those of uncertain origin, 29. With respect to immediate nest-cover, 45 were under stones, 21 associated with logs and stumps, 1 came from a grassy mound, 30 with miscellaneous or no cover, and 40 of uncertain status. One of the 30 nests in the miscellaneous category was under a beef marrow bone in a backyard in Ithaca, New York. There had been no evidence of the colony before putting out bones for dogs. Once the *claviger* workers were observed

Table 5. **Identification of 20 queen specimens of *claviger* from different localities, using 1 character at a time ***

Locality	Characters						
	No. 1	No. 2	No. 3	No. 4	No. 5	No. 6	No. 7
1. Suffolk Co., N. Y.	C	C	C	C	I	V	C
2. Tompkins Co., N. Y.	C	C	C	C	I	C	V
3. Queen Anne Co., Md.	C	C	I	C	C	C	C
4. Washington, D. C.	C	I	C	V	I	C	C
5. Co. unknown, Fla.	C	C	C	C	V	C	I
6. Suffolk Co., Mass.	C	C	C	C	I	C	C
7. Seneca Co., Ohio	C	C	I	C	C	C	I
8. Watseka Co., Ill.	C	I	V	C	V	C	I
9. Winona Co., Minn.	C	C	C	C	I	C	I
10. Lancaster Co., Nebr.	C	C	V	C	I	C	I
11. Chesterfield Co., Va.	V	V	V	V	I	C	V
12. Duplin Co., N. C.	V	V	I	V	I	V	C
13. Washington, D. C.	V	V	V	V	V	V	V
14. Wake Co., N. C.	V	V	V	V	V	V	V
15. Moore Co., N. C.	V	V	V	V	V	V	V
16. Montgomery Co., Va.	V	V	V	V	V	V	V
17. Montgomery Co., Md.	V	V	I	V	V	V	I
18. Montgomery Co., Pa.	C	C	I	V	I	V	I
19. Prince George Co., Md.	C	I	C	C	V	C	V
20. Washington, D. C.	C	I	C	C	I	V	V

* For each character and each specimen, one of 3 scores was given: C, typical *claviger*; V, variant form of *claviger*; I, intermediate form. See text for further discussion.

coming up in some numbers to collect fat, other bones were placed nearby. In several cases they brought workers to the surface. This should prove to be a useful method for locating ant nests otherwise difficult to find.

In addition to the data associated with specimens received for study; Carter (1962b) and Talbot (1963) have published data based on a large number of colonies. All the North Carolina records reported as *claviger* by Carter are correct except 2: the China Grove sample is *plumopilosus,* and the Morehead City sample is *subglaber*. He found *claviger* common throughout North Carolina except in the Coastal Plain. Nests were located under stones, in well-decayed stumps, and without cover in a variety of soil types ranging from red clay to loose sand. They occurred in fields of various ages and in forests ranging from young to mature. The forests were composed of various species of pines, oaks, and hickory. Talbot, working in southern Michigan, found *claviger* versatile in its nesting habits. Nests were about equally frequent in deep woods, open woods, and fields. In deep woods, most nests were associated with logs and stumps. In open woods, stones and old logs usually formed the immediate nest-cover. Nests located in the open often were not associated with stones or wood; small mounds frequently marked their location. The soil thrown up at the time of flight probably was overgrown with grass, eventually becoming permanent mounds. Some of them were up to 3 feet in diameter and 2 to 4 inches high. My own field observations on *claviger,* principally in Minnesota, New York, and North Carolina, indicate that the location and immediate cover of nests varies somewhat from one local to another. Before more precise quantitative statements than those indicated above can be made, a number of habitats in various parts of the range need to be uniformly investigated.

Alate dates. See discussion in the general treatment of nuptial flights.

Colony foundation. See general treatment. The results of an unpublished piece of work on *claviger* undertaken by W. L. Brown, Jr. with the help of several friends is of interest. They excavated a nest in Pennsylvania that went down about 4 feet in clay soil. After a complete excavation of the nest, no dealate queen was found. To arrive at any reasonably accurate nontheoretical assessment of polygyny in *claviger,* or in any other species of *Acanthomyops,* efficient methods are needed. Slow digging may easily allow the queen or queens to escape. Fast, high-powered digging equipment, although expensive, might enable an estimation of the average number of queens per colony. Before excavating a series of nests in this manner, the queen or queens and workers could be tagged with a suitable radioactive isotope. The techniques used by Kannowski (1959), perhaps with some modification, should suffice. **Guests.** In addition to the 2 or 3 dozen vials with aphids and coccids, and a few with mites, the following papers listed other insects associated with *claviger*: Evans (1961), *Pseudisobrachium ashmeadi* and

P. elongatum (Hymenoptera:Bethylidae). Schwarz (1890), *Batrisodes montrosus, B. ferox* (Coleoptera: Pselaphidae), *Panagaeus crucigerus* (Coleoptera: Carabidae), *Quedius molochinus, Homoeusa expansa* (Coleoptera:Staphylinidae), and the larvae of *Brachyacantha ursina* (Coleoptera:Coccinellidae), which were preying on the *Pemphigus* pastured by the ants. Wickham (1898), *Batrisodes frontalis* found in the galleries of a nest under a log. Park (1935), *Batrisodes globosus.* Park (1932) studied the myrmecocole, *Batrisodes globosus* in a *Lasius americanus* (prob. = *alienus*) colony. He concluded that this species may act occasionally as a predator of living host larvae, but more frequently aids the host colony by disposing of dead larvae. The habits of *B. globosus* are probably similar in the colonies of the closely related *A. claviger.*

2. *Acanthomyops coloradensis*

Lasius (*Acanthomyops*) *interjectus* subsp. *coloradensis*
Wheeler, 1917: worker, queen and male, p. 532.
Type locality: Manitou, El Paso Co., Colorado.
Location of types: Syntypes in the MCZ.

DIAGNOSIS. **Queen.** Quite similar to *claviger,* but SI at least 67, usually 70 or more. Antennal scapes and funiculi never more than slightly clavate. Somewhat more pilose and less pubescent. Body color darker, usually a very deep brown, often appearing nearly black to naked eye. **Worker.** Very closely similar to *claviger,* but averaging and ranging smaller. Standing body hairs more numerous and shorter; this difference between the two sibling species is especially evident on the dorsum of the gaster. Also the second and third femora frequently have at

Table 6. **Sample statistics for *A. coloradensis*: mean, standard deviation, and 3 standard deviation limits ***

Variate	X̄	S.D.	3 S.D. limits
	Workers (N = 56)		
SL	75.68	5.50	59.18– 92.18
HW	96.04	5.61	79.21–112.87
HL	100.21	6.14	81.79–118.63
AL	124.34	9.03	97.25–151.43
CI	95.86	2.08	89.62–102.10
SI	78.73	2.58	70.99– 87.47
	Queens (N = 16)		
SL	90.50	4.27	77.69–103.31
HW	128.56	7.38	106.24–150.70
HL	132.06	6.66	112.08–148.04
AL	218.38	14.97	173.47–263.29
FL	103.56	5.76	86.28–120.84
FW	35.25	3.00	26.25– 44.25
CI	97.31	1.66	92.33–102.29
SI	70.44	2.00	64.44– 76.44
FI	34.06	2.17	27.55– 40.57

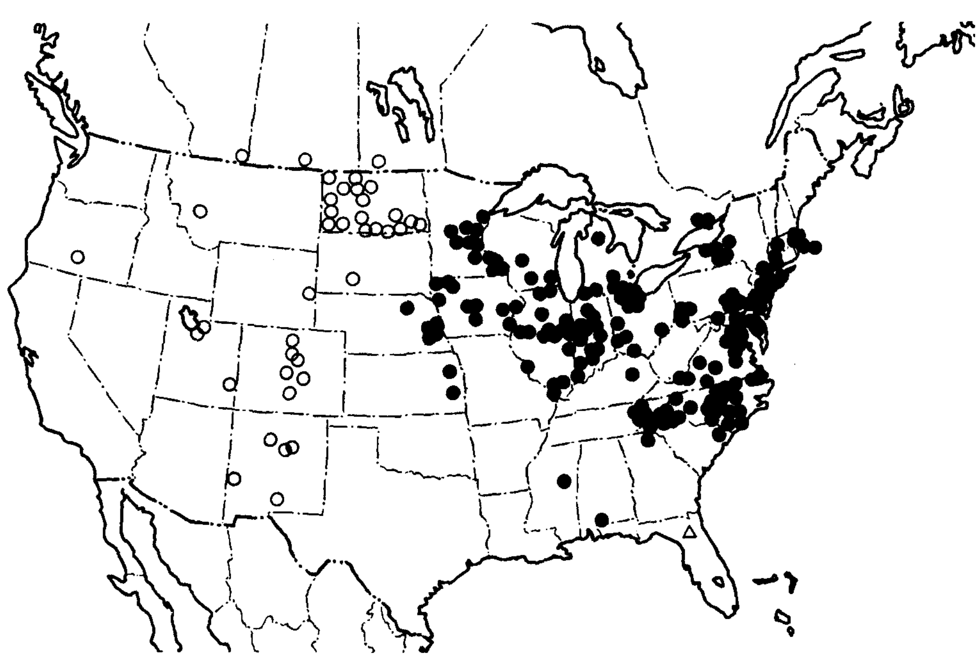
* Unit of measurement is 10^{-2} mm. Not over 2 specimens of a caste (usually 1) measured from any 1 nest.

least a few suberect standing hairs. Pubescence more dilute and longer. Body color averaging darker, usually a yellowish brown to brown. (See notes in the section following the treatment of variation for further diagnostic comments.) **Male.** Similar to *claviger,* but smaller; usually AL 1.50 mm or less, HW 0.99 mm or less, SL 0.62 mm or less, and terminal width of pygostyle 0.03 mm or less. Scale width at level of petiolar spiracles not over 1.3 times its height above spiracles. Pilosity moderate; pubescence dilute to very dilute. Body color dark brown, often appearing black or nearly black to naked eye.

Table 6 gives selected samples statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 46–54 give standardized illustrations. Figure 45 gives a sample regression of SL on HW for the workers of *coloradensis* and *claviger;* table 7 gives critical values of SL and HW. ALR = 1.76 (1.61 – 2.12, n = 10).

DISTRIBUTION. This species ranges from New Mexico, Colorado, and Utah north to Manitoba and west to Alberta and Oregon. The 70 samples available for study are plotted on map 1.

Most western records of this species have been published under *claviger,* with a few named *latipes, occidentalis, subglaber, interjectus,* and *parvulus.* Before this study, both *claviger* and *interjectus* were assumed to be common in the East and sporadic in the West. Although true for *interjectus,* a study of nearly 500 samples of *claviger* showed only 1 with a western label. This MCZ sample was labelled to place it in eastern



Map 1. Geographic distribution of *A. claviger,* solid circles and hollow triangle; and *coloradensis,* hollow circles. (See text for further details.)

Colorado. Under the treatment of *claviger,* I have discussed the reasons why it is likely that this sample is mislabelled. The *Acanthomyops* specimens of a certain extant Colorado collection were not made available, a lack that was keenly felt in dealing with the problem of delimiting the ranges of *coloradensis* and *claviger.*

VARIATION. Workers are about as variable as those of *claviger* for a number of conventional characters, such as pilosity, pubescence, and color. A moderate number of samples with queens and males was available for study; the sexual castes, especially the males, tended to show less variation in conventional characters than did those of *claviger.* The variability of metric characters over the range was difficult to assess because a high proportion of the samples originated in North Dakota. Measurement cards of workers were drawn at random; out of 33 cards, 23 were for North Dakota specimens. The fact that the proportion of extreme metric values for the North Dakota specimens was unusually high, suggests a rather high variability for workers in the northeastern part of the range.

SEPARATION OF COLORADENSIS AND CLAVIGER. All queens and nearly all males are readily separated by the use of the keys. Workers originating from well within the geographic range of either one of the species can be named on the basis of geographic origin. Difficulties may arise, however, if workers are collected from between the presently known ranges, or are of uncertain origin within some states. There is some evidence from moderately extensive collecting I have done in western Minnesota that a band may exist between the ranges of these two sibling species that is not inhabited by either. Further collecting over the entire area between the ranges is needed to settle this matter.

On the assumption that samples of one or both species may be collected in the area between the ranges, I tried to find conventional ways of separating the workers. Particular attention was given to the characters of worker specimens in samples with associated queens and males. Also, workers of *claviger* from the western part of its range were relied on heavily in these studies. Of the many methods tried, the results of most were highly discouraging or very difficult to convey in words. The definition of sibling species as taxa that are not separable by ordinary taxonomic means certainly applies well to this pair. Some characters tested turned out to be promising at first, but under most hypotheses, errors of placement increased as a function of sample size and geographic diversity.

An alternative approach was the generation of statistical statements about metric, meristic, and other characters. These statistical statements tended to have pronounced overlap, and were thus useful in identification only in an ancillary way. Although a person seeking to identify a given worker specimen desires reasonable assurance of completing the task correctly, it is not always possible to give assurance when dealing with workers of this pair. As statistical statements may help in the identification of some specimens, a few of these overlapping characters are included. In addition to the standard frequency tables and the tables of means, standard deviations, etc., the comparisons listed below were selected because they may some times be useful.

Standing body hairs are relatively less numerous and longer in *claviger.* The difference in the number and length of hairs on the dorsum of the gaster, although difficult to convey quantitatively, is evident when workers of these two taxa are compared. The number of standing hairs on the occiput typically ranges from 12 to 24 in *claviger,* and from 20 to 30 in *coloradensis.* In *claviger,* the length of the longer standing hairs on the gula is usually 0.13 mm or more; in *coloradensis,* 0.12 mm or less. Those on the propodeum of *claviger* are usually 0.16 mm or more, in *coloradensis* 0.15 mm or less. The pubescence of *coloradensis* is usually longer and more dilute than that of *claviger.* To separate these species, Creighton (1950) used the angle of inclination of pubescence over the scape — a method that has a diagnostic value much like the overlapping statistical characters now under discussion. A relatively greater number of *coloradensis* specimens show suberect pubescence, but a fair number of *claviger* workers have an essentially identical pattern. Also, many *coloradensis* workers have pubescence on scapes appressed or nearly so. In viewing a box containing workers of both species, one is immediately struck by the fact that *claviger* specimens tend to be larger, more robust and lighter in color than those of *coloradensis.* The size difference is borne out by the distribution of HW, which was 1.00 mm or less in 80 percent of the 56 workers of *coloradensis* measured. Of the 183 workers of *claviger* measured, HW was 1.01 mm or more in 76 percent. Since this *claviger* sample included a number of the smaller workers from North Carolina and Virginia, the percent with HW at or above 1.01 mm from the western part of the range was underestimated. The most useful single index for separating the workers is SI. An SI of 76 or less occurred in 79 percent of the 183 *claviger* workers. An SI of 77 or more occurred in 77 percent of the 56 *coloradensis* workers.

Inspection of the regression plots for various combinations of measurements led to the formulation of the empirical, linear relationship, $SL = 1.27(HW) - 0.505$ as a critical dividing line for these species. Most *coloradensis* workers fall above this line; most *claviger* workers fall on or below it. This relationship gave approximately 90 percent correct separation of the two species, largely on the basis of random singles in a sample of 56 *coloradensis* and 70 *claviger* workers. The exact figures for the errors of determination in this sample are given in the footnote to table 7. The sample of *coloradensis* represented all workers measured. The sample of *claviger* represented all workers measured in the western part of its range (Minnesota, Iowa, Nebraska, Kansas, Missouri, Illinois, and Wisconsin). In both samples only 1 worker

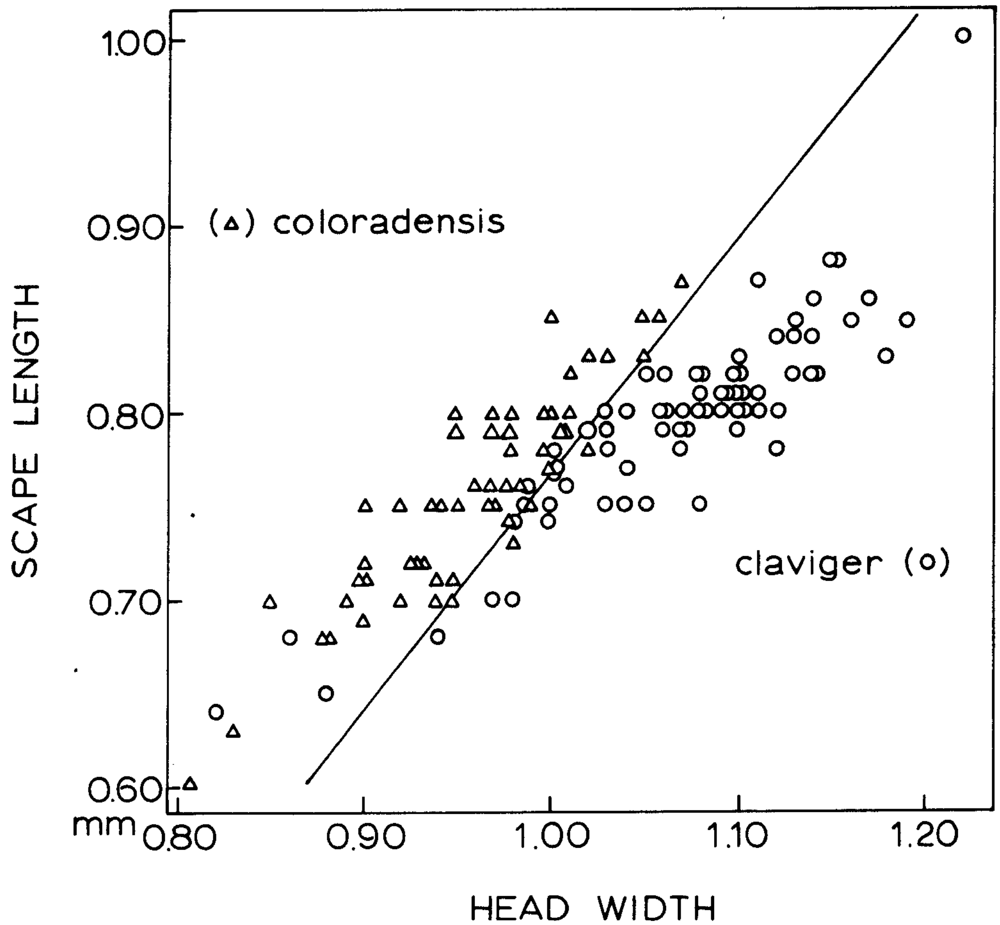


Fig. 45. Sample regressions of scape length on head width, and critical dividing line for workers of *A. claviger* (N = 70) and *coloradensis* (N = 56). Not over 2 workers measured per nest series, usually only 1. (See text for further discussion.)

per nest series was measured, with 2 or 3 exceptions, where not over 2 specimens were measured from a nest series.

It is evident from the regression plot in figure 45 that the errors of placement of *claviger* occurred in the smaller specimens, those with HW equal to 1.00 mm or less, and especially for those 0.88 mm or less. For *coloradensis,* the errors of placement were for the larger workers of that species, those with HW of 0.95 mm or more. On the basis of this sample of 126 workers, a person using the critical values of table 7 for single worker specimens of one of the two species from between the presently known ranges, could reasonably expect to correctly identify them about 90 percent of the time.

The range of variation in metric characters among members of the worker caste from a single colony requires detailed study. Confident statements cannot now be made about the limits of intranidal varia-

Table 7. **Critical values for 28 pairs of SL and HW in workers of *claviger* and *coloradensis* based on the relationship, SL = 1.27(HW) − 0.505 ***

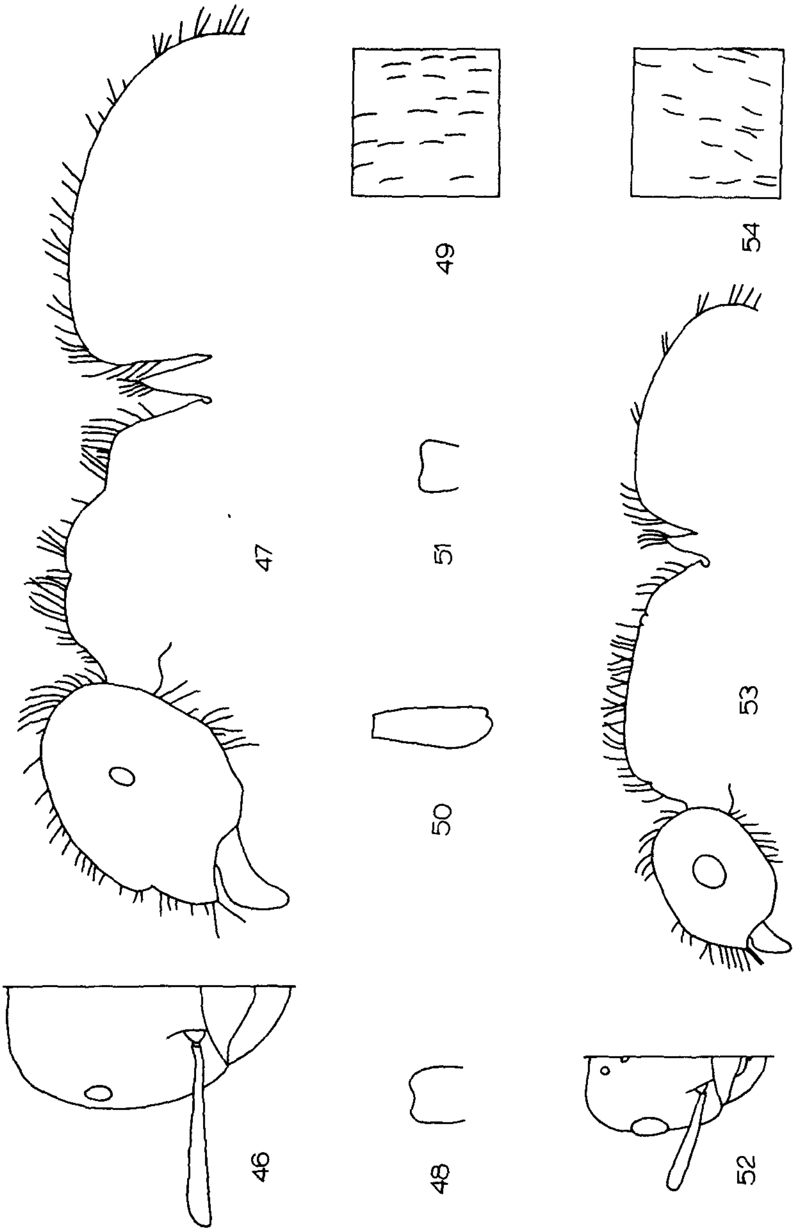
HW	SL	HW	SL
0.80	0.51	0.94	0.69
.81	.52	.95	.70
.82	.53	.96	.71
.83	.55	.97	.73
.84	.56	.98	.74
.85	.58	.99	.75
.86	.59	1.00	.77
.87	.60	1.01	.78
.88	.61	1.02	.79
.89	.63	1.03	.80
.90	.64	1.04	.82
.91	.65	1.05	.83
.92	.66	1.06	.84
.93	.68	1.07	.85

* SL was computed and rounded for each given value of HW. Sample errors of determination by the use of this table for the 126 random singles plotted in fig. 45 were: *coloradensis* (N = 56), 7; *claviger* (N = 70), 5. Measurements in mm. See text for further discussion.

tion. However, observations made during the course of this study indicate that intranidal metric variations of as much as 15 percent are not uncommon. This is based on randomly drawing and measuring additional specimens from a sample and comparing them with the first one. On this basis, the chances of correct identification of a series of 6 or more workers should exceed the 90 percent expectation for random singles. A few preliminary checks of this point make it seem possible that the chances of success may go well above 95 percent.

Much more work must be done on these two species along several lines, including extensive field work, before they can be dealt with taxonomically in an effective way.

ECOLOGY. **Habitat.** Of the 70 samples received for study, 6 had associated data on nests; 1 colony was under cow dung, 4 were under stones. Sandy soil was indicated in 2 of the 6 samples. Most of the samples reported as *claviger* by Wheeler and Wheeler (1963) are *coloradensis*. The data of their paper suggest that many *coloradensis* nests are covered by stones. In the paper by Cole (1954), the colonies reported as *coloradensis* are *latipes*. One of those reported as *latipes* is *coloradensis* (N. Beaverhead). Two of those reported as *claviger* are *coloradensis* (Bandelier and Mescalero National Monuments). The 2 nests of *coloradensis* that could be associated with the data of this paper were under stones on dry grassy slopes under cover of scattered trees. Based on data associated with specimens and that in the literature references cited above, the altitudinal range of this species is from below 2000 to above 7000 feet. **Alate dates.** Of the 13 dated samples containing alates, July 30 and September 16 are the extreme dates for those associated with workers. One sample collected on September 16 contained



Figs. 46–54. A. coloradensis. WORKERS (25×): 46, head; 47, body profile; 48, petiolar scale; 49, pubescence (50×). QUEENS (12.5×): 50, fore femur; 51, petiolar scale; 52, head; 53, body profile; 54, pubescence (50×). (For details, see p. 17 and fig. 8.)

alate and dealate queens but no workers. Another collected on December 27 contained only dealate queens. Wheeler and Wheeler (1963) listed September 16 as the latest date for collecting winged males and females of *claviger* (= mostly *coloradensis*). A comparison of the dates cited above with those given for *claviger* in the general section treating nuptial flights, indicates that the flights of *coloradensis* average much earlier than those of *claviger*. **Guests.** Schwartz (1895) reported that T. Ulke collected *Adranes* sp. near *lecontei* (Coleoptera: Pselaphidae) in the Black Hills of South Dakota. The host ant, listed as *claviger*, was probably *coloradensis*.

3. *Acanthomyops californicus*

Lasius (*Acanthomyops*) *interjectus* subsp. *californicus*
Wheeler, 1917: worker and queen, p. 531.
Type locality: Palmer's Canyon, San Gabriel Mts., near Clarmont, Los Angeles Co., California.[2]
Location of types: The single female collected by F. Grinnell, August 10, 1909 is hereby designated as the lectotype. Of the original series of 11 cotypes, 4 workers remain. All of these specimens are in the MCZ.

DIAGNOSIS. **Queen.** Similar to *interjectus*, but CI 98–103, with scapes shorter and more clavate. Penultimate segments of funiculus a little broader than long. Petiolar scale broad, its crest broadly emarginate, usually deeply so; its sides straight and converging dorsally, occasionally slightly convex. Basal margin of mandible usually without a denticle. Pubescence dilute to moderate; scapes with pubescence appressed to decumbent. Standing body hairs simple to finely barbulate. Wings only slightly infuscated basally. **Worker.** Bears a resemblance to both *interjectus* and *claviger;* closely related to *colei*, but with SI 81–84. Petiolar scale with crest emarginate, usually distinctly so; sides straight and parallel or slightly converging dorsally. Standing body hairs simple to finely barbulate. Gula and clypeus each with 10 or more standing hairs. A few standing hairs on alitrunk flexed. Dorsum of gaster with standing hairs fairly numerous to numerous, irregularly distributed. Pubescence on scapes appressed to decumbent. **Male.** Crest of petiolar scale moderately sharp to moderately blunt, feebly emarginate to straight; sides more or less straight and parallel. Length of longer hairs on crest and sides of scale and on clypeus less than 0.15 mm, those at posterior tip of gaster less than 0.25 mm. Standing hairs simple to finely barbulate, sparse; gula with 2 standing hairs located centrally. Pubescence on head moderate, on dorsum of gaster dilute.

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[2] In a recent letter, R. R. Snelling pointed out that *Palmer's* Canyon could not be located on any of their maps, nor did any residents of the area know of it. *Plummer's* Canyon, however, is in the San Gabriel Mountains, directly north of Claremont. He feels sure that the type locality was cited incorrectly.

Table 8 gives selected sample statistics.

Tables 27–41 give frequency distributions for measurements and indices. Figures 55–63 give standardized illustrations. ALR = 1.98.

FURTHER DESCRIPTION. **Queen.** Body color ranging from brown, with appendages lighter, to yellow throughout; feebly shining to highly glabrous. **Worker.** Pubescence on head dilute to moderately dense, that on gaster very dilute to moderate; body more or less shining. Color yellow to yellowish brown. **Male.** Surface of mesocutum and mesoscutellum finely sculptured, covered with dilute pubescence. Body color brown.

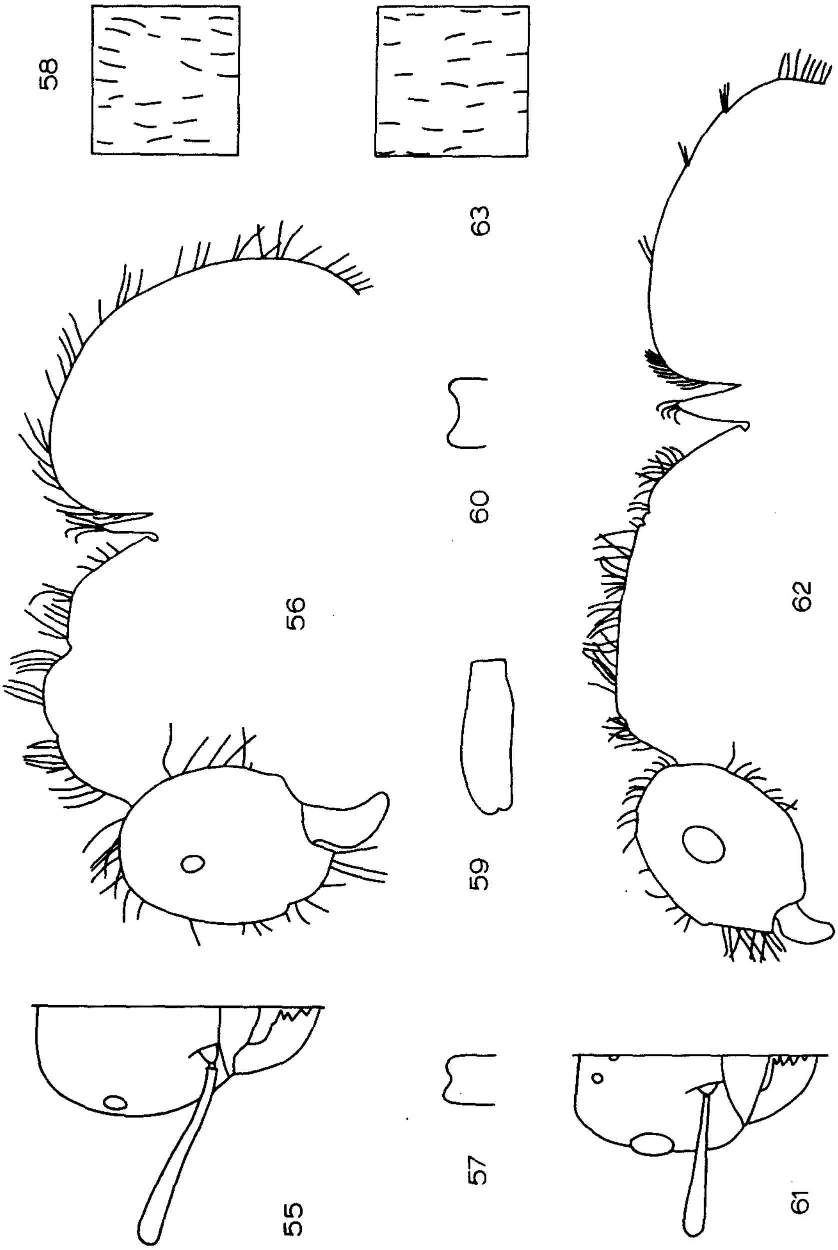
DISTRIBUTION. The 12 samples, all from southern California, are from 3 counties. Los Angeles County: Altadena, August 8, 1946, C. A. Hamsher; Arcadia, April 12, 1944; Palmer's Canyon, San Gabriel Mts., near Claremont, December 9, 1910, W. M. Wheeler, about 2000 feet; Mescal Creek, San Gabriel Mts., May 2, 1965, R. R. Snelling, 6600 feet, in soil under deeply imbedded stone; San Gabriel Mts., August 10, 1909, F. Grinnell, Jr.; Glendale, E. I. Schlinger, July 1941 and June 28, 1948. San Bernardino County: Camp Baldy, June 27, 1956, H. R. Moffitt; Camp Baldy, M. Pijoan. San Diego County: few miles south of Julian on Rte. 79, September 14, 1959, W. F. Buren, under stone, about 4000 feet; Julian, September 15, 1959, W. F. Buren, in canyon; Pine Valley, July 18, 1927, F. W. Kelsey.

VARIATION. The workers exhibit only minor variation in both metric and conventional characters. Queens, however, are extremely variable in primary measurments, color, degree of pubescence, and other characters. Coefficients of variation were computed for the queens. Range for primary measurements was 14.66 to 19.83, while that for indices

Table 8. **Sample statistics for *A. californicus:* mean, standard deviation, and 3 standard deviation limits** *

Variate	$\bar{X}$	S.D.	3 S.D. limits
	Workers (N = 6)		
SL	75.67	2.80	67.27– 84.07
HW	91.83	3.66	80.85–102.81
HL	96.17	3.71	85.04–107.30
AL	117.50	4.42	104.24–130.76
CI	95.67	.52	94.11– 97.23
SI	82.50	1.05	79.35– 85.65
	Queens (N = 5)		
SL	99.00	15.18	53.46–144.54
HW	139.00	23.18	69.46–208.54
HL	138.00	22.88	69.36–206.64
AL	232.80	34.14	130.38–335.22
FL	110.60	21.93	44.81–176.39
FW	36.20	6.61	16.37– 56.03
CI	101.00	1.87	95.39–106.61
SI	71.60	1.52	67.04– 76.16
FI	33.00	1.00	30.00– 36.00

* Unit of measurement is 10^{-2} mm. Not over 2 specimens of a caste (usually 1) measured from any 1 nest.



Figs. 55–63. *A. californicus.* WORKERS (25×): 55, head; 56, body profile; 57, petiolar scale; 58, pubescence (50×). QUEENS (12.5×): 59, fore femur; 60, petiolar scale; 61, head; 62, body profile; 63, pubescence (50×). (For details, see p. 17 and fig. 8.)

was 1.85 to 3.03. With larger sample size, such large coefficients of variation in primary measurements would indicate a mixture of more than one species. With only 5 queens measured, however, the inference is not necessarily true. The extreme range in both conventional and metric characters led me to first consider the smaller, yellow queens to be distinct from *californicus*, but the indices did not bear this out. Nor were any good conventional characters found that would clearly separate the larger, brown queens from the smaller, yellow ones. The obvious need is for the collection of a series of nest samples containing all 3 castes. Until this is done, *californicus* cannot be satisfactorily treated taxonomically. On the basis of the small amount of material available for study, and the fact that few species of *Acanthomyops* occur in California, I have lumped these two seemingly different queens. Lack of competition from close congeners could result in a more highly variable taxon than would be the case where several species of *Acanthomyops* were in competition.

ECOLOGY. **Habitat.** The small amount of information on this species is listed with the locality records above. A preference for mid-mountain localities is indicated. **Alate dates.** Extreme dates for alates are June 27 and August 10. Dealate queens were collected on July 18 and August 8. Flights may typically begin in late June and extend into August.

4. *Acanthomyops colei* n. sp.

Type locality: Cochise Stronghold, Dragoon Mts., Cochise Co., Arizona. Location of types: Holotype worker and 3 paratype workers in the MCZ, 2 paratypes in the USNM, 2 paratypes in the Cornell collection, and 10 paratypes in the collection of A. C. Cole.

DIAGNOSIS. **Queen.** Unknown. **Worker.** Somewhat similar to small *interjectus*; closely related to *californicus*, but SI 86–90. Petiolar scale with crest straight to weakly emarginate; sides straight and strongly converging dorsally, sometimes slightly convex. Standing body hairs finely to strongly barbulate, ranging and averaging longer than in *californicus*. Gula with 4 to 6 standing hairs, clypeus with 6 to 8. Alitrunk with most standing hairs flexed. Standing hairs on gaster fewer than on *californicus*, with somewhat irregular distribution, but mostly concentrated on or near posterior edges of tergites. Pubescence on scapes loosely appressed to strongly suberect. **Male.** Similar to *californicus*. Crest of petiolar scale sharp to very sharp, strongly to weakly emarginate; sides straight and converging dorsally, sometimes convex. Length of longer hairs on crest and sides of scale and on clypeus 0.18 mm or more, many flexed, those on posterior tip of gaster 0.27 mm or more. Standing body hairs weakly to strongly barbulate, a few, especially on alitrunk, with conspicuous bifurcate tips. Gula with 4 standing hairs. Pubescence on head dilute, that on dorsum of gaster very dilute.

Table 9 gives selected sample statistics. Tables 27–32 give frequency distributions for measurements and indices. Figures 64–67 give standardized illustrations.

FURTHER DESCRIPTION. **Worker.** Pubescence dilute, body shining. Color yellowish brown to brown. **Male.** Body light brown, head darker.

This species is named for Dr. A. C. Cole, University of Tennessee. He is the only collector other than W. M. Wheeler who has taken this species.

DISTRIBUTION. Nine samples from southern Arizona and 1 from southern New Mexico are as follows: **Arizona.** Cochise County: Dragoon Mts., July 29, 1954, A. C. Cole, 5 nest samples. Graham County: Post Cr. Canyon, Pinaleno Mts., July 15, 1917, W. M. Wheeler; Post Canyon, Pinaleno Mts., July 18, 1917, W. M. Wheeler, 5–6000 feet: Pima County: Apache Camp, S. Catalina Mts., July 27, 1917, W. M. Wheeler, 5500 feet; Stratton, S. Catalina Mts., July 27, 1917, W. M. Wheeler, 6–7000 feet. **New Mexico.** Grant County: Black Mt., Gila National Forest, August 14, 1952, A. C. Cole, 6600 feet.

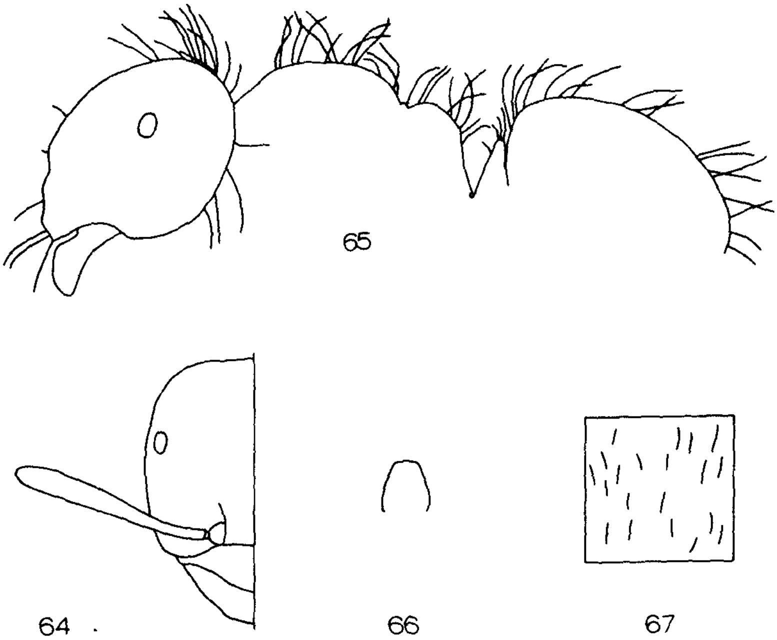
VARIATION. Only slight variation in metric characters with the exception of CI. Minor variation in pilosity, pubescence, color, etc., for both workers and males.

ECOLOGY. **Habitat.** Other than altitudinal data given above, no data were associated with the specimens studied. However, Cole (1954) lists biological data for 2 colonies he identified as *interjectus.* I have not seen the specimens from E. of Taos, New Mexico, but the Black Mt., New Mexico collection is *colei.* He stated that "Colonies were under stones on moist pine slopes. . . ." **Alate dates.** The only sample with sexual forms was the Stratton, Arizona collection of W. M. Wheeler. Thus July 27 is the only alate date available. Since the nest contained males and workers, it is possible that flights do not begin until August. Collection of nests with all 3 castes will not only make it possible to delimit the flight period, but also will throw further light on the degree of relationship between *colei* and *californicus.* From the evidence at hand they appear to be quite closely related, but a study of the queens will be of the greatest value in assessing the degree of relationship.

Table 9. **Sample statistics for *A. colei:* mean, standard deviation, and 3 standard deviation limits ***

Variate	$\bar{X}$	S.D.	3 S.D. limits
	Workers (N = 8)		
SL	81.75	3.65	70.80– 92.70
HW	93.00	4.57	79.29–106.71
HL	98.88	3.98	86.94–110.82
AL	118.63	7.80	95.23–142.03
CI	94.13	2.23	87.44–100.82
SI	88.00	1.51	83.47– 92.53

* Unit of measurement is 10^{-2} mm. Not over 2 specimens (usually 1) measured from any 1 nest.



Figs. 64–67. A. colei. WORKERS (25×): 64, head; 65, body profile; 66, petiolar scale; 67, pubescence (50×). (For details, see p. 17 and fig. 8.)

5. *Acanthomyops arizonicus*

Lasius (Acanthomyops) interjectus subsp. *arizonicus* Wheeler, 1917: worker, p. 532.

Type locality: Huachuca Mts., Cochise Co., Arizona.

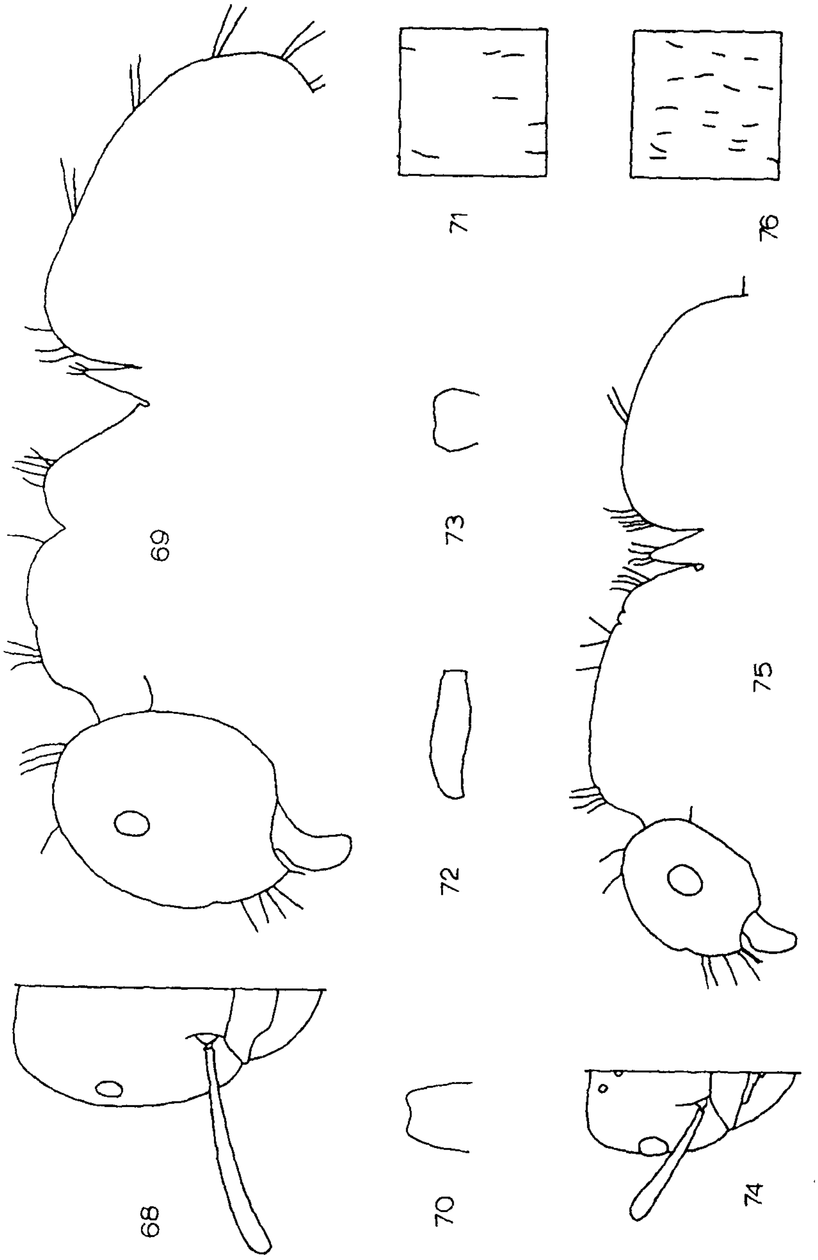
Location of types: Syntypes in the MCZ.

DIAGNOSIS. **All castes.** Similar in appearance to *interjectus,* but averaging and ranging smaller. Body pilosity very sparse and long; gula usually with no standing hairs, occasionally with 1 inconspicuous short hair, rarely with 2 or 3 standing hairs. Pubescence very dilute, especially on gaster; body surface highly glabrous.

Table 10 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 68–76 give standardized illustrations. ALR = 1.88(1.48, n = 1).

FURTHER DESCRIPTION. **Queen.** Crest of petiolar scale sharp to moderately sharp, weakly to strongly emarginate. Color reddish brown. **Worker.** Dorsum of propodeum convex, often strongly so. Crest of petiolar scale sharp to moderately sharp, weakly to strongly emarginate. Color, yellow to yellowish brown. **Male.** Crest of petiolar scale sharp to very sharp; emarginate, straight or convex. Color, dark brown.

DISTRIBUTION. All 40 nest samples of this species were collected in southeastern Arizona: Cochise Co., 30; Pima Co. (near Continental), 2; and Santa Cruz Co., 8. Southern Arizona is undoubtedly only the



Figs. 68–76. A. arizonicus. WORKERS (25×): 68, head; 69, body profile; 70, petiolar scale; 71, pubescence (50×). QUEENS (12.5×): 72, fore femur; 73, petiolar scale; 74, head; 75, body profile; 76, pubescence (50×). (For details, see p. 17 and fig. 8.)

Table 10. **Sample statistics for *A. arizonicus*: mean, standard deviation, and 3 standard deviation limits** *

Variate	$\bar{X}$	S.D.	3 S.D. limits
	Workers (N = 8)		
SL	91.13	5.79	73.76–108.50
HW	108.63	6.07	90.42–126.84
HL	109.75	6.45	90.40–129.10
AL	129.25	9.98	99.31–159.19
CI	98.88	2.30	91.98–105.78
SI	83.88	1.46	79.50– 88.26
	Queens (N = 4)		
SL	108.50	10.21	77.87–139.13
HW	145.50	12.66	107.52–183.48
HL	142.50	8.35	117.45–167.55
AL	243.25	25.18	167.71–318.79
FL	119.00	8.41	93.77–144.23
FW	36.25	3.77	24.94– 47.56
CI	102.00	4.24	89.28–114.72
SI	74.75	2.75	66.50– 83.00
FI	30.50	1.73	25.31– 35.69

* Unit of measurement is 10^{-2} mm. Not over 2 specimens of a caste (usually 1) measured from any 1 nest.

northern end of a range of uncertain extent; future collections from suitable habitats in Mexico will delimit the range of this species.

VARIATION. The specimens studied appeared to be fairly constant in conventional characters. This is probably true also of metric characters, but the few queens measured showed a considerable size range.

ECOLOGY. **Habitat.** Almost no biological data have been published on this species. Wheeler (1917) cited 3 localities in Cochise Co. from which the types were collected, giving an altitude of 5000 ft. for one collection. Data associated with the specimens at hand are meager. Four samples were taken under stones, 1 came from a "shaded canyon". Slightly over 20 samples had altitudinal data. With the one exception of a collection made at 2000 ft., they ranged from approximately 5000 to 8500 ft. **Alate dates.** Eight dated samples contained alates. The extreme dates are June 13 and August 8. On June 13, queens alone were captured on 2 occasions. Dealate queens were taken on July 6 and 8. It is likely that flights begin by mid-June. The collection on August 8 contained workers and males; it is probably a nest collection. Thus flights may still occur as late as early August.

6. *Acanthomyops interjectus*

Lasius interjectus Mayr, 1866: queen, p. 888, pl. 20, fig. 3.

Type locality: New Jersey.

Location of type: Dr. Per Inge Persson, Naturhistoriska Riksmuseum, Stockholm, kindly sent me information about the type, which is in their collection. It is a queen with the following data: "N. Yersey, Belfrage." Belfrage was a Swedish collector who moved to the USA in 1850. There are no type specimens located in the collections of the Naturhistorisches

Museum in Wien. I wish to thank Dr. Max Fischer for his kindness in lending me the material in the Mayr Collection.

DIAGNOSIS. **Queen.** Basal margin of mandible usually with 1 or more denticles. Head broad, HW almost always 1.53 mm or more, CI 102 to 110, usually 104 or greater. Antennae long and slender, penultimate and antepenultimate segments of funiculus at least as long as wide, usually longer than wide. SL almost always over 1.08 mm, SI 64–75, usually 67 or over. Crest of petiolar scale sharp to moderately sharp, usually narrowly but distinctly emarginate; sides convex. Body size moderate, AL of most specimens falls between 2.35 and 2.85 mm. Standing body hairs finely barbulate and simple, long, fairly numerous, especially on alitrunk; those on gula confined to its posterior ⅓ to ¾. **Worker.** Large, HW at least 1.08 mm, most specimens measuring 1.20 mm or more; AL at least 1.28 mm, most specimens measuring 1.50 mm or more. Head wide, CI at least 98, often 100 or more. Basal margin of mandible often with 1 or more denticles. Antennae slender; SI 75 to 86, most specimens falling between 78 and 85. Propodeum convex in profile, often strongly so. Crest of petiolar scale sharp to moderately sharp, usually narrowly but distinctly emarginate; sides usually convex. Standing body hairs simple to minutely barbulate, long; those on dorsum of gaster confined to rows along posterior edges of tergites beyond first; those on gula confined to its posterior ⅔. Pubescence on dorsum of gaster dilute, that on upper part of head moderate to dense. **Male.** Large, HW usually over 1.00 mm; AL at least 1.50 mm, usually 1.60 mm or more. Head fairly broad, CI 110 or more. Antennae slender, SL 0.70 mm or more, SI 70 or more. Crest of petiolar scale sharp to very sharp, usually distinctly emarginate; upper sides often straight and converging dorsally. Standing body hairs mostly simple, moderately numerous; many of those at posterior tip of gaster measuring over 0.27 mm; those on gula measuring 0.18 mm or more. Pubescence on dorsum of gaster dilute to very dilute, that on head and appendages moderate to dense.

Table 11 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 77–85 give standardized illustrations. Figures 16–18 give habitus figures of the 3 castes prepared by Mr. William Gotwald, Jr. M. R. Smith (1947, p. 610 and 1965, p. 88) gives habitus figures of the worker. ALR $= 1.62 (1.08 - 1.75, n = 10)$.

FURTHER DESCRIPTION. **Queen.** Head and appendages moderately to densely pubescent, other parts of body mostly with dilute pubescence. Standing hairs on dorsum of gaster confined to posterior edges of tergites beyond first. Body color of most specimens light brownish yellow, a few sordid yellowish brown, often with gaster darker than rest of the body. **Worker.** Moderately pilose. Pubescence on head and appendages moderate to dense, usually moderate to dense on base of gaster,

Table 11. **Sample statistics for *A. interjectus:* mean, standard deviation, and 3 standard deviation limits** *

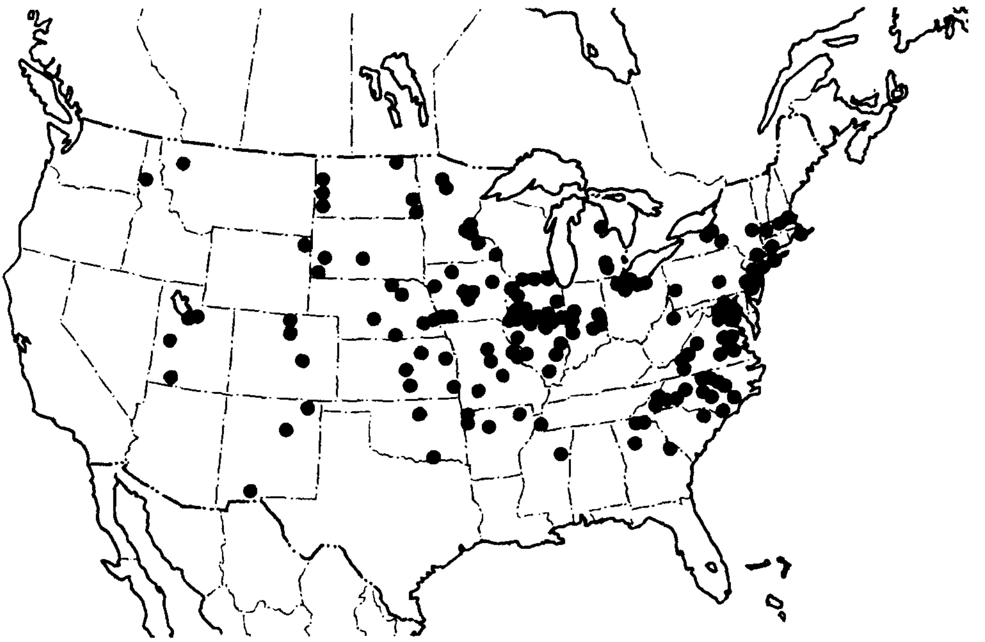
Variate	$\bar{X}$	S.D.	3 S.D. limits
	Workers (N = 157)		
SL	103.31	5.90	85.61–121.01
HW	126.97	7.05	105.82–148.12
HL	125.57	6.49	106.10–145.04
AL	160.68	9.75	131.43–189.93
CI	101.10	1.57	96.39–105.81
SI	81.38	2.10	75.08– 87.68
	Queens (N = 65)		
SL	116.51	5.20	100.91–132.11
HW	165.22	8.28	140.38–190.06
HL	155.65	7.05	134.50–176.80
AL	260.97	14.94	216.15–305.79
FL	131.72	6.66	111.74–151.70
FW	41.14	1.94	35.32– 46.96
CI	106.11	2.02	100.05–112.17
SI	70.60	2.11	64.27– 76.93
FI	31.28	1.22	27.62– 34.94

* Unit of measurement is 10^{-2} mm. Not over 2 specimens of a caste (usually 1) measured from any 1 nest.

elsewhere on body mostly dilute; surface of most parts of body shining. Antennal scapes with pubescence appressed to suberect. Body and appendages yellow to pale brownish yellow. **Male.** Antennal scapes with pubescence ranging from appressed to suberect. Alitrunk with pubescence variable, central areas of scutum and scutellum largely free of pubescence. Color of alitrunk brown, often with a reddish cast; head and sometimes gaster darker, appendages lighter.

DISTRIBUTION. All but a few of the 337 samples of this species had full locality data. The range of *interjectus* as indicated by these records is from southern New England and Georgia west to the Rockies. Map 2 shows the distribution. Experienced myrmecologists have tended to make relatively few mistakes in the identification of workers of this species. Thus literature records without voucher specimens are more likely to be correct than those for either *claviger* or *latipes*.

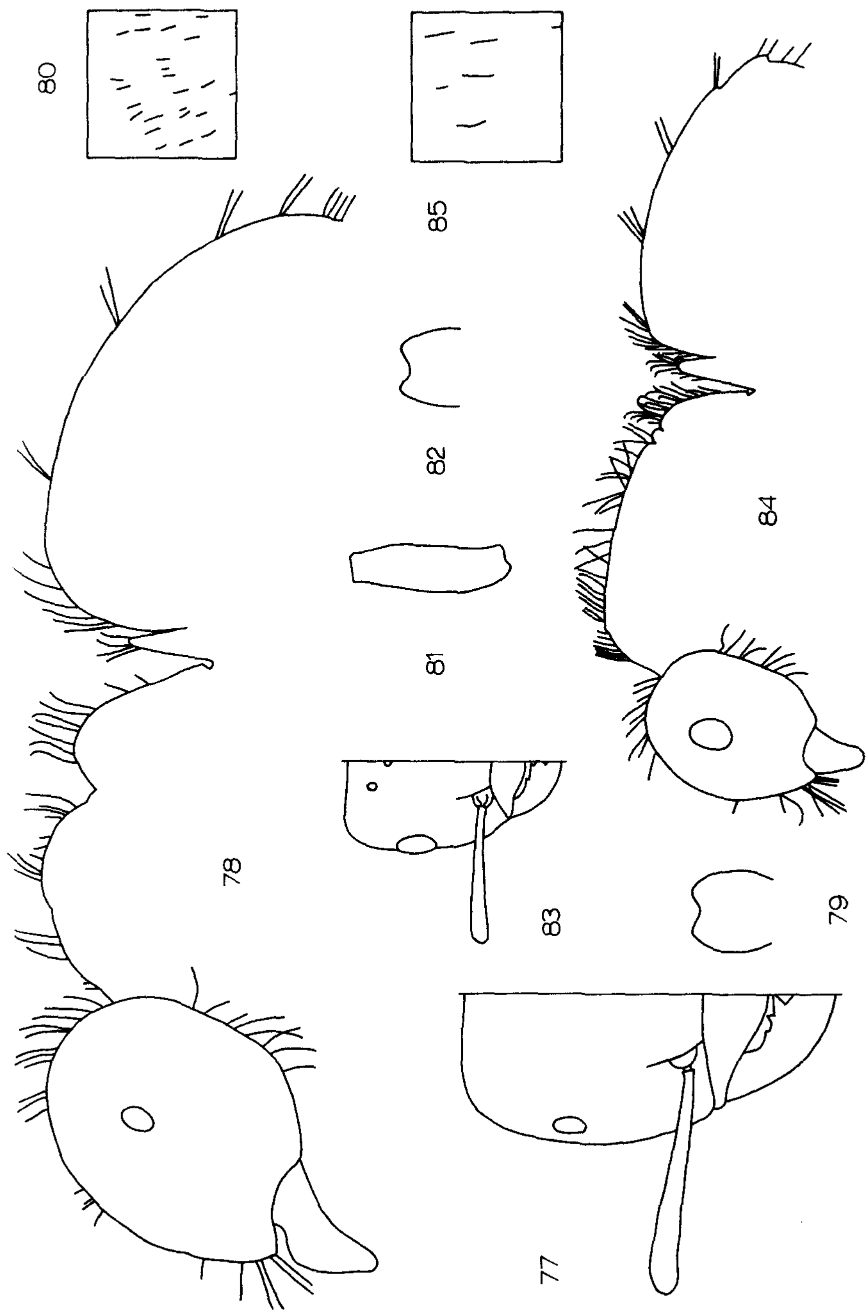
VARIATION. Measurement cards were drawn randomly, 100 for workers and 40 for queens. A review of these cards indicated that extreme values of measurements and indices are more or less randomly distributed throughout the range. The pattern of standing hairs on the gaster of workers and queens shows almost no variation. Because of its value in the routine sorting of workers, exceptions to the typical pattern of pilosity on the gaster are of interest. Two samples containing only workers showed gasters more or less uniformly covered by hairs. In both samples the specimens were otherwise typical of *interjectus*. The data on these samples are: Washington, D. C. April 21, T. Pergande, and Raleigh, North Carolina, March 5, 1949, R. L. Rabb, pine stump. Variation in queen characters tends to be minor except in color. Occasionally a queen specimen that has been studied by an



Map 2. Geographic distribution of *A. interjectus.* (See text for further details.)

experienced myrmecologist bears a label that indicates some doubt as to its status. Two such samples were reviewed critically. One sample bore the data: Champaign, Illinois, September 21, 1941, W. E. McCauley, in lawn, and the note "*Acanthomyops* sp." It contained 2 dealate queens, 12 males and 8 workers. The males and workers seemed to be typical in all respects. The queens showed minor deviations from the typical form. Their antennal scapes were slightly more clavate, the colors somewhat darker, and the pubescence a little more dense than usual. The pubescence covering the legs was suberect. There seemed, however, to be little reason to refer the sample to any taxon other than *interjectus*. The other sample bore the data: Iosco Co., Michigan, 7–16–38, R. R. Dreisbach, and the note "*Acanthomyops interjectus* n. ssp.?". It contained 5 queens, that showed minor deviations. Their antennal scapes were a little shorter and less slender than usual. The crest of the petiolar scale was somewhat blunted and quite convex. The body and appendages were a light reddish yellow. The chief reason for taking a second look is the rarity of the unusual conformation of the petiolar scale. The measurements, indices, and most of the conventional characters were well within the range of normal variation. There seems to be little reason for considering this single, somewhat aberrant sample from near the edge of the range as a new subspecies. One of a series of 6 queens from Woodstock, Illinois, exhibited marked deformities. The collection was made on July 10, 1942, by John Brock. The antennal scapes were strongly clavate, short, and sharply bent near their mid-points, giving them a V-shaped appearance. The external margins of the mandibles were indented near their mid-points. The head was somewhat compressed, reducing the width through the eyes. The outer margins of the middle and hind tibiae were shallowly indented. The petiolar scale was somewhat blunted and only faintly emarginate, and the pubescence on the gaster was a little more dense than usual in the deformed queen. The characters of the other queens of this sample were within the range of variation for *interjectus*.

ECOLOGY. **Habitat.** Of the 337 samples of this taxon, 66 had associated nest data. Nests in or adjacent to buildings numbered 27. Of the nests not associated with buildings, 10 were in the open, 16 in woods, and 13 of uncertain status. With respect to immediate nest-cover, 10 were under stones, 8 associated with wood, 1 in a mound, 11 with other or no cover, and 9 of uncertain status. The kind of immediate nest-cover did not appear to be correlated with whether nests were in woods or in the open. Carter (1962b) reported on 9 nests in North Carolina. Most records were from woods or associated with buildings. Nests were in rotted stumps, under stones, and without any visible covering object in soil ranging from compact red clay to loose sand. Talbot (1963) studied 9 colonies in southern Michigan. All of these colonies were either in woods or along their edges in places where leaves had accumulated on the ground. Old, well-galleried stumps accounted for 5, 1 occupied a well-galleried log and the soil under it, and 3 were in low mounds with diameters of 3 to 4 feet. One of the mounds had been built up around a stump, which later had rotted away. Wheeler and Wheeler (1963) reported 27 samples of *interjectus* from North Dakota; I have seen specimens from about ½ of these samples. Of the 19 nests observed, they found 7 nests in grassy mounds, 7 under stones, 3 under wood, and 2 under other cover. In North Dakota nests were usually in grasslands; 14 of the 19 were found in this habitat. Of the 5 other nesting situations, 4 were at the edges of woods and 1 in woods. They give 3 figures showing nest photographs on pp. 198–199. **Alate dates.** See discussion in the general treatment of nuptial flights. **Colony foundation.** See general treatment of colony foundation. **Guests.** A few of the vials received contained aphids and mites. A pointed worker specimen had a single pointed specimen of *Batrisodes montrosus* (Coleoptera: Pselaphidae) associated with it. Records of insects associated with *interjectus* from the literature are: Schwarz (1890), *Batrisodes montrosus, B. ferox,* and *Serica vespertina* (Coleoptera: Scarabaeidae). Wickham (1900) reported on the sifting of an old stump which contained worker ants, *Adranes lecontei, Ceophyllus monilis,* (Coleoptera: Pselaphidae), and *Limulodes paradoxus* (Coleoptera: Limulodidae). The ant species was determined by Wasmann as *Lasius "interjectionis"*; I believe that it is safe to assume that *interjectus* was the ant species associated with these guests.



Figs. 77–85. A. interjectus. WORKERS (25×): 77, head; 78, body profile; 79, petiolar scale; 80, pubescence (50×). QUEENS (12.5×): 81, fore femur; 82, petiolar scale; 83, head; 84, body profile; 85, pubescence (50×). (For details, see p. 17 and fig. 8.)

7. *Acanthomyops latipes*

Formica latipes Walsh, 1862: queen, worker, and male, p. 311.

Lasius (*Acanthomyops*) *latipes* (Walsh). Mayr, 1866: queen, p. 889, pl. 20, figs. 4a and 4b.

Lasius (*A.*) *latipes* beta-form: Wheeler and McClendon (1903) and subsequent authors.

Type locality: None stated. Dalla Torre (1893) cited Illinois in addition to Wisconsin (the defective queen described by Mayr, 1866) and New Jersey. Wheeler and McClendon (1903), perhaps in part because of the data in the von Dalla Torre catalogue, stated that Rock Island, Illinois was probably the type locality.

Location of types: None are known to exist despite efforts made to locate the Walsh specimens by the late William Morton Wheeler and others since the turn of the century. For this reason, I am designating a neotype queen. I wish to thank Margaret Doyle of the International Commission on Zoological Nomenclature for her help in this matter, especially with respect to the requirements of 75c of the Code. The neotype specimen bears 2 printed labels (Livingston Co., MICH., VIII–25–58, M. Talbot and Edwin S. George Reserve), a written code-label (238Ac–N), and a printed identification label with an added hand-printed "NEOTYPE" in red. I wish to thank Dr. Mary Talbot, the collector, for giving me this typical series of *latipes;* it contains all 3 castes which are consistent with Walsh's descriptions. It is virtually certain that Walsh's specimens came from one of the midwestern states, although the exact locality remains in doubt. Dr. Talbot's collection made in southern Michigan almost certainly originates from the general area where the Walsh types were taken. I am depositing the neotype in the MCZ along with another queen, 2 males and 4 workers from the nest series.

DIAGNOSIS. **Queen.** Head deformed. Scapes and funiculi extremely clavate; antepenultimate segment of funiculus at least 2.30 times wider than long. Gula with standing hairs covering its entire surface, usually numbering 40 to 80, their maximum length 0.35 to 0.80 mm, usually at least 0.40 mm. FW 0.80 to 1.02 mm, FI 58 to 70, genual plates of fore femora large and conspicuous. Petiolar scale large, with crest very blunt, not emarginate. Standing hairs numerous and more or less evenly distributed over head, alitrunk, legs, and petiolar scale, which is covered by 65 to 180 hairs. Pilosity on gaster variable, ranging from fairly sparse to dense. Pubescence on gaster dense to very dense. Body size large, AL ranging from 3.12 to 3.85 mm, with most specimens measuring at least 3.20 mm. **Worker.** Crest of petiolar scale blunt to very blunt, convex or straight, not emarginate. Standing body hairs numerous, more or less evenly distributed, most of moderate length. Entire surface of gula covered with 20 to 40 standing hairs, the longest of which measure

0.12 mm or more; those on dorsum of gaster measuring 0.13 mm or more. Fore femur with 12 or more standing hairs. **Male.** Antennal scapes stout, somewhat thickened apically, SL 0.70 mm or less, SI less than 70. Crest of petiolar scale blunt to moderately blunt, usually convex. Paramere with its apex usually truncate. Body size large, AL usually 1.70 mm or greater. Standing body hairs numerous. Entire surface of gula covered with 20 or more standing hairs. All femora quite pilose. Pubescence dense to moderately dense on dorsum of gaster, often suberect on antennal scapes.

Table 12 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 86–94 give standardized illustrations. In the treatment of interspecific hybrids, 4 sample regressions (figs. 10, 13–15) involve *latipes*. M. R. Smith (1965, p. 91) gives a habitus figure of the worker. Wheeler and McClendon (1903, p. 150) give a habitus figure of the queen, and (p. 155) figures of the antenna and mandible. ALR = 2.55 (2.30 – 2.92, n = 10).

FURTHER DESCRIPTION. **Queen.** Standing body hairs simple to finely barbulate, usually fairly numerous on basal segment of gaster, varying on dorsum of other segments from sparse to numerous, and either (1) covering entire surface, or (2) confined to rows on posterior edges of tergites, or (3) with an intermediate pattern. Standing hairs present on hind surface of fore femora, both surfaces of middle femora, and front surface of hind femora. Pubescence on head and pronotum dilute to moderate, that on scutum and scutellum dilute, surface shining. Body color varying from blond to reddish or castaneous brown, with a few specimens fairly dark. **Worker.** Standing body hairs simple to finely barbulate, usually fairly numerous on middle and hind femora. Pubescence on head and dorsum of gaster moderate, that on antennal scapes

Table 12. **Sample statistics for *A. latipes*: mean, standard deviation, and 3 standard deviation limits** *

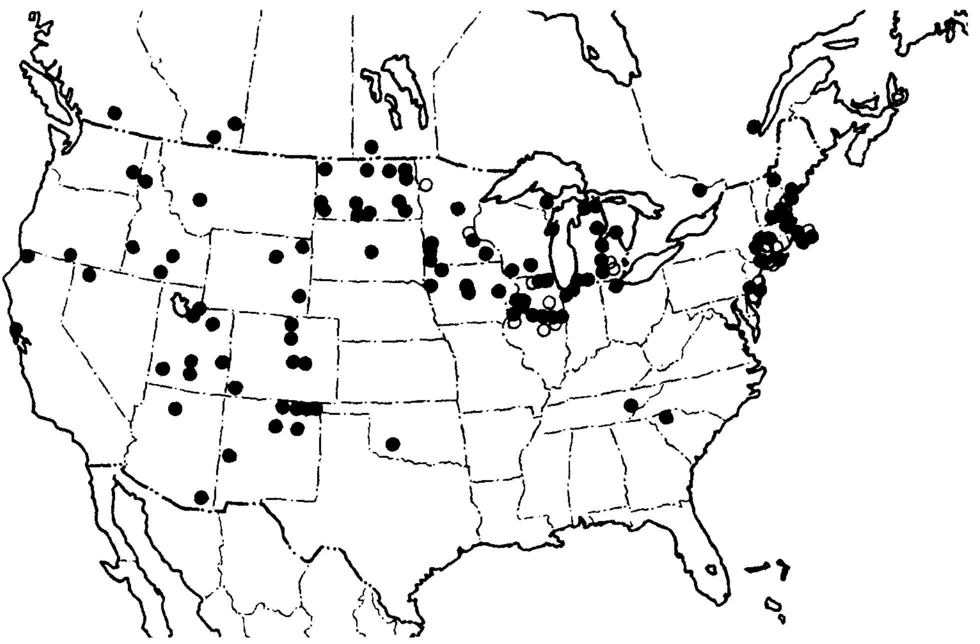
Variate	X̄	S.D.	3 S.D. limits
	Workers (N = 146)		
SL	77.22	4.72	63.06– 91.38
HW	100.42	6.36	81.34–119.50
HL	105.47	6.39	86.30–124.64
AL	134.68	10.21	104.05–165.31
CI	95.16	1.73	89.97–100.35
SI	76.95	2.49	69.48– 84.42
	Queens (N = 48)		
SL	95.06	4.37	81.95–108.17
HW	149.17	5.58	132.43–165.91
HL	160.67	6.05	142.52–178.82
AL	343.96	15.98	296.02–391.90
FL	143.75	7.48	121.31–166.19
FW	90.52	4.92	75.76–105.28
CI	92.85	1.60	88.05– 97.65
SI	63.88	2.00	57.88– 69.88
FI	63.00	2.69	54.93– 71.07

* Unit of measurement is 10^{-2} mm. Not over 2 specimens of a caste (usually 1) measured from any 1 nest.

often decumbent to suberect. Body and appendages yellow to brownish yellow, surface of body at least moderately shining. **Male.** Standing body hairs mostly simple, those on dorsum of gaster more or less evenly distributed. Pubescence on head, gaster, and legs moderate to dense, that on antennal scapes usually suberect. Color brown, head darker, appendages lighter.

DISTRIBUTION. Based on 258 samples, the distribution of this species is from coast to coast in southern Canada and the northern half of the continental United States, with southern extensions to Arizona and New Mexico and to South Carolina and Tennessee. A single queen specimen bears the data: Anchorage, Alaska, August 1947, F. R. DuChanois, No. 18. The remoteness of this station from the northern boundary of the range based on the other specimens, makes the record suspect. Wilson (1955, p. 101), was faced with the same data for *Lasius neoniger.* He cited ecological data on the Anchorage site from a letter of F. R. DuChanois, but withheld judgement pending the collection of additional specimens. I am taking the same viewpoint on the single *latipes* queen, which is not shown on the distributional map. The other 258 records are plotted on map 3. Some of the earlier published records of *latipes* based solely on worker specimens belong to other taxa in addition to hybrids of *latipes,* especially *murphyi, coloradensis* and *claviger.*

VARIATION. A random sample of 104 measurement cards, 71 for workers and 33 for queens, suggested that extremely high and low values of measurements and indices are more or less randomly distributed over the range. The queens of *latipes,* unlike those of *latipes* × *claviger,* which are usually dark, range from blond to dark brown. Lighter colored specimens are more common than the darker ones, but there is no indication of a geographic trend in coloration. The pattern of pilosity on the dorsum of the gaster of queens shows a hint of geographic trend. The less frequent pattern of pilosity, one with the standing hairs confined principally to the posterior edges of the tergites, is seen almost entirely in specimens of eastern origin. The more common pattern, one where the standing hairs more or less cover the entire surface of the gaster, is found throughout the range. Specimens with pilosity on gaster dense and evenly distributed are largely from the West. Those with pilosity on gaster moderate to more or less sparse, and often somewhat irregularly distributed are much more common in the East. Much of the extreme variability claimed for the queens of *latipes* by earlier students resulted from a study of mixed samples. When *latipes* and *latipes* × *claviger* queens are kept separate, samples of neither taxon exhibit unusually high variability. When the two taxa are lumped together, however, some characters, such as pilosity, pubescence, FW, FI, and others do exhibit extreme variability. If, for example, coefficients of variation for FW and FI were computed from the data given in this study, the results would vary greatly between



Map 3. Geographic distribution of *A. latipes,* solid circles; and *latipes* × *claviger,* hollow circles. (See text for further details.)

pure and mixed samples. Since the taxonomic separation of the two kinds of queens once lumped together under the name *latipes* is straightforward, no real problem exists. Problems do come up, however, when attempting to assess the variability of the workers. In making statements about variability, sample size obviously plays an important role. The very fact that *latipes, claviger,* and *interjectus* are successful, dominant species means that, unlike the situation in the rarer taxa, samples adequate to reveal something approaching the limits of their variability can be accumulated by the usual methods open to a reviser. Of these 3 species, only *latipes* poses any real problem relating to sample size. It is always taxonomically difficult, and often impossible, to separate *latipes* workers from those of its hybrids. Thus collections composed solely of workers are frequently mixtures of more than one taxon. Depending on geographic origin, samples may contain a greater or lesser number of hybrids such as *latipes* × *claviger,* or *murphyi* × *latipes.* These worker collections are often large and tend to be quite variable. If one restricts his attention solely to the workers of samples with associated queens or males, then the size of the collection that can be amassed as well as its variability is considerably reduced. Judging by the latter type of collection, the workers of *latipes* exhibit about the same amount of variability in a number of conventional and metric characters as do the workers of *claviger.* The sharpness of the crest of the petiolar scale is variable in both *latipes* and *claviger,* sometimes showing overlap. The scale crest of *claviger* is usually emarginate, at least feebly, while that of *latipes* is at most notched. The distribution of standing hairs on the gula is quite constant in *latipes*. Pilosity on the gula of *claviger* workers tends to be fairly constant except in the area in and around North Carolina and Virginia where *latipes* is seldom found. Thus over most of their common range the vast majority of worker specimens of these two taxa can be identified by a combination of diagnostic characters. In collections of workers from some of the eastern and central states, certain specimens may appear somewhat intermediate. When the distribution of standing hairs on the gula is essentially like *latipes*, and the crest of the petiolar scale approaches that of *claviger* in sharpness and emargination, there is a good possibility that *latipes* × *claviger* is the taxon at hand.

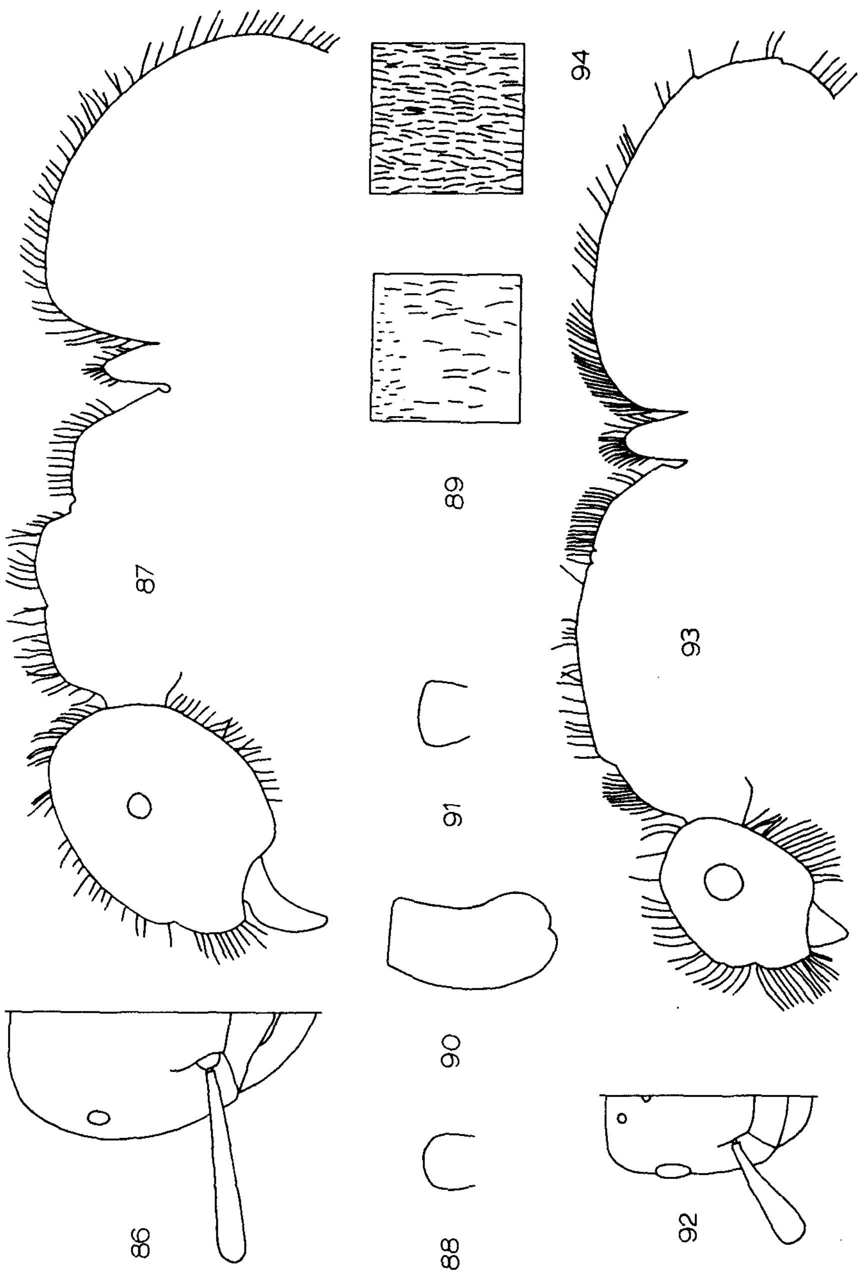
Mr. R. Sanwald kindly gave me a sample of *latipes* which included a male–female intergrade. This vial contained a queen, a male, and 4 workers, all normal, in addition to the single anomalous specimen. He collected the sample in Selden, Suffolk Co., New York in August 1961. Since only 1 other such *latipes* specimen has been described (Wheeler, 1919), I am depositing it in the MCZ along with the male, female, and a worker. A brief description of this sex intergrade is given below. Comparison with the description and figure presented by Wheeler (1919) indicates that the two specimens are quite similar in their overall appearance, but that they differ in a number of particulars.

The colors of this anomalous specimen do not always agree with the size and structure of parts typical of the corresponding sex. While the yellow areas are largely female and the black areas often male in terms of form and size, structures intermediate between male and queen may be either black or yellow. In general, typical male pilosity is associated with black, and female pilosity with yellow, and largely independent of the form and size of the underlying structure. **Head.** The right side is mostly male and black. The mandible, eye, median and right ocelli, and the slender, 12-segmented, antennal funiculus are clearly male. The right antennal scape is black but intermediate. The entire clypeus is black, but essentially that of a female including its pilosity. Most of the left side is yellow and female. The antennal scape and 11-segmented funiculus are typical of a female, as is the left ocellus. **Alitrunk.** AL measures about 3.1 mm (overall body length about 7 mm). Essentially like that of a smaller female in size and form. Mostly yellow in color, but with a number of black areas of varying size and shape. The 2 complete wings still attached to the right side are essentially those of a female. The legs are female-like for the most part, but reduced in size and with altered form. Color of legs varying from yellow to black. The parts of the legs most like those of a male and all black are the left hind tibia and tarsus and the right middle and hind tibiae and tarsi. **Petiolar scale.** All black, intermediate in size and shape.

Gaster. Predominately that of a large male, mostly black. The first segment is, partly female and yellow. Male genitalia on both sides are somewhat reduced in size, some structures showing an unusual form. The whole genitalic apparatus is turned noticeably to one side.

Reported anomalies in ants involving intergrades between males and the various female castes, mostly queens, are fairly numerous. Typically only 1 intergrade is found in a given nest. Donisthorpe (1949) stated that 126 such specimens had been described. In addition, there are some 4000 in the Wheeler collection awaiting study. Many species of the subfamily Myrmicinae (*Myrmica, Tetramorium, Aphaenogaster,* etc.) and a number in the Formicinae (*Formica, Polyergus, Camponotus,* etc.) figure in the reports of sex intergrades. Wheeler (1937), although primarily concerned with intergrades between the various female castes, does cite many of the earlier papers treating male–queen intergrades. Whiting (1938) suggested that many of the so-called sex and caste mosaics of ants may rather be intersexes and intercastes. This view was based largely on the fact that only the head is involved in a great majority of the cases. In a true sex-mosaic, the genetically produced anomalous condition tends to be distributed over the body more or less at random. Since this description fits both the specimen described above and the one described by Wheeler (1919), it might be assumed that they represent true sex-mosaics. There are at least two reasons, however, why this diagnosis is uncertain. First, the intersex may phenotypically resemble a true sex-mosaic, even though the intersex begins its development as one sex and shifts its developmental pattern to that of the opposite sex at a definite time in the embryonic sequence. The second point is based on the report of Donisthorpe (1946). He described 50 male–female anomalies in *Myrmica sabuleti.* Some of these specimens approached the two anomalous *latipes* specimens in that male and female parts were more or less randomly distributed over the body. In this paper Donisthorpe alluded to the work of van Sommeren, who had produced so-called gynandromorphs in Lepidoptera by vibrating the larvae. He then stated that a powerful lighthouse oscillator located on the small island caused considerable vibration in the ground. The fact that the 50 anomalous specimens were collected near the lighthouse would strongly suggest that their peculiarities may have been brought about by vibration, presumably at a critical point in their development. These 50 specimens showed a considerable spectrum of intergrading types, some of which approached Whiting's description of true gynandromorphs. Although some of the anomalous specimens reported in the literature may be true gynandromorphs, such as, for example, the *Epipheidole inquilina* specimen described by Wheeler (1903), the difficulties of interpretation make it seem wise to withhold judgement on the nature of the 2 aberrant specimens of *latipes.* The evidence cited above from Donisthorpe's paper and comments on the possible developmental effects of vibration made by W. L. Brown, Jr. suggest that suitable experiments involving vibration may lead to a better understanding of both sex and caste mosaics. Wheeler (1903) was apparently thinking along similar lines when he stated "...we can have no genuine understanding of gynandromorphism till this anomaly can be produced experimentally." It is entirely possible that the structural peculiarities observed in the Sample 5 (= *claviger*) workers may have resulted from excessive vibration. The nest from which these workers were collected was located near a hillside road in an area where bed rock occurs close to the surface of the soil.

ECOLOGY. **Habitat.** Of the 259 samples, 44 had data in some form relating to nest structure and location. Nests in the open numbered 25, those in woods and openings in woods 11, while the status of 8 samples was uncertain. With respect to immediate nest-cover, 19 were under stones, 3 associated with wood, 15 without immediate cover, and 7 of uncertain status. Cole (1954) listed 4 New Mexico records of *latipes* as *coloradensis.* The data associated with these nests indicated that they were under stones in open grassy areas with scrub oak, pine, and cedar at 7000 to 7200 feet. He listed 9 records under *latipes.* Of the 7 samples I have seen, 6 were *latipes,* and 1 *coloradensis.* The data associated with these samples that seem to apply to *latipes* is "Nests for the most part beneath stones on dry and moist, grassy, pine slopes. . . ." M. Talbot kindly sent me the 2 or 3 dozen samples that she collected in southern Michigan. The notes relating to these samples are set forth in her paper of 1963. Most nests were on the margins of fields with scattered oak trees. In many cases there was no externally visible evidence of the nest except at flight time. Some nests had immediate cover in the form of stones, wood, or mounds, the latter occurring in thick growths of grass. Kannowski (1956) discussed the structure of several nests in North Dakota; I have seen 6 of his samples. Most of the nests were in the open, under stones. In my own collecting, most nests have been found under stones either in the open, or clearings in woods, or on the borders of woods. This species is often found in sandy areas. **Alate dates.** See treatment in the general section on nuptial flights. **Colony foundation.** See treatment in the general section on colony foundation, and also that of *subglaber* and *latipes* × *claviger.* Apparently the fact that many parasites, especially endoparasites, produce extremely large numbers of offspring has given rise to a scattering of statements in the literature to the effect that *latipes* produces very large numbers of offspring. It is true that *latipes* does produce fairly large numbers of alates, but the statement tends to be misleading, since most other higher ant species also produce alates in large numbers. For example, some species of *Lasius* known to found their colonies independently produce on the average about the same number of alates as does *latipes,* and are subject to about the same amount of variation in numbers due to seasonal and other factors.



Figs. 86–94. A. latipes. WORKERS (25×): 86, head; 87, body profile; 88, petiolar scale; 89, pubescence (50×). QUEENS (12.5×): 90, fore femur; 91, petiolar scale; 92, head; 93, body profile; 94, pubescence (50×). (For details, see p. 17 and fig. 8.)

7a. *Acanthomyops latipes* × *claviger* hybrid

Lasius (*A.*) *latipes* alpha-form: Wheeler and McClendon (1903) and subsequent authors.

Digm locality: Selden, Suffolk Co., Long Island, New York.

Location of digms: A typical queen, male, and 2 workers from a single colony collected at the above locality by R. Sanwald are in the MCZ.

DIAGNOSIS. **Queen.** Intermediate between *latipes* and *claviger.* Head not or only slightly deformed. Antennal scapes and funiculi decidedly clavate; antepenultimate segment of funiculus greater than 1.55 and less than 2.30 times wider than long. Entire surface of gula covered with from 24 to 40 standing hairs, with maximum length usually less than 0.30 mm. FW 0.50 to 0.75 mm, usually at least 0.55 mm; genual plates of fore femora moderate, not conspicuous. FI 43–54. Crest of petiolar scale usually blunt to very blunt, not emarginate, rarely sharper and feebly emarginate. Scale covered with 50–75 standing hairs. Most standing femoral hairs confined to fore femora. **Worker.** Intermediate between *latipes* and *claviger,* but having the general appearance of *latipes,* from which it is not now reliably separable. **Male.** Typical of the males of *latipes* in all known respects.

Table 13 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 95–103 give standardized illustrations. Sample regressions for the queen and worker castes of *latipes* × *claviger* and its parent species are given (figs. 13–15) in the section on interspecific hybrids.

ALR = 2.12(1.93 – 2.50, n = 10).

Table 13. **Sample statistics for *A. latipes* × *claviger:* mean, standard deviation, and 3 standard deviation limits ***

Variate	$\bar{X}$	S.D.	3 S.D. limits
	Workers (N = 20)		
SL	80.55	4.76	66.27– 94.83
HW	106.85	5.82	89.39–124.31
HL	111.45	5.68	94.41–128.49
AL	140.85	10.34	109.83–171.87
CI	95.70	1.84	90.18–101.22
SI	75.35	1.93	69.56– 81.14
	Queens (N = 20)		
SL	95.70	4.94	80.88–110.52
HW	151.85	9.32	123.89–179.81
HL	159.00	8.94	132.18–185.82
AL	298.70	20.86	236.12–361.28
FL	132.90	8.57	107.19–158.61
FW	62.05	6.12	43.69– 80.41
CI	95.55	2.33	88.56–102.54
SI	63.15	2.89	54.48– 71.82
FI	46.55	2.61	38.72– 54.38

* Unit of measurement is 10^{-2} mm. Not over 2 specimens of a caste (usually 1) measured from any 1 nest.

Wheeler and McClendon (1903, p. 150) present habitus figures for the queens of *claviger, latipes* × *claviger* and *latipes.* Although not completely accurate in some details, these figures do give a good general idea of the appearance of the parent species and the intermediate nature of the hybrid taxon. A table on p. 153 of their article gives comparative measurements in micron units for 41 structures. This table was apparently based on 3 specimens, 1 of each taxon, considered to be typical. A tabulation on pp. 154–155 contrasts 12 points of difference between the queens of *latipes* and *latipes* × *claviger.* Figures of the antennae and mandibles for the queen caste of the 3 taxa are given on p. 155.

FURTHER DESCRIPTION. **Queen.** Pubescence on gaster from very dilute to very dense, that on rest of body usually much less dense, most of body usually shining. Pilosity on gaster variable, but most specimens have standing hairs largely confined to the posterior edges of tergites beyond first. Body color variable, most frequently a medium-dark castaneous brown. Some specimens are lighter yellowish brown, others are a dark grayish brown. **Worker.** Pubescence on gaster dilute to dense. Petiolar scale variable, but usually quite similar to that of *latipes.* Standing hairs on gula almost invariably cover the entire surface. Length of standing body hairs and body size average and range a little greater than in *latipes.* Body color yellow to brownish yellow.

DESIGNATION OF DIMORPHIC QUEENS IN LATIPES. Wheeler and McClendon (1903) discussed 4 possible ways to account for alpha and beta females. One suggestion was that they represented 2 species, another was that the alpha-form represented the normal queen of *latipes* while the betas were abnormal, diseased forms. Both ideas were rejected as being improbable. The third alternative, that the alpha queen is a hybrid produced by a *latipes* queen and a *claviger* male, caused considerable soul-searching, and the door was never really shut on this possibility. The hypothesis that the alpha and beta forms represented dimorphic queens was somewhat half-heartedly accepted and formally stated to be the answer to the riddle. That this renaming of the problem did not entirely satisfy Wheeler is evident; he indicated that only further observation and experiment would enable myrmecologists to decide which of the two alternatives, hybridism or dimorphism, was correct. I think that there is little doubt that Wheeler would have chosen the hybrid explanation had he done this work a few decades later. Once committed in print to the statement that *latipes* has dimorphic queens, however, he went on to the end of the paper with a discussion of the origin of wingless females in the Hymenoptera.

The problem, however renamed, remained a problem. No one ever saw more than a few specimens at a time. The fairly clear-cut and relatively constant diagnostic differences between the males of *latipes* and *claviger* went unnoticed. Measurements were rarely taken on the queens of the supposed parent species and their hybrid offspring, hence regression studies were out of the question. The very existence of the 1903 paper stating that these queens were dimorphs more or less ended the matter for most myrmecologists. We all tended to forget the substance of the paper, and remembered only its title.

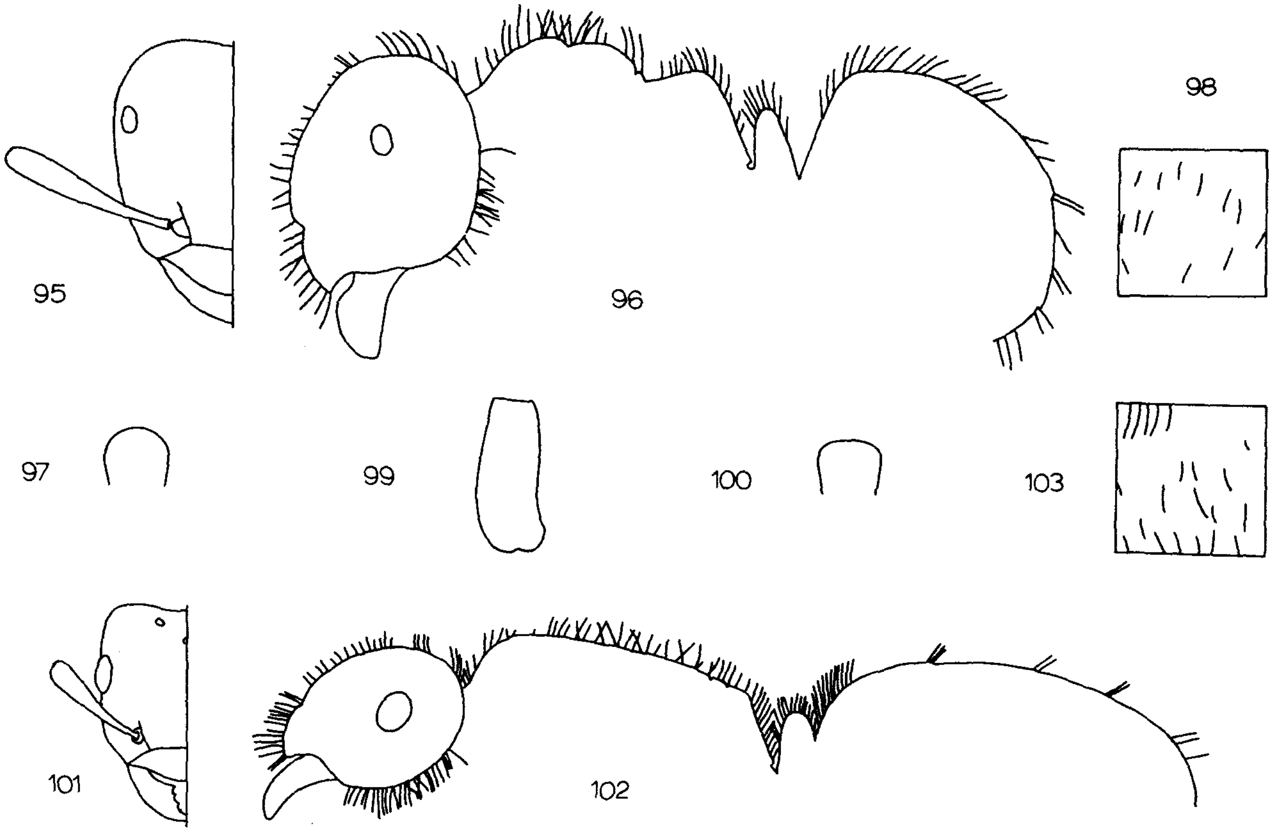
The solution offered in the present paper that the queen known as the alpha-form is a hybrid is simple, straightforward, and backed by considerable evidence. It is the solution that Wheeler almost gave in 1903, despite the fact that laboratory genetics was in its infancy and population genetics was unknown. The solution has at least one merit other than fitting a number of the known facts, it is, unlike esoteric hypotheses or a renaming of the problem, testable in several ways.

DISTRIBUTION. This sporadic form is recorded in a band from Minnesota and Central Illinois east to New England and New Jersey. It is by far the most common of all known hybrid taxa, most of which are known from only one or two collections. The samples containing only *latipes* × *claviger* queens, numbering 25, and the 1 sample collected by Wheeler at Rockford, Illinois, containing both *latipes* and *latipes* × *claviger* queens, are plotted on map 3 in the treatment of *latipes*. Comparison of the distribution of *latipes* × *claviger* with those of the parent species shows the absence of records between eastern New York and eastern Michigan for both *latipes* and *latipes* × *claviger*. Although *claviger* is common in this area, there are relatively fewer records of its capture here than on the eastern seaboard and in the western part of its range. It will be noted that all records of *latipes* × *claviger* are within or on the fringes of the known common range of the parent species, with 1 exception. The queen collected from a nest in Polk Co., Minnesota, and assigned to *latipes* × *claviger*, is between the known ranges of *claviger* and *coloradensis*. The metric data for this specimen are at the extreme low end of the range for *latipes* × *claviger* on all primary measurements except AL. A study of the regression sheets was inconclusive in deciding on the identity of the parent taxa. The status of this single queen is thus uncertain; it could be either *latipes* × *claviger* or *latipes* × *coloradensis*.

VARIATION. This taxon tends to be as variable or more so in all castes than either parent species, both of which are variable in a number of characters. Because of this, some characters diagnostically useful in restricted areas are of little value taken over the whole range. Of the queen characters cited in the diagnosis section, FI stands out as the best single character. Despite its rather extensive range, it has clearly separated the hybrid queens from those of both parent species in the more than 100 recorded cases, and in about as many more cases where FI computations were made but not formally recorded. In neither FI nor in a number of other fairly variable characters, such as pilosity, pubescence, and color, has there been any evidence of geographic trends. The size and structure of the petiolar scale tend to vary over the range. A queen collected by Wheeler at Colebrook, Connecticut had a gigantic swollen scale. She exhibited no other teratological trends, and the other queens in the series were normal in all respects.

The workers exhibit considerable variation, tending to follow the associated queens in degree and direction of variation. The variation in size, pilosity, and pubescence tends to stay more or less within the combined ranges of workers of the variable parent species. Since the distribution of standing hairs on the gula is quite constant, and almost invariably closely resembles that of *latipes*, nearly all *latipes* × *claviger* workers run to *latipes* in the key. When the scale is sharper than is usually the case in *latipes* × *claviger*, and especially if it is emarginate and not just notched, then the gula hair pattern keeps the specimen from running out to *claviger* in most cases. The *claviger* workers in the area in and around North Carolina and Virginia often mimic *latipes* in their pattern of gular pilosity. However, in the area where this variant of *claviger* is common, few *latipes* colonies are found. Comparison of groups of known *latipes* workers with groups of known *latipes* × *claviger* workers gives rise to overlapping statistical differences in a number of characters. At the present time, however, the variability of these taxa is too great to make reliable separation possible even for series of workers.

ECOLOGY. **Habitat.** Few data were associated with the specimens received for study. I collected a single alate queen at Kittery Point, York Co., Maine on September 4, 1946. She was found in the late afternoon in a dry open area between woods containing *latipes* colonies and a main paved road. W. L. Brown, Jr. found a single dealate queen on August 2, 1955 in an open area on sandy clay soil on Cape Cod, Barnstable Co., Massachusetts. I made a nest collection containing a single alate queen on August 27, 1950, near Crookston, Polk Co., Minnesota. This populous colony inhabited a nest with a few inconspicuous openings; it was located on a dry roadside. I collected a single dealate queen in Ramsey Co., Minnesota on August 31, 1950; this queen was running about on the ground associated with several *latipes* queens at 6 P.M. J. G. Franclemont collected a dealate queen on August 11, 1955 near Lakehurst, Ocean Co., New Jersey; this queen crawled up on an illuminated sheet at night along with several *latipes* queens. From the little evidence at hand, it seems likely that *latipes* × *claviger*, like *latipes*, prefers dry, usually sandy, areas. Until more data are available, however, the range of its habitat preferences are uncertain. **Alate dates.** Sexual forms associated with workers, presumably nest collections, range from July 31 to September 24, with 1 extremely late record on October 29. Alate queens taken without workers range from August 18 to September 16. Dealate queen dates run from August 2 to September 27. Probably most flights occur between mid-August and mid-September.



Figs. 95–103. A. latipes × claviger. WORKERS (25×): 95, head; 96, body profile; 97, petiolar scale; 98, pubescence (50×). QUEENS (12.5×): 99, fore femur; 100, petiolar scale; 101, head; 102, body profile; 103, pubescence (50×). (For details, see p. 17 and fig. 8.)

Colony founding. Wheeler and McClendon (1903) list 10 nests of *latipes,* 2 of which were stated to contain both alpha and beta queens. A search for these specimens turned up 4 of the 10, including the 2 mixed series. The Rockford, Illinois series still had both types of queens. The Colebrook, Connecticut series contained only betas, which probably means only that the alphas were completely removed from the MCZ along with the other 6 series. In addition to these 2 mixed colonies, Tanquary (1911) reported finding 1. The material sent to me for study, containing over 100 *latipes* nest series with queens, had no further mixed colonies. Single colonies producing both *latipes* and *latipes* × *claviger* queens are rarely collected.

The occurrence of these mixed colonies is of interest, since they may indicate the existence of polygyny in *latipes.* A possible explanation for the origin of these nests involves 2 *latipes* nest queens, one fertilized by *latipes* and the other by *claviger.* This would give rise to a colony with 2 kinds of daughter queens, 2 kinds of workers, and males of *latipes.* The infrequent occurrence of such nests agrees with expectation. The frequency of these nests is a function of both the relative proportion of *latipes* queens fertilized in the two ways, and the combinatorial aspects of queen-pair formation as evidenced by successful nest adoptions. That the origin of these nests may be accounted for in other ways is obvious. Perhaps 2 nests founded separately by single queens either merge into 1, or are combined in 1 sample by a collector because of their extreme proximity. Multiple fertilization of a single queen by males of the two species is another possible explanation for the mixed colonies. See the general section on colony founding, and the treatment of *subglaber.*

7b. ***Acanthomyops latipes* × *coloradensis* hybrid**

Lasius latipes: Weber, 1935: alpha female, p. 200.

Types: None, but 1 digm specimen, a dealate queen, in the MCZ.

DIAGNOSIS. **Queen.** Bears a close resemblance to *latipes* × *claviger,* from which it cannot readily be separated. **Worker** and **male** not seen.

Table 14 gives selected sample statistics. Tables 33–41 give frequency distributions for measurements and indices.

FURTHER DESCRIPTION. Ranging and averaging smaller for most metric characters, but with AL, CI, and FI about the same, and SI higher than in *latipes* × *claviger.* Minor differences from *latipes* × *claviger* in conventional characters are: antennal scapes slightly less clavate, petiolar scale crest a little less blunt, and slight color differences. The head and appendages are light yellowish brown; the rest of the body a darker brown. Only a small proportion of the *latipes* × *claviger* queens appear bicolorous; they range and average somewhat darker than *latipes* × *coloradensis.*

DISCUSSION. When the manuscript of the present revision was nearing completion, I noted that Weber (1935) had reported collecting alpha-

Table 14. **Sample statistics for *A. latipes* × *coloradensis:* mean, standard deviation, and 3 standard deviation limits ***

Variate	$\bar{X}$	S.D.	3 S.D. limits
	Queens (N = 2)		
SL	90.00	1.41	85.77– 94.23
HW	136.00	0	136.00–136.00
HL	142.00	2.83	133.51–150.49
AL	280.00	28.28	195.16–364.84
FL	121.00	12.73	82.81–159.19
FW	54.50	6.36	35.42– 73.58
CI	95.50	2.12	89.14–101.86
SI	66.00	1.41	61.77– 70.23
FI	45.00	0	45.00– 45.00

* Unit of measurement is 10^{-2} mm. Both queens measured from 1 nest series.

latipes queens on September 2, 1931 from Towner, McHenry Co., North Dakota. In this paper on *Formica obscuripes,* he reported on their collection as follows: "Live workers, males and dealate alpha and beta females of *Lasius latipes* Walsh were found in digging up an *obscuripes* nest at a depth of about two feet (61 cm.). They did not seem to be captive and were possibly an independent colony." Upon my request, Dr. Weber sent me a beta queen and 3 "alpha" queens, 1 lacking a head. He was unable to locate the workers and males. The study of these specimens was of particular interest, because I knew of no other alpha queens collected so far outside the known range of *claviger. Claviger* and *coloradensis* are so closely related that the previous absence of records of *latipes* × *coloradensis* seemed odd, especially since *latipes* × *claviger* is our most frequently collected hybrid taxon.

A study of these specimens showed the beta female to be a perfectly typical *latipes* queen. The three "alpha" females resembled *latipes* × *claviger* queens closely enough to pass for small variants of this hybrid. Assignment of these queens to *latipes* × *coloradensis* was based both on structural characters, largely metric, and the known ranges of *claviger* and *coloradensis.*

Measurements for the two complete specimens were entered on regression work sheets. Comparison for all standard regressions with *coloradensis* and *latipes* queens indicated that the Weber specimens could well be the hybrid offspring of these parents. The same comparisons with *claviger* and *latipes* queens gave from fairly good to very poor support for the hypothesis that these queens could be *latipes* × *claviger.* These conclusions are evident to a degree from the frequency distribution tables.

From the standpoint of geographical distribution alone, Weber's "alpha" queens would not be assigned to *latipes* × *claviger.* Towner, North Dakota is some 300 miles northwest of Todd Co., Minnesota, the westernmost point at which I have collected a *claviger* nest. Fairly extensive ant collecting in Minnesota leads me to believe that *claviger* nests will not be found much west of Todd Co., or much north of an eastern extension of the boundary line separating North and South Dakota. However, occasional records of single queens may occur farther north; Dr. C. E. Mickel collected a single dealate queen on the lake shore at Duluth.

The range boundaries of *claviger* expand and contract in response to changes in environmental factors, especially climate, as do those of other ant species. Weber (1941, 1942) reported on the results of sampling ants in and around North Dakota for the years 1934 and 1941. The extreme drought conditions of the early 1930's adversely affected the population density of all ant species not adapted to very dry conditions. *Claviger* is not well adapted to dry conditions. Thus it seems highly improbable that the range boundaries of *claviger* would have been expanding during the early 1930's to the extent necessary to place sexual individuals within cruising range of Towner, North Dakota.

Weber's collection may represent a nest producing both types of queens. For a possible explanation of the origin of a nest producing both *latipes* and *latipes* × *coloradensis* queens, see the discussion on polygyny under colony foundation in *latipes* × *claviger*.

8. *Acanthomyops murphyi*

Lasius (*Acanthomyops*) *Murphii* Forel, 1901: worker, p. 367; queen, p. 368; male, p. 369.

Type locality: Morganton, Burke Co., North Carolina.

Location of types: Syntypes in the MCZ, AMNH, and Forel Collection, Museum d'Histoire Naturelle, Geneva.

DIAGNOSIS. **Queen.** Hair tufts unevenly distributed, matted, beard-like; petiolar scale large, blunt, densely pilose; antennal scapes slender, head deformed; SI near or above 80, FI 40 or less. **Worker.** Numerous, short standing hairs covering very blunt petiolar scale and entire surface of the gula, and the very small eyes are sufficient to separate this species from all others except some specimens of *latipes*. Workers of *murphyi* have standing hairs of alitrunk concentrated largely on the propodeum, while *latipes* workers have pilosity more or less evenly distributed over alitrunk. **Male.** Petiolar scale blunt, gula with a few standing hairs usually restricted to its posterior ⅔, antennal scapes slender, with appressed pubescence; body pilosity moderate to sparse.

Table 15 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 104–112 give standardized illustrations. Smith (1965, p. 90) gives a habitus figure of the worker. In the treatment of interspecific hybrids, 2 sample regressions (figs. 10, 12) involve *murphyi*.

ALR = 2.26(2.04 − 2.37, n = 10).

Table 15. **Sample statistics for *A. murphyi:* mean, standard deviation, and 3 standard deviation limits** *

Variate	$\bar{X}$	S.D.	3 S.D. limits
		Workers (N = 30)	
SL	73.43	4.78	59.09- 87.77
HW	91.80	5.54	75.18-108.42
HL	96.10	6.11	77.77-114.43
AL	119.90	8.94	93.08-146.72
CI	95.63	1.43	91.34- 99.92
SI	79.97	1.81	75.54- 85.40
		Queens (N = 15)	
SL	104.13	3.02	95.07-113.19
HW	129.27	3.84	117.75-140.79
HL	144.27	3.45	133.92-154.62
AL	271.33	7.19	249.76-292.90
FL	131.27	3.31	121.34-141.20
FW	47.93	2.19	41.36- 54.50
CI	89.60	1.55	84.95- 94.25
SI	80.53	2.10	74.23- 86.83
FI	36.53	1.51	32.00- 41.06

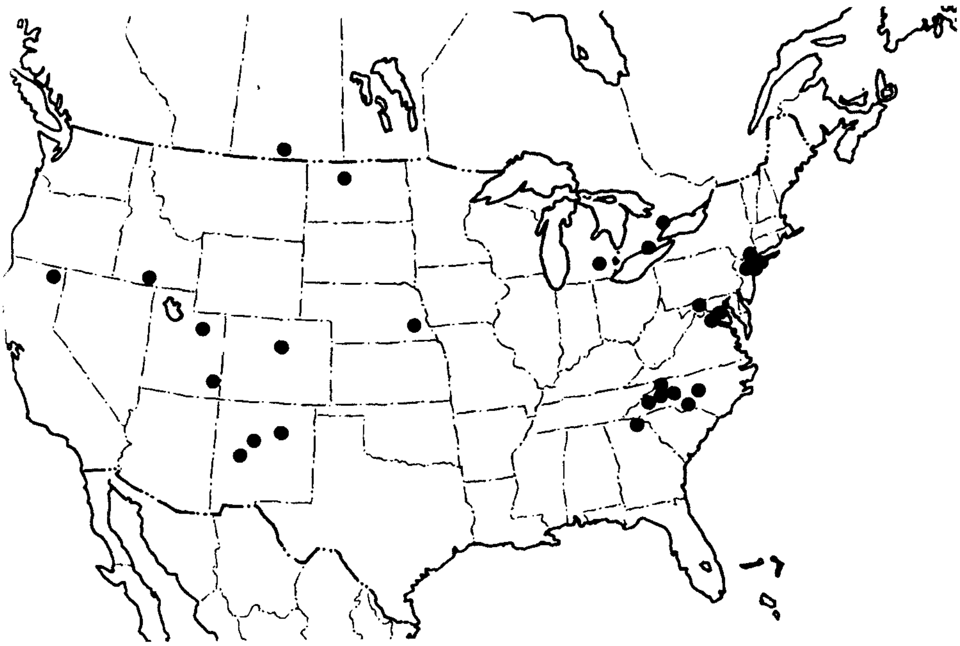
* Unit of measurement is 10^{-2} mm. Not over 2 specimens of a caste (usually 1) measured from any 1 nest.

FURTHER DESCRIPTION. **Queen.** The matted body hairs are coarse and whitish to golden in appearance; those on the fore femora are strongly reflexed, or looped, and not tightly matted to surface. Gaster with few or no standing hairs, moderately to densely pubescent. Body and appendages more or less dull, yellowish-brown. Forewings brownish basally, lighter apically. **Worker.** Standing body hairs numerous; pubescence moderate. Body and appendages shining, color ranging from yellow to brownish yellow. **Male.** Pubescence moderate; cuticle finely sculptured, feebly shining. Body color dark brown, appendages lighter. Infuscation of forewings as in queens.

DISTRIBUTION. Coast to coast in southern Canada and northern United States, with southern extensions to New Mexico in the Rocky Mountains and to Georgia in the Appalachians. The 49 samples of this sporadic species are plotted on map 4.

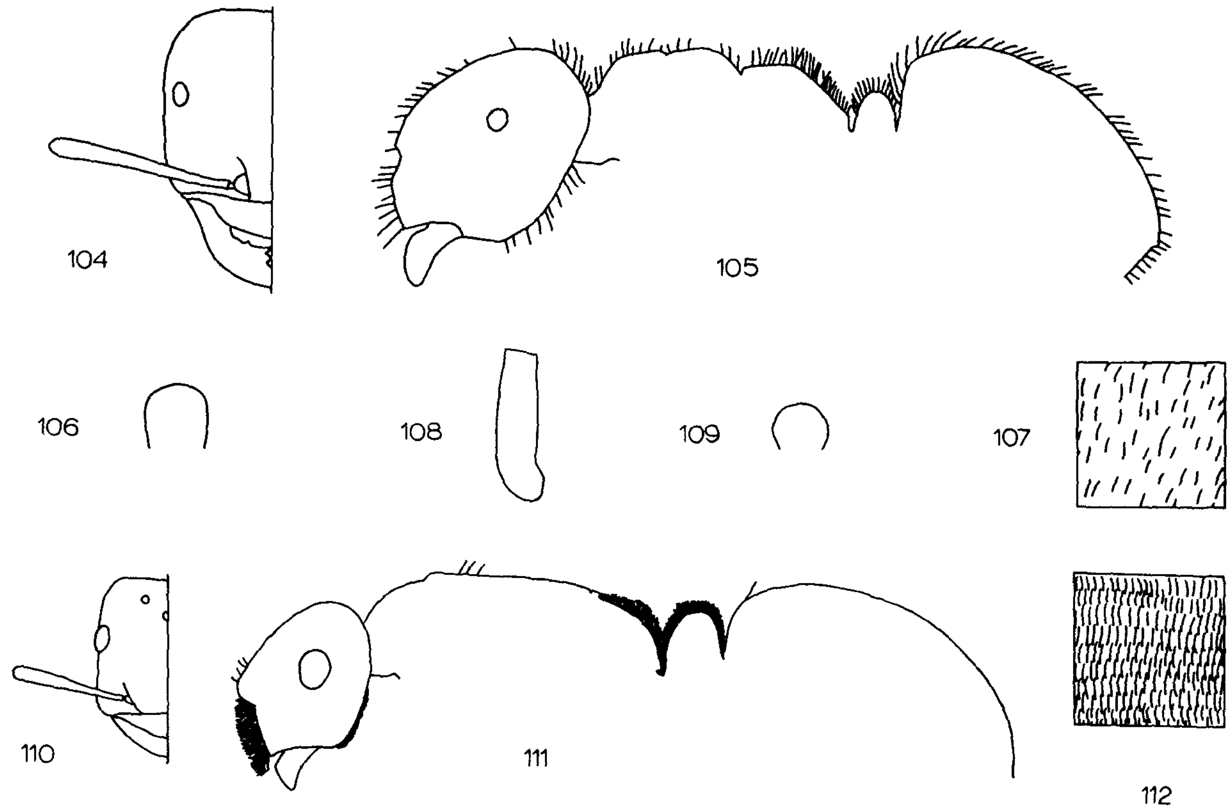
VARIATION. Worker samples are more variable than those of queens in both the conventional and metric characters studied, but neither caste exhibits notable variation. A review of 26 measured specimens failed to show any significant geographic trends in metric characters; these and other specimens revealed no notable geographic trends in conventional characters.

ECOLOGY. **Habitat.** This species usually nests under or adjacent to stones in open woods or on their edges; it shows a preference for sandy soil. Nests occur at altitudes ranging from sea level to above 6000 feet, with most southern records occurring at the higher altitudes. In North Carolina, for example, 7 of the 9 collections were from mountains. I have no direct evidence that this species nests under wood or maintains regular mounds anywhere in its range. I found a small colony on



Map 4. Geographic distribution of *A. murphyi.* (See text for further details.)

he edge of an open pine woods at Siler City, North Carolina. The nest vas under a small stone well covered by pine needles. Its main chambers ınd galleries were about 2 inches below the surface of the soil, and did ıot extend outward for more than a few feet. The dominant *Acan-thomyops* species in this woods and along its edges was *claviger*. Although most nests are in open woods, often pines in the Southeast, occasional nests are found in the open, without covering objects. Carter (1962b) found 1 colony in western North Carolina under a stone on a grassy roadside bank. Wheeler and Wheeler (1963) reported 1 nest from open grasslands in North Dakota. Talbot (1963) studied 11 nests in southern Michigan; they were located both in open fields and fence rows, and among young trees and in mature open oak woods. She found that nests often covered sizable areas. One colony that used 15 covering stones, extended for at least 5 yards. Another nest had clusters of exits extending for at least 13 yards during the flight period, but no trace of openings could be seen after flights were over. **Alate dates.** The 21 dated samples with alates showed extreme dates of June 28 and September 18. The June date was for a sample with larval queens. Forel (1901) reported that the types were having their nuptial flight on July 16. It is doubtful if flights occur much before mid-July. Talbot (1963) noted that the date of first flights was variable, but her records indicate that most take place in late July and early August. Since the flight period of this species is usually brief, most flights are probably over by middle



Figs. 104–112. A. murphyi. WORKERS (25×): 104, head; 105, body profile; 106, petiolar scale; 107, pubescence (50×). QUEENS (12.5×): 108, fore femur; 109, petiolar scale; 110, head; 111, body profile; 112, pubescence (50×). (For details, see p. 17 and fig. 8.)

to late August. She noted, however, that one colony, which produced only males in 1961, was still making flights on August 23, with males still left in the nest. Another nest still contained males and females on September 2. As in other species, rains usually provided the stimulus for the opening of the nests by workers and the subsequent flights. **Colony founding.** This species probably establishes its colonies parasitically in a manner similar to *latipes*. For further details see the general section on colony foundation.

8a. *Acanthomyops murphyi* × *latipes* hybrid

Lasius (*Acanthomyops*) *pogonogynus* Buren, 1950: queen and worker, p. 186.

Type locality: Red Feather Lakes, Larimer Co., Colorado.

Location of types: Holotype female and paratype females and workers in the USMN; paratype female in the MCZ.

DIAGNOSIS. **Queen.** Similar to *latipes,* but differing as follows: Standing body hairs unevenly distributed, bent, tangled, and twisted, but not matted to surface. Crest of petiolar scale more pilose. Gula with most hairs appressed. Antennal scapes and funiculi less clavate. Genual plates of fore femora less pronounced. Fore femora with hairs suberect to erect and mostly flexed, those on other femora fewer in number, mostly appressed to decumbent, and straight. SI over 70. FI 51 or less. **Worker.** Bears a close resemblance to *latipes,* from which it is not now separable. **Male.** A typical *murphyi* male associated with the Idaho collection indicates that this hybrid was produced by the cross, *murphyi* female × *latipes* male.

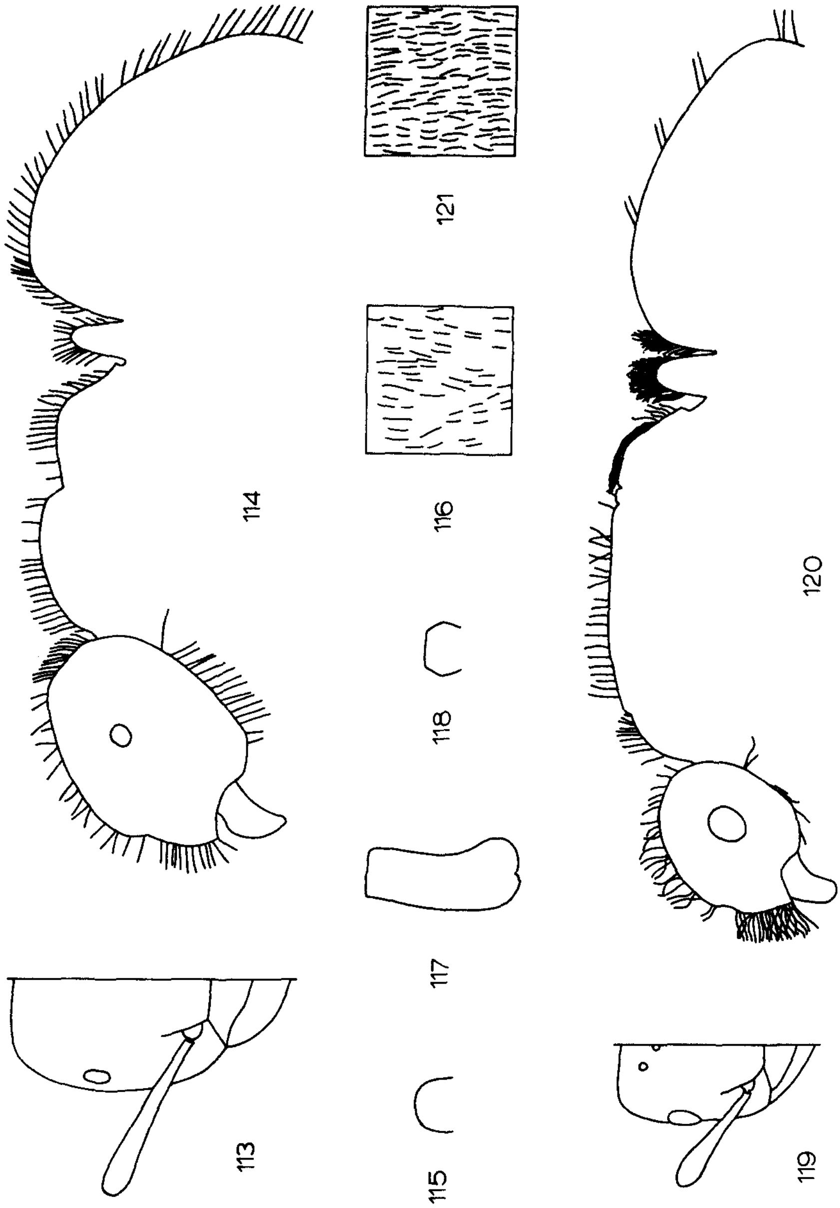
Table 16 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 113–121 give standardized illustrations. Figure 10 gives a sample regression of FW on FL for the queens of this hybrid taxon and its parent species.

ALR = 2.61(2.46 — 2.48, n = 2).

FURTHER DESCRIPTION. **Queen.** Pubescence on dorsum of gaster dense to moderately dense, elsewhere on body and appendages dilute to moderate. Color brown to yellowish brown. **Worker.** Body pilosity more dense than that of most *latipes* workers, otherwise no consistent differences have been noted. **Male.** See treatment of *murphyi.*

DISTRIBUTION. Five samples studied from 3 states. Red Feather Lakes, Larimer Co., Colorado June 14, 1933, under stone at an altitude of about 10,000 ft., V. S. L. Pate and A. B. Klots. Moscow, Latah Co., Idaho, June 26, 1962, J. V. Foy, from house. Ames, Story Co., Iowa, August 1, 1940, Vera Hagen. Sioux City, Woodbury Co., Iowa, C. N. Ainslie, August 2, 1921, from sidewalk; and Sioux City, Ainslie, July 24, 1926.

VARIATION. The few specimens available for study show little variation. Two samples containing only workers, referred to *latipes,* may



Figs. 113–121. A. murphyi × latipes. WORKERS (25×). 113, head; 114, body profile; 115, petiolar scale; 116, pubescence (50×). QUEENS (12.5×): 117, fore femur; 118, petiolar scale; 119, head; 120, body profile; 121, pubescence (50×). (For details, see p. 17 and fig. 8.)

Table 16. **Sample statistics for *A. murphyi* × *latipes*: mean, standard deviation, and 3 standard deviation limits** *

Variate	$\bar{X}$	S.D.	3 S.D. limits
	Workers (N = 3)		
SL	77.33	.58	75.59– 79.07
HW	96.67	.58	94.93– 98.41
HL	101.33	.58	99.59–103.07
AL	125.33	.58	123.59–127.07
CI	95.33	.58	93.59– 97.07
SI	79.67	1.15	76.22– 83.12
	Queens (N = 3)		
SL	103.00	1.00	100.00–106.00
HW	142.00	3.46	131.62–152.38
HL	157.67	2.52	150.11–165.23
AL	326.67	15.28	280.83–372.51
FL	141.67	1.53	137.08–146.26
FW	68.67	2.52	61.11– 76.23
CI	90.00	2.00	84.00– 96.00
SI	72.67	1.53	68.08– 77.26
FI	48.33	2.52	40.77– 55.89

* Unit of measurement is 10^{-2} mm. Not over 2 queens measured from any 1 nest, but the 3 workers measured were from the type nest.

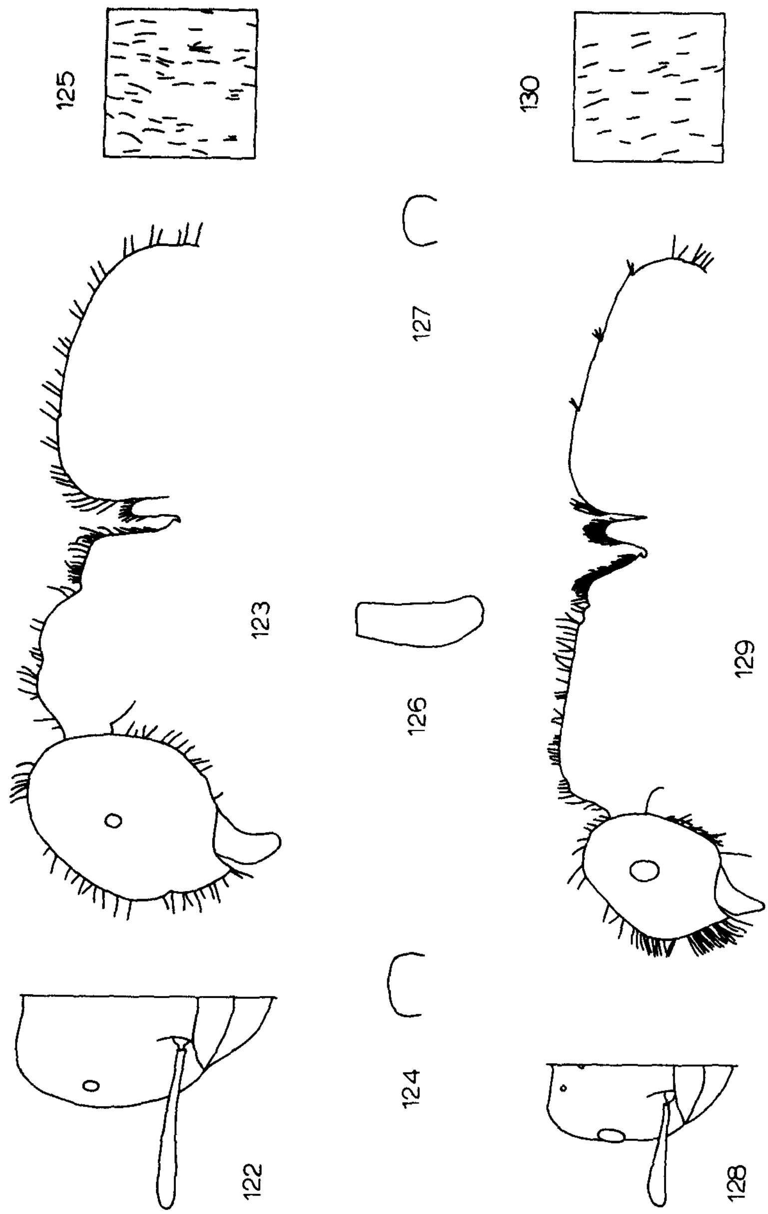
be *murphyi* × *latipes*; the body pilosity on both of these samples was unusually dense. Their data are: Boulder Can., Boulder Co., Colorado 8300 ft., April 19, 1959, H. Levi; and Grand Canyon, Coconino Co., Arizona, 6500 ft., March 1919, W. M. Wheeler Collection.

ECOLOGY. *Habitat.* No biological information is available other than that listed above in the distribution section. **Alate dates.** Queens in the type nest on June 14, and males and queens from a house in Moscow, Idaho on June 26 indicate that flights may begin in June. Dealate queens from Iowa collected in late July and early August indicate that flights may continue at least throughout July.

8b. *Acanthomyops murphyi* × *subglaber* hybrid

Previously undescribed.
Digm locality: Medford, Suffolk Co., New York.
Location of digms: A queen and 2 workers in the MCZ.

DIAGNOSIS. **Queen.** Somewhat similar in form and size to larger *subglaber* specimens. Body pilosity coarse, often with tips blunt, unevenly distributed in a pattern suggesting *murphyi.* Pilosity on gula appressed to suberect; on propodeum tangled and flexed. Scale densely pilose, with crest blunt and sometimes with a median notch. Antennal scapes moderately clavate, covered with suberect and decumbent pubescence. Head somewhat deformed. SI 71–74, CI 94–96. **Worker.** Resembles a small *latipes* specimen with standing body hairs fewer and shorter. Pubescence on antennal scapes predominantly suberect. Eyes very small. CI 96 or more. **Male.** Unknown.



Figs. 122–130. A. murphyi × subglaber. WORKERS (25×): 122, head; 123, body profile; 124, petiolar scale; 125, pubescence (50×). QUEENS (12.5×): 126, fore femur; 127, petiolar scale; 128, head; 129, body profile; 130, pubescence (50×). (For details, see p. 17 and fig. 8.)

Table 17. **Sample statistics for *A. murphyi* × *subglaber*: mean, standard deviation, and 3 standard deviation limits** *

Variate	$\bar{X}$	S.D.	3 S.D. limits
		Workers (N = 2)	
SL	72.50	4.95	57.65– 87.35
HW	94.00	8.49	68.53–119.47
HL	96.50	9.19	68.93–124.07
AL	119.00	12.73	80.81–157.19
CI	97.50	.71	95.37– 99.63
SI	77.00	1.41	72.77– 81.23
		Queens (N = 2)	
SL	94.00	4.24	81.28–106.72
HW	130.00	1.41	125.77–134.23
HL	136.50	3.54	125.88–147.12
AL	249.00	15.56	202.32–295.68
FL	118.50	3.54	107.88–129.12
FW	41.00	0	41.00– 41.00
CI	95.00	1.41	90.77– 99.23
SI	72.50	2.12	66.14– 78.86
FI	34.50	.71	32.37– 36.63

* Unit of measurement is 10^{-2} mm. Not over 1 specimen of a caste measured from any 1 nest.

Table 17 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 122–130 give standardized illustrations. Figure 12 gives a sample regression of FW on FL for the queens of this hybrid taxon and its parent species. ALR = 2.09(1.86 — 2.36, n = 2).

FURTHER DESCRIPTION. **Queen.** Pubescence dilute to moderate. Color yellowish brown. **Worker.** Crest of petiolar scale often with a median notch. Pubescence dilute to moderate, denser on front of head than on dorsum of gaster. Color yellow to pale brownish yellow.

DISCUSSION. This taxon is known from only 2 collections made by R. Sanwald in Suffolk Co., Long Island, New York: Medford, August 1961, and N. E. Patchogue, September 1960, in moist open woods. Two detached wings in the Medford vial indicate that at least one of the two dealate queens of this sample were winged at the time of capture. The single queen in the Patchogue vial was dealate. These two samples comprising only a few individuals exhibited only slight variation, as might be expected. Flights may begin in August and extend into September.

9. *Acanthomyops subglaber*

Lasius claviger var. *subglaber* Emery, 1893: worker, queen and male, p. 642.

Lasius (*A*) *clavigeroides* Buren, 1942: worker, p. 406; queen and male, p. 407.

Acanthomyops subglaber: Creighton, 1950: worker, p. 433. (*clavigeroides* synonymized).

Type locality: Washington, D.C.

Location of types: A queen, a worker, and a male in the AMNH bear the following data: Washington, D.C., Aug. 2, 1891, No. 386. These three specimens, labelled "cotypes", were presumably collected by T. Pergande. Creighton (1950) stated that types were in the USNM and AMNH. However, the USNM material sent to me for study did not contain any *subglaber* types. There is material in the MCZ that bears a type label. These "type" specimens were given to the MCZ by the Curator of the Emery Collection; they represent a sample of the specimens collected by Wheeler at Rockford, Illinois. It thus appears that the only types located in this country are in the AMNH. I wish to thank Dr. J. G. Rosen for his kindness in lending me the AMNH cotypes for study.

DIAGNOSIS. **Queen.** Superficially similar to smaller *claviger* specimens. Standing body hairs delicate, short, and fairly sparse. Standing hairs on dorsum of gaster largely confined to posterior edges of tergites beyond first. Crest of petiolar scale moderately blunt, straight, very feebly emarginate or slightly convex. Anterior and posterior surfaces of scale flat; upper sides more or less straight. Scapes and funiculi somewhat clavate. Body size small, HW usually 1.37 mm or less. Pubescence on gula and appendages, especially scapes, usually suberect and conspicuous, at least decumbent. Amount of pubescence on gaster, number of standing hairs on gula, and body color variable; see discussion under the section on variation. **Worker.** Superficially similar to *claviger,* closely similar to *occidentalis.* Standing body hairs delicate to fairly delicate, mostly short, sparse to moderately numerous. Gula usually has few or no standing hairs. Propodeum usually convex in profile. Crest of erect petiolar scale usually below level of propodeal spiracles, moderately blunt and not emarginate in most cases. Antennal scapes with pubescence decumbent to strongly suberect. Pubescence on gaster and head ranging from moderately dilute to dense. See section on variation for separation of *subglaber* from several other species, especially *occidentalis.* **Male.** Similar to *occidentalis,* but larger, AL 1.35 to 1.60 mm. Crest of petiolar scale moderately sharp, straight or nearly so. Standing body hairs delicate; gula has few very short hairs, or none. Antennal scapes short, robust, covered with suberect pubescence; SL greater than 0.60 mm, SI less than 70. Head quite pubescent, gaster with pubescence varying from moderate to dilute. Body color very dark brown.

Table 18 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 132–140 give standardized illustrations. Figure 131 gives sample regressions of SL on HW for the workers of *subglaber* and *occidentalis*; Table 19 gives critical values of SL and HW. In the treatment of interspecific hybrids, 2 sample regressions (figs. 11, 12) involve *subglaber.*

Table 18. **Sample statistics for *A. subglaber*: mean, standard deviation, and 3 standard deviation limits** *

Variate	X̄	S.D.	3 S.D. limits
	Workers (N = 54)		
SL	70.56	4.49	57.09– 84.03
HW	95.33	5.92	77.57–113.09
HL	99.67	5.79	82.30–117.04
AL	122.15	8.22	97.49–146.81
CI	95.63	1.86	90.05–101.21
SI	73.96	2.07	67.75– 80.17
	Queens (N = 22)		
SL	82.73	5.51	66.20– 99.26
HW	127.23	7.48	104.79–149.67
HL	128.41	6.88	107.77–149.05
AL	208.82	14.99	163.85–253.79
FL	98.45	6.68	78.41–118.49
FW	35.05	3.46	24.67– 45.43
CI	99.00	2.41	91.77–106.23
SI	65.05	2.17	58.54– 71.56
FI	35.64	2.06	29.46– 41.82

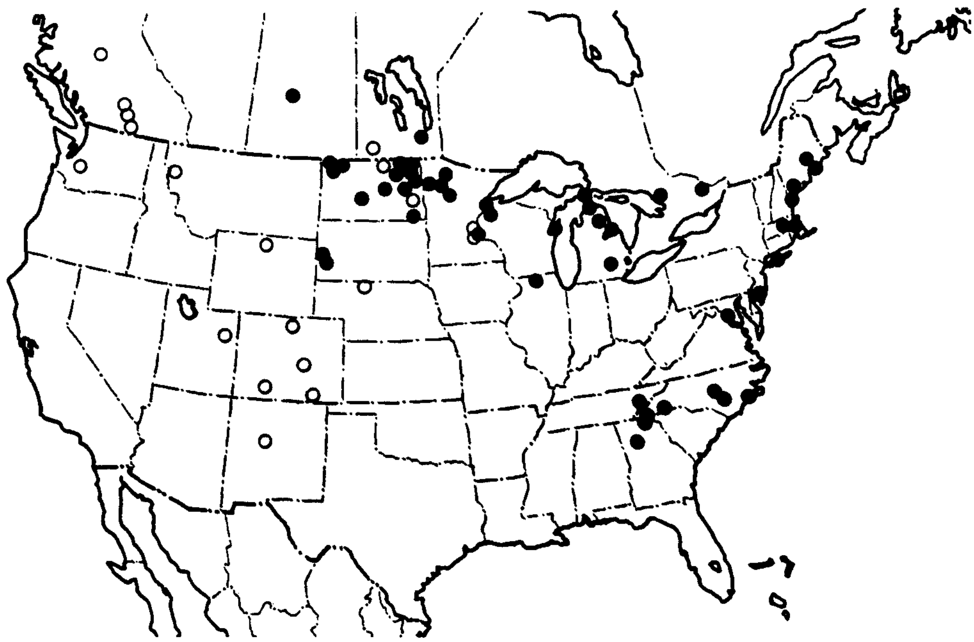
* Unit of measurement is 10^{-2} mm. Not over 2 specimens of a caste (usually 1) measured from any 1 nest.

ALR = 1.71 (1.66 – 2.20, n = 10).

DISTRIBUTION. The known range extends in a band from Saskatchewan and the Black Hills of South Dakota, east to central Maine and southern New York, with a southern extension into eastern North Carolina and northern Georgia. The 68 sample records are plotted on map 5. Gregg (1963) reported the collection of a sample of *subglaber* from Boulder, Colorado; the caste composition was not stated. This sample may well be referable to *occidentalis.*

VARIATION. Measurement cards were selected randomly, 33 for workers, 16 for queens. Extreme values of one or more measurements or indices were exhibited principally by specimens from Maine, Minnesota, North Dakota, South Dakota, and Manitoba. The only other extreme values were one each from Michigan, North Carolina, and Tennessee. The more numerous values of measurements and indices that fell between the extremes were shown by specimens from all of the 16 political divisions of the sample. Significantly greater variability in measurements and indices for both castes at the northeastern and northwestern ends of the range would probably be shown by a more detailed study. Perhaps specimens from the southern tip of the range might also exhibit significantly greater variability in metric characters than specimens from the more central parts of the range.

Queens show considerable variation in several of the conventional characters that exhibit statistical trends geographically. Standing hairs on gula typically number from few to none north and west of southern New York; hairs are typically more numerous from southern New York southward. Occasional specimens reverse this trend. A queen from North



Map. 5. Geographic distribution of *A. subglaber,* solid circles; and *occidentalis,* hollow circles. (See text for further details.)

Dakota, for example, had pilosity on gula like that of typical southern specimens. Pubescence on gaster of both female castes typically ranges from moderately dense to very dense north and west of southern New York, while specimens from southern New York and in the southern extension of the range typically have pubescence on gaster moderate to extremely dilute. Pubescence on head, although more constant than that on gaster, is typically more dense north and west of southern New York than for specimens collected farther south. Body color is quite variable. Queens with a fairly deep brown color were seen from Ontario, Wisconsin, Minnesota, North Dakota, North Carolina, and New York. Some of these specimens showed a reddish cast, others a yellowish cast in the lighter areas. Specimens that were lighter brown in color, some with a reddish and some with a yellowish cast, were seen from Georgia, New York, Maine, and Manitoba. Thus, of the 3 characters — pubescence, pilosity and color — pubescence shows the clearest geographic trends, pilosity next, with color a very poor third.

Buren (1942) named *clavigeroides* as a new species closely related to *subglaber.* Buren (1950), treating *clavigeroides* as a subspecies of *subglaber,* used color and pubescence to separate the queens in his key. Creighton (1950) sank *clavigeroides* as a synonym of *subglaber,* basing his decision on both female castes. I must concur with Creighton's action in this matter, since the characters used to separate southern demes from those of the North often show overlap and lack of concordance.

In worker specimens, pilosity and pubescence vary, while color is a fairly constant yellow to yellowish brown. Standing body hairs vary from relatively sparse to moderately numerous. This variation is not clearly associated with the geographic origin of the samples. Pubescence on gaster tends to be moderately dense to dense in northern specimens, and often much more dilute in those from the South. Some specimens, however, show pronounced deviation from this geographic pattern.

One worker of a series collected by R. Sanwald in Medford, Suffolk Co., New York had a 4-segmented maxillary palpus on the left side. The palp on the right side, as well as all palpi of other specimens in the series, were normal.

Males seem to show less variation than queens and workers. Pubescence on the head is quite constant. Pubescence on the gaster tends to be more dilute in the South and denser in the North.

Workers of *subglaber* have been misidentified to various taxa, but especially to *claviger, coloradensis,* and *occidentalis.* The shorter, more delicate standing body hairs, the more abundant pubescence on the head, and the decumbent to suberect pubescence on the antennal scapes separate this taxon from *claviger* and *coloradensis,* and sometimes from *occidentalis.* Some workers of *claviger* and *coloradensis,* more commonly the latter, have suberect pubescence on the scapes, but it is coarser in texture than in *subglaber.* The separation of atypical workers of *subglaber* and *occidentalis* often presents a number of difficulties. The section that follows treats this problem.

SEPARATION OF SUBGLABER AND OCCIDENTALIS. Queens and males of these two species present no significant problems anywhere in their ranges. Use of the keys will separate all queens and presumably all males. Separation of atypical worker specimens is not always possible by the use of the key alone. Inasmuch as the most serious problems of separation occur principally away from the range common to the two species, a measure of character displacement is evident in the worker caste. Even though sympatric collections of these species generally present fewer and less serious problems of separation, some problems do exist. When only the worker caste is available, it is helpful to have fairly good sized series at hand for study. Uniques may on occasion be undeterminable. To assist in separating atypical workers of these two species, some of their differences are given in the following comparative list, together with approximate frequency statements.

1. Standing body hairs, degree of coarseness and number. *Subglaber*: Delicate to very delicate and not especially numerous. Major exceptions are on East Coast, where usual coarseness and greater numbers are common. *Occidentalis*: Usually coarse and fairly numerous throughout range.

2. Pubescence on dorsum of gaster. *Subglaber*: Usually dense to very dense and short on center of first tergite, and not thinning out

significantly before third tergite. In many eastern specimens, dilute to moderate on first tergite and often thinning out more quickly. *Occidentalis*: Usually dense to moderate and longer on first tergite, and beginning to thin out a little on second tergite.

3. Pubescence on antennal scapes. *Subglaber*: Usually strongly suberect to decumbent, very rarely appressed. *Occidentalis*: Often appressed to decumbent, less commonly suberect.

4. Standing hairs on fore femora, number and length. *Subglaber*: Hairs usually numbering 0 to 3, but up to 7 in some eastern specimens. Length usually 0.03 to 0.05 mm, but as long as 0.06 mm, or a little more, mostly in eastern specimens. *Occidentalis*: Hairs usually numbering 5 to 8, but a few as low as 3 or 4 in some southwestern specimens. Length almost always 0.06 to 0.09 mm.

5. Standing hairs on gula, number, distribution and length of longer hairs. *Subglaber*: Number variable and without distribution pattern, often none present. Length usually well under 0.10 mm, but a few at or a little more than 0.10 mm. *Occidentalis*: Number somewhat variable, but often with a pattern of 3 longer hairs more or less symmetrically placed on each side of gula. Length almost always 0.10 mm or more.

6. Standing hairs on front of head between clypeus and vertex as seen in side view, number and length of longer hairs. *Subglaber*: Generally none to very few. Length almost always 0.06 mm or less, often only 0.02 or 0.03 mm, but as long as 0.08 mm in a few specimens, mostly eastern. *Occidentalis*: Few to many. Length almost always 0.06 to 0.09 mm.

7. Standing hairs on pronotum, length of longer hairs. *Subglaber*: Length usually 0.11 mm or less, but a very few may measure up to 0.13 or 0.14 mm anywhere in range. *Occidentalis*: Length usually 0.13 mm or more, some as long as 0.20 mm, but a very few may be as short as 0.11 or 0.12 mm anywhere in range.

8. Propodeum, shape of dorsum in side view. *Subglaber*: Usually convex, often distinctly so. *Occidentalis*: Usually more flattened, but sometimes weakly convex.

9. Crest of petiolar scale in anterior view. *Subglaber*: Usually straight or weakly emarginate, very rarely with pronounced emargination, a few convex. *Occidentalis*: Weakly to distinctly emarginate, rarely straight, and almost never convex.

10. Crest of petiolar scale in side view. *Subglaber*: Almost always moderately blunt, rarely fairly sharp. *Occidentalis*: Usually sharp to moderate, a few moderately blunt.

11. Height of erect petiolar scale with respect to propodeal spiracle. *Subglaber*: Crest usually at or below level of spiracle, but in a few cases, mostly eastern specimens, above it. *Occidentalis*: Crest usually at, above, or well above level of spiracle, very few below it.

12. Posterior border of head, shape in perfect full-face view. *Sub-*

glaber: Almost always straight throughout range. *Occidentalis*: Some specimens weakly to distinctly emarginate, others straight.

13. Measurements and indices of various parts of body. See tables 27–32.

14. Regression of SL on HW for workers. See figure 131 and table 19. *Subglaber*: Most specimens fall on or below the line, SL = 0.962(HW) — 0.181. *Occidentalis*: Most specimens fall above this line.

ECOLOGY. **Habitat.** Field notes were available for 15 samples that I had collected in Maine, Minnesota, and North Carolina. in addition, 6 of the samples sent to me for study had associated biological data. The summary below includes the data on these 21 samples plus some notes from the literature, where identity of species could be verified. The sample of workers from Morehead City, Carteret Co., North Carolina, reported by Carter (1962b) as *claviger*, is *subglaber*. About ⅔ of the colonies were collected in woods or in small clearings in woods; the rest were found nesting in the open. Stones formed the immediate cover for nearly ½ of the nests, with low but often sizable mounds accounting for about ¼ of the colonies. The rest were found nesting in soil associated with stumps, logs, roots, etc. Perhaps the most unusual nest was one located west of Old Town, Maine in an open area overgrown by *Crataegus* bushes. I found this populous colony nesting in an abandoned *Formica exsectoides* mound. These mounds

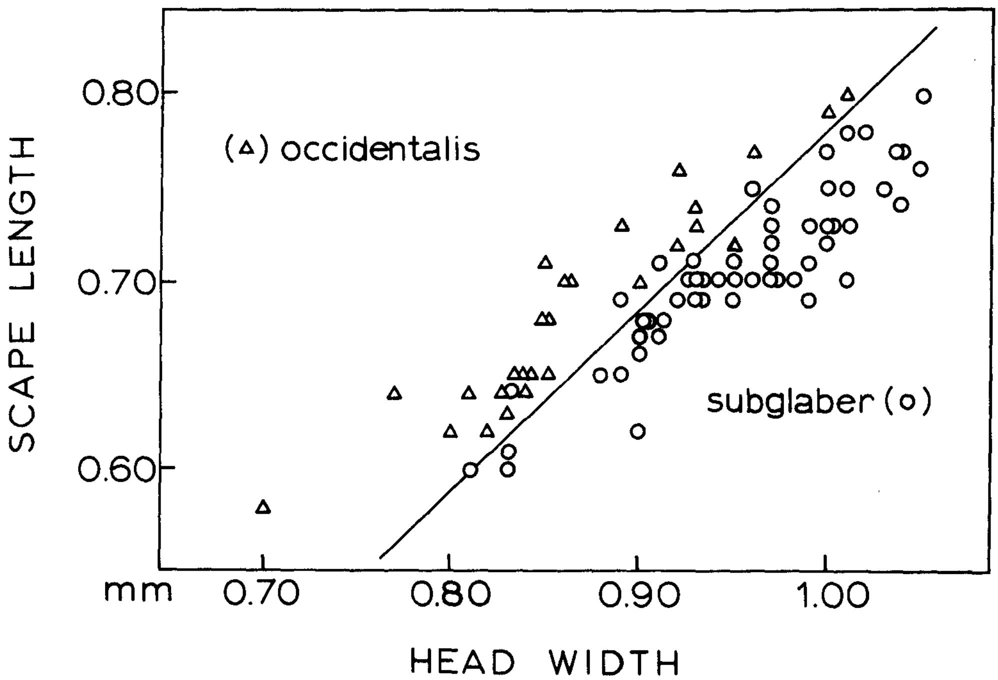


Fig. 131. Sample regressions of scape length on head width and critical dividing line for workers of *A. occidentalis* (N = 27) and *subglaber* (N = 54). Not over 2 workers measured per nest series, usually only 1. (See text for further discussion.)

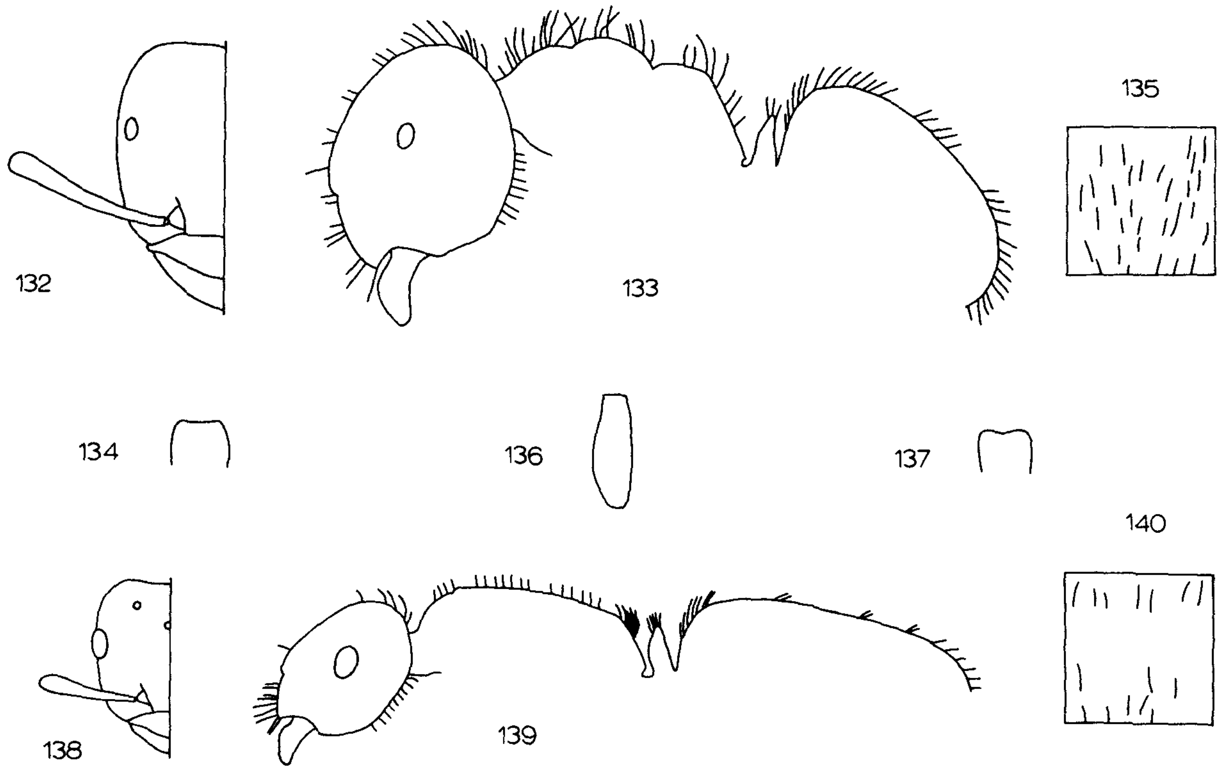
Table 19. **Critical values for 30 pairs of SL and HW in workers of *subglaber* and *occidentalis* based on the relationship, SL = 0.962(HW) − 0.181 ***

HW	SL	HW	SL
0.75	0.54	0.90	0.69
.76	.55	.91	.69
.77	.56	.92	.70
.78	.57	.93	.71
.79	.58	.94	.72
.80	.59	.95	.73
.81	.60	.96	.74
.82	.61	.97	.75
.83	.62	.98	.76
.84	.63	.99	.77
.85	.64	1.00	.78
.86	.65	1.01	.79
.87	.66	1.02	.80
.88	.67	1.03	.81
.89	.68	1.04	.82

* SL computed and rounded for each given value of HW. Errors of determination by the use of this table for the 81 random singles plotted in fig. 131 were: *subglaber* (N = 54), 4; *occidentalis* (N = 27), 1. Measurements in mm. See text for further discussion.

were common in the area, but all that I checked other than the nest in question were populated by *exsectoides*. The *subglaber* colony occupied the approximate half of the nest that faced southeast, and the rest of the mound was totally unoccupied. The chambers and galleries dug or reconstructed by the *subglaber* workers extended well into the ground. Several other *subglaber* nests in the immediate area were situated in the shade of an overhanging bank; all but one of these nests were covered by stones. The 21 samples of *subgaber* from throughout the range appeared to show no more than random association between the type of immediate nest-cover and whether the nests were in woods or in the open. Kannowski (1956) gives notes on a nest that he collected on the North Dakota prairie. The altitudinal range for the *subglaber* samples was from about sea level to 5000 feet. Most nests were collected at low altitudes, usually well under 1000 to 1100 feet. However, some of the few collections from the Black Hills of South Dakota, western North Carolina, eastern Tennessee, and northern Georgia ranged up to about 5000 feet.

Alate dates. Dated samples with one or both sexual forms numbered 25. Several colonies with queen pupae or callows were found in the last half of July. Adult alates associated with workers had the extreme dates of July 28 and September 7. Dates for alate queens not associated with workers ranged from August 1 to September 21. A single dealate queen was found overwintering under trash in woods in Sampson Co., North Carolina on November 22, 1954. Wheeler (1908) reported nuptial flights on July 23, but the only MCZ specimens that I have seen bear the date of July 28. In either case these flights



Figs. 132–140. A. subglaber. WORKERS (25×): 132, head; 133, body profile; 134, petiolar scale; 135, pubescence (50×). QUEENS (12.5×): 136, fore femur; 137, petiolar scale; 138, head; 139, body profile; 140, pubescence (50×). (For details, see p. 17 and fig. 8.)

were probably somewhat earlier than is usual for this species in most years. The 25 samples indicate that flights usually begin in early August and perhaps extend into September in some years.

Colony founding. Virtually nothing is known about this taxon. One literature reference, which is something of an enigma, gives evidence for polygyny in *subglaber, latipes,* or *latipes* × *claviger.* Gaige (1916) reported the collection on June 13, 1914 of a small *latipes* colony on Whitefish Point, Chippewa Co., Michigan. He stated that the colony contained about 50 workers and 2 dealate queens. The nest was beneath the bark on the underside of a rotten log. The only specimens that I received for study from this sample were 3 workers belonging to *subglaber.* The identity of the queens remains uncertain. If they were actually *latipes* or *latipes* × *claviger,* this would account for the sample determination of *latipes.* Either of the two queens then considered to be dimorphs of *latipes* are so distinct that a mistake could hardly be made in their determination. Once Gaige had seen the queens, he probably gave the workers a cursory glance at most. In making routine determinations of samples, many of us are often guilty of depending solely on distinctive queens — an excellent way, of course, to miss recognizing mixed colonies. Whatever the identity of the queens, polygyny is indicated. If, however, the queens were not *subglaber,* then workers all or partly referable to *subglaber* would suggest a mixed colony with *subglaber* as the host species.

9a. *Acanthomyops subglaber* × *plumopilosus* hybrid

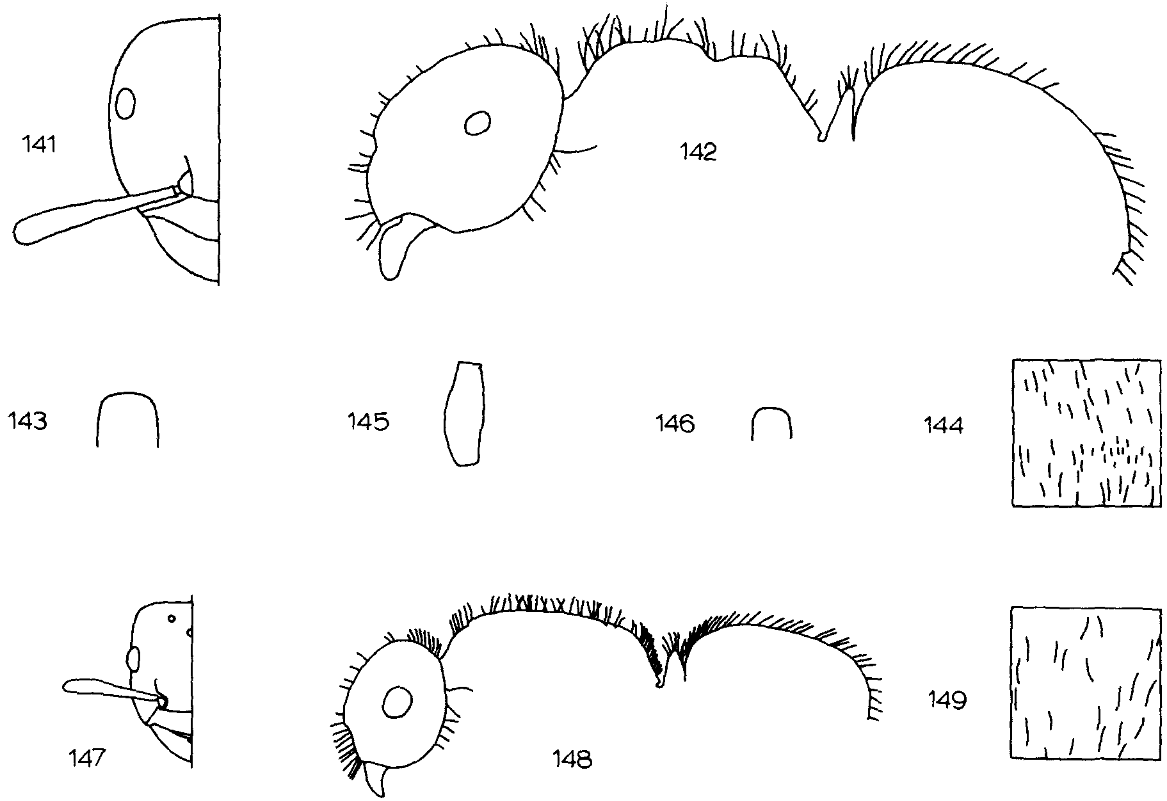
Previously undescribed.
Digm locality: Selden, Suffolk Co., New York.
Location of digms: A queen and 2 workers in the MCZ.

DIAGNOSIS. **Queen.** Resembles a small *subglaber* specimen with exceptionally low HW. Standing body hairs strongly barbulate, coarser, and a little more numerous than in *subglaber.* Dorsum of gaster with pilosity somewhat irregularly distributed, but chiefly confined to posterior edges of tergites. **Worker.** Similar to *subglaber* in general appearance and size, but with standing body hairs much coarser, strongly barbulate, and pubescence on antennal scapes conspicuously suberect. **Male.** Unknown.

Table 20 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 141–149 give standardized illustrations. Figure 11 gives a sample regression of HL on HW for the queens of this hybrid taxon and its parent species.

ALR = 1.62(1.54 — 1.69, n = 2).

FURTHER DESCRIPTION. **Queen.** Antennal scapes with pubescence loosely appressed to decumbent. Body and appendages with moderately dense pubescence except on posterior dorsum of gaster where it is fairly dilute. Crest of petiolar scale moderately blunt, not emarginate. Color brown, more or less like that of darker *claviger* queens. **Worker.** Crest of petiolar



Figs. 141–149. A. subglaber × *plumopilosus.* WORKERS (25×): 141, head; 142, body profile; 143, petiolar scale; 144, pubescence (50×). QUEENS (12.5×): 145, fore femur; 146, petiolar scale; 147, head; 148, body profile; 149, pubescence (50×). (For details, see p. 17 and fig. 8.)

Table 20. **Sample statistics for *A. subglaber* × *plumopilosus*: mean, standard deviation, and 3 standard deviation limits** *

Variate	$\bar{X}$	S.D.	3 S.D. limits
		Workers (N = 3)	
SL	68.33	3.21	58.70– 77.96
HW	93.33	1.53	88.74– 97.92
HL	96.00	1.73	90.81–101.19
AL	119.67	3.06	110.49–128.85
CI	97.33	.58	95.59– 99.07
SI	73.33	2.31	66.40– 80.26
		Queens (N = 2)	
SL	74.50	2.12	68.14– 80.86
HW	112.00	1.41	107.77–116.23
HL	113.50	2.12	107.14–119.86
AL	193.50	6.36	174.42–212.58
FL	86.00	1.41	81.77– 90.23
FW	32.00	0	32.00– 32.00
CI	98.50	.71	96.37–100.63
SI	66.50	.71	64.37– 68.63
FI	37.50	.71	35.37– 39.63

* Unit of measurement is 10^{-2} mm. All queens and workers measured from 1 nest.

scale moderate, often faintly emarginate. Pubescence moderate to moderately dense over most of body and appendages, but that on posterior dorsum of gaster dilute. Color yellow to brownish yellow.

DISCUSSION. I received a single sample collected by R. Sanwald in Selden, Suffolk Co., New York, August 1961, in sandy area. The vial contained 2 dealate queens, 6 workers and 2 detached wings. Flights may occur sometime during August.

10. *Acanthomyops plumopilosus*

Lasius (*Acanthomyops*) *plumopilosus* Buren, 1941: queen, p. 231; worker and male, p. 232; fig. 1.

Type locality: Backbone State Park, Delaware Co., Iowa.

Location of types: Holotype female, USNM: paratypes in several collections including the MCZ.

DIAGNOSIS. The distally plumose hairs and small body size of all castes make recognition of this species straightforward.

Table 21 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 150–158 give standardized illustrations. In the treatment of interspecific hybrids, a sample regression (fig. 11) involves *plumopilosus*. ALR = 1.44(1.39 — 1.48, n = 3).

FURTHER DESCRIPTION. **Queen.** Standing body hairs numerous, mostly with strongly plumose tips. Pubescence moderately sparse, body shining. Body color brown, legs lighter. **Worker.** Standing body hairs fairly numerous, many with moderately plumose tips. Pubescence more or less sparse, body shining. Body and appendages yellow to brownish yellow. **Male.** Standing body hairs moderate to sparse, a few of which have weakly

Table 21. **Sample statistics for *A. plumopilosus*: mean, standard deviation, and 3 standard deviation limits***

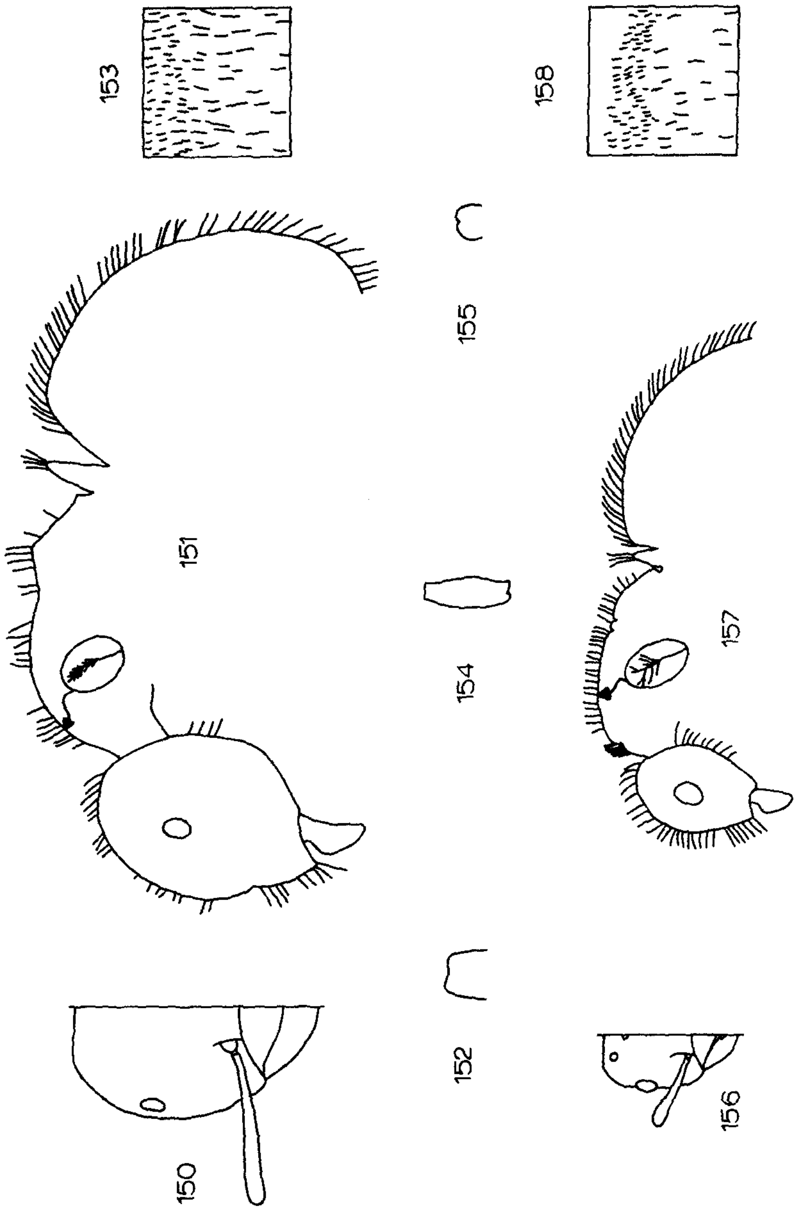
Variate	$\bar{X}$	S.D.	3 S.D. limits
		Workers (N = 6)	
SL	64.83	3.13	55.44- 74.22
HW	89.67	4.08	77.43-101.91
HL	92.50	3.02	83.44-101.56
AL	114.00	5.22	98.34-129.66
CI	97.00	1.79	91.63-102.37
SI	72.17	2.14	65.75- 78.59
		Queens (N = 3)	
SL	66.00	2.65	58.05- 73.95
HW	96.00	2.65	88.05-103.95
HL	96.33	2.08	90.09-102.57
AL	163.67	6.66	143.69-183.65
FL	74.00	3.00	65.00- 83.00
FW	25.33	1.15	21.88- 28.78
CI	99.67	.58	97.93-101.41
SI	68.67	1.53	64.08- 73.26
FI	34.33	2.52	26.77- 41.89

* Unit of measurement is 10^{-2} mm. Not over 2 specimens of a caste (usually 1) measured from any 1 nest.

plumose tips and are confined chiefly to occiput and dorsum of alitrunk. Pubescence sparser than in the female castes, cuticle finely sculptured, body surface only moderately shining. Body color very dark brown, almost black.

DISTRIBUTION. Four collections from the type locality, Backbone State Park, Iowa, are: Sept. 13, 1940, W. F. Buren; June 23, 1941, W. F. Buren; Sept. 14, 1941, W. F. Buren; and 5 mi. E. Lamont, August 22, 1952, R. Gregg, log, stage 3, basswood-maple forest. Other collections are: Winterset, Madison Co., Iowa, June 27, 1941, W. F. Buren. Ann Arbor, Washtenaw Co., Michigan, May 6, 1914, F. M. Gaige, No. 137. Pequot, Crow Wing Co., Minn., July 8, 1940, W. F. Buren. China Grove, Rowan Co., North Carolina, W. G. Carter, No. 23, August 1960, in rotten stump (reported as *claviger* by Carter, 1962b). The overall distribution of this species is notably patchy; judging from the typical distribution pattern of very rare species, it is probably strongly clumped locally.

VARIATION. There are few differences among the available samples, with 1 exception. The homogeneous sample of 6 workers from Pequot, Minnesota requires special comment. Notable among its differences is that the pilosity is very weakly plumose to strongly barbulate. The distribution of these weakly plumose hairs is typical of normal workers, *i.e.*, especially numerous on the occiput and alitrunk. The pubescence on the gaster is notably denser than in normal workers. Measurements (in mm) and indices for 1 variant worker are: SL, 0.65; HW, 0.86; HL, 0.90; AL, 1.10; CI, 96; and SI, 76. HW, HL, and AL are in the low end of the *plumopilosus* range; SL and CI are in the midrange; and SI is well out of the range; without its inclusion, the SI range for



Figs. 150–158. A. plumopilosus. WORKERS (25×): 150, head; 151, body profile; 152, petiolar scale; 153, pubescence (50×). QUEENS (12.5×): 154, fore femur; 155, petiolar scale; 156, head; 157, body profile; 158, pubescence (50×). (For details, see p. 17 and fig. 8.)

plumopilosus would be 70–73.

This variant sample was referred to *plumopilosus* with some uncertainty. The available evidence makes it difficult to determine with much assurance whether it represents a hybrid. If a hybrid, the other parent may be *occidentalis*. The reasons for this conjecture are as follows: *occidentalis* is the only species known or likely to occur in the general area that has the proper combination of flight dates and other characteristics to make it a candidate. Comparison of regressions for SL/HW, AL/SI, and AL/CI clearly eliminate *subglaber*. Structure of the petiolar scale of the variant specimens make it improbable that *murphyi* is one parent species. The process of elimination leaves *occidentalis*, which meets expectation in several ways, including density of pubescence on gaster and shape of petiolar scale.

ECOLOGY. **Habitat.** The type nest was under a stone on a hillside. Another colony from the type locality was collected from a stage 3 log in a basswood-maple forest. The North Carolina collection was from a rotten stump. Habitat data are unavailable for other samples. **Dates of alates.** Queens and males of the type series were collected on Sept. 13; those from North Carolina were taken sometime during August. Flights may occur during both of these months.

COLONY FOUNDING. Collections of mixed colonies are lacking for *plumopilosus*, yet the small size and peculiar hairs of the queens strongly suggest that they are parasites. These peculiarities may indicate a mode (or modes) of colony founding quite different from those of *latipes* or *murphyi*. Buren (1944) suggested that *plumopilosus* may be a temporary social parasite of *claviger*. If true, this would make it one of the rare social hyperparasites. *Lasius* (*Dendrolasius*) *fuliginosus* (and probably *L.* (*D.*) *spathepus*) parasitizes *L.* (*C.*) *umbratus*, which utilizes *L.* (*L.*) *niger* and relatives as its host. Few myrmecologists have seemed inclined to accept Buren's view in this matter. The rarity of this species makes it unlikely that his hypothesis will soon be tested. By virtue of their small size alone, *plumopilosus* queens would have to depend heavily on conciliation. Although conciliation doubtless plays a role in the adoption of *latipes* queens, their great size relative to the host worker, plus their heavy armor, may make it ancillary.

The extreme rarity of *plumopilosus* suggests that Wilson's (1963) comments on social modifications related to rareness may well apply to this species. It seems likely that *plumopilosus* colonies may contain multiple queens; perhaps colonies are founded by two or more queens working together.

11. *Acanthomyops bureni* n. sp.

Type locality: Comstock, Barron Co., Wisconsin.

Location of types: Holotype queen, paratype queen, 2 paratype males, and 4 paratype workers in the MCZ. Paratypes, 2 of each caste, in both the USNM and Cornell Collections. Rest of the type series in the W. F. Buren Collection.

DIAGNOSIS. **Queen.** *Lasius*-like in appearance; closely related to *pubescens.* Crest of erect petiolar scale on level with propodeal spiracles, sharp to moderately sharp, broadly and distinctly emarginate; sides more or less straight and diverging dorsally. Standing body hairs moderate in number and length, those on dorsum of gaster largely confined to posterior edges of tergites beyond first. Standing hairs on crest and sides of scale numbering 10 or more, with a maximum length 0.16 mm or more; those on gula numbering 8 or more, their maximum length 0.20 mm or greater, those on fore femur numbering about 8, with a maximum length 0.10 mm or more. Alitrunk with longer standing hairs measuring 0.28 mm or more. Antennae very slightly clavate, SI 70-73. Body size moderate, HW 1.20 mm or more. Pubescence on dorsum of gaster dense, its surface dull. Body color deep castaneous brown, appendages a little lighter. **Worker.** *Lasius*-like, similar to *pubescens,* but SI 81 or less. Crest of petiolar scale about on a level with propodeal spiracles; sharp to moderately sharp, rarely blunt; emarginate. Longer standing hairs on gula usually measuring at least 0.12 mm, those on crest of scale usually numbering 4 to 6 or more. Pubescence dense and short on dorsum of gaster, dilute to moderate and longer on gula. **Male.** Crest of petiolar scale sharp to moderately sharp, weakly and broadly emarginate. In profile, scale is approximately an equilateral triangle. A few of the longer hairs at the posterior tip of the gaster 0.20 mm or a little longer. Standing hairs on gula not exceeding 0.12 mm. Pubescence on dorsum of gaster short, dense, that on most of the rest of the body dense to moderately dense, but scutellum nearly free of pubescence, shining. Body color dark brown, appendages a little lighter, head black.

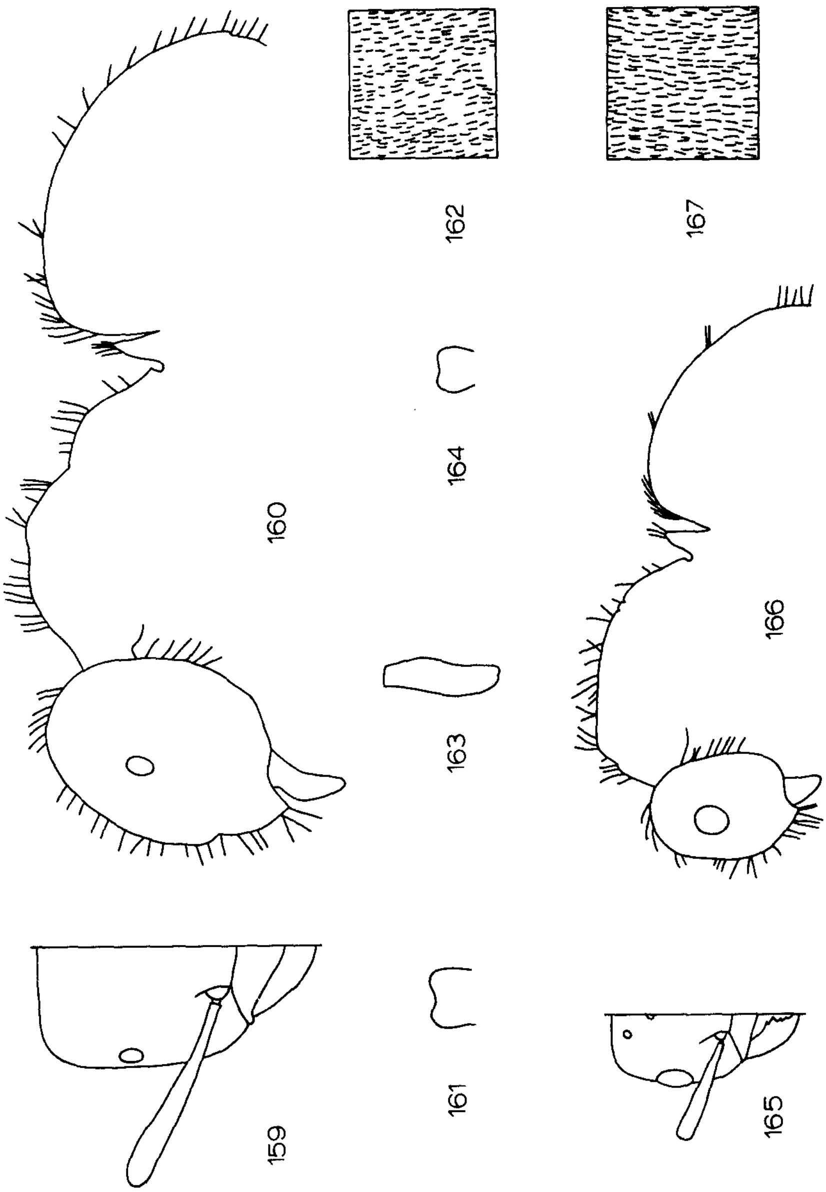
Table 22 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 159–167 give standardized illustrations. ALR $= 1.60(1.41 - 1.77, n = 3)$.

FURTHER DESCRIPTION. **Queen.** Pubescence on head moderately dense. Dorsum of alitrunk and declivitous face of propodeum below spiracles glabrous. **Worker.** Most of body quite pubescent, but dorsum of alitrunk relatively free of pubescence, shining. Color brown to yellowish brown.

DISTRIBUTION. Known only from the types collected by W. F. Buren on August 16, 1941 at Comstock, Barron Co., Wisconsin. The type series is composed of 20 queens, 39 males, and 60 workers.

This species is named for the collector, Dr. W. F. Buren, U.S. Department of Health, Education and Welfare, Bethesda, Md.

VARIATION. The 6 workers measured from the 1 nest exhibit a fair range for some metric characters; little variation is evident in nonmetric characters. One of the larger workers had the petiolar scale crest rather



Figs. 159–167. A. bureni. WORKERS (25×): 159, head; 160, body profile; 161, petiolar scale; 162, pubescence (50×). QUEENS (12.5×): 163, fore femur; 164, petiolar scale; 165, head; 166, body profile; 167, pubescence (50×). (For details, see p. 17 and fig. 8.)

Table 22. **Sample statistics for *A. bureni:* mean, standard deviation, and 3 standard deviation limits** *

Variate	$\bar{x}$	S.D.	3 S.D. limits
	Workers (N = 6)		
SL	80.50	5.32	64.54– 96.46
HW	101.00	6.07	82.79–119.21
HL	104.00	7.13	82.61–125.39
AL	130.83	9.33	102.84–158.82
CI	97.00	1.26	93.22–100.78
SI	79.50	1.64	74.58– 84.42
	Queens (N = 3)		
SL	89.67	1.53	85.08– 94.26
HW	125.67	4.04	113.55–137.79
HL	125.00	4.36	111.92–138.08
AL	209.00	7.81	185.57–232.43
FL	98.33	3.79	86.96–109.70
FW	29.67	2.31	22.74– 36.60
CI	100.67	.58	98.93–102.41
SI	71.33	1.53	66.74– 75.92
FI	30.33	1.15	26.88– 33.78

* Unit of measurement is 10^{-2} mm. All queens and workers measured from type series.

blunt and somewhat below the level of the propodeal spiracles. Simultaneous variation of several diagnostic characters in 1 specimen might make separation from *pubescens* rather difficult. The queens, however, differ in enough characters to pose few problems of identification.

ECOLOGY. No data other than that cited above.

12. *Acanthomyops pubescens*

Lasius (*Acanthomyops*) *pubescens* Buren, 1942: worker and female, p. 405.

Type locality: Jenkins, Crow Wing Co., Minnesota.

Location of types: Holotype queen in the W. F. Buren Collection; paratypes in the collections of the MCZ, USNM and Iowa State College.

DIAGNOSIS. **Queen.** *Lasius*-like, similar to *bureni.* Crest of erect petiolar scale below level of prodpodeal spiracle, blunt to very blunt, without emargination; sides slightly convex. Standing body hairs less numerous and shorter than in *bureni.* Standing hairs on crest and sides of scale and on gula each numbering 6 or less, with a maximum length not over 0.12 mm; those on fore femur numbering about 6, with a maximum length not over 0.08 mm. Alitrunk with longer standing hairs measuring 0.20 mm or less. Antennal scapes longer, SI 77–78. Body size smaller, HW 1.10 mm or less. Pubescence on dorsum of gaster very dense. Body color deep grayish brown, appendages lighter. **Worker.** *Lasius*-like, similar to *bureni,* but SI 83 or more. Erect petiolar scale with crest below level of propodeal spiracles; blunt, not emarginate. Standing hairs on gula measuring 0.10 mm or less, those on crest of scale usually numbering 2, one on each corner. Pubescence short, dense over most of body. **Male.** Unknown.

Table 23. **Sample statistics *for A. pubescens:* mean, standard deviation, and 3 standard deviation limits ***

Variate	X̄	S.D.	3 S.D. limits
	Workers (N = 8)		
SL	79.75	1.98	73.81– 85.69
HW	95.38	2.83	86.89–103.87
HL	98.00	3.30	88.10–107.90
AL	123.50	4.00	111.50–135.50
CI	97.38	1.41	93.15–101.61
SI	83.75	.89	81.08– 86.42
	Queens (N = 2)		
SL	84.00	1.41	79.77– 88.23
HW	108.50	2.12	102.14–114.86
HL	107.50	2.12	101.14–113.86
AL	185.50	.71	183.37–187.63
FL	87.50	.71	85.37– 89.63
FW	24.50	.71	22.37– 26.63
CI	101.00	0	101.00–101.00
SI	77.50	.71	75.37– 79.63
FI	28.00	1.41	23.77– 32.23

* Unit of measurement 10^{-2} mm. Queens and 4 workers measured from type series; other 4 workers measured from only other known nest.

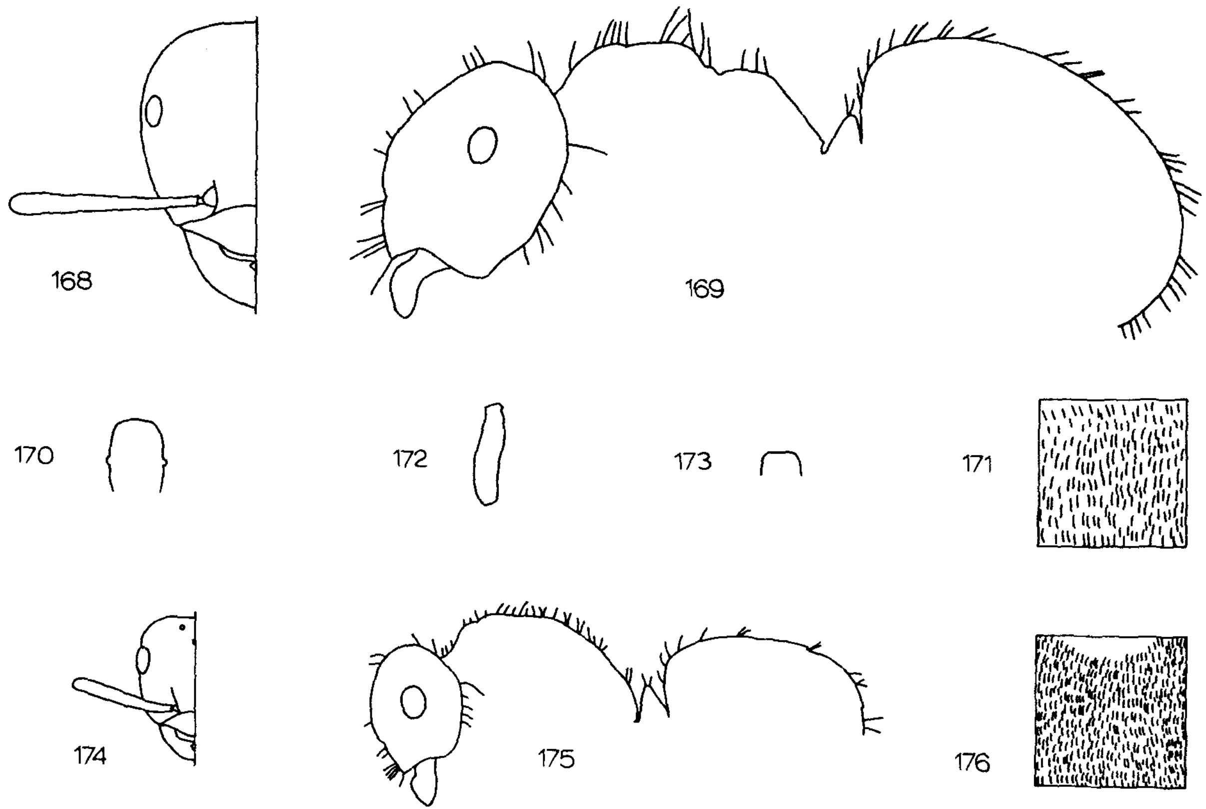
Table 23 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 168–176 give standardized illustrations. ALR = 1.50(1.42 – 1.59, n = 2).

FURTHER DESCRIPTION. **Queen.** Pubescence denser on gaster than elsewhere on body, fairly sparse on alitrunk. Declivitous face of propodeum below spiracles highly glabrous. **Worker.** Averaging and ranging smaller than *bureni.* Color yellow to brownish yellow.

DISTRIBUTION. Only 2 nest samples of this species are known to have been collected. I collected one of them near McGrath, Aitkin Co., Minnesota on August 29, 1950. It was a populous colony in a low mound in open woods. At the time of the collection I saw a dealate queen go into the aspirator along with the series of workers, but she was apparently lost in transferring the sample to alcohol. The type series was collected by W. F. Buren on August 11, 1941, near Jenkins, Crow Wing Co., Minnesota. This colony also was nesting in a sandy, low mound in open woods.

VARIATION. The 2 queens of the type series available to me for study were measured, as were 4 workers from each nest series. The queens showed almost no variation, the workers very little in either metric or conventional characters.

ECOLOGY. **Habitat.** That this species was nesting in a low mound in open woods in both cases is the only available data. **Alate dates.** The Buren nest series had only 4 queens and no males. He took this to indicate that all major flight activity had occurred before the collection date, August 11, 1941.



Figs. 168–176. A. pubescens. WORKERS (25×): 168, head; 169, body profile; 170, petiolar scale; 171, pubescence (50×). QUEENS (12.5×): 172, fore femur; 173, petiolar scale; 174, head 175, body profile; 176, pubescence (50×). (For details, see p. 17 and fig. 8.)

13. ***Acanthomyops creightoni* n. sp.**

Type locality: Warner Ranger Station, La Sal Mts., Moab, Grand Co., Utah.

Location of types: Holotype female, 2 paratype females, 3 paratype males, and 3 paratype workers in the MCZ.

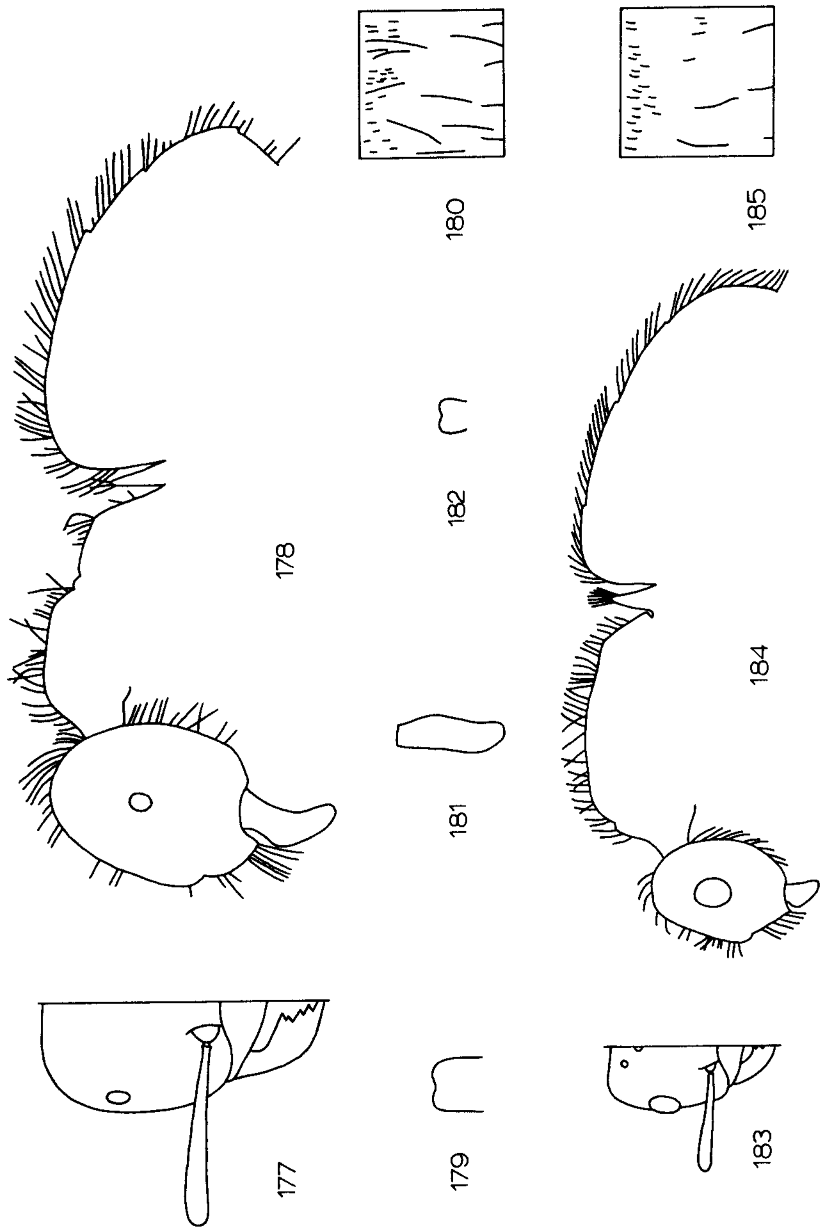
DIAGNOSIS. **Queen.** Distinct from all other known species of *Acanthomyops*. Body pilosity fairly dense, simple to finely barbulate, delicate, whitish to silvery in appearance. Pubescence dilute to moderately dense, also whitish to silvery, much of it unusually long, loosely appressed to suberect, conspicuous on antennal scapes, gula, and gaster. Antennae slender. Crest of petiolar scale moderately sharp, shallowly emarginate; sides straight, converging slightly dorsally. Color light brownish yellow, appendages lighter, body shining. **Worker.** Pilosity and pubescence similar to that of queen, but somewhat less dense. Antennae slender. Crest of petiolar scale broadly and shallowly emarginate, sides more or less straight. Color pale yellow, body shining. **Male.** Pilosity and pubescence as in queen, but considerably less dense. Longer hairs at posterior tip of gaster 0.20 mm or more. Crest of petiolar scale moderately sharp to sharp, feebly and broadly emarginate. Antennae slender, SI 70 or greater. HW 0.85 mm or less, CI less than 105. Scutum and scutellum finely sculptured, largely free of pubescence. Color light brown, head darker, appendages lighter, body somewhat shining.

Table 24 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 177–185 give standardized illustrations. ALR = 1.53(1.34 – 1.72, n = 3).

Table 24. **Sample statistics for *A. creightoni:* mean, standard deviation, and 3 standard deviation limits ***

Variate	$\bar{X}$	S.D.	3 S.D. limits
	Workers (N = 3)		
SL	79.00	1.73	73.81– 84.19
HW	97.33	5.13	81.94–112.72
HL	101.33	5.51	84.80–117.86
AL	131.33	8.08	107.09–155.57
CI	96.00	1.00	93.00– 99.00
SI	81.33	2.52	73.77– 88.89
	Queens (N = 3)		
SL	85.00	2.65	77.05– 92.95
HW	116.67	3.06	107.49–125.85
HL	117.33	3.21	107.70–126.96
AL	200.33	12.50	162.83–237.83
FL	95.00	2.00	89.00–101.00
FW	28.67	2.89	20.00– 37.34
CI	99.33	1.53	94.74–103.92
SI	73.00	1.73	67.81– 78.19
FI	30.33	3.21	20.70– 39.96

* Unit of measurement 10^{-2} mm. All queens and workers measured from type series.



Figs. 177–185. A. creightoni. **WORKERS** (25×): 177, head; 178, body profile; 179, petiolar scale; 180, pubescence (50×). **QUEENS** (12.5×): 181, fore femur; 182, petiolar scale; 183, head; 184, body profile; 185, pubescence (50×). (For details, see p. 17 and fig. 8.)

This species is named for the collector, Dr. W. S. Creighton, Emeritus Professor of Biology, City College of New York.

DISCUSSION. Known only from the types. Professor Creighton's collection located in the MCZ consisted of 3 specimens of each caste. The date on the specimens was July 1933. Wilson (1955) cites a collection of *Lasius fallax* made by Creighton at the Warner Ranger Station, Moab, Utah, on July 19, 1933. Because he collected over a wide area during the summer of 1933, it is likely that *A. creightoni* was taken on or near July 19. Little variation is evident in either metric or conventional characters. The only ecological data is that the Warner Ranger Station is at an altitude of about 4000 feet. Nuptial flights may not have started at the time of collection, since all 3 castes were in the nest; flights may occur sometime in late July or early August.

14. *Acanthomyops occidentalis*

Lasius (Acanthomyops) occidentalis Wheeler, 1909a: worker, queen and male, p. 83.

Type locality: Colorado Springs, El Paso Co., Colorado.

Location of types: Syntypes in the MCZ.

DIAGNOSIS. **Queen.** With rare exceptions this is the only taxon that has the posterior border of the head broadly and distinctly emarginate as seen in full-face view. Antennal scapes short, their tips reaching to a little beyond the posterior margins of the eyes. Scapes and funiculi only slightly clavate. Crest of petiolar scale sharp to moderately sharp; usually emarginate, often deeply so. Scale with sides straight, its width about equal to height from spiracle to crest. Body and appendages with pubescence moderately dense to dense. Scutellum with central area free of pubescence. CI 98 or less. **Worker.** Body size and eyes small; similar in appearance to some *subglaber* and most *mexicanus* specimens. Standing body hairs not delicate; posterior border of head as seen in full-face view feebly emarginate in some specimens. Pubescence moderate to dense and fairly short. Crest of petiolar scale sharp to moderate, usually emarginate. Crest of erect scale at or above level of propodeal spiracles. Sides of scale usually more or less straight and parallel. Propodeum in profile more or less straight, rarely convex. See treatment of *subglaber* for further diagnosis of these two closely related taxa. **Male.** Small, AL 1.05 — 1.30 mm, SL under 0.60 mm. Crest of petiolar scale sharp to moderately sharp, emarginate to straight, and with a row of flexed hairs. Width of scale about equal to its height above petiolar spiracles. Scutellum with pubescence absent centrally. Longer hairs at posterior tip of gaster less than 0.20 mm, often 0.15 mm or less.

Table 25 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 186–194 give standardized illustrations. Fig. 131, in the treatment of *subglaber,* gives sample regressions of SL on HW for the workers of *occidentalis* and *subglaber.* ALR $\doteq$ 1.86(1.78 — 1.95, n = 4).

Table 25. **Sample statistics for *A. occidentalis:* mean, standard deviation, and 3 standard deviation limits ***

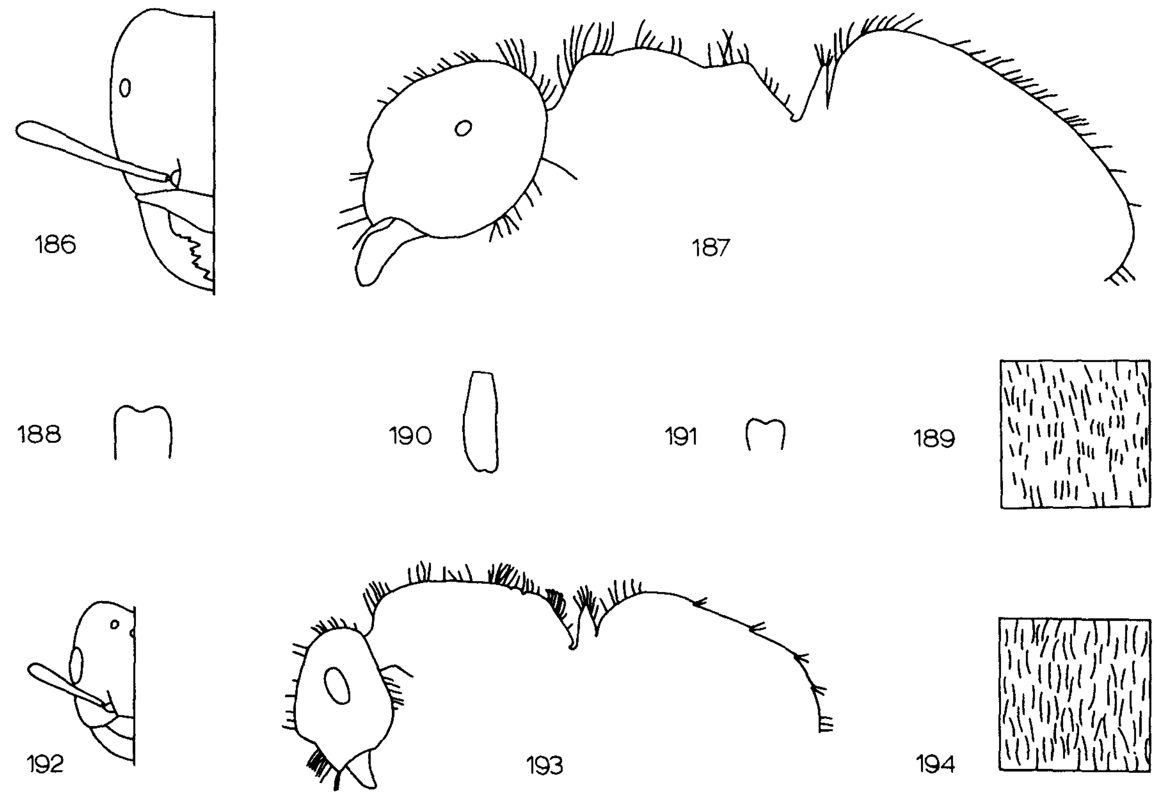
Variate	$\bar{X}$	S.D.	3 S.D. limits
	Workers (N = 27)		
SL	68.67	5.66	51.69– 85.65
HW	86.85	6.88	66.21–107.49
HL	92.93	6.56	73.25–112.61
AL	110.96	10.50	79.46–142.46
CI	93.37	2.44	86.05–100.69
SI	79.04	2.47	71.63– 86.45
	Queens (N = 5)		
SL	73.00	3.08	63.76– 82.24
HW	117.80	2.77	109.49–126.11
HL	124.20	2.77	115.89–132.51
AL	206.40	11.78	171.06–241.74
FL	95.60	3.21	85.97–105.23
FW	36.00	2.92	27.24– 44.76
CI	95.00	1.73	89.81–100.19
SI	62.20	2.59	54.43– 69.97
FI	37.80	2.17	31.29– 44.31

* Unit of measurement is 10^{-2} mm. Not over 2 specimens of a caste (usually 1) measured from any 1 nest.

FURTHER DESCRIPTION. **Queen.** Color yellowish brown. **Worker.** Body and appendages pale yellow to brownish yellow, head often a little darker. **Male.** Pubescence fairly dilute, body shining. Body and appendages brown, head piceous brown.

DISTRIBUTION. British Columbia and Washington east to Manitoba and Minnesota with a southern extension to New Mexico. The 3 samples reported as *claviger* by Buckell (1932) are *occidentalis*. The 34 samples of this sporadic species are plotted on map 5, in the treatment of *subglaber*.

VARIATION. A randomly chosen subsample of 19 workers included 6 with extreme values of 1 or more measurements or indices. Of these 6 extremes, 5 were from Brandon, Manitoba; Towner Co., North Dakota; and Anoka Co., Minnesota. A sixth, a worker with an SI of 84, was from Mineral Co., Colorado. Thus a high proportion of workers with extreme values came from the northeastern part of the range. This suggests that a detailed analysis of variation based on more specimens may well show that the northeastern part of the range has significantly more variable specimens than other parts have. A review of all mounted specimens revealed minor variation in a number of nonmetric characters. These included degree of sharpness and emargination of the crest of the petiolar scale, proportion of suberect pubescence hairs on scapes, and profile of alitrunk. The variation exhibited by these characters was more or less randomly distributed over the range. A hint of a geographic trend is evident, however, in the degree of density of the pubescence, especially on the dorsum of the gaster, in all castes. In all parts of the range the queens are most densely pubescent and males least; the workers are intermediate. Specimens from Washington and British Colum-



Figs. 186–194. A. occidentalis. WORKERS (25×): 186, head; 187, body profile; 188, petiolar scale 189, pubescence (50×). QUEENS (12.5×): 190, fore femur 191, petiolar scale; 192, head; 193, body profile; 194, pubescence (50×). (For details, see p. 17 and fig. 8.)

bia were notably less pubescent than those throughout the rest of the range. Specimens from eastern Minnesota were distinctly more pubescent than typical specimens; all queens and many workers were as densely pubescent as corresponding specimens of *A. pubescens*. The specimens from Albuquerque, New Mexico were densely pubescent, but not as much so as the Minnesota specimens. Further study may establish east–west and north–south trends in this character.

ECOLOGY. **Habitat.** Data associated with specimens are scanty, and very little has been published on this species. The types came from several different nests, all under stones, in or near Colorado Springs, Colorado. The 4 collections I made in Anoka Co., Minesota all came from dry sandy soil. The 2 nests with alates taken in July had very low mounds, but it is by no means certain that mounds would be visible at other than flight time; these nests are discussed below. The other 2 nests were collected from under logs in the early spring. A Nebraska collection was made in sandy soil. A nest sample from Washington and one from Montana were both under stones. A nest sample from British Columbia was taken under a stone on a dry hillside. The altitudinal data available for a few of the 34 samples ranged from a little below 1000 to over 8000 ft. **Alate dates.** Of 13 dated samples containing one or both sexes, only 1 did not include workers. These 12 samples are assumed to represent nest collections. A single queen was collected at light in Fort Collins, Colorado on July 26, 1935. The extreme dates for these collections are July 14 and August 17. The only available biological data on colonies with alates are from my field books. These notes cover 2 colonies collected in Anoka Co., Minnesota on July 21, 1950. The nests were in the middle of a sandy private road with sparse vegetation growing in its center. The workers had opened up the first nest by excavation; many were walking about on the surface of the ground near the nest openings. The collection was made in the early afternoon of a warm day with an overcast sky. Males and workers were collected by digging into the upper few inches of the nest. The second nest was located several yards down the road. All comments made on the first nest apply to this one, except that queens, males, and workers were taken from this nest. Both nests seemed ready to begin flights, awaiting the right combination of environmental conditions. From the meager data at hand it is not possible to delimit the flight period. However, it probably extends from mid-July to mid-August or later.

15. *Acanthomyops mexicanus*

Lasius (*Acanthomyops*) *interjectus* subsp. *mexicanus* Wheeler, 1914: worker and queen, p. 55; male p. 56.
Type locality: Guerrero Mill, State of Hidalgo, Mexico.
Location of types: Syntypes in the MCZ.

DIAGNOSIS. **Queen.** Similar to *occidentalis,* but posterior border of head as seen in full-face view straight or nearly so. Scutellum completely covered with long, dilute pubescence. Width of petiolar scale across spiracles clearly greater than height from spiracle to crest. Crest and sides of scale with fewer standing hairs. Pubescence over dorsum of gaster dilute, thinner on posterior surface than anteriorly. An occasional specimen may have pubescence moderate to moderately dense and more irregularly distributed. In all cases the gaster is at least moderately shiny. CI 100 or more. **Worker.** Closely similar to *occidentalis,* but petiolar scale broader, its width across spiracles clearly greater than height from spiracle to crest. Dorsum of gaster with pubescence dilute to moderate and long, its surface shining. In profile, propodeum usually distinctly convex. Posterior border of head as seen in full-face view straight or nearly so. Crest of petiolar scale usually emarginate, sides often convex. **Male.** Similar to *occidentalis,* but much larger; AL 1.40 mm or more, SL 0.60 mm or more. Scutellum entirely covered with dilute long pubescence. Pilosity at posterior tip of gaster with longer hairs measuring 0.20 mm or more. Petiolar scale broad, crest emarginate.

Table 26 gives selected sample statistics. Tables 27–41 give frequency distributions for measurements and indices. Figures 195–203 give standardized illustrations. ALR = 1.79(1.72 — 1.74, n = 2).

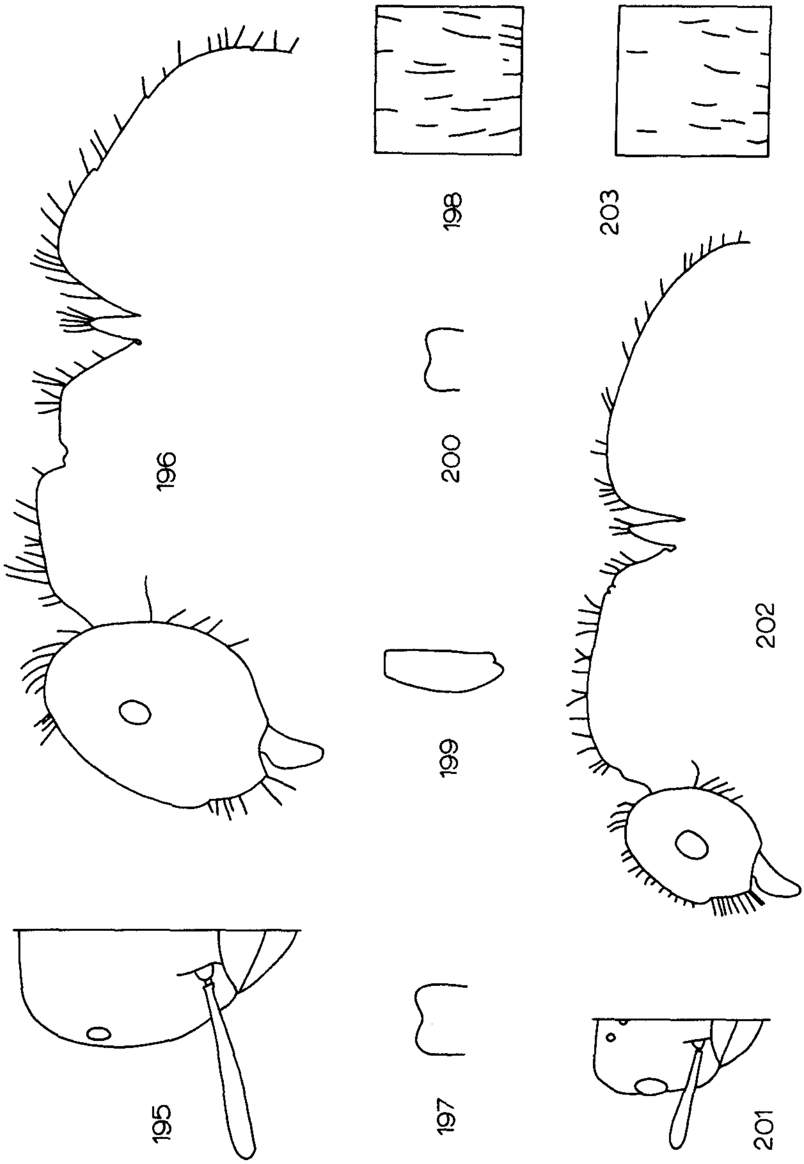
FURTHER DESCRIPTION. **Queen.** Color brown to yellowish brown. **Worker.** Color yellow. **Male.** Pubescence on gaster dilute, surface shining. Body color brown, head darker, appendages lighter.

DISTRIBUTION. In addition to the types collected by W. M. Mann, L. B. Carney collected a single queen 3 mi. W. Pachua, Hidalgo, Mexico, June 16, 1961. L. B. and T. M. Carney collected workers

Table 26. **Sample statistics for A. *mexicanus*: mean, standard deviation, and 3 standard deviation limits ***

Variate	$\bar{X}$	S.D.	3 S.D. limits
	Workers (N = 5)		
SL	77.00	4.06	64.82– 89.18
HW	98.00	5.61	81.17–114.83
HL	105.60	7.77	82.29–128.91
AL	122.40	11.80	87.00–157.80
CI	93.00	1.87	87.39– 98.61
SI	78.60	1.14	75.18– 82.02
	Queens (N = 3)		
SL	80.00	8.19	55.43–104.57
HW	124.67	4.93	109.88–139.46
HL	122.67	5.51	106.14–139.20
AL	218.67	2.31	211.74–225.60
FL	99.00	5.57	82.29–115.71
FW	38.00	2.00	32.00– 44.00
CI	101.67	1.53	97.08–106.26
SI	64.33	4.04	52.21– 76.45
FI	38.33	.58	36.59– 40.07

* Unit of measurement 10^{-2} mm. Not over 2 queens measured from any 1 nest, but 3 of the workers measured were from the type series.



Figs. 195–203. A. mexicanus. WORKERS (25×): 195, head; 196, body profile; 197, petiolar scale; 198, pubescence (50×). QUEENS (12.5×): 199, fore femur; 200 petiolar scale; 201, head; 202, body profile; 203, pubescence (50×). (For details, see p. 17 and fig. 8.)

from a populous nest, 13 mi. N. W. San Martin Texmelucan, Puebla, Mexico, July 26, 1963.

VARIATION. The 3 samples at hand reveal only slight variation.

ECOLOGY. **Habitat.** Type collections were made within a radius of a couple of miles of the ore mill, which was situated on the eastern slope of the high mountain range east of Pachuca. This country was covered with woods, mostly oaks and pines. The area around the mill was dry at certain times of the year; the altitude was between 8500 and 9000 feet. The type series includes specimens from more than one nest; all were collected from under large stones, mostly in pine woods. No habitat data other than altitude are available for the other two collections. The single queen was collected at 7900 feet, the nest of workers at 8600 feet. **Alate dates.** The type alates were taken sometime during May 1913, while the Carney queen was collected June 16. This species begins its flights early in the season.

Frequency Distributions for Metric Data

Tables 27–41 give univariate frequency distributions of measurements and indices for workers (27–32) and queens (33–41). The species codes used in these tables are listed below along with the species-numbers:

1. CLA (t) .... claviger, "typical" form
1. CLA (v) .... claviger, "variant" form
1a. PAR .... parvulus (= claviger)
1b. SM5 .... Sample 5 (= claviger)
2. COL .... coloradensis
3. CLF .... californicus
4. CLE .... colei
5. ARZ .... arizonicus
6. INT .... interjectus
7. LAT .... latipes
7a. LAT × CLA .... latipes × claviger
7b. LAT × COL .... latipes × coloradensis
8. MUR .... murphyi
8a. MUR × LAT .... murphyi × latipes
8b. MUR × SUB .... murphyi × subglaber
9. SUB .... subglaber
9a. SUB × PLU .... subglaber × plumopilosus
10. PLU .... plumopilosus
11. BUR .... bureni
12. PUB .... pubescens
13. CRT .... creightoni
14. OCC .... occidentalis
15. MEX .... mexicanus

Table 27. **Frequency distributions by taxa of SL in workers**

Variate range (mm)	1. CLA	1a. PAR	1b. SM5	2. COL	3. CLF	4. CLE	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
1.16–1.18								1													
1.13–1.15								2													
1.10–1.12								18													
1.07–1.09								36													
1.04–1.06								22													
1.01–1.03								34													
0.98–1.00	1						1	16													
0.95–0.97	0						2	13													
0.92–0.94	0						1	8													
0.89–0.91	4						2	6	3	2											
0.86–0.88	17			1		2	1	1	4	2							1				
0.83–0.85	24			6		0	0		6	0							2	1			
0.80–0.82	59			7		5	1		40	7	1			1			0	4	1	1	1
0.77–0.79	33			10	2	1			32	5	8	3		5			1	3	2	2	3
0.74–0.76	25			13	3				27	3	9		1	7			1			2	0
0.71–0.73	7		1	9	1				22	1	7		0	12	1		1			5	0
0.68–0.70	6	1	0	8					10		2		1	19	0	1				5	1
0.65–0.67	3	0	0	0					2		1			5	2	3				4	
0.62–0.64		1	1	1							0			2		1				7	
0.59–0.61				1							2			3		1				0	
0.56–0.58																				1	
Totals	179	2	2	56	6	8	8	157	146	20	30	3	2	54	3	6	6	8	3	27	5

Table 28. **Frequency distributions by taxa of HW in workers**

Variate range (mm)	1. CLA	1a. PAR	1b. SM5	2. COL	3. CLF	4. CLE	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
1.47–1.49								1													
1.44–1.46								0													
1.41–1.43								2													
1.38–1.40								5													
1.35–1.37								11													
1.32–1.34								12													
1.29–1.31								44													
1.26–1.28								31													
1.23–1.25								12													
1.20–1.22	2							17		1											
1.17–1.19	16							9		0											
1.14–1.16	17						2	6		3											
1.11–1.13	21						1	4	5	0											
1.08–1.10	38						1	3	15	1											
1.05–1.07	28			4			2		22	9				2			2				
1.02–1.04	18			3		1	1		24	4				5			2		1		
0.99–1.01	17			12		0	1		22	0			1	12			0	1	0	2	4
0.96–0.98	12		1	12	1	1			27	2	6	3	0	9			0	4	1	1	0
0.93–0.95	4		0	12	2	1			12		11		0	10	2	2	2	1	1	3	0
0.90–0.92	3		0	7	2	5			11		8		0	9	1	2		2		3	0
0.87–0.89	2		0	3	0				8		2		1	3		0				1	1
0.84–0.86	1	1	0	1	1						1			0		2				10	
0.81–0.83		1	1	1							0			4						4	
0.78–0.80				1							0									1	
0.75–0.77											1									1	
0.72–0.74											1									0	
0.69–0.71																				1	
Totals	179	2	2	56	6	8	8	157	146	20	30	3	2	54	3	6	6	8	3	27	5

Table 29. **Frequency distributions by taxa of HL in workers**

Variate range (mm)	1. CLA	1a. PAR	1b. SM5	2. COL	3. CLF	4. CLE	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
1.40–1.42.....								2													
1.37–1.39.....								3													
1.34–1.36.....								6													
1.31–1.33.....								18													
1.28–1.30.....								42													
1.25–1.27.....								27													
1.22–1.24.....	3							18		2											
1.19–1.21.....	16							23		1											
1.16–1.18.....	21						1	4	5	2											
1.13–1.15.....	21						3	5	14	1											
1.10–1.12.....	46			3			0	8	32	6				1			2				2
1.07–1.09.....	25			8		1	1	1	20	5				4			1		1		2
1.04–1.06.....	14			5		0	2		16	2	1			8			1		0	2	0
1.01–1.03.....	17		1	11		1	0		27	1	5	3	1	11			0	2	1	1	0
0.98–1.00.....	8		0	12	3	2	1		14		9		0	16	1		0	3	0	3	0
0.95–0.97.....	4		0	10	1	4			9		7		0	5	2	2	2	2	1	2	0
0.92–0.94.....	1		0	1	1				7		5		0	2		1		1		7	1
0.89–0.91.....	2	1	0	4	1				2		0		1	3		3				6	
0.86–0.88.....	1	1	1	1							1			3						5	
0.83–0.85.....				0							0			1						0	
0.80–0.82.....				1							0									0	
0.77–0.79.....											2									0	
0.74–0.76.....																				1	
Totals	179	2	2	56	6	8	8	157	146	20	30	3	2	54	3	6	6	8	3	27	5

Table 30. **Frequency distributions by taxa of AL in workers**

Variate range (mm)	1. CLA	1a. PAR	1b. SM5	2. COL	3. CLF	4. CLE	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
1.85–1.87								1													
1.82–1.84								1													
1.79–1.81								2													
1.76–1.78								3													
1.73–1.75								5													
1.70–1.72								19													
1.67–1.69								14													
1.64–1.66								18													
1.61–1.63								15													
1.58–1.60								30		2											
1.55–1.57	2							18	4	0											
1.52–1.54	0							3	2	2											
1.49–1.51	11							11	6	0											
1.46–1.48	5			1				3	9	1											
1.43–1.45	15			0				5	10	2											
1.40–1.42	31			0			2	5	24	7							2		1		
1.37–1.39	13			3			0	2	16	0				1			0		0		
1.34–1.36	24			3			1	1	14	1				2			1		0	1	1
1.31–1.33	13			6			1	0	11	1	1			4			0		0	0	0
1.28–1.30	21			9		2	1	1	19	3	3		1	7			0	1	1	1	1
1.25–1.27	13			6		0	0		8	0	8	3	0	7			1	2	0	2	1
1.22–1.24	10			10		0	1		2	0	1		0	10	1		1	3	1	0	0
1.19–1.21	6		1	9	3	1	1		10	1	7		0	10	1	2	1	1		4	1
1.16–1.18	3		0	0	2	2	0		3		4		0	2	1	0		1		0	0
1.13–1.15	6		0	2	0	0	1		5		3		1	4		1				1	0
1.10–1.12	3		0	4	0	3			3		0			4		2				5	0
1.07–1.09	1		0	1	1						0			1		1				4	0
1.04–1.06	2		0	0							1			0						2	0
1.01–1.03			0	1							0			1						3	1
0.98–1.00		1	1	1							0			1						3	
0.95–0.97		1									1									0	
0.92–0.94											1									0	
0.89–0.91																				1	
Totals	179	2	2	56	6	8	8	157	146	20	30	3	2	54	3	6	6	8	3	27	5

Table 31. **Frequency distributions by taxa of CI in workers**

Variate	1. CLA	1a. PAR	1b. SM5	2. COL	3. CLF	4. CLE	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
105								3													
104								8													
103								12													
102	1						1	43													
101	3						2	37													
100	14			1			0	31						1							
99	27			5			1	13	1					4		1	1	2			
98	46			8		1	2	10	12	3	2		1	4	1	2	1	2		1	
97	42			6		0	0		19	5	8		1	8	2	1	1	2	1	2	
96	28	1		12	4	1	2		34	4	6	1		10		1	3	1	1	3	1
95	12	0	1	11	2	1			30	4	7	2		8		0		1	1	4	0
94	3	1	0	6		2			24	1	6			13		1				1	0
93	2		1	4		1			18	1	0			6						6	2
92	1			2		1			6	2	1									5	1
91				0		1			1											0	1
90				1					0											4	
89									1											1	
Totals	179	2	2	56	6	8	8	157	146	20	30	3	2	54	3	6	6	8	3	27	5

Table 32. **Frequency distributions by taxa of SI in workers**

Variate	1. CLA	1a. PAR	1b. SM5	2. COL	3. CLF	4. CLE	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
90						1															
89						3															
88						1															
87						1															
86						2		5													
85				1			4	4			1							2			
84				1	1		1	11			0							2	1	1	
83				2	2		2	32			0							4	0	3	
82	1			4	2		0	24	7		6								0	1	
81	0			7	1		1	27	9		2	1					2		1	2	
80	2			7				26	11		9	0					2		0	4	1
79	2	1	1	7				15	14		7	2					0		1	3	2
78	11	1	0	6				8	13	2	3		1	3			1			4	1
77	20		0	10				3	24	4	1		0	3			1			4	1
76	17		0	6				1	17	3	1		1	6	1	1				5	
75	39		0	2				1	29	7				8	0	0					
74	30		0	3					12	2				13	0	0					
73	24		1						9	0				9	0	1					
72	16								1	1				7	2	1					
71	10									0				2		2					
70	4									1				1		1					
69	2													2							
68	1																				
Totals	179	2	2	56	6	8	8	157	146	20	30	3	2	54	3	6	6	8	3	27	5

Table 33. **Frequency distributions by taxa of SL in queens**

Variate range (mm)	1. CLA (t)	1. CLA (v)	2. COL	3. CLF	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	7b. LAT × COL	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
1.30–1.32						1														
1.27–1.29						1														
1.24–1.26						2														
1.21–1.23					1	8														
1.18–1.20				1	0	18														
1.15–1.17				0	0	16														
1.12–1.14				0	0	6														
1.09–1.11				1	1	10				2										
1.06–1.08				0	1	1		2		2										
1.03–1.05			1	0	0	1	2	0		5	2		1							
1.00–1.02	4		0	0	0	1	6	1		6	1		0							
0.97–0.99	10	3	0	0	0		13	2				1	0							
0.94–0.96	6	0	0	0	1		9	9				0	0							
0.91–0.93	4	8	6	1			11	4	1			1	0			1				
0.88–0.90	4	3	6	1			4	1	1				1			2				
0.85–0.87	1	3	3	1			3	1					4				1	2		1
0.82–0.84		0											3				1	1		1
0.79–0.81		1											10							0
0.76–0.78													3	1					1	0
0.73–0.75														1					2	0
0.70–0.72																			1	1
0.67–0.69															1				1	
0.64–0.66															2					
Totals	29	18	16	5	4	65	48	20	2	15	3	2	22	2	3	3	2	3	5	3

Table 34. **Frequency distributions by taxa of HW in queens**

Variate range (mm)	1. CLA (t)	1. CLA (v)	2. COL	3. CLF	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	7b. LAT × COL	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
1.89–1.91						2														
1.86–1.88						0														
1.83–1.85						0														
1.80–1.82						0														
1.77–1.79						3														
1.74–1.76						3														
1.71–1.73						4														
1.68–1.70	2			1		10	1	1												
1.65–1.67	1	1		0		10	0	1												
1.62–1.64	3	0		0		13	1	2												
1.59–1.61	9	2		0	1	11	1	0												
1.56–1.58	3	0		1	0	4	1	4												
1.53–1.55	4	0		0	0	4	6	0												
1.50–1.52	2	3	1	0	1	0	15	4												
1.47–1.49	2	1	0	0	0	0	9	2					1							
1.44–1.46	1	5	0	0	0	0	6	0			1		0							
1.41–1.43	1	1	0	0	0	0	6	4			0		0							
1.38–1.40	0	4	0	0	1	0	2	2			2		0							
1.35–1.37	0	0	0	0	0	1			2	2			3							
1.32–1.34	1	0	4	0	0					2			1							
1.29–1.31		0	0	1	1					5		2	6							
1.26–1.28		0	6	0						3			0			2				2
1.23–1.25		0	3	0						3			4			0				0
1.20–1.22		1	1	1									6			1		1	1	0
1.17–1.19			1	1									0					0	3	1
1.14–1.16													1					2	0	
1.11–1.13														2					1	
1.08–1.10																	1			
1.05–1.07																	1			
1.02–1.04																				
0.99–1.01																				
0.96–0.98															2					
0.93–0.95															1					
Totals	29	18	16	5	4	65	48	20	2	15	3	2	22	2	3	3	2	3	5	3

Table 35. **Frequency distributions by taxa of HL in queens**

Variate range (mm)	1. CLA (t)	1. CLA (v)	2. COL	3. CLF	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	7b. LAT × COL	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
1.77–1.79						1	1													
1.74–1.76						1	0	2												
1.71–1.73	1					0	2	0												
1.68–1.70	0			1		0	3	1												
1.65–1.67	2	2		0		1	5	2												
1.62–1.64	5	0		0		7	9	3												
1.59–1.61	9	1		0		16	12	2			1									
1.56–1.58	4	0		0		3	7	1			1									
1.53–1.55	3	1		1		12	4	6			1									
1.50–1.52	2	4		0	1	17	4	1		2										
1.47–1.49	1	3	1	0	0	5	1	1		1			1							
1.44–1.46	0	2	0	0	2	1		0	1	6			0							
1.41–1.43	1	4	0	0	0	0		1	0	3			0							
1.38–1.40	0	0	2	0	0	0			1	3		1	0							
1.35–1.37	1	0	2	0	0	0						0	3							
1.32–1.34		0	2	1	0	1						1	2							
1.29–1.31		1	5	0	1								5							
1.26–1.28			2	0									3			2			2	1
1.23–1.25			1	0									4			0			2	1
1.20–1.22			1	0									3			1		1	1	0
1.17–1.19				2									0					0		1
1.14–1.16													1	1				2		
1.11–1.13														1						
1.08–1.10																	1			
1.05–1.07																	1			
1.02–1.04																				
0.99–1.01																				
0.96–0.98															2					
0.93–0.95															1					
Totals	29	18	16	5	4	65	48	20	2	15	3	2	22	2	3	3	2	3	5	3

Table 36. **Frequency distributions by taxa of AL in queens**

Variate range (mm)	1. CLA (t)	1. CLA (v)	2. COL	3. CLF	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	7b. LAT × COL	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
3.81–3.87							1													
3.74–3.80							0													
3.67–3.73							2													
3.60–3.66							7													
3.53–3.59							4													
3.46–3.52							8													
3.39–3.45							12	1			1									
3.32–3.38							2	1			0									
3.25–3.31							6	0			1									
3.18–3.24							3	2			0									
3.11–3.17							3	2			0									
3.04–3.10								1			1									
2.97–3.03						1		4	1											
2.90–2.96						1		1	0											
2.83–2.89						1		4	0	1										
2.76–2.82	3	2		1		6		2	0	3										
2.69–2.75	8	0		0	1	11		1	0	6										
2.62–2.68	4	2		0	0	9		0	0	4										
2.55–2.61	6	1	1	1	0	17		1	1	1		1								
2.48–2.54	4	1	0	0	1	9						0	1							
2.41–2.47	2	4	0	0	1	7						0	0							
2.34–2.40	1	5	1	0	0	2						1	0							
2.27–2.33	1	1	0	1	0	0							0							
2.20–2.26		1	6	0	0	0							3							2
2.13–2.19		0	3	0	0	0							5			2		1	2	1
2.06–2.12		1	2	0	1	0							4			0		0	1	
1.99–2.05			2	2		1							4			1		1	0	
1.92–1.98			1										3	1				0	2	
1.85–1.91													1	1			2	1		
1.78–1.84													1							
1.71–1.77																				
1.64–1.70															2					
1.57–1.63															0					
1.50–1.56															1					
Totals	29	18	16	5	4	65	48	20	2	15	3	2	22	2	3	3	2	3	5	3

Table 37. **Frequency distributions by taxa of FL in queens**

Variate range (mm)	1. CLA (t)	1. CLA (v)	2. COL	3. CLF	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	7b. LAT × COL	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
1.65–1.67							1													
1.62–1.64							0													
1.59–1.61							0													
1.56–1.58						1	2													
1.53–1.55						0	2													
1.50–1.52						1	7	1												
1.47–1.49						0	3	1												
1.44–1.46						0	11	0												
1.41–1.43						1	4	0			2									
1.38–1.40				1		7	10	4		1	1									
1.35–1.37				0		9	1	1		1										
1.32–1.34				0		10	3	3		3										
1.29–1.31	3			0	1	18	4	5	1	8										
1.26–1.28	5			1	0	9		2	0	1										
1.23–1.25	2	2		0	0	7		1	0	1										
1.20–1.22	10	1	1	0	1	1		1	0			1								
1.17–1.19	3	0	0	0	0	0		0	0			0	1							
1.14–1.16	2	2	0	0	1	0		0	0			1	0							
1.11–1.13	3	6	0	0	0	1		1	1				0							
1.08–1.10	0	4	2	0	1								0							
1.05–1.07	0	2	0	0									1							1
1.02–1.04	0	0	6	1									3							0
0.99–1.01	1	0	6	0									7			2				0
0.96–0.98		1	1	0									4			0		1	4	1
0.93–0.95				0									2			1		2	0	1
0.90–0.92				2									2						1	
0.87–0.89													1	1			2			
0.84–0.86													1	1						
0.81–0.83																				
0.78–0.80																				
0.75–0.77															1					
0.72–0.74															1					
0.69–0.71															1					
Totals	29	18	16	5	4	65	48	20	2	15	3	2	22	2	3	3	2	3	5	3

Table 38. **Frequency distributions by taxa of FW in queens**

Variate range (mm)	1. CLA (t)	1. CLA (v)	2. COL	3. CLF	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	7b. LAT × COL	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
1.01–1.03							2													
0.98–1.00							4													
0.95–0.97							1													
0.92–0.94							10													
0.89–0.91							17													
0.86–0.88							7													
0.83–0.85							5													
0.80–0.82							2													
0.77–0.79																				
0.74–0.76								1												
0.71–0.73								2			1									
0.68–0.70								1			1									
0.65–0.67								2			1									
0.62–0.64								2												
0.59–0.61								8	1											
0.56–0.58								2	0											
0.53–0.55								1	0	1										
0.50–0.52	6							1	1	2										
0.47–0.49	10	2								9										
0.44–0.46	6	2		1		9				3										
0.41–0.43	5	7		1	1	26						2	1							
0.38–0.40	1	6	4	0	0	29							4						1	2
0.35–0.37	0	1	5	1	2	0							9						3	1
0.32–0.34	1		6	0	1	1							4	2				1	1	
0.29–0.31			1	2									3			2		0		
0.26–0.28													1		2	1		2		
0.23–0.25															1		2			
Totals	29	18	16	5	4	65	48	20	2	15	3	2	22	2	3	3	2	3	5	3

Table 39. **Frequency distributions by taxa of CI in queens**

Variate	1. CLA (t)	1. CLA (v)	2. COL	3. CLF	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	7b. LAT × COL	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
110						3														
109						7														
108						8														
107						9														
106					1	9														
105					1	14														
104					0	9							1							
103	1			1	0	5							0							1
102	3			1	0	1							3							1
101	2	4	1	2	0								1			2	2	1		0
100	6	1	0	0	1								3		2	1		0		1
99	8	4	1	0	0			2					5	1	1			1		
98	3	1	7	1	0			3					5	1				1	1	
97	2	5	2		1			3	1				1						0	
96	3	1	3				1	1	0			1	2						0	
95	1	1	1				6	6	0			0	0						1	
94		1	1				11	0	1			1	0						3	
93							14	3					1							
92							3	1		2	1									
91							10	1		3	0									
90							2			3	1									
89							1			1	0									
88										6	1									
Totals	29	18	16	5	4	65	48	20	2	15	3	2	22	2	3	3	2	3	5	3

Table 40. **Frequency distributions by taxa of SI in queens**

Variate	1. CLA (t)	1. CLA (v)	2. COL	3. CLF	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	7b. LAT × COL	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
84										1										
83										2										
82										3										
81										2										
80										1										
79										2										
78					1					4							1			
77					0												1			
76					1															
75			1		0	2												1		
74			0	1	0	2					1	1						0		
73			1	0	1	6					1	0				1		0		
72			2	1	1	12					0	0				0		2		
71			3	2		17					1	1				1				
70			5	1		7									1	1				
69			1			9							1		1					
68			2			5	1	3					0		0					1
67			1			3	0	1	1				5	1	1					0
66	1	3				1	12	1	0				5	1						0
65	1	2				0	9	1	1				3						1	1
64	1	0				1	6	1					4						0	0
63	5	1					7	3					1						2	0
62	3	6					5	2					1						1	0
61	4	0					7	6					1						0	0
60	7	5					0	0					1						0	1
59	3	0					1	2											0	
58	1	1																	1	
57	2																			
56	1																			
Totals	29	18	16	5	4	65	48	20	2	15	3	2	22	2	3	3	2	3	5	3

Table 41. **Frequency distributions by taxa of FI in queens**

Variate	1. CLA (t)	1. CLA (v)	2. COL	3. CLF	5. ARZ	6. INT	7. LAT	7a. LAT × CLA	7b. LAT × COL	8. MUR	8a. MUR × LAT	8b. MUR × SUB	9. SUB	9a. SUB × PLU	10. PLU	11. BUR	12. PUB	13. CRT	14. OCC	15. MEX
69–70							1													
67–68							3													
65–66							9													
63–64							15													
61–62							11													
59–60							6													
57–58							3													
55–56																				
53–54								1												
51–52								0			1									
49–50								3			0									
47–48								5	1		1									
45–46								7	1		1									
43–44								4												
41–42	5	1																	1	
39–40	8	2								1			3						1	1
37–38	9	9	2							6			4	2	1				1	2
35–36	6	6	5							8		1	8		0				2	
33–34	1		4	3		10						1	6		1			1		
31–32			5	2	2	39							1		1	2		0		
29–30					2	15										1	1	1		
27–28						1											1	1		
Totals	29	18	16	5	4	65	48	20	2	15	3	2	22	2	3	3	2	3	5	3

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Index of Scientific Names

All species cited in the text are arranged alphabetically by species name. Included also are the references to genera and subgenera. All species except those of *Acanthomyops* are followed by their genus name. Synonymic citations are followed by the current species name only in cases where doubt might arise; most have been moved from *Lasius* to *Acanthomyops* without a change in name.