DIMORPHIC QUEENS IN AN AMERICAN ANT
(LASIGUS LATIPES WALSH)

W. M. WHEELER AND E. L. MERRICK

On the afternoon of September 17 of the current year the
senior author had occasion to witness the nuptial flights of several
species of Lasius in an open wood near Rockford, Illinois. These
flights occurred almost simultaneously from mound nests of
Lasius niger var. mimus, L. interjectus, L. interjectus, and L. latipes. The last
species is ubiquitous in all open country in the Northern States,
especially where the soil is sandy or sandy. Owing to the dingy
color of the workers, males, and females, and the relatively small
size of the colonies, the nuptial flight of this species offers nothing
of special interest or beauty. It is quite otherwise with some
of the yellow-colored species, which are more common in the
United States, namely: L. aphidesco Walsh, species inediti, Eurytoma Ewing, species Fordi, etc., etc.

The last is known only from North Carolina and Colorado. L. inter-
jectus, L. interjectus, L. interjectus, and L. latipes build large mound nests,
often a foot or more in diameter and several inches high, either
in open grassy places or about the bases of rotten stumps. These
mounds are shot through with living grass and covered with little
openings for the ingress and egress of the ants. L. latipes in some localities prefers to build its nests under rather
large stones. This is the case at Colebrook, Connecticut, for
example. Unlike L. niger and L. interjectus the yellow species of
the genus appear to be nocturnal in their habits and L. niger
largely subterranean. At any rate the workers of these various
species are not seen to leave the nests in the day-time, except
during the nuptial flight of the males and virgin females.
This flight, especially in the case of *L. latipes*, presents a beautiful spectacle. At the moment when the great swarming impulse seizes the colony, the shining amber-yellow workers, together with the host of sable males and large tawny-red females, break in a flood from the main openings of the nest.
The winged forms hasten up the slender grass-blades on which they rock for a few moments, while filling their tracheae with the pure air of the upper world, then one by one spread their glittering wings and soar into the air like sparks rising from a fire.

While watching a colony during this interesting culmination of its annual development, the senior author noticed females of two different kinds issuing in numbers from the same openings of the grass-covered mound. The majority of these females were the remarkably pilose individuals, of a rich fulvous red, with extremely broad and flat legs and abnormally short, feeble tarsi, which have always been regarded as the true females of *L. latipes*. Among these, however, there were several hundred females which were perceptibly smaller, of a deep brown color, much less pilose, with only moderately broadened and compressed legs and with much longer tarsi. Both forms mingled with the workers and males and took flight together within the same half hour. Although the unusual character of this observation was fully appreciated at the time, circumstances made it impossible to excavate the nest and search its environs for the females of these very different virgin females. It seemed best to leave the nest for careful study at some future time and to collect a large number of the workers, males and females at the surface.

In this paper we will designate as the $\beta$-female the highly aberrant form (Fig. 1, $\epsilon$) with the excessively flattened legs, i.e., the form which has hitherto passed as the true and only female of *L. latipes*, the other (Fig. 1, $\beta$) we will call the $\delta$-female. These designations will suffice for present purposes and will leave the facts uncolored by the conjectural meaning of this singular dimorphism.

A few days after the above recorded observations were made the senior author returned to Texas, and soon afterwards, with the aid of the junior author, undertook an examination of all the material of *L. latipes* collected during three consecutive summers in three different localities. This was easily possible because the specimens from different nests had been kept by themselves in separate vials of alcohol. There were, in all, collections from ten separate nests, as recorded with the date of capture and the personnel of each colony in the following table:

Nest No. 1. Woods Hole, Mass., Aug., 1900. $\varphi, \delta, \beta, \gamma$.

Nest No. 2. Woods Hole, Mass., Aug., 1900. $\varphi, \beta, \gamma$. 
Page Missing From Book
<table>
<thead>
<tr>
<th>Measurement</th>
<th>L. charip.</th>
<th>L. tagetes</th>
<th>L. tagetes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of thorax</td>
<td>2.517</td>
<td>2.969</td>
<td>3.627</td>
</tr>
<tr>
<td>Length of gaster</td>
<td>3.959</td>
<td>3.511</td>
<td>3.473</td>
</tr>
<tr>
<td>Length of petiole</td>
<td>3.126</td>
<td>3.503</td>
<td>3.829</td>
</tr>
<tr>
<td>Height of petiole</td>
<td>2.795</td>
<td>3.873</td>
<td>4.064</td>
</tr>
<tr>
<td>Length of antennal scape</td>
<td>1.609</td>
<td>1.323</td>
<td>1.374</td>
</tr>
<tr>
<td>Apical breadth of antennal scape</td>
<td>1.478</td>
<td>1.379</td>
<td>1.347</td>
</tr>
<tr>
<td>Length of funiculus</td>
<td>1.600</td>
<td>1.519</td>
<td>1.579</td>
</tr>
<tr>
<td>Breadth of funiculus</td>
<td>1.578</td>
<td>1.628</td>
<td>1.605</td>
</tr>
<tr>
<td>Length of fore femur</td>
<td>1.519</td>
<td>1.486</td>
<td>1.535</td>
</tr>
<tr>
<td>Length of middle femur</td>
<td>1.593</td>
<td>1.573</td>
<td>1.682</td>
</tr>
<tr>
<td>Length of hind femur</td>
<td>1.536</td>
<td>1.548</td>
<td>1.592</td>
</tr>
<tr>
<td>Length of fore tibia</td>
<td>1.081</td>
<td>1.043</td>
<td>0.979</td>
</tr>
<tr>
<td>Length of middle tibia</td>
<td>1.041</td>
<td>1.015</td>
<td>0.960</td>
</tr>
<tr>
<td>Length of hind tibia</td>
<td>1.015</td>
<td>1.011</td>
<td>0.999</td>
</tr>
<tr>
<td>Length of fore spur (among)</td>
<td>0.938</td>
<td>1.029</td>
<td>0.989</td>
</tr>
<tr>
<td>Length of middle spur</td>
<td>0.731</td>
<td>0.707</td>
<td>0.689</td>
</tr>
<tr>
<td>Length of hind spur</td>
<td>0.697</td>
<td>0.667</td>
<td>0.667</td>
</tr>
<tr>
<td>Length of whole fore tarsus</td>
<td>1.043</td>
<td>1.005</td>
<td>0.999</td>
</tr>
<tr>
<td>Length of fore free tarsal joints</td>
<td>0.978</td>
<td>0.971</td>
<td>0.971</td>
</tr>
<tr>
<td>Length of protarsal free tarsal joints</td>
<td>0.879</td>
<td>0.866</td>
<td>0.866</td>
</tr>
<tr>
<td>Length of hind free tarsal joints</td>
<td>0.772</td>
<td>0.755</td>
<td>0.755</td>
</tr>
<tr>
<td>Length of fourth free tarsal joints</td>
<td>0.672</td>
<td>0.672</td>
<td>0.672</td>
</tr>
<tr>
<td>Length of fore free tarsal joint</td>
<td>0.636</td>
<td>0.622</td>
<td>0.622</td>
</tr>
<tr>
<td>Length of middle free tarsal joint</td>
<td>0.615</td>
<td>0.602</td>
<td>0.602</td>
</tr>
<tr>
<td>Length of hind free tarsal joint</td>
<td>0.590</td>
<td>0.590</td>
<td>0.590</td>
</tr>
<tr>
<td>Length of fourth hind tarsal joint</td>
<td>0.567</td>
<td>0.567</td>
<td>0.567</td>
</tr>
</tbody>
</table>

* The dimensions are in microns.

...signed to the limbo of useless specific diagnoses except for the mention of the extraordinarily flattened legs in the male, a character which is, moreover, emphasized in the specific name.

Walsh had only two specimens of the μ-female. The locality of the types is not given, but was probably Rock Island, Illinois. It was the flattening of the legs of L. charip., a trait still more pronounced in L. tagetes and visible also in L. tagetes and, the more recently discovered *Murphyi* that led Mayr ("ibid., p. 51") to separate these forms as the genus *Acromyrmex*. Later he reduced...
this genus to subgeneric rank under *Lasius*, where it is still used to include those species which have 3- instead of 6-jointed maxillary palpi. Mayr redescribed ('66, p. 889) the β-female from a defective specimen from Wisconsin, and says that he was at first tempted to place it in a new genus on account of its remarkable appearance. That he refrained from doing this is evidence of his keen taxonomic insight. Later writers, like Emery ('93, p. 638), have included the β-female in the table of *Lasius* species as distinguishable from all other females by having "the hind tarsus shorter than the much flattened tibia." The discovery of the α-female, which has the hind tarsus longer and the tibia much less dilated, makes it more difficult to recognize the species. This has induced us to make a closer study of *L. latipes* and of the allied *claviger* in all the sexual phases.

Comparison shows that the α-female is almost intermediate between the β-female and the female of *claviger*. This is clearly shown in the figures, in the table of measurements on p. 153, drawn up by the junior author, and in the two-column statement of the principal differences between the α- and β-females, as compared with the female of *L. claviger* as a standard:

---

**α-female of *Lasius latipes***

1. Dark brown, like *L. claviger* ♀.
2. A little more pilose and pubescent than *L. claviger* ♀.
3. A little larger.
4. Thorax longer in proportion to the gaster.
5. Mesonotum and scutellum as in *claviger* ♀.
6. Petiole thicker, higher and more rounded above than in *claviger* ♀.
7. Mandibles similar to those of *claviger* ♀.

---

**β-female of *Lasius latipes***

1. Fulvous red, in one nest (No. 5) dark brown like the α-female.
2. Much more pilose and pubescent.
3. Considerably larger and longer.
4. Thorax much longer in proportion to the gaster.
5. Mesonotum and scutellum flatter.
6. Petiole considerably thicker, higher and more rounded above.
7. Mandibles with fewer teeth than in *claviger* ♀ (Fig. 3 C).
8. Antennal scape and funiculus shorter and broader. (Fig. 2, B.)

9. Trochanters, femora and tibiae broader and more flattened.

10. Strigil a little smaller.

11. Tarsi rapidly tapering.

12. Middle and hind tarsi nearly as long as the tibiae. Much shorter than the tibia.

Turning now to a comparison of the two species, latipes and claviger, as exhibited by the workers and males, we find but few
points of difference, so that we are compelled to regard the two species as very closely related to each other. The worker *latipes* has a thicker petiole, which is distinctly blunt and rounded above, and the hairs are somewhat more abundant and evenly distributed on the dorsal surface of the gaster. In the worker *claviger*, on the other hand, the petiole is thinner anteroposteriorly and sharply constricted above when seen in profile, and the gaster is less uniformly hairy and somewhat more shining. The males of the two species differ much as do the workers in the shape of the petiole. Moreover the male *claviger* is decidedly larger, more robust and blacker than the male of *latipes*. These differences, especially in the males, are easily appreciated in the living specimens when they are seen in numbers, but are necessarily more obscure in dried cabinet specimens.

From these comparatively slight differences between the males and workers of the two species we should naturally expect to find a corresponding similarity in the females. It is quite obvious that the α-female is the very form which satisfies this requirement, whereas the β-female presents extreme characters which make it appear like a decided sport or aberration from the normal type of *Lasius* female. It would seem, therefore, that the β-female is the one for which we are most in need of an explanation, although it is connected with the females of normal form by a rather complete series of gradations, *i.e.*, through the females of the following species, beginning with the most extreme form: *L. Muripl*, α-female of *latipes*, *claviger*, *interjectus*. The remarkable configuration of the legs and antennae, the color and pilosity of the β-female all suggest some peculiarity of habit or habitat the nature of which remains to be determined by further observation and experiment.

We come now to the important question: What is the meaning of this dimorphism in the females of *L. latipes*? From the fragmentary data at our command it would seem that four different hypotheses might be advanced to explain this peculiar phenomenon:

1. It may be suggested that the α- and β-females really belong to two distinct species. According to this view the α-female might be regarded as the true queen of *latipes*, whereas the
β-form would represent the queen of some inquiline or symbiotic species. Although this explanation is readily suggested by the well-known cases of dulosis and xenobiosis in ants, we are, nevertheless, bound to reject it for the following reasons: Though the β-females were taken in several nests and, in one case, were seen to celebrate their nuptial flight at the very same time as the α-females, no males or workers which could represent any species except latipes were to be found in the nests. The same argument would hold mutatis mutandis, were we to consider the β-form as the only true female of latipes. The workers and males of all the known North American Lasii have been accounted for, and there is still a female form left over, so that there is no species known that could be enslaved by, or live as an inquiline with, L. latipes. We should have to suppose that the inquiline species was represented by females only, and this is most improbable.

Finally, the deep coloration above noted as occurring in the β-females of nest No. 3 would indicate that both the α- and β-females belong to the same species. We believe, therefore, that this hypothesis may be safely rejected.

Secondly: It may be suggested that the α-female is the normal female of latipes, whereas the β-females are diseased forms—individuals afflicted with some strange emumet elephantiasis or acromegaly! But even apart from the very frequent occurrence and uniform development of the β-females, dissection shows that such a view cannot be seriously entertained. Their internal structure is in no respect abnormal. The fat body is well developed and the ovaries are in the same stage and have the same normal structure as the ovaries of the α-females. If anything, the β-females are more vigorous, somewhat larger and supplied with more fatty tissue (even in the distal lobes of the large fore femora!) than the α-females. In a word, the β-females are somewhat above normal, while the α-females, so far as we are able to judge, are quite normal. Hence this hypothesis, also, may be safely rejected.

3. The dimorphism may be regarded as the result of hybridism between L. elangor and L. latipes. This view is supported by the following considerations:

(a) Both species occur in the very same localities, and latipes is much rarer than elangor. Hence the queens of the latter may
find cross-fertilization by males of their own species from other nests very difficult and fertilization by males of *claviger* a relatively easy matter.

(4) The nuptial flights of the two species may occur simultaneously. In fact, the senior author witnessed a flight of *claviger* from a nest not twenty feet away from the *lapis* nest and at the very same time (4:30 p.m.) as the above-described flight of the latter species. And it may also be stated that both these nests were large and must therefore have existed side by side for some years. We could suppose that a β-female of *lapis* in some previous year had been fertilized during her nuptial flight by a male *claviger* and had returned into the parental nest to give birth to the α-females which celebrated their nuptial flight on the 17th of September, 1902.

(c) This view is also supported by the fact that the α-female is so clearly intermediate in nearly all its characters between the female *claviger* and the β-female, as has been shown in the above tables.

The arguments that can be brought to bear against the hypothesis are the following:

(a) We have failed to find any hybrid workers in the nests containing the α and β-females. This should be the case unless we suppose that all the hybridized β-females produced only queens.† But it must be borne in mind that the hybrid between the worker *claviger* and worker *lapis* would differ presumably from the parent species only in intermediate piosity and in having a petiole intermediate in shape. Such differences would not be easily detected, as anybody will confess who has examined a large series of workers of the two species. The workers are of small size and the petiole is sometimes decidedly variable even within the limits of the same species of *Lapis*.

(8) It is improbable that hybridization could occur so frequently in a state of nature as appears to be indicated by the high percentage of nests containing α-females and their occurrence in such widely separated localities. If we are really confronted by a case of hybridism we are almost compelled to believe

† Obviously the male offspring of the hybridized queen would not be affected, since they arise from unstimulated eggs.
that the ω-female must be sterile, notwithstanding her well-developed ovaries, or the two species would long since have merged into one.

(c) It seems improbable that such an aberrant creature as the β-female would mate with the male of another species, but this argument loses much of its force when we stop to reflect that the ω-female male is very similar to the lekper male even in the structure of its genitalia.4

4. We may suppose that we are dealing with a true case of dimorphism in the female sex. On first thought this seems improbable because dimorphic queens, in the strict sense of the term, are unknown among ants. But when we stop to consider that the social bees and wasps exhibit an essentially similar dimorphism, except that one of the two winged forms, the worker, is sterile (and this may also be the case with the ω-female of L. laeviceps?) there is nothing preposterous in this view. Moreover, in ants, the wingless workers have themselves in many species become dimorphic, developing soldier and typical worker forms, either perfectly distinct from each other or connected by a series of intermediates. Why, then, may we not expect the winged queens in some cases to exhibit dimorphism among themselves, especially when dimorphism "runs in the blood," so to speak, of all the social Hymenoptera? And why may not L. laeviceps be such a species in which the old and deeply-rooted tendency is breaking out in a novel form? This would at least complete the theoretical possibilities in female ants as represented in the following diagram:

```
<table>
<thead>
<tr>
<th>Worker, or sterile female.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Worker minor, or soldier.</td>
</tr>
<tr>
<td>ω-female.</td>
</tr>
<tr>
<td>β-female.</td>
</tr>
<tr>
<td>Queen, or fertile female.</td>
</tr>
</tbody>
</table>
```

It thus appears that of the four hypotheses, two may be rejected as too improbable to be entertained, and that the true meaning of

1 (Unless, indeed, the Mendelian law be supposed to operate with supernormal degrees in this particular case.

2 In this connection, however, it is necessary to note that Marshall (ibid. p. 43) failed to reduce worker between two very closely allied species of wasp (V. spiniger and V. auratus).
the dimorphism of the females of *L. latipes* is to be sought in the
direction of hybridism or of dimorphism *sensus stricto*. Only
further observation and especially experiment can enable us to
decide which of these interesting alternatives confronts us.

For the present we incline to the belief that the α- and β-females
of *L. latipes* represent true dimorphic forms, and see in this
condition an interesting repetition of what may have led to the
differentiation of the primitive winged female ant into workers and
queens. It is granted on all sides that insects like the ants,
social wasps and bees, which present three sexual phases, viz.,
males, queens and workers, are to be derived from forms with
only a single female form. In the bees and wasps there can be
no question that this original female form was winged like the
male, and we should expect this to be the case also with the ants,
but so eminent a myrmecologist as Professor Emery takes quite
a different view of the matter. (95a, p. 775). He says: “If the
above considered derivation of ants from Mutillid-like Hymenoptera be granted, we must suppose, furthermore, that in primiti-
tive ants, as in the Mutillids, the males were winged, but the
females wingless, and that the latter subsequently reacquired
wings. This supposition is upheld by the fact that wingless
females are most commonly met with among the Doryline and
Ponerine, i.e., in those very groups of ants which are the most
primitive, more rarely among the Myrmicine, and most rarely,
and, so far as I am aware, only as individual anomalies, in the
Dolichoderinae and Camponotinae. The frequency of occurrence
of wingless females is, therefore, inversely as the phyletic stage
of development of the different groups of ants.

1 In the Leptospermoidea and Hymenoptera, if we except a few cases like the Tachy-rid
Chalicesidae, the female sex seems to be more prone to dimorphism than the male. In
Lepidoptera the low records cases of dimorphism occur in males, i.e., in the Brazilian
*Carapa nortusimia* (E. H. Mueller, '81: Owen Seckel, '83) and the North American
*Sympis Mutila simulcaformis* (Williston, '85). Among the Coloaptena *Syphle-'
cal presents dimorphism in the females, while some of the Antshibidae are said to
show it in the males. The dimorphism seen in the “high” “and “low” males of
the Scarabaeide among the Coloaptena and the “high” and “low” male Dermapter-
a (Frisia steneura, Dorn: observed by Boisni (94, pp. 40-42), resembles that of
the female *L. latipes* in having a normal and excess development of the individuals
of the same sex. In the latter case, however, the two forms are not conducted by
intermediate variations.
"Not only is the normal occurrence of wingless females among existing species evidence of a similar condition among the primitive ants, but it also furnishes the most natural explanation of the origin of the wingless workers. I surmise that the ancestral ants consisted of small societies of wingless females, among which sterile individuals were subsequently differentiated as workers. The wings, so readily decidual in the queens of existing ants, were newly acquired from rudiments still persisting in the ontogeny, by a process of reversion to the winged ancestors."

We are unable to assent to this view, for the following reasons:

1. While there is no end of evidence to show that the most diverse insects have lost their wings during phylogeny, there is not, to our knowledge, a single insect which can be satisfactorily shown to have reacquired these organs. At any rate the losing of wings is a much easier process than their acquisition.

2. Existing waaps and bees certainly show the possibility of differentiation into workers and queens prior to the loss of wings.

3. This is an interesting case of a principle to which Huxley ('73, pp. 105, 119) has recently called attention: "The sudden loss of horns brings out a point to which, I think, attention has never been directed in discussions on pinnipeds. The evolution of new characters is a gradual process requiring ages of time. Geology shows that the pinnipeds have grown step by step from small beginnings. But they might be completely lost in a single generation. The horns of cattle, through less magnificence, are more the less the slow product of ages of unaltered selection. But by a sudden flash they disappear entirely in an individual here and there, or leave only a dying vestige attached to the skin.

These evolutionists, who love symmetrical theories, mapped out regardless of observed facts, imagine a process of reversion by which all the wings are restored in order of succession. What actually happens is entirely different. An elaborate organ is suddenly much reduced and apotephal or suddenly disappears altogether.
And there is no strong evidence to show that this condition did not exist in the ancestral ants, for the Doryline are hardly in the direct line of Formicid descent, and the Ponerine, though very primitive, still show the differentiation into winged queens and wingless workers in some of their most generalized genera (Cephalotes, Synaphanta, Proceratium, etc.).

That the most natural way of accounting for the wingless workers is through loss of the organs of flight in one of the two winged female forms, is also indicated by the phenomena of ergatogomorphism among male ants. It is known that in a few sporadic species belonging to several genera the males are wingless and have assumed a worker-like form, especially in the development of the thorax. These species are, Anogerates atratulus (Schenck '52), Formicorhynchus minutulus (Adler 64), Cardiocondyla Siambulofu (Ferel '92), Forren punctatissima (Emery '99) and P. ergatoides (Ferel '93). This same reduction of the wings is shown in a more or less advanced condition in some male Mutillidae. All these cases are most naturally explained by loss of the organs of flight, and we are justified in adopting the same explanation to account for the wingless condition of the workers. Our view of the matter, therefore, would differ from Emery's in assuming that in the ancestors of the ants all three forms--workers, queens and males--were alike winged, and that the workers lost their wings either suddenly in accordance with Heinle's principle, or concomitantly with the atrophy of the ovaries and the assumption of the other worker characters. Thus it would be the workers that have lost their wings and the queens have not reacquired, but retained these organs which came to them as the common heritage of all the Pterygota insects.

BIBLIOGRAPHY.

Adler, C.


Malison, W.


Emery, C.

Emery, C.

Emery, C.

Fernald, A.

Fernald, A.

Handley, F. W.

Hampe, Paul.

Mayr, O. L.

Mayr, O. L.

Monill, Frl.
1895 Metamorphosis of a Worker Termite. Insecta, X., 1895, pp. 29-37, 1 Tab.

Oettel, Sacken, C. F.

Schaeffer.

White, R. D.

Williamson, G. W.

AUSTIN, TEXAS
December 5, 1902.