

A Gynandromorph of *Smithistruma* (Hymenoptera: Formicidae)

JACK R. MUNSEE, Department of Life Sciences
Indiana State University, Terre Haute, Indiana 47809

Introduction

Among ants collected in an undisturbed stripmine area, Vermillion County, was a unique individual belonging to the genus *Smithistruma*. The latter is represented by small ants, less than to slightly more than 2 mm. A description of a worker of *S. filitalpa* Brown collected in the abandoned stripmine adjacent to the location noted above has been cited from Indiana (4). Contained in the description are the characteristics of the Tribe Cdaetini which is represented by ants of this genus. The specimen in question represents the reproductive castes in a single individual, although Wilson (9) recognizes male ants as a caste only in the loosest sense. At least, the right side of the body is predominantly male, while the left is female. Such an anomaly is a bilateral gynandromorph.

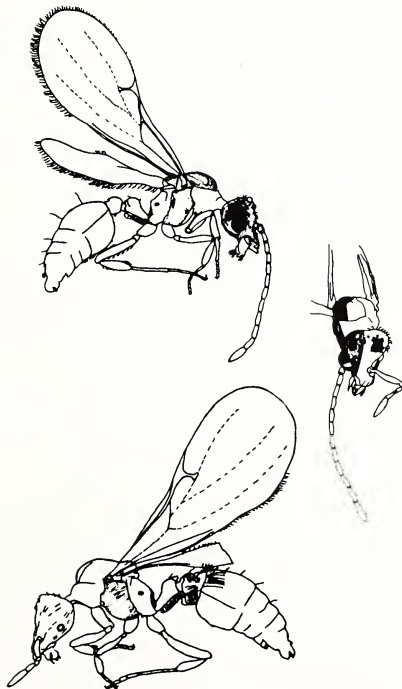
The problem of gynandromorphism is associated with caste determination in ants. As to the latter, two opposing views developed among myrmecologists: One argued that caste was determined genetically, or blastogenically; the other view, trophogenic, claimed that caste was determined by nutrition or caused by environmental effects (6, 7, 9). Wheeler (6) supported the blastogenic view, and according to Wilson (9) did not distinguish between normal functional castes and true anomalies. In 1937, Wheeler (6) published a detailed account of his study of an entire preserved colony of the fungus ant, *Acromyrmex octospinosus* Reich, from Trinidad. There were over 8000 normal and 163 aberrant individuals in the collection. Among the latter were 10 gynandromorphs. The female component in each was confined to the head, except in one specimen in which the genitalia was bisexual. According to Wheeler the body of these ants was that of a "perfectly formed male." Whiting (7) suggested that these "gynandromorphs" were male intersexes of varying forms with more or less superficial female traits. He cited Goldschmidt who determined that intersexes result when there is a shift at a specific point in development from one sex to that of the opposite. According to Whiting (7), intersexuality may result from trophogenic or other environmental factors, besides resulting genetically from race-crossing.

Whereas Wheeler's "gynandromorphs" may be more accurately considered as intersexes, the single specimen of *Smithistruma* in the present study is a true gynandromorph. In true sexual mosaics the male and female parts of the body are distributed more or less at random (7). Thus, male regions may be limited to anterior or posterior half, to right or left sides, or in a female head or abdomen there may be an island or spot of male tissue. Whiting's opinion of Wheeler's "gynandromorphs" has come to be accepted and lends further evidence to the trophogenic view of caste determinations in ants (9); furthermore, Wilson cited

the separate works of Brian, Weir, Wesson, *et al.*, in which nutritional and environmental factors have been demonstrated to be important factors in caste determination in some ants. An interesting side-light related to ant nutrition came from Dr. George C. Wheeler (personal communication). Upon enquiring if, in his extensive studies of ant larvae, he had noted the presence of anomalous forms of these stages, he indicated that he had not. Although true mosaics, including bilateral gynandromorphs, are viable adults, an anomalous larva would die if it could not receive nourishment from nurse ants.

Methods

The gynandromorph was compared with a normal male and a normal female of this genus. The three specimens were studied in glycerin in deep depression slides, using a stereomicroscope with 10X and 15X eye pieces, and having 1X, 3X, 6X, and 8X objectives. The comparisons began with head



FIGURES APPROXIMATELY 25X

FIGURE 1. Gynandromorph of *Smithistruma*: Male side represented by 13-segmented antenna, large compound eye and ocelli, reduced spongiform processes of pedicel, lack of gastric costulae, and pigmentation (above).

FIGURE 2. Gynandromorph of *Smithistruma*: Female side represented by 6-segmented antenna (one funicular segment obscured), reduced compound eye, well-developed spongiform processes of pedicel, presence of gastric costulae, and general lack of pigmentation (below).

FIGURE 3. Front view of gynandromorph showing pyriform head, male and female compound eyes and ocelli, mandibles, antennae, distribution of head and thoracic pigment, and reticulation (shown in part) of head capsule (right).

structures and proceeded posteriorly. Attention was given to differences in size, form, and color of sclerites being compared in each region on male and female sides. An ocular micrometer was used to measure certain structures, including mouthparts. The latter are very small and detection of slight differences in sizes cannot be determined otherwise. Lateral male and female habitus are shown in Figures 1 and 2. Figure 3 is a frontal view of head and thorax. Drawings were done with the aid of a camera lucida.

Discussion and Results

The head is divided laterally into distinct regions with the right side predominantly male, and the left, female; the latter representing more of the total head surface (Fig. 3). Head shape also more closely approaches that of the normal female, thus affecting the normal teardrop head shape of the male, since that of the female is more flattened and pyriform. The right side bears a typical, filamentous, 13-segmented male antenna, while the left is 6-segmented and elbowed as found in the workers and queens of this genus. The preocular laminae on the female side (Fig. 3) is missing from the other side. The large compound eye on the right is that of the male, and on the left is its much smaller female counterpart. Two ocelli, right lateral and medial, are similar in size and shape to those found in normal males. The left lateral ocellus, however, is small and rudimentary, most closely resembling that of the female. Anteriorly, the clypeus is sharply separated into male and female portions. The male part of this structure is small and subtends the female part which is conspicuous and well developed (Fig. 3). Lateral and anterior margins of the female clypeus are bordered by stout, antero-medially projecting hairs with similar cover rather closely distributed over much of that side of the head. On the male side, shorter, stout curved hairs are sparse and lacking from the clypeal margins. Both male and female head surfaces are distinctly reticulate (partly shown in Figs. 1 and 3). Below the clypeus is the labrum, which in this genus of ants is two-pronged, united basally, and usually projects beyond the anterior border of the clypeus. The right element of the labrum is reduced and represents the male structure, while the female counterpart is much longer and robust; however, each projects beyond the anterior borders of their respective clypei. Beneath the clypei are the mandibles, the right, small, toothless, and spike-like, typical of the male of this genus (Fig. 3). In males of *Smithistruma*, the mandibles are shorter than, or at least not greater in length than the greatest diameter of the eye, according to Brown (1). In the anomalous ant, the length of the male mandible is about .03 mm compared with .19 mm, the male eye diameter (Figs. 1 and 3). The left mandible is distinctly like that of the female and worker, bearing apical and intermediate (principal) teeth, as well as a tooth at the basal inner border (1). The maxillary and labial components are quite small, as noted by Kennedy and Schramm (3) who determined that the length of the mentum and submentum of a worker (*S. dietrichi*) of this genus measured .02 in. (about .5 mm), while the labial palp was .001 in. (.025 mm). Since the maxillae appear to be essentially the same size and form, and the intervening labium appears normal in shape and size when compared with these structures of the normal female, it is assumed that they are not anomalous. The mentum of the anomalous ant is about .08 mm, while that of the normal female is .11 mm in length. Some of the differences may

be accounted for due to measurements being made *in situ* on the former, while this structure was removed for measurement from the normal ant. Although the mentum of the male is about the same length as that for the normal female, it appears to be distinctly marginate, which is not seen in the mentum of either the anomaly or normal female.

Viewed laterally, the outline of the alitrunk corresponds nicely to that of the male (Fig. 1, 2). It follows, therefore, that the sclerites of this tagma reflect male influence for the most part. The pronotum is predominantly male, although it lacks the dark pigmentation of that sex. Especially noticeable is the mesoscutum which in males is bulbous and rounded above, while in females it is flattened. On the male side this sclerite is higher than on the left, or female side (Fig. 3). It is also distinguishable from the left side since it is darkly pigmented as in the normal male. On the right, anteriorly and dorsally, may be seen a vestige of the Mayrian furrow (Fig. 1), but a parapsidal suture on the same side is not evident. Both foregoing traits are often found in male ants. Dorsally, between the mesoscutum and scutellum is a transverse sclerite found in alate ants and known as the parapteron. On the male side, the lateral portion of this sclerite is well-developed and distinctly angular. Its opposite extremity on the female side is less conspicuous and rounded. Continuing posteriorly to the scutellum, on the female side the margin curves evenly toward the apex, while on the male side the curve to the apex is more abrupt. Also, it is darker. The metanotum of the gynandromorph is longer at the midline (.04 mm) than that of either the normal female or male (.02, .03 mm, respectively). However, since its length more closely matches that of the latter, it is felt that it is a male sclerite. Bilaterally, the mesosterna, mesepisterna, and mesepimera are somewhat similar in form and size, and reflect male influence. On the male side these sclerites are darker. Similarly, the corresponding sclerites of the metathorax exhibit male size and form but are not as deeply pigmented as those of the mesothorax. The basal and declivous faces of the epinota of the normal male and female meet at distinct angles, with that of the male being more acute and therefore more distinct. Spongiform plates on these faces form epinotal spine-like structures. The basal and declivous faces of the epinotum of the anomaly are joined by a curve but they are distinct. The characteristics of this sclerite in the anomaly most closely resembles that of the normal male. It is darkly pigmented. Finally, the stigma, or spiracle, of the epinotum on the male side is more conspicuous than on the female side.

A characteristic of dacetine ants is the presence of spongiform collars and/or plates associated with the epinotum, petiole, and post-petiole (Figs. 1, 2). The same spongiform material forms the preocular laminae, noted previously. These processes are well developed in workers and normal females. In the anomaly, two inconspicuous thin lamellae parallel one another on either side of the declivous face of the epinotum, the left being slightly larger (Figs. 1, 2). In the normal male these lamellae are inconspicuous.

The alate forms of the genus have a much reduced venation in both pairs of wings, according to Brown (1). Since basic studies of ant wings have been largely confined to the mesothoracic or fore wings, most of the following applies to these. The complement of veins found in the gynandromorph was the same as in

the normal male and female. Prominent in each are R + Sc, the stigma, and 2r; also easily seen are the "basalis" veins (1), which are the first free abscissae of the radial sector (Rs) and the Media (M), or Rsfl and Mfl, respectively. Other veins were represented by furrows resulting from disturbances of the pattern of microtrichia. These furrows were seen in reflected light only, and represent the presence of former veins (2). Differences in wing lengths between those of the anomaly and those of the normal ants were noted. On the basis of this, it is believed that the wings of the anomalous ant, which appeared identical, are female. Approximate wing lengths for the normal male and female were 1.9 mm and 2.1 mm, respectively. For the gynandromorph wing length was 2.2 mm. The metathoracic or hind wing of the anomalous ant is slightly longer than that of either the normal male or female, although for these, it is about the same length. (The left hind wing of the gynandromorph is broken off beyond the hamuli.) As observed by Brown (1), the only vein in the hind wing is found in the basal part of the costal region. The 4 hamuli appear normal, decreasing in length toward the apex of the wings.

The petiole of the anomalous ant tends toward maleness, being about the same length as in the normal male (.28 mm), compared with the normal female (.26 mm). The node is rounded above but more angular in the female. From above, the petiole appears asymmetrical, the male part of the node is longer and rounded laterally, while the node on the female side is clearly more angular. Also, the petiolar stalk on the male side is ridged and projects laterally beneath the node, while on the other side the projection is less pronounced with the side somewhat straight as seen from above. The median ventral spongiform plate is present in all three ants; however, it is much more developed in the normal female than in either the gynandromorph or the normal male, although degree of development most closely approaches that of the latter. Whereas conspicuous and well-developed "wings" of spongiform substance, interconnected by a bridge, flank the node of the petiole posteriorly in the normal female, in the gynandromorph only the left "wing" is seen. Extending laterally toward the right or male side is a single low, inconspicuous spongiform plate as seen in the normal male.

The postpetiole clearly displays male and female characteristics. Most notable are the shape of the node, as seen from above, and the distribution of the spongiform substance. On the female side the node is angular-ovoid, and on the male side it is rounded, the two sides corresponding in form to their respective sides in the normal ants. On the female side the spongiform substance is seen as a mass covering this side of the postpetiole, although it is not as dense as in the normal female. On the male side this substance is lacking, except for a thin transverse plate subtending this segment, which is the condition found in the normal male (Figs. 1, 2).

The gaster of the anomalous ant is larger than that of either normal ant. Because in preserving, swelling or shrinking of the gaster occurs, it is difficult to assess actual sizes for comparison. Dorsally, the first gastric segment is nicely separated into male and female regions by the basal costulae. These are absent in the male, but are represented by about a dozen conspicuous striae in the female

region of this tergite. The male region, which represents about one-half the dorsal surface, is smooth and shining as it is over the entire tergite in the normal male.

Most myrmecine female ants bear a sting (5), which is well developed in the queens. The sting is plainly visible in the normal alate female, but absent in the gynandromorph. Also, in the latter there appears to be no distinct genital capsule as in the normal male. Structures of the genitalia present are positioned toward the left or female side. A poorly developed genital capsule is recognizable, and it bears a single left volsella flanked on the right by a stipe. On the left is a stipe-like mass which may or may not be the partner to the structure on the right. The sclerotized volsella is not similar in form to the pair in the normal male; therefore, it is assumed that the volsella of the anomalous ant represents a different species of the genus. According to Brown (1), volsellae appear to vary with species or species-groups.

To account for an anomaly such as exhibited in the gynandromorph of *Smithistruma*, Wigglesworth (8) states that in all cases of gynandromorphism in insects some of the cleavage nuclei are male and some are female. Such nuclei reaching the cortical zone of the egg become determined for a given part of the body, and patches of one or the other sex develop depending on the constitution of the cells from which they happen to be formed. In this ant instead of patches, whole sclerites, or parts of sclerites, as well as entire structures exhibit characteristics of one sex or the other. Male cleavage nuclei reaching the presumptive compound eye region of the embryo resulted in its partner being female. Differential sexual development of other characteristics of the gynandromorph ant may be similarly accounted for. The mosaic pattern of distribution of maleness and femaleness shown in the anomaly indicates that it is a true gynandromorph, quite unlike Wheeler's "gynandromorphs" of *Acromyrmex*.

Literature Cited

1. BROWN, WILLIAM L., JR., 1953. Revisionary studies in the Ant Tribe Dacetini. Amer. Midl. Natur. **50**(1):1-137.
2. BROWN, WILLIAM L., JR., and W. L. NUTTING. 1950. Wing venation and the phylogeny of the Formicidae. Trans. Amer. Entomol. Soc. **75**:113-132.
3. KENNEDY, C. H., and M. M. SCHRAMM. 1953. A new *Strumigenys* with notes on Ohio species (Formicidae: Hymenoptera). Ann. Entomol. Soc. Amer., **26**:95-104.
4. MUNSEE, J. R. 1976. *Smithistruma filitalpa* W. L. BROWN. An Indiana dacetine ant. Proc. Ind. Acad. Sci. **86**: (in press).
5. WHEELER, W. M. 1910. Ants, Their Structure, Development and Behavior. Columbia Univ. Press., N.Y. 663 pp., illus.
6. WHEELER, W. M. 1937. Mosaics and other anomalies among ants. Harvard Univ. Press, Cambridge, Mass. 95 pp., illus.
7. WHITING, P. W. 1938. Anomalies and case determination in ants. Jour. Heredity **29**(5):189-193.
8. WIGGLESWORTH, V. B. 1974. Principles of Insect Physiology. Chapman and Hall Ltd., London. 7th ed. 827 pp., illus.
9. WILSON, E. O. 1971. The Insect Societies. Harvard Univ. Press, Cambridge, Mass., 548 pp., illus.