In 1878 Dewitz published an important contribution to our knowledge of the postembryonic development of the appendages in insects. Among the forms which he studied were the worker larvae and pupae of a common European ant (Formica rufa). He investigated their imaginal discs and discovered minute vestiges of wings which could be traced into the pupa stage. Concerning these structures he says (p. 82): "The imaginal discs of the vestigial wings arise later than those of the legs but nevertheless before the last larval ecdysis. They are situated on the sides of the two posterior thoracic segments, near their hind margins, and are drawn down close to the ventral surface [Plate XIV, Fig. 1 b and c]. Hence they are much further from the row of stigmata than from the leg-discs and lie just above the broad muscle band that runs along each side of the ventral surface. An elongate thickening with its two ends directed towards the ventral and dorsal surfaces and having a long slit-shaped invagination, arises in the hypodermis. The disc enlarges while the invagination progresses inward, so that two parts are differentiated, as in the development of the legs: an enveloping membrane and lying within it a more massive portion, the rudiment of the wing."

The further development of these "wing-pockets corresponds exactly with that of the leg-pockets. Each is an invagination of the hypodermis towards the interior of the body and opens outward by means of an orifice. In both cases growth is accompanied by an enlargement of the enclosed appendage."

During the pupal stage of the worker "the wings do not increase in size, since they have reached the acme of their growth in the fully developed larva." Traces of the wings are still visible in the semi-pupa but the little sacs finally flatten out and apparently become portions of the general hypodermis in the older pupa. Dewitz shows, nevertheless, a small vestige of the hind wing in a profile view of the thorax of a completed worker pupa (Plate XIV, Fig. 2 b).


2 According to Dewitz the term semipupa was introduced by Packard (Observations on the Development and Position of the Hymenoptera, with Notes on the Morphology of Insects. Proc. Boston Soc. Nat. Hist., Vol. X, Boston, 1866) and the term pseudonymph was subsequently given to the same stage by von Siebold (Beiträge zur Parthenogenese der Arthropoden, Leipzig, 1871, p. 35). Although von Siebold's term seems to be the more generally used, especially in Germany Packard's term not only takes precedence but is simpler and more appropriate.

[405]
Owing to the high degree of variability so characteristic of vestigial organs, we should expect occasionally to find adult worker ants bearing these structures, especially traces of the larger anterior pair of wings, in a more or less imperfect state of development. And the probability of finding such workers would seem to be the greater on account of the vast number of these insects born into the world during every month of the warm season. Among the thousands of workers that have come under my observation during the past six years, I have, in fact, succeeded in finding four winged individuals belonging to two colonies of two different species. While this is a very small percentage of the total number of specimens examined, it must be borne in mind that the wing-vestiges are sometimes very minute and easily detached, so that workers actually hatched with these interesting appendages may rub them off while excavating, or have them torn off by their sister workers while undergoing final ecdysis, or while submitting to the mutual shampooing to which these insects devote so much of their leisure.

Sept. 5, 1904, I found at Bronxville, New York, a small colony of a form of Myrmica rubra scabrinodis near the variety schencki Emery. This colony comprised about 150 workers and a dealated female of rather small size. Three of these workers bear vestiges of anterior wings but are in every other respect perfectly normal individuals. In the structure of the thorax there is not the slightest approach to the female type. Each of the three specimens represents a different condition in the development of the wings. In one (Fig. 3) the wing vestiges are nearly 1.7 mm. long, spatulate in outline and very slender at their bases where they are furnished with small but distinct tegulae. The appendages are yellowish brown, translucent and covered with minute hairs like those on the normal wings of females, but without any traces of venation. In another worker (Fig. 4) the wings are barely .4 mm. in length and are merely little opaque pads or sacs, without even a trace of hairs on their surfaces, although they have minute tegulae at their bases. In the third specimen (Pl. XIV, Fig. 5) the wings are even more vestigial, the right being represented by a small nodular appendage and its tegula, the left by a minute papilla. In all of these workers the vestiges represent anterior wings, as is shown by their insertion just behind the suture which sharply separates the pro- and mesothoracic segments in the region of the pleurae but not on the dorsal surface. It is very probable that the ants were quite unable to move these appendages. In the dead specimens they are applied to the mesopleuræ with their tips directed ventrally and
posterily, like the wing-pads in the pupæ of normal males and females, and do not stand off at right angles from the thorax as represented, for the sake of clearness, in the figures. The two specimens with more considerable vestiges are a trifle larger than the majority of the workers in the colony, but this, apart from the wings, is the only character in which they approach the female.

The only other worker ant with wing vestiges in my collection is a soldier of Cryptocerus aztecs Forel taken Dec. 27, 1900, by myself from a normal colony that was living between the leaves of an epiphytic Tillandsia near Cuernavaca, Mexico. This specimen (Fig. 6) is in every respect a perfectly normal worker major, or soldier of its species, except that it bears on the external angles of the mesonotum a pair of symmetrical organs representing anterior wings. These are shaped very much like those in the first of the above-described Myrmica scabrinodis workers. They are .8 mm. long, spatulate, yellowish brown in color, opaque at the base but semi-transparent towards their tips. Their surfaces are transversely wrinkled but hairless. The tegulæ, if present, are extremely minute. In the dried specimen the vestiges are directed ventrally and posteriorly like the wing rudiments in the normal female pupæ of Myrmicine ants.1

We must assume that in all the above cases the wing vestiges which, in worker ant larvæ, are extremely minute and normally disappear in the pupa stage, have, so to speak, been fanned into greater activity of growth by some unusual and unknown stimulus during ontogeny and have persisted till the imaginal stage without, however, attaining to any functional significance.

The specimens above described not only confirm but emphasize Dewitz’s conclusion that worker ants must once have possessed functional wings like those of the existing workers of social bees and wasps. This is evidently only a special case of what Dewitz expresses as a general law, now universally accepted by entomologists: “If only one of the sexes of an insect species is winged we must regard the wingless condition of the other as acquired during phylogenetic development.” This statement is also clearly applicable to ants, provided we insert the words “one phase of a sex” in the place of “one of the sexes.”

The above-described workers with vestigial wings evidently belong to the category of abnormal forms intermediate between normal worker and female ants, like the ergatoid females and pseudogynes.

1 This same winged soldier of Cryptocerus aztecs is also briefly described by my former pupil Miss Margaret Holliday in her paper entitled ‘A Study of Some Ergatogynic Ants.’ Zool. Jahrb. Abth. f. Syst., XIX, 4, 1903, p. 315.
While these latter, however, tend to resemble the normal female in the structure of the thorax but, like normal workers, lack wings, the workers above described have vestiges of wings but show no similarity to the female in the structure of the thorax. They therefore represent a distinct and hitherto apparently unknown group of gynæcoid abnormalities for which I would suggest the name *pterergates*.

**Postscript.**

While this paper is going through the press I find in a collection of ants made in Isle Royale near the northern shore of Lake Superior and sent me by Dr. Chas. C. Adams of the University of Michigan, three peculiar workers of a new variety of *Myrmica rubra sulcinodis* Nyl. They resemble one another and approach the female in the structure of the thorax. The mesonotum is delimited anteriorly by a distinct suture, is larger and more convex than that of the normal worker, and has finer longitudinal rugæ. There is a small and indistinct scutellum but no traces of ocelli. Two of the specimens have vestigial fore wings but on the left side only. In one the vestige is a minute nodule like that on the left side in one of the *M. scabrinodis* workers above described (Pl. XIV, Fig. 5). In the other the vestige is about the size of those shown in the worker represented in Fig. 4, but more shrivelled. These three abnormal *sulcinodis* workers resemble a worker of the same species described by Wasmann (Die ergatogynen Formen bei den Ameisen und ihre Erklärung, Biol. Centralbl., XV, No. 16 u. 17, 1895, p. 609) except in possessing wing vestiges. I believe it would be best to regard them all as pseudogynes, although these forms, which are well known in certain Camponotine genera (*Formica, Polyergus*, and *Camponotus*) are described by Wasmann as “stets ungeflügelt” (loco citato, p. 606).

**Explanation of Plate XIV.**

**Fig. 1.** — Anterior portion of adult worker larva of *Formica rufa* showing imaginal discs for legs at a, and at b and c vestigial imaginal discs for the hind and fore wings, respectively. After Dewitz.

**Fig. 2.** — Thorax and petiole of adult worker pupa of *Formica rufa* showing vestige of hind wing at b. After Dewitz.

**Fig. 3.** — Worker of *Myrmica rubra scabrinodis* Nylander var. with vestigial fore wings.

**Fig. 4.** — Thorax of a second worker of the same ant with more reduced fore wing vestiges.

**Fig. 5.** — Thorax of a third worker with still more reduced fore wing vestiges

**Fig. 6.** — Soldier of *Cryptocerus aztecus* Forel with vestigial fore wings.