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Description of a New Species of Slave-making Ant in the *Formica Sanguinea* Group (Hymenoptera: Formicidae)

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DESCRIPTION OF A NEW SPECIES OF SLAVE-MAKING ANT IN THE *FORMICA SANGUINEA* GROUP (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

The new species, *Formica gynocrates*, is described and illustrated from all the castes. This slave-making species is a member of the *sanguinea* group and is most similar to *F. pergandei*. The type locality is the E. S. George Reserve, Livingston County, Michigan. Specimens were also examined from North Dakota, Wyoming, and Colorado. A key is provided for the separation of the described North American members of the *sanguinea* group. The most commonly associated slave species is *F. vinculans* Wheeler, a member of the *neogagates* group. It is our opinion that *F. vinculans* is a valid species and not a synonym of *F. neogagates*, as has been previously supposed.

The following new species is described in order that the name might be available for use by Dr. Mary Talbot, who has studied its behavior and ecology. This species was long ago recognized as new by WFB and a preliminary description was drawn up. Following the death of WFB in 1983, and the acquisition of his collection by the Natural History Museum of Los Angeles County (LACM), RRS was asked to complete the description for publication.

The *Formica sanguinea* group is a small, Holarctic complex of dulotic (slave-making) ants that enslave species belonging to other species groups in the genus *Formica*. Most frequently, enslaved species belong to the *fusca, neogagates*, or *pallidefulva* groups. Occasionally species in other groups may be enslaved. Sometimes, also, two or more slave species may be present in a single nest.

Creighton (1950), following Wheeler (1913) and others, placed within *Raptiformica* all species of *Formica* with the apical clypeal margin more or less sharply notched or incised. While many species of *Raptiformica* were known slave-makers, others clearly were not. The non-dulotic species were removed from this group by Wilson and Brown (1955), who also rejected *Raptiformica* as a subgenus. The few, known slave-making species were grouped into the *sanguinea* group, a total of six species (including the Eurasian *F. sanguinea*) after five names were placed in synonymy.

Buren (1968) reviewed the group and recognized a total of 10 species, after he resurrected four names from the synonymy of Wilson and Brown. One new species was described. The only recent changes include one new synonymy by Snelling (1969) and the return of *F. obtusopilosa* to the *sanguinea* group by Wheeler and Wheeler (1963). Considerable work remains to be done in the systematics of this group, particularly in western North America, but that is beyond the scope of the present paper.

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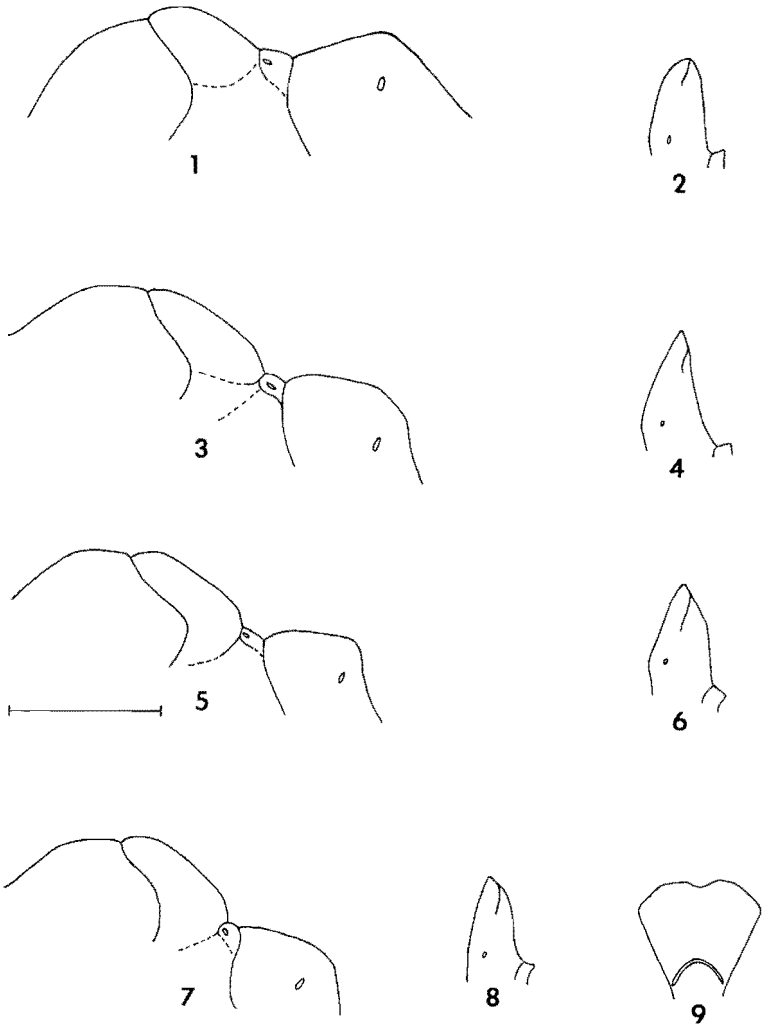

Fig. 1–9. Worker thoracic and petiolar profiles, respectively, of (1–2) *Formica subintegra*; (3–4) *F. rubicunda*; (5–6) *F. pergandei*; (7–8) *F. gynocrates*; (9) scale of petiole, anterior view, *F. gynocrates*. Scale line = 1.0 mm.

The following key will separate the presently described members of the *sanguinea* group in North America, including the new species described below. It replaces the earlier key by Buren (1968), which has proven to be unsatisfactory. Specimens from Colorado, Montana, Nebraska, and Wyoming may present difficulties since undescribed species are present in those States.

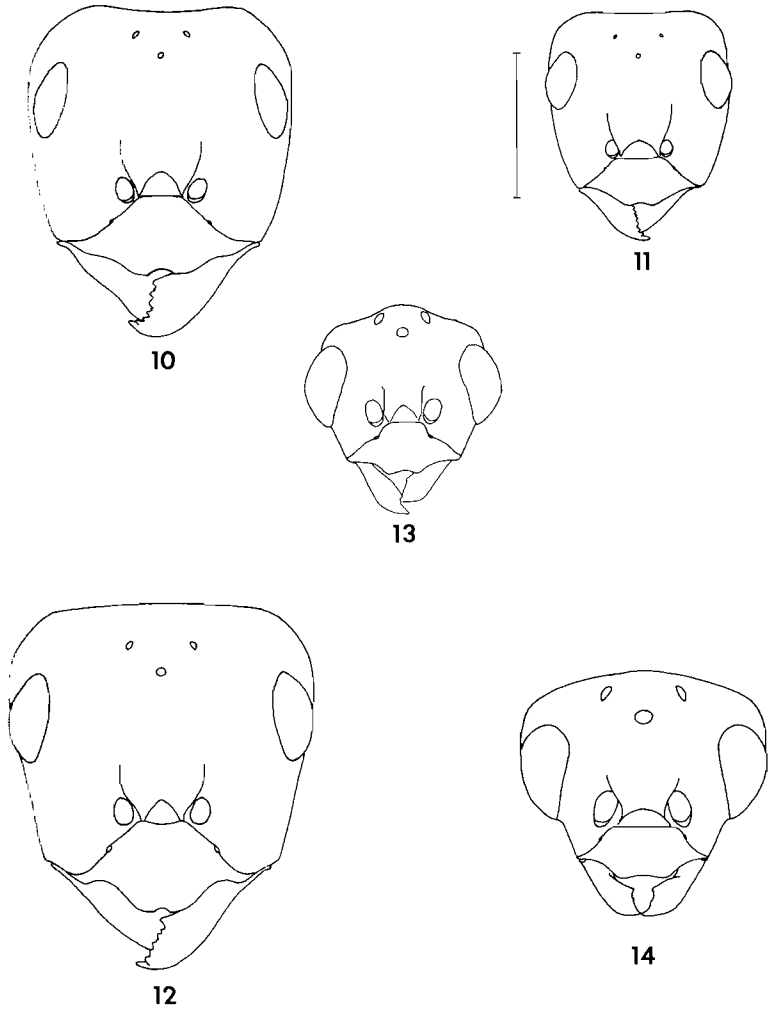

Fig. 10–14. *Formica gynocrates*, frontal view of head of (10) large worker (head width 1.86 mm); (11) small worker (head width, 1.23 mm); (12) female; (13) small male (head width 1.28 mm); (14) large male (head width, 1.63 mm). Scale line = 1.0 mm.

KEY TO NEARCTIC SPECIES, *FORMICA SANGUINEA* GROUP

1. Gula without erect hairs *and* pronotal dorsum with no erect setae or with fewer than six very short (less than 0.006 mm long), stiff, blunt bristles; crest of petiole without erect setae. 2
1′. Gula with one or more erect hairs on each side *and (or)* pronotal dorsum with six or more flexuous bristles, at least some of which are more than 0.10 mm long; crest of petiole with conspicuous erect setae. 3

2(1). Crest of petiole sharp, petiole broadly fan-shaped in posterior view; longest hairs on disc of second tergum about 0.06 mm long; clypeal disc distinctly very finely striate along middle and often laterad along apical margin .... *subnuda* Emery

2′. Crest of petiole blunt, petiole narrowly fan-shaped in posterior view; longest hairs on disc of second tergum about 0.10 mm long; clypeal disc without very fine striae along middle ..... *emeryi* Wheeler

3(1′). Erect hairs of thoracic and gastric dorsa short (0.06–0.14 mm long), stiff and bristle-like, usually more or less flattened and blunt-tipped, or abruptly tapering 4

3′. Erect hairs longer, (0.10–0.25 mm long), evenly tapering to tip 6

4(3). Scape shorter than head length; *either* (a) mesonotum and propodeum without erect hairs (or very nearly so) *or* (b) propodeum is subangulate in profile and crest of petiole is sharp 5

4′. Scape longer than head length; mesonotum and propodeum with numerous fully erect hairs; propodeum broadly rounded between basal and declivous faces; crest of petiole blunt in profile ..... *obtusopilosa* Emery

5(4). Thorax "saddle-backed" (Fig. 1); crest of petiole, in profile, blunt (Fig. 2) ..... *subintegra* Emery

5′. Thoracic profile less angulate (Fig. 3); crest of petiole, in profile, sharp (Fig. 4) ..... *rubicunda* Emery

6(3′). Pubescence of antennal scape fine and entirely appressed. 7

6′. Pubescence of antennal scape coarse and at least partly decumbent to sub-erect ..... *puberula* Emery

7(6). Eyes large and protruding beyond sides of head in frontal view in all sizes; female microgynous 8

7′. Eyes not protruding beyond sides of head, at least in large workers; known females normal, much larger than largest workers 9

8(7). Petiole with blunt crest, broadly fan-shaped in posterior view and usually with median notch; head often darker than thorax, but may be merely infuscated in occipital area ..... *wheeleri* Creighton

8′ .Petiole with sharp crest, narrowly fan-shaped in posterior view, more or less angularly convex across crest and without median notch .... *curiosa* Creighton

9(7′). Head as broad as long or broader, *and (or)* scape length distinctly less than head length; gaster with abundant erect hairs, those on disc of second tergum separated by less than their own lengths, longest at least 0.13 mm long and usually over 0.15 mm 10

9′. Head distinctly longer than broad in all sizes; scape longer than head; gastric hairs less than 0.13 mm long and on disc of second tergum separated by more than their own lengths ..... *creightoni* Buren

10(9). Mesopropodeal impression deep (Fig. 5); one or two hairs usually present on each side of gula; head usually broader than long and outer margins of eyes well removed from lateral margins of head in frontal view ..... *pergandei* Emery

10′. Mesopropodeal impression shallow (Fig. 7); gular hairs variable, but often absent; head longer than broad (rarely as broad as long) and outer margins of eyes approaching or exceeding head margins in frontal view (Fig. 9) *gynocrates*, new species

Formica gynocrates, **new species**

Figures 7–15

WORKER. Diagnosis: Superficially similar to *F. pergandei*, but differing in the shapes of the head and thorax, and in the sculpture, especially of the head. Head longer than broad in all sizes, and in large workers with weakly, nearly uniformly convex sides, and faintly

excised across posterior margin. Meso-propodeal impression weak and shallow. Integument opaque on nearly all surfaces, distinctly and consistently less shiny than in *F. pergandei*. Erect hairs numerous, arranged in pattern similar to that of *F. pergandei*, including long, slender, tapering hairs on gaster.

Measurements: Head length 1.39–1.97; head width 1.23–1.89; thorax length 1.90–2.65; pronotal width 0.87–1.29; total length 5.2–7.6 mm.

Head longer than broad in all sizes; CI 86–97 (mean CI = 91); in frontal view, sides of head strongly convex in small workers (Fig. 11), wider dorsad, but less strongly so than in other species of *sanguinea* group; minimum head width 0.70–0.80 times maximum width (mean = 0.76); occipital margin weakly excised. Scape length varying from a little shorter than, to distinctly shorter than, head length, SI 82–91 (mean SI = 87). Median carina of clypeus nearly obsolete; apical notch moderate. Eye length 0.64–0.84 times oculomandibular distance; in full frontal view eyes protruding beyond margins of head in all small workers (Fig. 11) and in some moderate-sized workers, but not in largest (Fig. 10).

Thorax (Fig. 7) moderately robust, promesonotal outline more moderately convex than in *F. pergandei* (Fig. 5); base and declivity of propodeum about equal in length; meso-propodeal suture weak; metathoracic spiracles little projecting.

Petiole (Figs. 9–10) narrowly to moderately fan-shaped in anterior view; crest moderately sharp and uneven, usually without median notch, but if notch is present, it is weak and shallow.

Nearly all surfaces opaque and very finely punctate. Mandible and legs subopaque. All surfaces duller than corresponding surfaces in *F. pergandei*, but similar to those of such species as *F. subintegra* and *F. rubicunda*.

Pubescence dense and fully appressed on dorsal surfaces of thorax and gaster, and on antennal scapes; moderate on vertex and occiput and on anterior surfaces of femora and tibiae. Erect hairs about as in *F. pergandei*, present on clypeus, frons, vertex (but absent from occiput behind eyes), and venter of head; numerous and elongate on disc of pronotum, present anteriorly and posteriorly on mesonotum, and on angle of propodeum; present across crest of petiole; numerous, long (0.15–0.20 on disc of second tergum), and tapering on gaster.

Head (including mandibles and antennae), thorax, legs, and petiole uniformly dull ferruginous; mandibles, anterior margin of clypeus, and lower portion of gena may be darker. Gaster dull, dark brown to blackish.

FEMALE. Diagnosis: Head large, wider than thorax; scape short, surpassing occipital corner by less than length of first funicular segment; sides of head very slightly convex to nearly straight; crest of petiole sharp, without median notch; integument dull, as in worker; pilosity about as in *F. pergandei*.

Measurements: head length 2.00–2.15; head width 2.00–2.12; scape length 1.51–1.70; thorax length 3.12–3.40; pronotal width 1.63–1.95; total length 8.2–9.6 mm.

Head shape (Fig. 12) trapezoidal as in other eastern members of the *sanguinea* group; cephalic index 98–102 (mean = 97); eyes large, OI 28–31, and 0.70–0.86 times oculomandibular distance; scape very short and stout, barely exceeding occipital corner; SI 73–80 (mean = 77).

Integument opaque and finely punctate on nearly all surfaces including gena. Mandible striate, but moderately shiny.

Pilosity pattern essentially as in *F. pergandei*; erect hairs present on median portion of head and median area of pronotum, around anterior and lateral margins of scutellum, a few on metanotum, across crest of petiole, and on gaster mostly confined to single row near posterior margins of terga. Head, antennae, thorax, legs, and petiole dull dark grayish ferruginous; gaster dull black. Wings infuscated with brown.

MALE. Diagnosis: See DISCUSSION.

Measurements: head length 1.19–1.48; head width 1.28–1.70; scape length 1.09–1.33; eye length 0.57–0.74; pronotal width 1.49–1.95; thorax length 2.47–3.16; total length 6.9–8.6 mm.

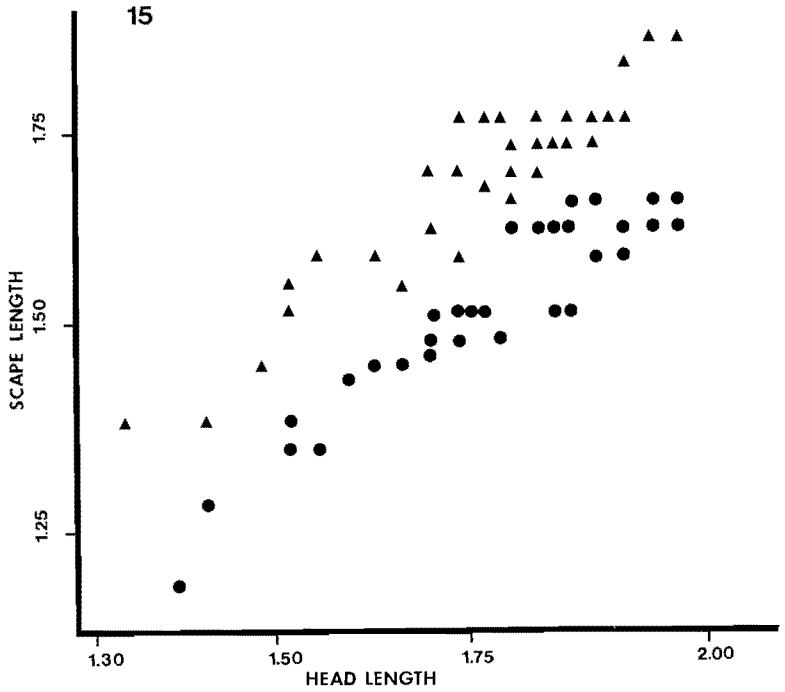

Fig. 15. Regression of scape length (SL) on head length (HL) in workers of *Formica gynocrates* (●) and *F. pergandei* (▲). Each symbol represents 1–3 specimens. For both species, $n = 50$.

Head (Figs. 13, 14) trapezoidal; cephalic index 106–117. Clypeal notch weak. Mandible with large apical tooth and two or three additional teeth basad, these usually blunt or obsolete, sometimes absent. Eye large, ocular index 47–50. Interocellar distance 2.3–3.8 times anterior ocellus diameter; ocellocular distance 2.3–3.3 times anterior ocellus diameter. Scape index 87–95.

Petiole rectanguloid in posterior view; median notch present, but usually weak.

All surfaces dull and opaque, except subopaque gaster.

Erect hairs present on clypeus, frons, vertex, disc of pronotum, scutellum, metanotum, and dorsal corners of petiole; absent from gastric dorsum. Appressed pubescence abundant on all surfaces.

Head and thorax dull black; mandibles light to medium brownish; legs yellowish; gaster dark brown. Wings infuscated with brown.

TYPE MATERIAL. Holotype worker, paratype workers, paratype females, and paratype males, all collected by Mary Talbot at the Edwin S. George Reserve, Livingston County, Michigan; the holotype was collected on 5 August 1972, and the remaining specimens were collected on this and various other dates. Holotype and most paratypes in Natural History Museum of Los Angeles County; paratypes deposited in American Museum of Natural History, Museum of Comparative Zoology, and United States National Museum of Natural History.

ETYMOLOGY. The specific name combines the Greek *gyne* (woman) and *krateo* (rule), in reference to the dulotic habits of this species.

DISCUSSION. Workers of *F. gynocrates* are most similar to those of *F. pergandei*, but may be distinguished by the differences in head shape and by the considerably duller integument, especially on the side of the head and thorax. Workers may be further differentiated by the consistently shorter scape of *F. gynocrates*. Figure 15 demonstrates the regression of scape length on head length. It will be seen that while there is broad area in the middle zone where the values are contiguous, but not overlapping, there are pronounced divergences at both lower and upper values.

The other two common eastern species, *F. rubicunda* and *F. subintegra*, both have workers in which the erect hairs on the dorsum of the thorax are very short, stiff and blunt or with abruptly tapering apices; the thoracic and petiolar shapes also differ (see key and figures). The differences in head shape, and in the sparse pilosity, will separate *F. gynocrates* from both *F. creightoni* and *F. subnuda*. The key should easily separate *F. gynocrates* from the described western species.

Females of *F. gynocrates* closely resemble those of the other eastern species, all of which are present at the George Reserve: *F. pergandei, F. rubicunda, F. subintegra*, and *F. subnuda* (those of *F. creightoni* are unknown). From *F. pergandei, F. gynocrates* may be separated by lack of short erect hairs on the lateral one-third of the occipital margin; females of *F. pergandei* have at least three or four on each side that are situated on the occiput above the eyes and there may be hairs on the occipital corners. Females of *F. pergandei* commonly possess 3–5 erect hairs on each side of the gula, while those of *F. gynocrates* have two or fewer, often none, on each side.

The disc of the first gastric tergum of *F. rubicunda* is without erect or suberect hairs, though fewer than eight may be present immediately below the summit of the declivous face. There often are none. In *F. gynocrates* females there are 15 or more suberect to erect hairs across the basal portion of the disc and the summit of the declivous face. While the number is variable, we have seen no specimens with fewer than 11 such hairs. The hairs of the mesoscutum and front of the head in both *F. rubicunda* and *F. subintegra* are flattened, which is not true of *F. gynocrates*, but the difference is less pronounced than is true of the workers.

Females of *F. subintegra* have a characteristic mandibular structure that will separate them from those of *F. gynocrates*. When the mandible is viewed from the side, there is a large, roughly triangular, flat basal area. In *F. subintegra* this area is polished and shiny between fine, well separated striae. In *F. gynocrates* this basal area is dull over most of its area because the interspaces between the striae are contiguously punctulate; the striae are often partially effaced. Also, in *F. subintegra* the petiolar scale, in profile, is blunt, much as in the workers, rather than sharp as in *F. gynocrates*. In the females of *F. subnuda*, the head width is consistently at least as great as head length, and consistently greater in sympatric populations (CI 100–109, $\bar{x} = 104$). The scape is proportionately longer (SI 88–92, $\bar{x} = 90$). There are usually no erect gular hairs in *F. subnuda* females and the mesoscutum is moderately shiny, with distinct piligerous punctures.

As is so commonly true of male ants, this caste is morphologically conservative and their identification fraught with uncertainties. Among the species of the *sanguinea* group present at the type locality, only the male of *F. pergandei* is easily recognized. In this species erect and suberect hairs are present across the entire width of the occipital margin. The remaining species have such hairs limited to the middle one-half, or less, of the occipital margin.

Males of *F. rubicunda* and *F. subintegra* both have proportionately larger ocelli than do those of *F. gynocrates*. The interocellar distance in *F. rubicunda* is 2.0–2.7, and usually less than 2.4, times the diameter of the anterior ocellus and the ocellocular distance is 1.8–2.4, and usually less than 2.3, times the diameter of the anterior ocellus. Males of *F. subintegra* and *F. subnuda* are similar, with the interocellar distance 2.0–2.5, usually less than 2.4, times the diameter of the anterior ocellus, and the ocellocular distance 2.1–2.5, usually less than 2.4, times the diameter of the anterior ocellus. Although the interocellar distance in *F. subintegra* is usually less than the ocellocular distance, they may be equal or the ocellocular distance may be the greater.

In *F. gynocrates* males, the interocellar distance is usually at least 3.0 times the diameter of the anterior ocellus and the ocellocular distance is usually more than 2.5 times the diameter of the anterior ocellus. The interocellar distance is at least equal to, and generally exceeds, the ocellocular distance.

The genital structures of all species were examined in situ. Infraspecific variation was so great that no obvious interspecific differences were seen and so these structures were not studied in greater detail.

Twenty-two males of *F. gynocrates*, associated with nest-mate workers, have been available. These males, as a whole, are variable in head shape. In frontal view, the occipital margin in large males (Fig. 14) tends to be broadly convex, with weak, or no, occipital angles, and the ocellar area weakly elevated. In smaller males, the occipital margin shows distinct lateral angles and the ocellar area is usually abruptly elevated (Fig. 13). The cephalic index in large males ranges from 110 to 120 and in smaller males the range is 106–108.

Of the 22 males, 16 (72.7%) have head widths ranging between 1.53 and 1.70 mm. The six remaining males (27.3%) have head widths ranging between 1.28 and 1.38 mm. There is a definite indication of two size categories of males, based on head width with a gap of about 0.15 mm between them. These males are from two colony samples and individuals of both size classes occur in only one colony sample, where they ae almost equally common (60% small, 40% large). The other sample includes only large males.

Whether or not males of *F. gynocrates* are actually dimorphic, as these data suggest, can only be determined by measuring many more specimens than are presently available. The apparent dimorphism may be an artificial result of a too limited sample size.

ADDITIONAL RECORDS. Stanton, NORTH DAKOTA, 20 July 1972 (A.C.F. Hung, no. 72–18; LACM); Wheatland, WYOMING, 24 July 1941 (W.F. Buren; LACM); Yellow Jacket Pass, 7700 ft el., Archuleta Co., COLORADO, 21 July 1955 (R.E. Gregg; LACM).

SLAVE-SPECIES. The principle slave-species of *F. gynocrates* at the type locality is *F. vinculans* Wheeler; a secondary slave species is *F. lasioides* Emery. Both are members of the *neogagates* group. *Formica vinculans* was originally described as a variety of *F. neogagates* by Wheeler (1913), but later was synonymized by Creighton (1950). We believe that *F. vinculans* should be resurrected from synonymy.

In the extensive Michigan material submitted by Dr. Talbot, *F. vinculans* seems to be consistently different from sympatric material of *F. neogagates*. In *F. vinculans* the thorax is paler than the head and gaster, the gastric pilosity is longer and the appressed pubescence is much less sparse than in *F. neogagates*. Nests of *F. vinculans* are more populous and are apparently always in open, sunny, prairie-like locations utilizing some vegetative debris. When nests are disturbed the workers display aggressive alarm.

In contrast, *F. neogagates* nests in woodlands under various covering objects, and the nest superstructure is a mound of soil. Disturbed workers exhibit panic alarm behavior.

ECOLOGY. At the type locality, Talbot (1985) found that nests of *F. gynocrates* were always in open, prairie-like situations. She also found that this species is more heat tolerant than other eastern members of the *sanquinea* group, capable of carrying on raiding activities at surface temperatures at which *F. subintegra* becomes disorganized (Talbot and Kennedy 1940). The enslaved species were always members of the *neogagates* group, usually *F. vinculans*, but occasionally *F. neogagates*. At the George Reserve, *F. gynocrates* was observed not to raid nests of species belonging to the *fusca* and *pallidefulva* groups, although these are regularly utilized as slaves by *F. subintegra, F. pergandei*, and *F. rubicunda* in this area.

Talbot's observations on *F. gynocrates*, as well as on *F. creightoni*, suggest that *F. gynocrates, F. creightoni, F. curiosa*, and *F. wheeleri*, form a subgroup within the *sanguinea* group that utilizes mainly or only *neogagates* group species as slaves. Following the postulate that parasitic ant species are often phylogenetically derived from their hosts or from lineages that are closely related to the host lineage (''Emery's Rule,'' Wilson 1971), the *sanguinea* group could be derived from species within the generalized

fusca group or *rufibarbis* group. The latter group, in particular, includes species that form populous colonies of aggressive workers.

That species of the *wheeleri* subgroup enslave members of the *neogates* group may be a secondarily derived specialization. This specialization has taken place in North America where the *neogagates* group arose and diversified with its half dozen or more species. The *neogagates* group is especially diverse in western North America with most of these species adapted to open habitats, such as prairies, forest clearings, and sagebrush desert. Most of the species of the *wheeleri* subgroup are also western, and those that are not nest in open prairie-like situations.

The sociobiological ramifications of this specialization are of interest. Talbot (1985) has observed that raiding workers of *F. gynocrates* rush forward among the *F. vinculans* defenders, then quickly retreat. During these sorties, raiders were not observed to spray defenders. This is an action not previously reported for raiding species of the *sanguinea* group.

Thus, if they were releasing any type of allomone, as surmized by Talbot, the method of release and the glands and substances involved may be different from the "propaganda" acetates from the enlarged Dufour's gland sprayed by *F. subintegra* and *F. pergandei* during their raids on *fusca* group species (Regnier and Wilson 1971). If different actions and different glandular products are used in subjugating *neogagates* group colonies, then it seems possible that evolutionary selection might enhance the tendency toward raiding *neogagates* group nests and becoming obligate slavers on this species group.

Whatever the degree of specialization necessary for the raiding workers to enslave *neogagates* group species, it is tempting to suggest that the behavior of nest-founding females may also be specialized. Within the *wheeleri* subgroup, *F. curiosa, F. wheeleri,* and an undescribed western species are known to have microgynous females; *F. creightoni* is believed to share this characteristic, based on the samll size of the male (Buren 1968). Within this subgroup, only *F. gynocrates* is known to have normal-sized females. *A. priori*, it may be assumed that the method by which the microgynes gain acceptance into a host colony must be different from those displayed by *F. sanguinea* in Europe (Huber 1810, Forel 1847, Wasmann 1891); the females of *F. sanguinea* are normal-sized. At present, nothing is known of colony-founding methods of any of the North American members of this group.

For all that has been written about the dulotic species of *Formica* we know remarkably little. With the pioneering work of Regnier and Wilson (1971) on the "propaganda" substances, the careful work of Talbot in demonstrating that host selection can be species-specific and that there are measurable ecological differences between the species, and with the recent advances in the taxonomy of the group, the time seems propitious for a major comparative sociobiological study of these interesting ants.

ACKNOWLEDGMENTS

We are especially indebted to Mary Talbot for making available long series of *F. gynocrates* and of other *sanquinea* group members sympatric with it at the E. S. George Reserve. Thanks are extended to James C. Trager for his generous assistance in expediting the transfer of the Buren collection to LACM, and for locating WFB's manuscript notes.

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