THE NATURAL HISTORY OF MANICA (Hymenoptera: Formicidae)[1]

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ABSTRACT

Manica was long regarded as a subgenus of *Myrmica*; the differences between these two genera are shown in a table. Keys are given to the species of *Manica*. *M. rubida* is Eurasian; *bradleyi*, *hunteri*, *mutica*, and *parasitica* occur in North America west of the hundredth meridian and north of the thirty-fourth parallel. *M. rubida* inhabits the mountains of Europe, Asia Minor, northern Asia, and the Caucasus; *bradleyi* occurs in the mountains of California and adjacent western Nevada; *parasitica* is known from only two localities in the Sierra Nevada; *hunteri* is the northern montane species. *M. mutica* has the most xeric, the most extensive (Great Plains and Great Basin and northward to Alaska) and the lowest (down to 1,100 feet in British Columbia) range; nevertheless it is also found in mountains (above 7,000 feet) in California, Colorado, New Mexico, and Wyoming. Spot maps illustrate the distribution of the four American species. Throughout the ranges distribution is sporadic, but any species may be locally abundant.

In spite of the remarkable anatomical similarity among the five species, it is difficult to generalize about their ecology and habits. Since almost nothing is known about *Manica parasitica*, except that it is presumably a social parasite on *M. bradleyi*, it is not considered further. *M. bradleyi* and *hunteri* are typically found in openings in coniferous forests; *mutica* and *rubida* occur in a greater variety of habitats. *M. mutica* is the most xerophilous; the others prefer moderately moist soil and can even tolerate mud. The basic nest structure is probably the same for all four: a reticulum of chambers and galleries connected with chambers under stones opening to the surface by holes in the bottom of one or more small craters constructed of excavated soil; but great plasticity is manifest in the variations on the basic plan. The nests are usually polycalic and their limits almost impossible to determine. Food is an unsolved mystery. Workers do take insects into the nest; but (in *bradleyi* and *hunteri*) only a few are out at any time, for only a few hours during the day and rarely at night; surely they cannot support a flourishing colony. Colonies are small; we would guess a thousand workers to be the maximum for a mature colony. A polycalic colony probably has many queens. Little is known about the nuptial flight.

The ants of this genus are not aggressive, but when their nest is disturbed the workers sting promptly and effectively. The sting has been reported to be very painful, but we have found it only moderately so with three of our American species.

The gait of workers of three of our American species is characteristic: steady, deliberate and unhurried, but never sluggish.

The three common American species—*bradleyi*, *hunteri*, and *mutica*—are treated under the headings: description, nuptial flight, census, relations with other ants, miscellaneous notes, range, records, and literature. The discussion of *M. rubida* is based on the literature.

EPIGRAPH

"What was formerly called natural history is the perennial foundation of the biological sciences. It has given rise to all the theoretical branches and will no

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doubt give rise to others in the future, and all the practical applications of biology have their roots in ecology, which is one of the basic branches of natural history, dealing with the behavior of organisms in relation to one another and to their environment. It formulates most of the basic problems which the experimentalists and biometricians are endeavoring to solve. Its concrete, sensuous, esthetic character will always attract the observer and the thinker, because it attaches itself to the individual organisms, and the individual is always essentially inscrutable and indefinable. The naturalist and the nature lover will, therefore, always be with us. No matter how far the naturalist may specialize in his study of single groups of organisms or of the faunas and floras of particular regions or geological ages, he is always keenly aware both of the limitations of his specialty and of its relations to the whole realm of living things. Such modesty is not always apparent in the biologist in the strict sense, because he is not engaged in sympathetically exploring the contours of nature, but in determining the extent to which phenomena conform with his experimental, metrical and therefore highly rational procedure." (W. M. Wheeler 1931: 11–12.)

The genus *Manica* has received scant attention from laymen, entomologists, and myrmecologists. There are good reasons for this neglect: (1) the workers are just medium-sized; (2) the colors are drab in comparison with those of many common insects; (3) these ants lack unusual structures (scrobes, spines, tubercles, grotesque heads); (4) while the sting is potent, they rarely have an opportunity to use it on man; (5) they exhibit no unusual habits, such as slave-raiding, fungus-growing, or harvesting; (6) their economic importance is almost nil.

We became interested in *Manica* during our study of the ants of North Dakota. The ranges of several western species of ants reach their limit in the southwestern corner of that state. To seek an explanation we devoted several summers to observing and collecting in western states and provinces. One of these species was *Manica mutica*, and our interest gradually spread to its congeners.

In 1967 we joined the staff of the Desert Research Institute of the University of Nevada System. In summers the Mobile Unit of the Institute's Laboratory of Desert Biology is stationed in Little Valley (Fig. 1), Washoe County, Nevada, which is 20 miles south of Reno at an elevation of 6,400 feet. The Valley is part of the George Whittell Forest and Wildlife Area and comprises a mountain meadow surrounded by coniferous forest and traversed by Franktown Creek. We have spent parts of three summers with the Unit and found the Valley a very favorable place for the study of *Manica* because the ranges of two species end there with a slight overlap: *M. mutica* flourishes on the meadow, while openings in the coniferous forest seem ideal for *bradleyi*.

THE GENUS *MANICA* JURINE

The genus *Manica* was established by Jurine in 1807, but Mayr in 1855 placed the type species (*rubida*) in the genus *Myrmica* and W. M. Wheeler in 1910 considered both *rubida* and *mutica* to be in *Myrmica*. In 1914, however, W. M. Wheeler wrote: "The large and handsome *Myrmica rubida* Latreille remained for many years the only species

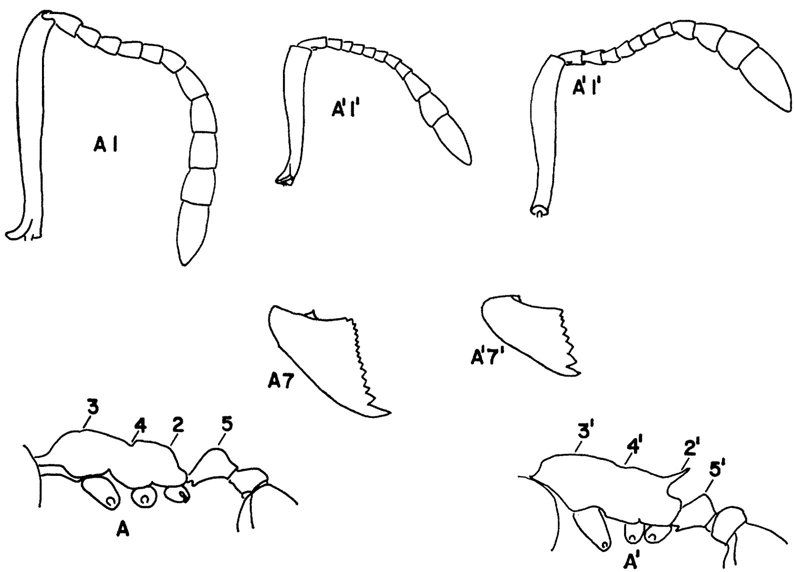
FIG. 1. Little Valley, Washoe County, Nevada (T. 16 N., R. 19 E., sec. 17). The light area is the meadow on the floor of the valley (6,200′). Franktown Creek meanders the length of the meadow. The range of *Manica bradleyi* descends from the mountains on the west (upper left) and ends in the forest on the lower right. *Manica mutica* is common in Washoe Valley (5,000′), two miles to the east, and terminates its range on the meadow, where it is locally abundant. (Courtesy of the Whittell Forest Board of Control.)

of an aberrant group within its genus. . . . As all five of the species now recognized are closely related to one another and constitute a sharply defined group, I propose to separate them from *Myrmica sens. str.* as a subgenus, *Oreomyrma, subgen. nov.*, with *M. rubida* Latr. as the type." Emery in 1921 and W. M. Wheeler in 1922 used the correct subgeneric name of *Manica*. Finally, Weber (1947) and Creighton (1950) independently separated the subgenus from *Myrmica* and elevated it to generic rank.

Manica and *Myrmica* are still regarded as closely related and among the least specialized genera in the tribe Myrmicini (subfamily Myrmicinae). Nevertheless, it is difficult to understand why the two taxa were ever placed in the same genus, unless it was an aversion to monotypic genera (when *rubida* was the only known species of *Manica*). But why did W. M. Wheeler, who recognized the aberrance (see above), maintain a subgenus even when five species were known? The two groups have little in common (aside from tribal characters). W. M. Wheeler, in his 1922 key, combined them on rather dubious characters: "Funiculus of antennae slightly swollen into a 3- to 5-jointed club.

Under side of head without psammophore. Head longer than broad." In addition to these, Emery (1921) listed for *Myrmica s. lat.*: no dimorphism; masticatory border long, furnished with many teeth; maxillary palps of 6 segments, labial of 4; thorax with an impression or a very conspicuous notch at the level of the mesoëpinotal suture; female winged, not much larger than the worker; male of the same size as the female; mandibles of male narrower than those of the worker, with the border dentate; male with the Mayrian furrows distinct; forewing of male with a closed cubital cell (which is incompletely divided), one discoidal cell and one open radial cell.

By contrast, the differences are numerous and distinctive, as shown in the following comparison. The accompanying illustrations are lettered and numbered to correspond with the characters below that they illustrate.



MANICA

A. WORKER

1. Antennal club 5-segmented.
2. Epinotum unarmed, spines replaced by blunt projections.
3. Promesonotal suture faint but visible on dorsum.
4. Mesoëpinotal suture strongly impressed.

MYRMICA

A.' WORKER

1'. Antennal club 3- or 4-segmented.
2'. Epinotum armed with spines or teeth.
3'. Promesonotal suture absent.
4'. Mesoëpinotal suture moderately impressed.

5. Petiolar node evenly rounded.
6. Sculpture less rugose, especially on thorax where rugae occur in parallel lines.
7. Each mandible with a prominent apical tooth and a prominent subapical tooth; the remaining 12–14 teeth minute.
8. Averaging notably larger, length 3½–8 mm.

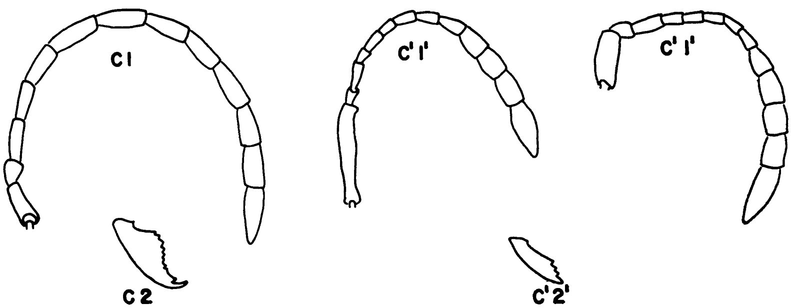
5′. Petiolar node usually with an angular crest.
6′. Rugae on the thorax (and usually elsewhere as well) strongly reticulate, even in smoother forms.
7′. Each mandible with 7–12 well developed teeth increasing in size toward apex.
8′. Averaging notably smaller, length 3–6½ mm.

B. Female

1. Averaging notably larger, length 7–12 mm. (Like worker in 1, 2, 6, and 7 above.)

B′. Female

1′. Averaging notably smaller, length 4–7 mm. (Like worker in 1, 2, 6, and 7 above.)



C. Male

1. Antenna without a club.
2. Mandibles similar to those of worker in length and dentition.
3. Averaging notably larger, length 6½–10 mm.

C′. Male

1′. Antenna with a 4- or 5-segmented club.
2′. Mandibles smaller than those of worker; with 4–8 teeth.
3′. Averaging notably smaller, length 3½–7 mm.

D. Larva

1. Without anchor-tipped hairs.

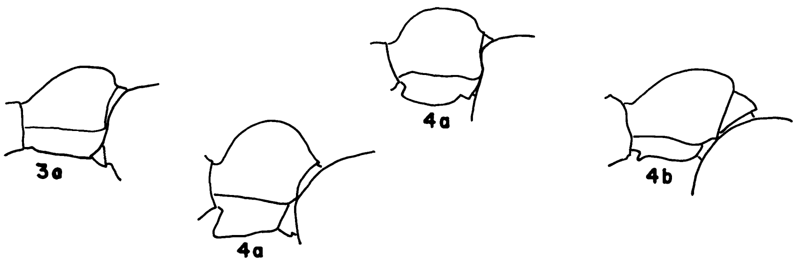
D′. Larva

1′. With anchor-tipped hairs.

In 1934 *Manica* comprised six species, but in 1956 Cole synonymized W. M. Wheeler's *aldrichi* into *hunteri*, leaving a total of five—one Palearctic, *rubida* (Latreille), and four Nearctic: *bradleyi* (W. M. Wheeler), *hunteri* (W. M. Wheeler), *mutica* (Emery), and *parasitica* (Creighton).

Key to the Workers and Females of *Manica*

(In the accompanying drawings some key characters are illustrated; the numbers are those of the key couplets illustrated.)



1a. Head and gaster black or dark brown; thorax much lighter (light brown to reddish yellow); thoracic sculpture prominent, surface scarcely shining .... *bradleyi*
1b. Concolorous or head and gaster only slightly infuscated and darker than thorax 2
2a. Black or very dark brown; shining .... *parasitica*
2b. Red, reddish yellow, or yellow 3
3a. Postpetiole without any ventral tooth or projection .... *mutica*
3b. Postpetiole with a distinct ventral projection 4
4a. Postpetiole with a large conoidal ventral protuberance, protuberance larger and more rounded than petiolar projection; North American .... *hunteri*
4b. Postpetiole with a small slender ventral projection, projection smaller than ventral petiolar projection; Eurasian .... *rubida*

Key to the Known Males of *Manica*

1a. Concolorous black .... *bradleyi*
1b. Bicolored 2
2a. Head, thorax, petiole, and postpetiole black, gaster brown .... *mutica*
2b. Black, except posterior portion of gaster yellowish brown 3
3a. Eurasian .... *rubida*
3b. North American .... *hunteri*

SIZE. Among Nearctic ants, *Manica* species are large. Only *Neoponera, Odontomachus, Pogonomyrmex, Atta, Camponotus, Myrmecocystus,* and *Formica* include larger workers. But three of these genera are outside the range of *Manica*. Therefore, within its range, the size of the largest *Manica* workers would be exceeded only in certain species of *Pogonomyrmex, Camponotus, Myrmecocystus,* and *Formica.*

HABITAT. The typical habitat of *M. bradleyi* and *M. hunteri* is an opening in a coniferous forest (preferably lodgepole pine, *Pinus murrayana* Grev. and Balf.). We have never found them in deciduous forests, pinyon-juniper woodlands, or dense forests of any kind. The nest is near (but not under) trees, so that it is shaded for part of the day. Ground cover is scant and at least half the surface is bare. The

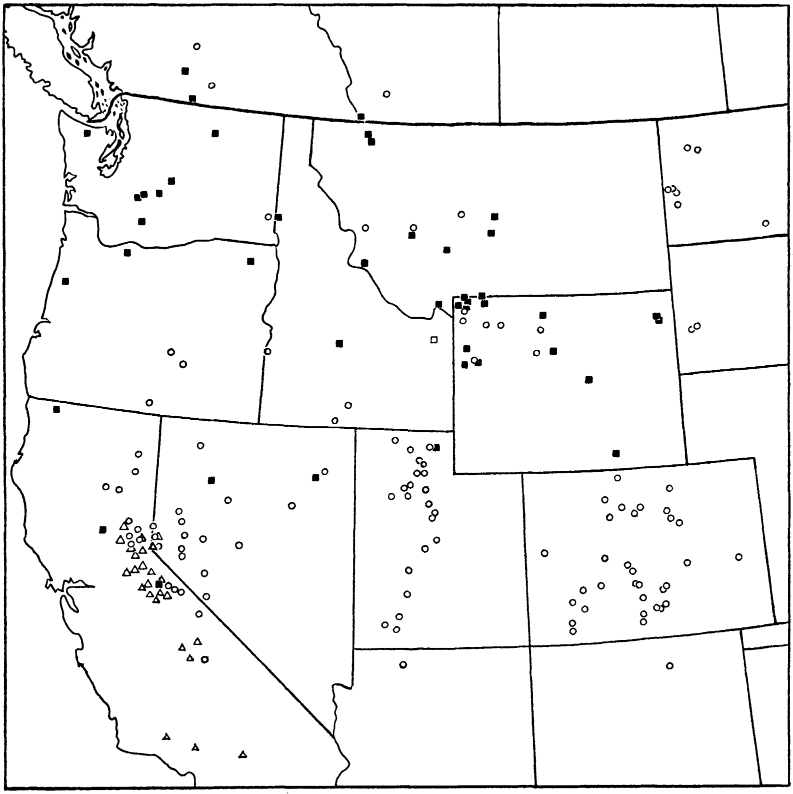


FIG. 2. Geographic distribution of *Manica bradleyi* △; *M. hunteri* ■ (two Alberta localities—Edmonton and Jasper Park—not shown; they are about one inch north of upper border of map); *M. mutica* ○ (Alaskan record not shown).

slope is steep, with a southern exposure. The soil is a sandy loam containing many small stones and with flat stones on the surface.

But there is considerable deviation in *hunteri* and still more in *bradleyi*. We have found nests of *bradleyi* in small pockets of soil on the granite domes in Yosemite National Park, on level ground, in soil free from stones, under the sidewalk on a motel lawn, in wet soil under a stone in a mountain meadow, and in mud near an overflowing spring. Always, however, these atypical sites were near conifers.

Not only does *M. mutica* have the largest range by far of any American species, but it also occurs in the greatest variety of habitats: openings in coniferous forests, deciduous forests (river fringes), pinyon-juniper woodlands, grasslands, and cold deserts. It is also quite at home

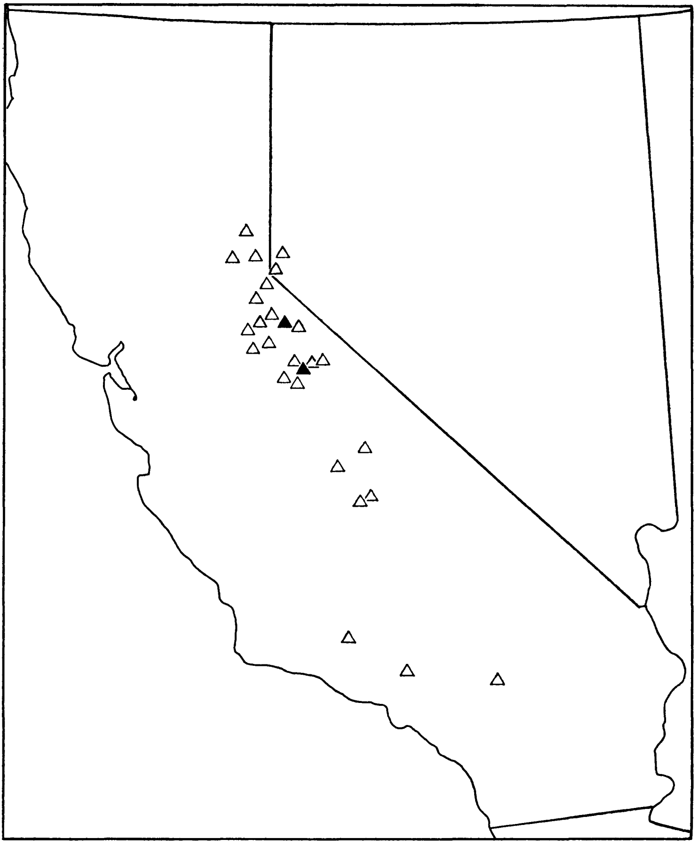


FIG. 3. Geographic distribution of *Manica bradleyi* △; the two mixed colonies of *M. bradleyi* and *M. parasitica* ▲.

in such disturbed areas as parks, lawns, and the shoulders and ditches along highways; it occurs as often in areas with low vegetation as in bare areas. We have never found it in tall grass or forbs nor in densely wooded areas.

Throughout Switzerland *M. rubida* is very common in humid places, more common in the northern part than in the southern. It occurs everywhere in swamps and woods, along brooks and rivers and in moist meadows. In the Alps it attains its climax in the subalpine zone. One does not find it on arid slopes that are exposed at midday, nor in dry places in general. In his 1915 article on Swiss ants Forel wrote:

FIG. 4. Typical habitat of *Manica bradleyi* near Tioga Pass (10,000′) in Yosemite National Park, California.

"Sporadic to 1500 m. Common on the banks of rivers, where it builds nests in the sand, which open by craters. Also on roads, in earth nests."

NEST. The basic nest plan for the genus includes a reticulum of chambers and galleries in the soil, connecting with chambers under stones lying on the ground, and opening by holes in the bottom of one or more craters of excavated soil. The entrance holes and galleries are approximately ¼ inch in diameter; the chambers are 1 or 2 inches in diameter and ¼ inch high. The craters are 3 to 4 inches in outside diameter and ½ inch high at the rim; they are constructed of coarse pellets of soil excavated below ground by the workers, and are slightly eccentric. If an entrance is at the edge of a stone, the crater is semi-circular. But variations are infinite, depending upon size of colony, terrain, soil, habitat, and doubtless many other factors.

In *M. bradleyi* there may be only one crater or only one stone (Fig. 6) or craters only (Fig. 7) or stones only. In our records the smallest covering stone was 7 × 7 × 1 inches and the largest 24 × 20 × 15 inches.

The entrances in craters serve for ingress and egress, but since workers are seldom seen on the surface and the craters may be numerous, we suspect that they have another function, ventilation. There is no evidence that they are feeding stations. By far the commonest activity

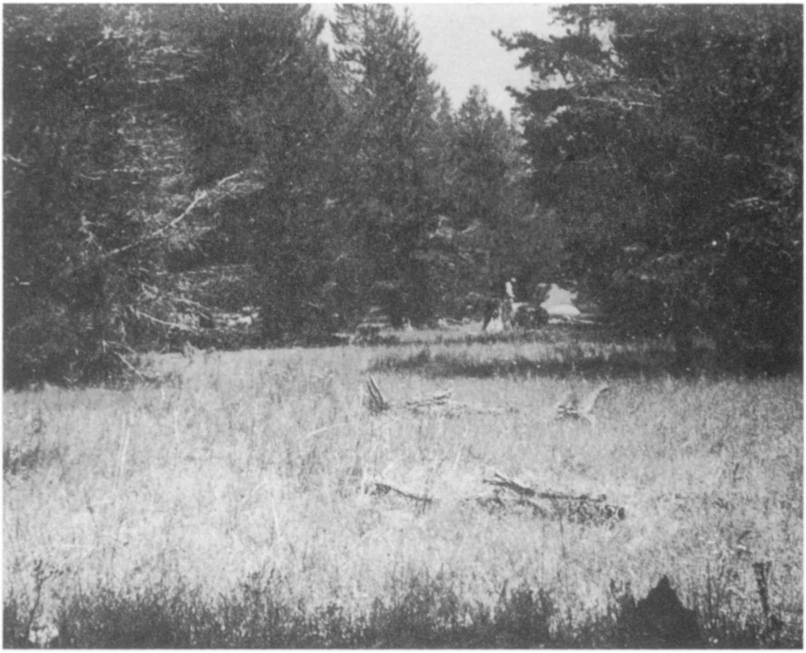


FIG. 5. Typical habitat of *Manica bradleyi* in Little Valley, Washoe County, Nevada: opening in coniferous forest.

of *bradleyi* and *hunteri* on the surface is excavation: workers emerge from the entrance carrying a load of earth in the mandibles; they go to the rim or edge of the crater and drop the load; then they return immediately to the entrance and descend. Marking individuals at craters suggests that certain workers are permanently detailed to keep an entrance open and to reopen it after a storm.

The greatest depth of any *bradleyi* nest we have excavated was 27 inches. We found brood in chambers at various depths from just beneath the surface to 11 inches. Brood chambers are never large: 1 or 2 inches in diameter and about ¼ inch high. In our observation nests the brood chambers were flat-floored dilatations of a gallery and about 10 mm in diameter; galleries are usually about 5 mm (see Figs. 8–10).

The largest—in surface area—*bradleyi* nest we have observed was in Little Valley (Washoe County, Nevada). It was in an elliptical opening (125 × 90 feet) in a Jeffrey pine forest. The nest was in the northern half of the ellipse. The craters were scattered over a roughly triangular area of about 800 square feet; in this area we counted 64 craters (Fig. 11).

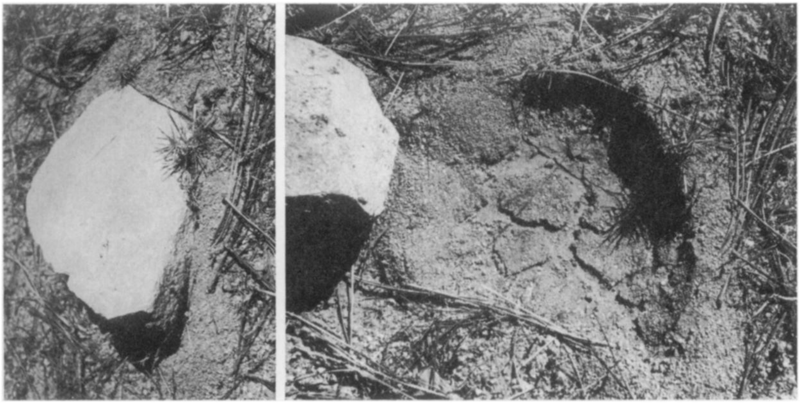


FIG. 6. Nest of ***Manica bradleyi*** under a stone. The photograph on the left shows the undisturbed stone; note the excavated earth at its edges; one entrance is visible. In the photograph on the right the stone has been lifted to show chambers and galleries. Little Valley, Washoe County, Nevada.

The question posed by the nest mentioned (and by most of the other *Manica* nests we have examined): is this the work of one colony? We do not have the answer, since we have never found a queen-mother in any *bradleyi* colony. In many other species of ants a colony is intolerant of other colonies of the same species. But this is not true of *bradleyi*. We shall return to this question later.

Since the colonies of *Manica* are usually polycalic,[4] we have not been able to determine the limits of a nest.

[4] We prefer Forel's "polycalic" (Gr. *poly-* many + Gr. *kalia* hut, barn, bird-nest) = having many nests, to the bastard derivative "polydomous" (Gr. *poly-* many + L. *domus* house, home). One might also coin "polydomatous" which is all Greek or "multidomous" (all Latin).

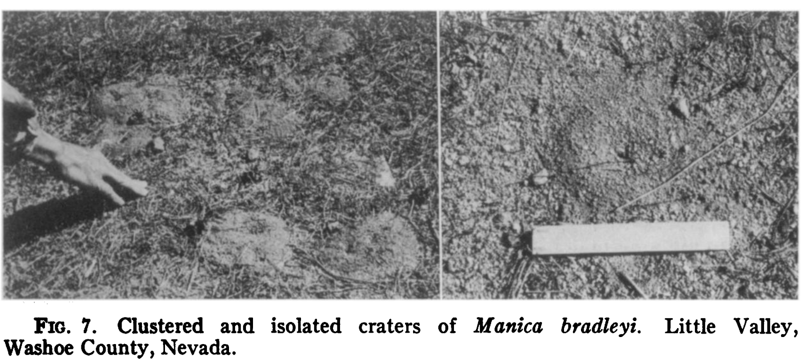


FIG. 7. Clustered and isolated craters of ***Manica bradleyi***. Little Valley, Washoe County, Nevada.

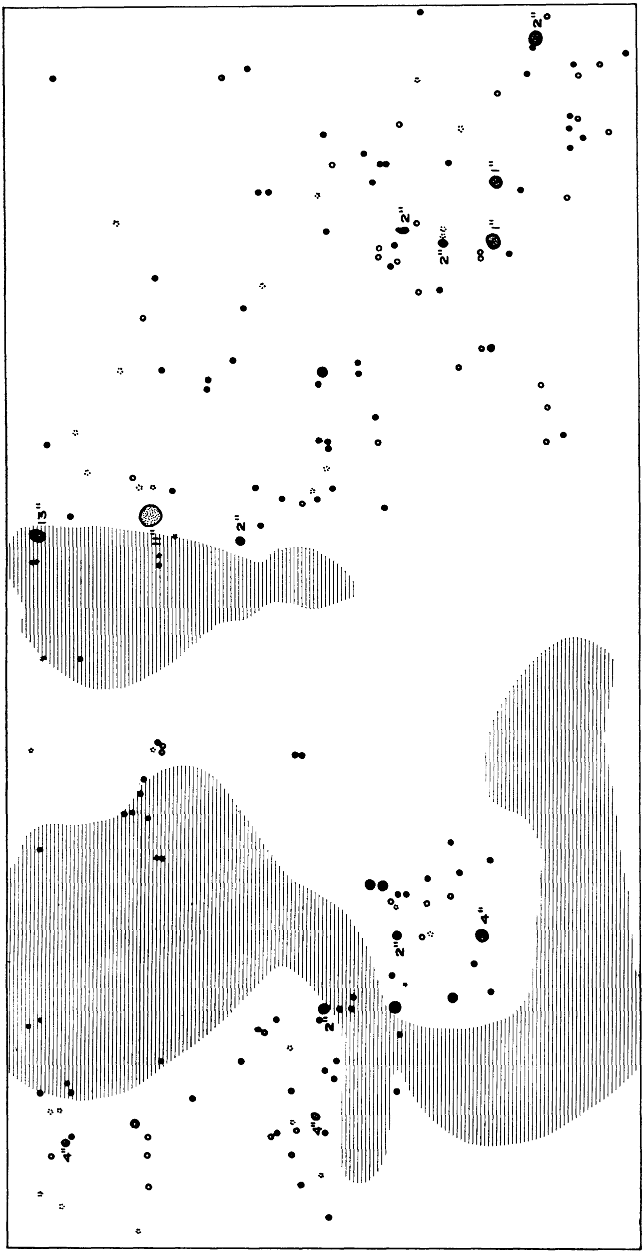


FIG. 8. Map of a nest of *Manica bradleyi* in Little Valley, Washoe County, Nevada. An area 5 × 10 feet was marked off on mostly bare ground; the hatching indicates a low cover of vegetation. All entrances were shown on the map by solid circles. Then the superficial soil was removed to a depth of four inches and galleries were added as dotted circles. The new surface was watered thoroughly; after it had dried, the new entrances were added as open circles. The brood chambers were added as stippled circles and the depth of each chamber (below the original surface) was written beside it.

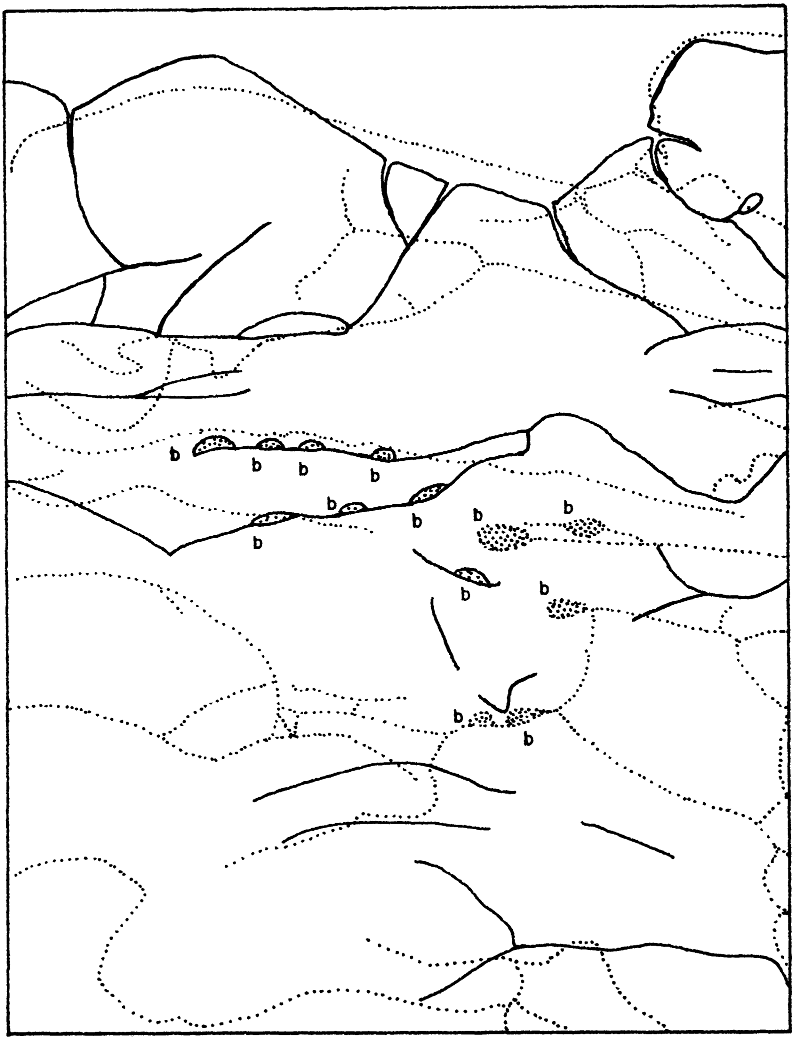


FIG. 9. Map of a vertical observation nest 13 × 9½ × ½ inches housing *Manica bradleyi*. The galleries and brood chambers (b) tunneled in the soil are shown by solid lines for the near side of the nest and by dotted lines for the far side.

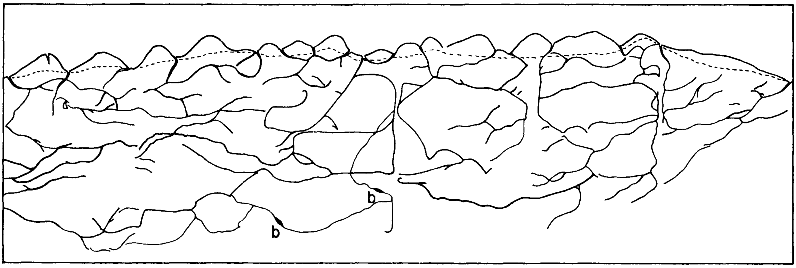


FIG. 10. Map of a vertical observation nest 72 × 24 × ¾ inches housing *Manica bradleyi*. The galleries tunneled in the soil next to the plastic wall on one side are shown by solid lines; brood chambers (b) are stippled. The broken line indicates the dry-moist soil boundary near the surface.

Nest structure is less variable in *hunteri*; for example, craters are more rare than with *bradleyi* and *mutica*. We have, however, encountered two extreme deviants: in one the *hunteri* colony was in the edge of a mound occupied by *Formica fusca*; in the other the *hunteri* colony occupied an earthen mound which had been apparently constructed and formerly occupied by *F. fusca*.

In *M. mutica*, irregular craters are often constructed among plants. Craters on bare ground may be so close together that they merge into a low messy mound. We have counted 14 distinct craters in an area of 14 square feet.

In Switzerland (according to Forel) *M. rubida* nests are nearly always in very fine sand at the border of torrents from the Alps. The craters are constructed from this sand.

Eidmann (1926:782) found *rubida* only once in the vicinity of Munich—a gigantic colony spread over an area of a hundred square meters, with dozens of entrances, each surrounded by a small sand crater.

FOOD. The food of *Manica* is a complete mystery to us. One rarely sees the American workers wandering far from a crater. Occasionally we have seen them carrying seeds and living or dead insects into the nest. Furthermore, the workers are active on the surface for such short periods that it seems improbable they could bring in enough forage to feed a populous colony. Our captive colonies have thrived on insects alone or on a mixture of honey, sugar, and yolk of hard-boiled egg; we are still trying to learn their source of natural foods. The lack of activity on the surface suggests an underground source, and the nest locations suggest that the food may involve the root-mycorrhiza association. There is also the possibility that *M. hunteri* feeds on the brood of other ants (see discussion under "Nest").

LOCOMOTION. The locomotion of *Manica* workers may be described as deliberate and moderately fast but not sluggish and never hurried; "sedate" would be a good anthropomorphism.

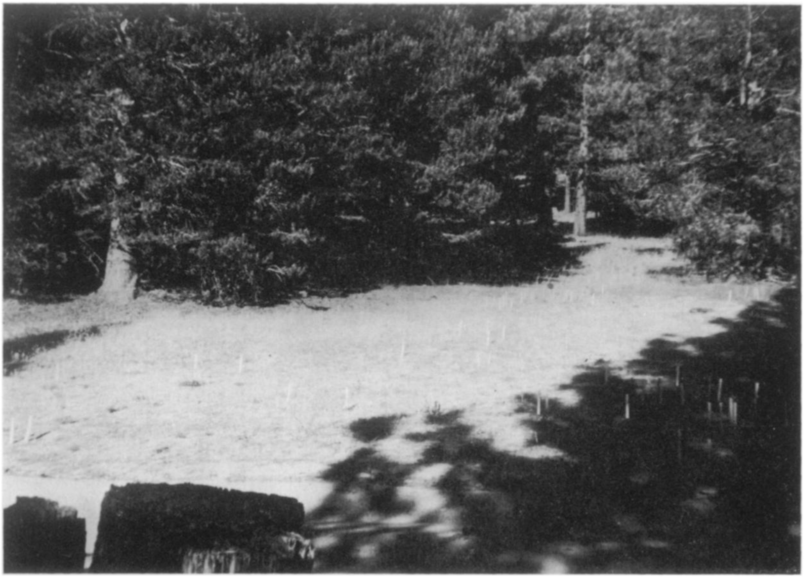


FIG. 11. Sixty-four craters (marked with stakes about one inch wide) in an area of 800 square feet; presumably all are part of one polycalic *bradleyi* nest. Little Valley, Washoe County, Nevada.

DEFENSE. The workers of this genus are not very aggressive, but if a nest is disturbed they attack *en masse* and sting promptly. The typical position for stinging: the skin is gripped with the mandibles; the gaster is curled under the thorax and the sting is inserted into the skin. But a worker may also sting with the gaster in either a horizontal or a vertical position.

The effects of ant stings are the results of so many variables in both the aggressor and the victim that it is difficult to generalize. But, since *Manica mutica* and *M. rubida* have been reported to inflict very painful stings, we are recording our own experiences. We have suffered many stings by *bradleyi*, *hunteri*, and *mutica*, but the effects on us have never been severe or very painful. (Certainly they are much less painful than the stings of *Pogonomyrmex*.) At the worst we would describe them as mildly painful, or merely as annoying. There is always a burning sensation, which may begin immediately or after a delay of 15 minutes; this lasts for 15 to 60 minutes. Usually there is erythema in the vicinity of the puncture and sometimes a minute white spot at the site. For a day or two there may be erythema and itching if the site is rubbed.

A colleague found that the sting of *bradleyi* on the middle finger at 7:00 P.M. was annoying for 15 minutes but was not noticeable after an hour. During the night the site began to itch; on the following morning there was a white spot at the site; around this there was erythema that extended onto the back of the hand, which was swollen near the finger; swelling and severe itching persisted for 48 hours.

The effect of the sting on other ants is lethal.

"Tout le monde craint la piqûre des fourmis," said Forel, who seemed almost obsessed with the sting of *rubida*. "C'est sans contredit l'espèce la plus redoubtable des fourmis d'Europe." In fact, he referred to it in his list of Swiss ants as "la grande fourmi rouge des sables et du bord des rivières, qui pique sévèrement." "The sting . . . is really very painful: the pain is, in my opinion, at least as severe and above all sharper than that of the common social wasps." [In German he was more laconic: "Sticht furchtbar."] But its nests are in exposed places and, therefore, easily avoided. Furthermore, it is not aggressive (much less so than, for example, *Myrmica laevinodis*). Forel never witnessed an unprovoked attack on other colonies. But he did perform (July 1863) some experiments that illustrated ferocity under provocation. He emptied a sackful of *Formica pratensis* on a *rubida* nest; the *rubida* workers surrounded the greater number of *pratensis* workers and stung them all to death in less than an hour. On another occasion (July 1871) he placed a few *rubida* workers on a large polycalic nest of *Formica cinerea*; they survived for two hours among the myriads of their enemies, killing many more than their own number.

Eidmann (1926:782) said that *rubida* was *wehrhaft und wegen ihrer Stiche gefürchtet.*

COLOR AND POLISH. As ants go, *Manica* is beautifully colored. The workers range from yellow to red to brown to black. The queens are somewhat more colorful—yellowish red through red to black. The males have the head and thorax black; the gaster may be yellowish red or black or black with brown sides. There is, however, not much patterning of the color in this genus.

The color is enhanced by the polished surface of some parts, notably the gaster, which looks as if it had been burnished. Even the dull surfaces are attractive under low magnification, which reveals a variety of fine sculpturing.

In our description of color we have followed the practice, started in our "Ants of North Dakota," of using the Munsell system.[5] With this system, one may be both precise and approximate, e.g., yellowish red (5YR 5/8). To interpret the Munsell notation, one must compare the ant with Munsell color chips, but for most purposes "yellowish red" would suffice. Such adjectives are certainly preferable to vague terms like "ferrugineous," "fuscous," or "piceous."

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[5] Munsell Soil Color Charts may be obtained from Munsell Color Company, Inc., 10 East Franklin Street, Baltimore, Maryland. They will suffice for the colors of Nearctic ants.

RANGE. *Manica* is essentially a genus of high altitudes. The Old World species occurs in the mountains of Europe, northern Asia, Asia Minor, and the Caucasus (Emery 1921:43). In the New World it occurs in the United States and Canada (Figs. 2, 3), between the 100th meridian and the Pacific coast and from the 34th to the 61st parallels. The easternmost record is in the Missouri River valley in south-central North Dakota; the westernmost is in the Coast Ranges of Oregon about 20 miles from the coast; the southernmost is in the San Bernardino Mountains in southern California; the northernmost is near Anchorage, Alaska. The range in altitude is from 1,100 feet at Penticton, British Columbia to 10,000 feet in the Sierra Nevada in California. Although 1,100 feet is not a high altitude, biogeographically speaking, high altitude is roughly equal to high latitude. The elevation of 8,400 feet in southern California at 34°N approximates 1,100 feet in southern British Columbia at 50°N.

The spot maps (Figs. 2, 3) are based on data from our own collection (164 records from 65 localities), to which we have added data supplied by others (see "Acknowledgments"). The grand total for the genus (in America) is 331 records from 225 localities.

PHENOLOGY. See Table 1.

EVOLUTION. We offer the following hypotheses concerning evolution within the genus *Manica*. *Mutica* may be regarded as ancestral for two reasons: (1) it is the most plastic (least restricted) species in habitat and habits; (2) its range is by far the largest. *Bradleyi*, *hunteri*, and *rubida* evolved directly from *mutica*; *parasitica* evolved from its host, *bradleyi*. Western North America may be considered the center of origin (see Wheeler, 1914:122) because four of the five species occur here, including the putative ancestral species, *mutica*. The Eurasian species, *rubida*, probably evolved in the Old World. Two facts support this: (1) *mutica* occurs in Alaska; (2) *rubida* is more similar to *mutica* than to any of the other species.

LITERATURE: See Creighton 1950:107; W. M. Wheeler 1914: 118, 122.

Manica bradleyi (W. M. Wheeler)

DESCRIPTION. *Worker*. Length 4–8½ mm. Head very dark gray (2.5YR 3/0) to black (2.5 YR 2/0); thorax dull brown (7.5YR 4/4) to yellowish red (5YR 5/8); gaster black (N/0). Head moderately shining; thorax dull; gaster very shining. *Female*. Length 10½ mm. Epinotum, petiole, and postpetiole yellowish red (5YR 5/8) to red (2.5YR 4/8); tarsi and mandibles yellowish red (5YR 5/8) to very dusky red (2.5YR 2/2); head, thorax, and gaster black (7.5YR 2/0 to 2.5YR 2/0). Head dull, thorax moderately shining, gaster very shining. *Male*. Length 6–8½ mm. Black (7.5YR 2/0). Head dull; thorax dull to moderately shining; gaster shining. *Brood*. Color variable; larvae often creamy white with a dirty gray meconium showing through from interior; becoming yellowish, especially at anterior

TABLE 1. Phenology of members of the genus *Manica*.
(Elevation, expressed in hundreds of feet, indicated in parentheses below dates.)

Locality	Eggs	Larvae	Pupae	Winged females	Winged males	Nuptial flights	Sexuals (not in nest)
				M. bradleyi			
California	—	22-25-VI (60–100)	22-VI (100)	23-VI-17-IX (60–93)	6-17-IX (60–80)	—	—
Nevada	27-VI, 5-VIII (64)	11-VII-8-VIII (63–88)	1-8-VIII (64–88)	18-VII (64)	10-18-VIII (64)	20-23-VII (64)	—
	1-VII (72)	—	—	20-IX	—	—	—
				—			
				M. hunteri			
Alberta	—	21-VIII	31-VII	—	—	—	—
British Columbia	—	—	—	—	28-VII (40)	—	—
Montana	—	1-21-VIII (50–58)	1-VIII (50)	—	16-21-VIII (50–75)	—	—
Washington	—	22,23-VII (33–50)	22-VII (50)	21-VII (35)	20,23-VII (33–34)	—	—
Wyoming	4,31-VIII (80)	14-IV-1-IX (64–80)	4-VIII-1-IX (80)	26-VIII-1-IX (70–80)	26-VIII-1-IX (70–80)	—	—
				M. mutica			
Alberta	—	—	—	—	—	—	♂♂ 23-IX
British Columbia	—	—	—	—	—	—	♀♀ 18-IX

Table 1. (*Continued*)

Locality	Eggs	Larvae	Pupae	Winged females	Winged males	Nuptial flights	Sexuals (not in nest)
California	—	14-VIII (56)	14-VIII (56)	30-VII (62)	14-VII (56)	—	—
						—	—
	—	—	—	—	30-VII (62)	—	—
Colorado	—	—	—	— —	—	—	♀♀ 19-V; ♂♂, ♀♀ 29-VII
Nevada	—	24-VII (64)	24-VII (64)	20-VII (50)	20-VIII (50)	20-IX (64)	—
							—
North Dakota	—	10-VI-2-VIII (18–25)	10-VI-2-VIII (18–25)	6-IX (25)	13-VII-6-IX (20–25)	—	—
Utah	—	—	—	—	—	—	♂♂ 20-VII, 22-X ♀♀ 20-X
Wyoming	—	31-VIII (58)	—	4-VIII (58)	—	—	—
				M. rubida			
Switzerland	—	—	—	16-V (Black Forest); 16-VI (Wasen nr Fluelen); 17-VIII (Rhone nr Yvorne); 30-VIII (nr summit Mt. Tendre)	16-V (Black Forest); 16-VI (Wasen nr Fluelen; 17-VIII (Rhone nr Yvorne); 30-VIII (nr summit Mt. Tendre)	—	♂♂ 24-VI (Sion); ♀♀ 19-V (Wildegg); 26-VI (Sierre); 7-VII (Bregaglia); 18-VII (Lintthal); 21-VII (Gadman)
Germany	—	—	—	—	—	—	16-V (Munich)

end; semipupae and pupae usually yellow; but brood of same size may be white, yellow, or orange.

NUPTIAL FLIGHT. On August 20, 1967, in Little Valley (Nevada) we noted a worker dragging (by one leg) a deälated female toward a crater. We rescued the female and placed her in a petri dish. By the following day she had laid a batch of eggs. The eggs were all gone (presumably eaten) by August 31. On September 10 we transferred her to a tube separated from a colony of workers by a cotton plug. After a few hours she had gotten through the plug and had been accepted by the workers, four of which were avidly licking her thorax and gaster. These observations suggest that fecundated queens may leave the parent nest sporadically and be adopted by established colonies.

Notes on a nuptial flight in Little Valley, 6,400 feet, 1967: September 17–18 it rained all night (1.11 inches), minimum 42 F. (The last previous rain, 0.34 inches, had fallen on September 4.) September 18, cloudy all day, maximum 56 F. September 19, minimum last night 34 F, maximum today 68 F. September 20, minimum last night 34 F, maximum today 71 F; nuptial flight in afternoon; two deälated females were excavating. September 21, minimum last night 32 F, maximum today 76 F. September 22, minimum last night 36 F, maximum today 69 F. On bare patches in a mountain meadow near the edge of a pine forest, many deälated females were excavating burrows. Soil was brought out in the mandibles, head first, and dumped in a pile; small stones, some larger than the head, were also brought out in the mandibles, but the female backed out of the burrow. Usually a female worked alone, but we observed two excavating from one hole and three from another. On the following morning, most of the holes were plugged with excavated soil. On September 28 we dug out two of the closed burrows; one contained a single queen, the other five queens.

On August 3, 1968 we found an incipient nest. The entrance was ⅛ inch in diameter; it was in the center of a disc of fine excavated dust; a few nanitic workers were seen on the surface occasionally. On August 24 we excavated the nest and found two dead queens and three living workers.

On September 23, 1967, at 9 A.M., in the warm (70 F) laboratory, we noticed that winged females and males confined in a jar-nest were attempting to fly. When released into a cage about three feet high, the males promptly flew to the top and most of the females hid on the floor, but two also flew to the top. A male caught one in flight and the pair fell to the floor in copulo. Males attempted to copulate with workers.

CENSUS. Until the limits of a nest can be established and an entire colony excavated, no reliable census can be made. The following counts are the best we can offer:

Alpine Co., California, 3 mi NE Clark Fork Campground, Stanislaus National Forest, 6,100 ft: Sept. 7, 17, 1967, 379 workers, 1 winged female, 53 males, 5 female pupae, 2 sexual semipupae, 26 larvae. Sept. 17, 1967, 225 workers, 8 winged females, 47 males. July 24, 1968, 291 workers, 5 female pupae, 8 male pupae, 3 worker pupae, 11 larvae.

Mono Co., California, 1 mi E Sonora Pass, 9,300 ft: Sept. 5, 1967, 696 workers, 48 female pupae, 207 male pupae, 178 worker pupae, 4 larvae. July 24, 1968, 465 workers, 2 winged females, 28 female pupae, 168 worker pupae, 66 larvae. These two samples were from the same polycalic colony.

Tuolumne Co., 3 mi W Sonora Pass, 8,000 ft: Sept. 17, 1967, 227 workers, 8 winged females, 15 males, 29 male pupae, 36 worker pupae.

Washoe Co., Nevada, Little Valley, 6,400 ft: July 19–31, 1967, 1,045 workers, 38 worker pupae, 36 sexual larvae, 511 larvae. August 18, 1966, 283 workers, 1 winged female, 8 males. Sept. 14, 1967, 140 workers, 5 female pupae, 54 worker pupae, 2 sexual semipupae, 26 larvae.

RELATIONS WITH OTHER ANTS. In Little Valley, *Formica* (*Proformica*) *lasioides* Emery lives in the same habitat as *Manica bradleyi*. It is, in fact, the only other species of ant that nests and wanders among the craters of the latter. Its nest-mounds are of about the same size as those of *bradleyi*, but are irregular and messy and are usually at the base of a clump of grass, whereas the mounds of *bradleyi* are neat and nearly symmetrical craters that are rarely near plants. The workers of *lasioides* are shining black and smaller. They move erratically, i.e., a fast spurt for about 12 inches, a sudden stop and then another spurt with a change of direction; this is in marked contrast to the slower gait and steadier course of *bradleyi*. *F. lasioides* is active all day, whereas *bradleyi* is usually out only for brief periods in early morning and in the evening. Also the workers of *lasioides* avoid encounters with *bradleyi*. Should such encounters occur, the results are suggested by occasional observations of *bradleyi* carrying *lasioides* into its nest.

Another ant common in the *bradleyi* range is *Formica sibylla* W. M. Wheeler, which is black and somewhat larger than the largest *bradleyi* workers. The members of this species construct craters in dry sandy areas that are usually bare of vegetation. Frequently an enormous number of craters are clustered in a small area. Such areas are often contiguous with clusters of *bradleyi* craters; sometimes there is overlap but never are the clusters of the two species coextensive. The two kinds of craters are easily distinguishable: *sibylla* craters are larger (6 to 7 inches in diameter vs. 3 to 4 inches), higher (1 inch vs. ¼ to ½ inch), with a larger entrance (½ to ¾ inch vs. ¼ inch) and dustier (in contrast with the more granular structure of *bradleyi* craters). We have witnessed no encounters between workers of these two species.

As a general rule, different colonies of ants, even of the same species, are mortally hostile to each other. Therefore, the behavior of *bradleyi* and its congener *Manica mutica* in captivity was surprising. We placed a group of workers of each species in separate observation nests connected by tubing plugged with cotton. We intended to leave the plug in place for several days so that nest odors could intermingle. But the workers soon extracted the cotton and wandered freely in both nests. There was no conflict, but a *mutica* worker would pick up a *bradleyi* worker, carry it to the refuse dump and drop it; the *bradleyi* worker simply curled up until dropped; then it got onto its feet and wandered back into the crowd. Some *bradleyi* workers were carried to the dump several times. Finally this behavior ceased and the two species lived together harmoniously and behaved alike, even to interspecific feeding and grooming.

That such harmony may exist in nature is suggested by our observation in Little Valley, where the ranges of the two species meet and overlap slightly: we have seen *mutica* working in a crater 7 inches from a *bradleyi* crater.

Manica parasitica (q.v.) has been found twice in *bradleyi* nests.

MISCELLANEOUS NOTES. As a general rule *Manica bradleyi* workers are to be seen on the surface only in the early morning and in the evening, when the air temperature is between 65 and 75 F. Usually it is only the excavators that are seen; each brings out a pellet, drops it on the outer slope of the crater and immediately re-enters. Often single workers will be seen wandering a few inches or a few feet from the craters. We have seen no evidence of systematic foraging but have occasionally seen single workers carrying insects into the entrances. Once we saw a dozen workers drag home an inch-long caterpillar and pull it down the entrance tunnel. The amount of foraging observed would be inadequate to supply even a small colony. As a result of marking experiments, we suspect that each excavator is permanently stationed at a certain crater. If such be the case, then she must be fed by other workers inside the nest. We have, however, taken a marked worked at an entrance 21 inches from the one at which she was marked.

On mild nights, especially after a rain, the workers were active on the surface after dark.

We soon found that workers could gnaw cork; so we were forced to use rubber stoppers in observation nests.

Winged daughter females often participate in such nest work as excavating and carrying out dead. They are able to feed themselves, as are the males.

In captivity, *bradleyi* workers were observed sweeping fine soil particles toward their mandibles with their front feet as they tilt the lower part of the head backward and close the mandibles. If, during the sweeping, the worker contacted a particle one millimeter or more in diameter, she immediately stopped sweeping and carried it away with her mandibles.

The average weight of the largest *bradleyi* workers is 5.5 mg.

Workers in an observation nest responded instantly and simultaneously by bouncing to certain human vocalizations. Unlike *hunteri* not more than half the workers reacted.

RANGE. This species is known only from the Sierra Nevada Mountains in California and western Nevada and the Transverse Ranges in southern California. The northernmost record is Sagehen Creek, Nevada County, California and the southernmost is Big Bear Lake in the San Bernardino Mountains. The lowest and highest records are in Yosemite National Park, 4,000 feet on the Valley Floor and 10,000 feet at Tioga Pass. Though sporadically distributed within its range, this species may be locally very abundant.

LOCALITY RECORDS. CALIFORNIA. Alpine Co.: 3 mi NE Clark Fork Campground, Stanislaus National Forest 6,100′; Lake Alpine, 7,400′; Wood's Lake 8,400′. Calaveras Co.: 1 mi W Big Trees 4,500′; 14 mi NE Big Trees 6,500′. El Dorado Co.: Luther Pass 7,700′; Lake Tahoe. Fresno Co.: Kings Canyon National Park 6,000′. Los Angeles Co.: Blue Ridge (San Gabriel Mts.) 7,400′. Mariposa Co.: Yosemite National Park (Gin Flat 7,200′, Glacier Point, Polly Dome 8,200′, 8,600′, 2 mi W Polly Dome 8,400′, Valley Floor 4,000′). Mono Co.: Lee Vining 7,500′; 2 mi SE Sonora Pass 8,400′; 1 mi E Sonora Pass 9,300′; Tioga Road 8,000′; T. 5 N., R. 22 E. 8,000′. Nevada Co.: Sagehen Creek (T. 18 N., R. 16 E.) 6,400′. Placer Co.: 13 mi E Forest Hill. San Bernardino Co.: Big Bear Lake (San Bernardino Mts.). Tulare Co.: General Grant National Park; Sequoia National Park 6,000′, 6,500′, 9,000′. Tuolumne Co.: Dodge Ridge S Pinecrest 6,000′; Long Barn 4,700′; Pinecrest 5,300′, 5,400′; Sonora Pass 9,600′; nr Sonora Pass 8,500′; 3 mi W Sonora Pass 8,000′; Strawberry Lake (T. 4 N., R. 18 E.) 5,800′; Yosemite National Park (Crane Flat 6,000′, Tioga Pass 10,000′, Tuolumne Meadows 9,000′, 5 mi E Tuolumne Meadows 9,300′, White Wolf Lodge 8,200′). Ventura Co.: Mt. Pinos 7,200–7,800′. NEVADA. Douglas Co.: Lake Tahoe 6,600′. Washoe Co.: nr Hobart Creek Reservoir 7,200′; Little Valley 6,400′; nr Mt. Rose (T. 17 N., R. 19 E., sec 19) 8,800′. Type locality: Alta Meadow, Tulare Co., California.

LITERATURE. Cole (1957: 212) and Mallis (1941: 65) describe nests. Wheeler and Wheeler (1960: 6, 9) described and figured the larva. W. M. Wheeler (1909: 78) referred to *bradleyi* as a "beautiful species."

Manica hunteri (W. M. Wheeler)

DESCRIPTION. *Worker*. Length 5½–7½ mm. Head strong brown (7.5YR 5/8) through dark reddish brown (5YR 3/2) to dark red (2.5YR 3/6) with variable dark reddish brown (2.5YR 2/4) infuscation; thorax yellow (10YR 7/8) through yellowish red (5YR 5/8)

FIG. 12. Typical habitat of *Manica hunteri*, Big Horn Mountains, Sheridan County, Wyoming; six miles east of Burgess Junction on U. S. Highway 14 (T. 55 N., R. 88 W.), 8,000′.

to red (2.5YR 4/6); gaster yellow (10YR 7/8) through yellowish red (5YR 4/8) to reddish brown (5YR 4/4) with variable transverse bands of very dusky red (7.5YR 2/2) infuscation. Head and thorax feebly to strongly shining; gaster strongly shining. *Female.* Length 8–10 mm. Yellowish red (5YR 4/8) or reddish yellow (7.5YR 6/8) with a narrow dusky red (2.5YR 3/2) or brown (7.5YR 4/4) band near posterior margin of first gastric segment and sometimes with three black lines on thorax. Mesonotum, petiole, postpetiole, and gaster strongly shining; elsewhere dull. *Male.* Length 6½–9 mm. Black (N/0), except sides of gaster strong brown (7.5YR 5/6). Mesonotum, petiole, postpetiole, and gaster strongly shining; elsewhere dull.

CENSUS. Under a single stone 7 × 4 × 1½ inches lying on the ground, at 8,000 feet on Casper Mountain in Wyoming on September 1 we collected what may have been an entire colony: 1,279 workers, 2 deälated females (= queens), 6 winged females, 75 males, 110 worker pupae, 63 female pupae, 40 male pupae, 434 larvae, and 666 eggs.

Since we have not been able to determine the limits of a nest or colony, we can hardly approximate the population, but we suspect that the above census represents the maximum for a mature flourishing colony.

MISCELLANEOUS NOTES. In an observation nest the workers gnaw corks; rubber stoppers must be used.

Males feed themselves. Workers groom males.

The large larvae of *hunteri* are active, flexible and extensible. When the honey-sugar-yolk food was placed near larvae, they fed upon it. Larvae were observed feeding on a dead fly: the mouth parts, which were half-buried in fly tissues, made pumping movements; the mandibles did not move from side to side; when a worker picked up and moved the fly, three larvae remained attached.

On August 4, 1965, in the Big Horn Mountains in Wyoming, at 8,000 feet, under a half-buried stone 10 × 5 × 5 inches, we found a populous colony of *hunteri* crowded around a physogastric queen. Her gaster was so swollen that the widely separated sclerites showed as conspicuous bands across the paler intersegmental membranes, which were greatly stretched. In fact, she resembled very closely the physogastric queens of the smaller species of army ants (*Neivamyrmex*). In an observation nest (August 8) the workers again pressed in upon her, avidly licking her gaster; there were many eggs in the nest. On August 12 we suspected she was dead but could not be sure because of the workers crowded around her; on August 16 she was obviously dead, but workers were still attracted.

All the workers in a colony respond instantly and simultaneously by a slight bounce to certain human vocalizations e.g., *but* and *co-* of "colony" (but not to *and*). They did not respond to finger-snapping.

The workers must touch larvae with their antennae in order to find them; otherwise the workers walk on and over the larvae without realizing their presence.

Notes on the surface activity of *hunteri* at Cooke City, Montana, 7,500 feet, August 2, 1965: 9:30 A.M., warm and sunny, usually two or three workers near each entrance. At 10:00 A.M., warmer, none out. By late afternoon they began to appear on the surface. At 7:30 P.M., mild cloudy twilight, two or three near each entrance. At 9:00 P.M., dark and cloudy, 64 F, two or three near each entrance. Usually there are no workers on the surface after dark, presumably because night temperatures are too low.

RANGE. This northern montane species ranges at elevations somewhat lower than those of *bradleyi* from northern Utah and northern Nevada to central California, thence northward into southern Canada. The southernmost record is in the Sierra Nevada in California, in Tuolumne County, 3 miles west of Sonora Pass at 8,000 feet; the northernmost is Edmonton, Alberta, at 2,200 feet; the easternmost is Sundance, Wyoming, at 6,700 feet; the westernmost is Mary's River, Oregon, at 4,100 feet, about 20 miles from the Pacific Ocean. The lowest record is 2,200 feet at Edmonton, Alberta and the highest 9,000 feet at Angel Lake (near Wells), Nevada.

It is strange that this species does not occur in Colorado (Gregg, 1963). We found it in abundance on Casper Mountain, Wyoming, which is 125 miles north of the Colorado boundary, and there is a record from Centennial, Wyoming, only 20 miles north of the boundary.

LOCALITY RECORDS. ALBERTA. Gorge Creek; Hillhurst (Edmonton) 2,200′; Jasper Park; Waterton Lakes National Park—3 mi NNE Cameron Lake 4,300′. BRITISH COLUMBIA. Manning Provincial Park Hq. 4,000′; Merritt. CALIFORNIA. Sierra Co.: Sierra Buttes. Siskiyou Co.: 3 mi W Donomore Meadow (Siskiyou Mts.) 6,300′. Tuolumne Co.: Chipmunk Flat (3 mi W Sonora Pass) 8,000′. IDAHO. Custer Co.: Stanley; 5 mi S Stanley 6,300′. Freemont Co.: 16 mi N Warm River 6,400′. Latah Co.: Moscow 2,600′. MONTANA. Fergus Co.: Camp Maiden (Judith Mts.) 5,000′; Rock Creek (Big Snowy Mts.) 5,800′. Gallatin Co.: "Madison R., nearly opposite mouth of Beaver Creek" 7,500′ (Type); Earthquake Lake 7,000′. Glacier Co.: Glacier National Park (Rising Sun Camp Ground 4,500′, St. Mary's Entrance 4,500′, Sunpoint Overlook 4,600′, Two Medicine Camp Ground 5,200′). Lewis and Clark Co.: Helena. Meagher Co.: 18 mi E Townsend 5,000′. Park Co.: Cooke City 7,500′. Ravalli Co.: Sula. NEVADA. Elko Co.: Angel Lake (nr Wells) 9,000′. Pershing Co.: Pole Canyon (E Humbolt Mts.). OREGON. Hood River Co.: Salmon River Meadows (Mt. Hood). Lincoln Co.: Mary's Peak 4,100′. Wallowa Co.: Anaeroid Lake (Wallowa Mts.) 7,000′. WASHINGTON. Clallam Co.: Olympic National Park (Hurricane Ridge 5,200′, 5,500′, 5,600′). Kittitas Co.: Blewett Pass 2,300′. Okanogan Co.: 18 mi E, 9 mi S Omak 3,400′. Pierce Co.: Mt. Ranier National Park (Cougar Rock Picnic Area 3,300′, Longmire 2,800′, trail to Emmons Glacier, 2 mi E Sunrise Lodge 5,000′). Yakima Co.: Mt. Adams; Hells Crossing (American River) 3,500′. WYOMING. Albany Co.: Centennial 8,800′. Big Horn Co.: Meadow Lark Lake 8,500′. Crook Co.: Sundance 6,700′; 5 mi NW Sundance 6,400′. Natrona Co.: Casper Mt. 8,000′. Park Co.: Clark's Fork Yellowstone River, 15 mi SE Cooke City, Montana. Sheridan Co.: 6 mi E Burgess Junction on Highway 14, nr Prune Creek (Big Horn Mts.) 8,000′. Teton Co.: Grand Teton National Park; Moran; U.S. Highway 89 nr Snake River (3 mi S entrance to Yellowstone National Park 7,000′). Yellowstone National Park (Canyon Junction, Grizzly Lake 7,400′, Mammoth Hot Springs, 1.2 mi W Tower Falls).

Manica mutica (Emery)

DESCRIPTION. *Worker*. Length 3½–6½ mm. Head, thorax, petiole, and postpetiole dark reddish brown (5YR 3/3) to yellowish red (5YR 4/8); gaster dark reddish brown (2.5YR 3/4) to yellowish red (5YR 5/8). Head and thorax dull to moderately shining; gaster

FIG. 13. Crater of *Manica mutica*. Little Valley, Washoe County, Nevada. The card is 5 inches long.

strongly shining. *Female*. Length 7 mm. Head and thorax red (10R 4/6) to dark red (10R 3/6) infuscated with very dusky red (10R 2/2) to black (N/0); gaster red (2.5YR 4/8) to dark red (2.5YR 3/6). Head moderately shining, thorax shining, gaster strongly shining. *Male*. Length 6½–7 mm. Head and thorax black (N2/0); petiole and postpetiole mostly black (N 2/0) with spots of red (2.5YR 4/8) on dorsum; gaster yellowish red (7.5YR 5/8) with infuscated transverse bands of very dusky red (2.5YR 3/2). Head and thorax dull, petiole and postpetiole moderately shining, gaster strongly shining.

NUPTIAL FLIGHT. A nuptial flight occurred in Little Valley on September 20, 1967, concurrently with the recounted flight of *bradleyi*. On a bare patch in a mountain meadow near the edge of a pine forest, a deälated female was excavating a burrow. On other bare areas on the mountain meadow, where *mutica* craters were abundant, we observed numerous deälated females running about on the surface of the ground and many others digging burrows. We excavated many of the closed burrows. Some contained only one deälated female, but just as many contained two or more; the maximum was nine. Under a medium-sized stone there was a cluster of 28 deälated females.

CENSUS. We collected two young colonies from nests under isolated craters on August 24 in Little Valley. In one we found 98 workers, 45 pupae, 24 larvae, and many eggs; in the other 1 queen, 73 workers, 28 pupae, 15 larvae, and 9 eggs. From an older nest under an isolated crater we took 388 workers, 22 males, and 1 larva.

RELATIONS WITH OTHER ANTS. As a general rule different colonies of the same species of ant are mortally hostile to each other. However, two colonies may sometimes be combined if air is allowed to circulate freely between them so that they acquire the same nest-odor. We selected for an experimental union colonies of *mutica* from localities 25 miles apart. At this distance we could be sure they did not belong to the same colony. We connected their two observation nests by tubing plugged with cotton. After a few days the plug was removed. Soon workers from each nest were circulating freely in the other nest and there was no evidence of hostility. When we tried the same experiment using a colony of *mutica* and a colony of *Formica fusca*, the *mutica* workers immediately began to move through the tube into the *fusca* nest, when the plug was removed; an hour and a quarter later all *fusca* had been killed by *mutica* workers.

For relations with *M. bradleyi* see under that species.

MYRMECOPHILES. The histerid beetle *Tribalus californicus* was taken from the nests of *Manica mutica* in Washington (W. M. Wheeler 1910:388).

"In 1902 C. V. Chamberlin discovered, near Salt Lake City, three mixed nests consisting of *Manica mutica* and a small guest ant to which Wheeler subsequently gave the name *Symmyrmica chamberlini*. Despite much subsequent examination of *mutica* colonies, no additional specimens of *chamberlini* have been taken. As a result, our knowledge of the habits of this insect is slight. Chamberlin observed that the inquiline constructed its own nest chambers so that they communicated with those of its host. . . . The general structure of the worker of Symmyrmica is closely similar to that of certain species of Leptothorax but Symmyrmica may be easily separated because of its peculiar, ergatoid male." (Creighton 1950: 280–281).

On August 31, 1964, in the Big Horn Mountains in Wyoming (four miles west of Shell Creek Bridge, 5,800 feet) we found larvae of the tick *Dermacentor albipictus* (Packard) (det. C. M. Clifford) in a *mutica* nest. The larvae were in two dense masses each half an inch in diameter in chambers under a stone.

MISCELLANEOUS NOTES. *Manica mutica* might become a minor local pest by constructing messy earthworks in lawns and by stinging children.

The slender young larvae are very active, waving the anterior end of the body at the slightest stimulus. They are capable of limited locomotion by the inch-worm technique.

On July 23 and 24, 1966, we kept records of the surface activity of *M. mutica*. At 5:40 A.M. we could see workers come to the entrance of the nest and then move back down; the air temperature was 44 F.

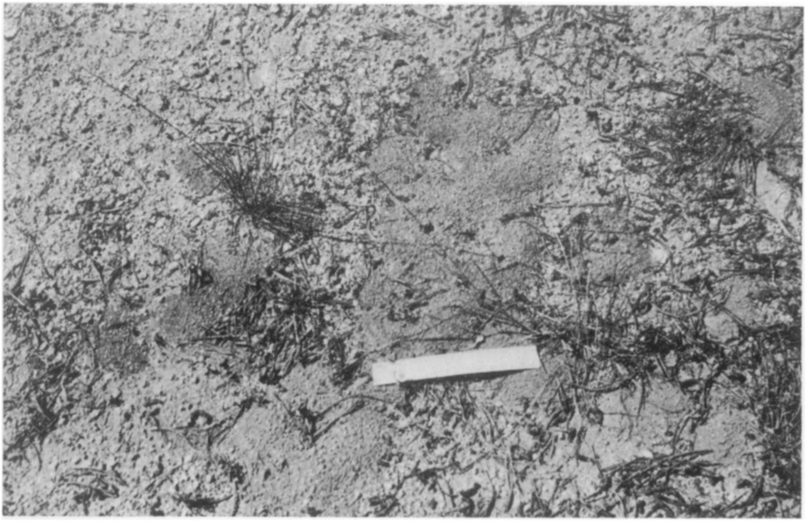

Fig. 14. Merged craters of *Manica mutica*. Little Valley, Washoe County, Nevada. The ruler is 6 inches long.

By 6:30 a.m. (air temperature 52 F) workers began to bring excavated material out and deposit it on the crater; a few wandered away from the crater. This activity continued until 8:30 a.m. (surface temperature 94 F). All surface activity had ceased at 9:30 a.m. (air temperature 74 F, surface temperature 95 F). No further activity was observed while the temperature rose; the highest observed were air 78 F, surface 116 F, at 3 p.m. By 5 p.m. workers were again actively bringing soil particles out to the edge of the crater and at 6 p.m., when the soil had cooled to 68 F, some were wandering away from the nest crater. Activity was reported until 10 p.m., after which no further observations were made. Not more than 3 workers were seen on the surface of a crater at any one time; the greatest number of trips was 48 in one 5-minute period. In any 5-minute period only 2 workers were seen leaving the crater. None was seen bringing in food at any time.

Range. *Manica mutica* might be called the species of the Great Plains and the Great Basin, in contrast to *bradleyi* and *hunteri*, which are essentially montane. Yet there are exceptions: in Colorado up to 8,600 feet and mostly above 7,500 feet; on the Yellowstone Plateau at 7,400 feet; in northern New Mexico at 7,300 feet; on the eastern slope of the Sierra Nevada up to 7,200 feet. Outside Colorado it occurs, on the average, at lower elevations than *bradleyi* and *hunteri*.

Its range is more extensive than that of either of the other two species: from the eastern slopes of the Sierra Nevada and Cascade Ranges to northeastern New Mexico, the Black Hills (South Dakota), and southwestern North Dakota; northward into southern British Columbia and Alberta, with one record from Alaska. The southernmost records are near Lone Pine, California, at 4,500 feet and Taos, New Mexico, at 7,300 feet; the easternmost is in the Missouri River valley in south-central North Dakota at 1,700 feet; the westernmost is Portola, California, at 4,800 feet; the northernmost is "Anchorage, Valdez," Alaska. The lowest record is 1,100 feet at Penticton, British Columbia, the highest, 8,600 feet in Mosca Canyon, Colorado.

LOCALITY RECORDS. ALASKA. "Valdez, Anchorage." ALBERTA. McLeod 3,100′. ARIZONA. Jacob Lake 7,900′ (Cole 1937: 135). BRITISH COLUMBIA. Kamloops 1,200′; Penticton 1,100′; Summerland. CALIFORNIA. Inyo Co.: Bishop 4,200′; Lone Pine 3,900′; 1.4 mi SW Lone Pine 4,500′. Lassen Co.: Susanville 4,200′; 14 mi W Susanville 5,600′; Thermo. Modoc Co.: Likely. Mono Co.: Bodie State Park; Bridgeport 6,500′; 7 mi S Bridgeport 6,400′; Fales Hot Springs 7,300′. Nevada Co.: Donner State Park 8,000′; 8 mi E Donner Pass (= Donner Camp) 6,400′; Sagehen Creek (T. 18 N., R. 15 E. 7,000′ and T. 18 N., R. 16 E. 6,400′). Plumas Co.: Portola 4,800′. Sierra Co.: Cottonwood Creek Camp Ground (T. 20 N., R. 15 E.) 6,200′. COLORADO. Alamosa Co.: Alamosa 7,500′; Great Sand Dunes National Monument 8,500′; Mosca Canyon 8,600′; 2 mi N Mosca 7,500′. Boulder Co.: Boulder (Baseline Lake) 5,300′. Chaffee Co.: Princeton Hot Springs; Salida. Cheyenne Co.: Wild Horse 4,500′. Cimarron Co.: Blue Creek Canyon (10 mi E Cimarron 8,300′). Denver Co.: Denver (City Park) 5,300′; Turkey Creek (Denver) [Denver is the type locality]. El Paso Co.: Colorado Springs. Fremont Co.: Adelaide (Phantom Canyon) 7,000′; Canyon City. Grand Co.: Granby; 5 mi W Granby 8,000′; Grand Lake 8,400′; Monarch Lake 8,300′; Parshall 7,600′. Gunnison Co.: 5 mi E Gunnison 8,200′. Hinsdale Co.: Carson City. Huerfano Co.: 10 mi NW Gardner 8,500′. Jackson Co.: 9 mi W Cowdrey 8,500′. Jefferson Co.: Leyden 5,700′. La Plata Co.: Durango 6,500′; 4 mi N Hermosa 7,000′. Larimer Co.: Ft. Collins (Rist Canyon). Mesa Co.: De Beque 4,800′. Pitkin Co.: Aspen 8,100′. Routt Co.: Rabbit Ear Pass. Saguache Co.: Villa Grove. IDAHO. Canyon Co.: Parma. Twin Falls Co.: Twin Falls; 35 mi S Twin Falls. MONTANA. Cascade Co.: Belt 3,800′. Lewis and Clark Co.: Sieben (25 mi N Helena). Missoula Co.: Missoula. NEVADA. Churchill Co.: 40 mi W Austin; Fallon 3,900′. Elko Co.: 6 mi E Wells on U.S. Highway 40, 6,200′. Esmeralda Co.: Fish Lake Valley. Eureka Co.: South Fork Creek (Diamond Mts.). Humbolt Co.: Summit Lake. Lyon Co.: Old Fort Churchill 4,300′; Wabuska 4,300′. Mineral Co.: Walker Lake 3,400′. Pershing Co.: 9 mi NE Lovelock 3,900′. Washoe Co.: Lake Tahoe 6,600′; Little Valley (T. 16 N., R. 19 E.) 6,400′; Pyramid 3,800′; Pyramid Lake; Washoe Lake 5,000′. NEW MEXICO. Taos Co.: 12 mi E Taos 7,200′; 15 mi E Taos

8,000′ (Cole 1953: 243). NORTH DAKOTA. Billings Co.: T. 144 N., R. 102 W. 2,500′; Mikkelson 2,300′. Golden Valley Co.: T. 144 N., R. 103 W., sec. 6 2,400′. Sioux Co.: T. 132 N., R. 79 W., sec. 9 1,700′. Williams Co.: T. 154 N., R. 95 W., sec. 22 1,800′; T. 154 N., R. 97 W., sec. 21 1,800′. OREGON. Deschutes Co.: Hampton. Harney Co.: 44 mi SW Burns 4,200′. Lake Co.: Lakeview 4,800′. SOUTH DAKOTA. Pennington Co.: Hill City 5,000′; Rapid City 3,200′. UTAH. Cache Co.: Benson; Hyrum. Box Elder Co.: Blue Creek; Corrine; Tremonton 4,300′. David Co.: Layton; Woods Cross. Garfield Co.: SE Panguitch. Iron Co.: Cedar Breaks. Kane Co.: Long Valley. Piute Co.: Junction 6,000′. Salt Lake Co.: NE Antelope Island; Midvale 4,500′; Murray; S end Great Salt Lake 4,200′; Salt Lake City 4,200′; Taylorsville (=Salt Lake City). Sanpete Co.: Chester; Fayette. Sevier Co.: Osiris (not located). Tooele Co.: Iosepa; Lake Point; Tooele 5,000′. Utah Co.: Lehi; Salem; Springville. Weber Co.: Ogden 4,500′; Plain City. WASHINGTON. Whitman Co.: Pullman. WYOMING. Big Horn Co.: 4 mi W Shell Creek Bridge (T. 53 N., R. 90 W.) 5,600′. Park Co.: 8 mi W Cody 5,000′; 35 mi W Cody 6,000′. Teton Co.: Moran 6,700′. Washakie Co.: Worland 4,000′. Yellowstone National Park (Gibbons Falls 7,000′, Old Faithful 7,400′).

LITERATURE. Ant nests and their distributions were discussed by Cole (1934: 223; 1942: 368; 1953: 243), Creighton (1950: 109), Gregg (1963: 316–317), Wheeler and Wheeler (1963: 109–110), and W. M. Wheeler (1904: 6). The larva was described and figured by Wheeler and Wheeler (1960: 5, 9). W. M. Wheeler (1910: 150) noted that *Manica mutica* "is hardly more than a subspecies of the European *M. rubida.*"

Manica parasitica (Creighton)

This species is known from only two collections in two localities, both in the Sierra Nevada Mountains in California: (1) Polly Dome, Yosemite National Park, Mariposa County, 8,600 feet, 13 workers, 1932 (Creighton, 1934); (2) three miles northeast of Clark Fork Campground, Stanislaus National Forest, Alpine County, 6,100 feet, 2 workers, 1967 (Wheeler and Wheeler, 1968).

Since both collections were from nests of *Manica bradleyi*, a parasitic relationship is inferred, although very little is known about *parasitica*. Creighton reported that *parasitica* workers took their share of activities and were treated as ordinary nest mates by the *bradleyi* workers. We kept one of our *parasitica* workers with *bradleyi* workers in an observation nest for three months. It was able to feed itself. It was quite easily distinguished by its quicker response to disturbances, by its faster gait, and by the bouncing of the anterior end as it walked.

Creighton described his workers as follows: length 5 mm; head piceous; thoracic dorsum and petiolar nodes blackish brown; gaster a darker brown than petiolar nodes but not so black as head; head and thorax feebly shining to shining, gaster smooth and shining. Our living worker was 6 mm long and black (5YR 2/1) throughout.

Manica rubida (Latreille)

Aside from the works of Forel, we have been able to find only a few references to this species. Therefore, unless otherwise noted, the following account is based on his work (see "Literature Cited").

DESCRIPTION. *Worker*. Length 5–8 mm. Reddish yellow or brownish red; darker on middle of gastric dorsum. *Female*. Length 10½–12 mm. Brownish red. *Male*. Length 8½–10 mm. Black except posterior half of the gaster which is yellowish brown (Forel, 1874, 1915).

MISCELLANEOUS NOTES. In Switzerland, the workers are able to form regular files which serve to connect two nests of a colony or to lead to food.

The female of *Manica rubida* has a very small seminal receptacle; this is related to the small population of the colony and with the fact there are usually several queens in each colony (Bernard 1951: 1017).

Ehrhardt 1931: Young workers tend brood and queen but do not forage. Older workers forage and defend the nest but do not tend brood. Young workers take to the field earlier when there is a shortage of older workers.

On May 16, 1925, Eidmann (1926: 783–784) captured a deälated queen, which was running about on the ground, and placed her in an observation nest. By May 20 she had excavated a passage in the soil. On May 25 she laid 12 eggs, which she licked and kept in a large chamber she had excavated. By June 15 the packet comprised 30 to 40 eggs, many more than laid by other species that practice independent colony-founding. The first larva hatched on June 27; by July 6 all had hatched. "We can therefore assert with considerable certainty that the colony-founding of *M. rubida* is independent and that it is completed in the year of the nuptial flight."

A myrmecophilous beetle *Lomechusa strumosa* (Staphylinidae) was placed in an observation colony by Wasmann. At first it was seized by several workers and even threatened with stinging, but after 15 minutes it was apparently adopted and workers were licking its trichomes, hair-tufts which diffuse an aromatic secretion (Forel, 1921: 97).

Goetsch (1934: 362–363) found that *rubida* lays scent trails.

For other references see the genus; see also W. M. Wheeler 1910: 150, under *mutica*.

RANGE. Emery (1921: 42) stated that the range of *Manica rubida* "extended from the Alps into Siberia," but on p. 43: "mountains of Europe, northern Asia, Asia Minor, Caucasus." W. M. Wheeler (1914: 118) gave the range as "Central and Southern Europe and as far east as the Caucasus in Asia Minor and Eastern Siberia." It does not occur in the Pyrenees (Bernard, 1958: 310).

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