This page intentionally left blank.

MALE GENITALIA AND THE TAXONOMY OF POLYERGUS
(HYMENOPTERA: FORMICIDAE)[1]

JEANETTE WHEELER, *Department of Biology, University of North Dakota, Grand Forks*[2]

Creighton (1950, p. 556) gave color as the only satisfactory character for the separation of the 2 subspecies *Polyergus rufescens bicolor* Wasmann ("head brownish red, gaster piceous brown and distinctly darker than the head") and *P. r. breviceps* Emery ("head, thorax and gaster ferrugineous to brownish red"), although he admitted (p. 558) that color was frequently not reliable in these subspecies. During the preparation of our book (1963) on the ants of North Dakota I had difficulty trying to separate *P. r. bicolor* and *P. r. breviceps* consistently, because I found so much internidal variation in color. I should not have been so surprised, however, because Smith (1947, p. 150–151) had remarked on the great amount of variation within a species or even in one nest of fresh specimens in the genus *Polyergus*. I arranged all of our material in "classes" according to color. Those ants without any infuscation I classed as "0" and those with slight infuscation as "+." We had material which Dr. Smith (*in litt.*) had identified as *P. r. breviceps* (0) and as *P. r. fusciventris* Wheeler (+). Since Creighton (1950, p. 559) sank *fusciventris* to a synonym of *breviceps*, I called these specimens all *breviceps*. We also had material which Dr. Smith (*in litt.*) had called *P. r. bicolor*; these were either moderately (++) or heavily (+++) infuscated. This infuscation involved the gaster, legs and sometimes the petiole. However, when I took all the specimens from a nest and tried to classify each one, I found that the color could range from 0 to ++ or from + to +++ in the same nest. On the other hand, some samples contained specimens of only one or two classes. It should be noted that we said (1963, p. 276): "In no case . . . has the total possible range of color been found in one nest." With the usually short series of *Polyergus* workers collected and the variability observed we decided to call our North Dakota material *P. rufescens* Latreille.

This was not a satisfactory situation. But I could not agree with Kannowski (1956, p. 185) in recognizing *P. breviceps* as a separate species nor with Gregg (1963, p. 635–638) who raised *P. bicolor* to specific rank by the use of the color of the workers as the separatory character.

Forbes and Brassel (1962) suggested the use of the male genitalia

---

[1] University of North Dakota Faculty Grant in aid #4422 assisted with the cost of photography.

[2] Present address: Desert Research Institute, University of Nevada, Reno 89507. GB 6681 (Renewal Grant 3873) assisted with the cost of photography.

for separating the subspecies of *P. rufescens*. I did not see this paper nor did I have enough males before our book was published to try to untangle our North Dakota subspecies on these characters. By September, 1965, I had collected or received several samples containing large series of males. In *bicolor*: Hauge #340 from the University of North Dakota Forest River Biology Area, about 35 miles northwest of the Oakville Prairie Biology Area, 26 males; Sather #58 from Turtle River State Park, 10 miles northwest of the Oakville Prairie Area, 25 males; Wheeler #2030, Billings County, near the western edge of the state, 9 males. In *P. r.* ssp?: Wheeler #125 from Teton County, Wyoming, 25 males. In *breviceps*: A. C. Cole, collected near Cimmaron, New Mexico, 1 male; R. E. Gregg from Harvey, Illinois, 1 male; Limvere, Oakville Prairie Biology Area of the University of North Dakota, 3 separate nests with 25 males each; Wheeler #2166, same locality, 5 males; Wheeler #2252 about 1½ miles south of the Oakville Prairie Area, 15 males. In *umbratus* Wheeler: A. C. Cole from Moran, Wyoming, 6 males; R. R. Snelling from Los Angeles County, California, 2 males. In *P. lucidus* Mayr: Collected by W. M. Wheeler—1 male from Colorado Springs, Colorado; 1 from Bronxville, New York, 1905; 1 from Bronxville, New York, 1908. Total: 193 males.

Borgmeier (1950, fig. 18–31) showed intranidal differences, and even bilateral asymmetry, in the genital apparatus of *Atta sexdens* L. Clausen (1938) gave the number of specimens studied for each species, drew outlines showing the variations for the genital plates and also gave the extremes and means for all the various measurements on numerous species. For *Formicia rufa rufa* L. he had 100 males from one nest (but probably from different queens). Here he gave the extremes, the means, the standard deviation and the coefficient of variation for each character which he had measured on the left and right halves of the genital plates (tables 14–17, p. 303–306) and he concluded (p. 310) "das die Variabilität des Geschlechtsapparates grösser ist als die Variabilität der Merkmale des äussern Körperbaues." Weber (1948, pl VII, p. 280) showed four samples of variation in the middle valve (= volsella) of 26 forms in the genus *Myrmica* and mentioned the differences in his descriptions (1947, 1948, 1950). Forbes and Brassel (1962), however, did not mention any variability in the 10 male specimens of *P. lucidus* or the three specimens of *P. r. breviceps*; nor did they mention any bilateral asymmetry in those males nor in their single specimens of *P. r. bicolor* and *P. r. umbratus*. This is the only paper in which Forbes gave the number of specimens examined. In none of his other papers on the male genitalia was the sample size mentioned nor was any variability noted (Forbes 1954 and 1956; Forbes and Do-Van-Quy, 1965; Forbes

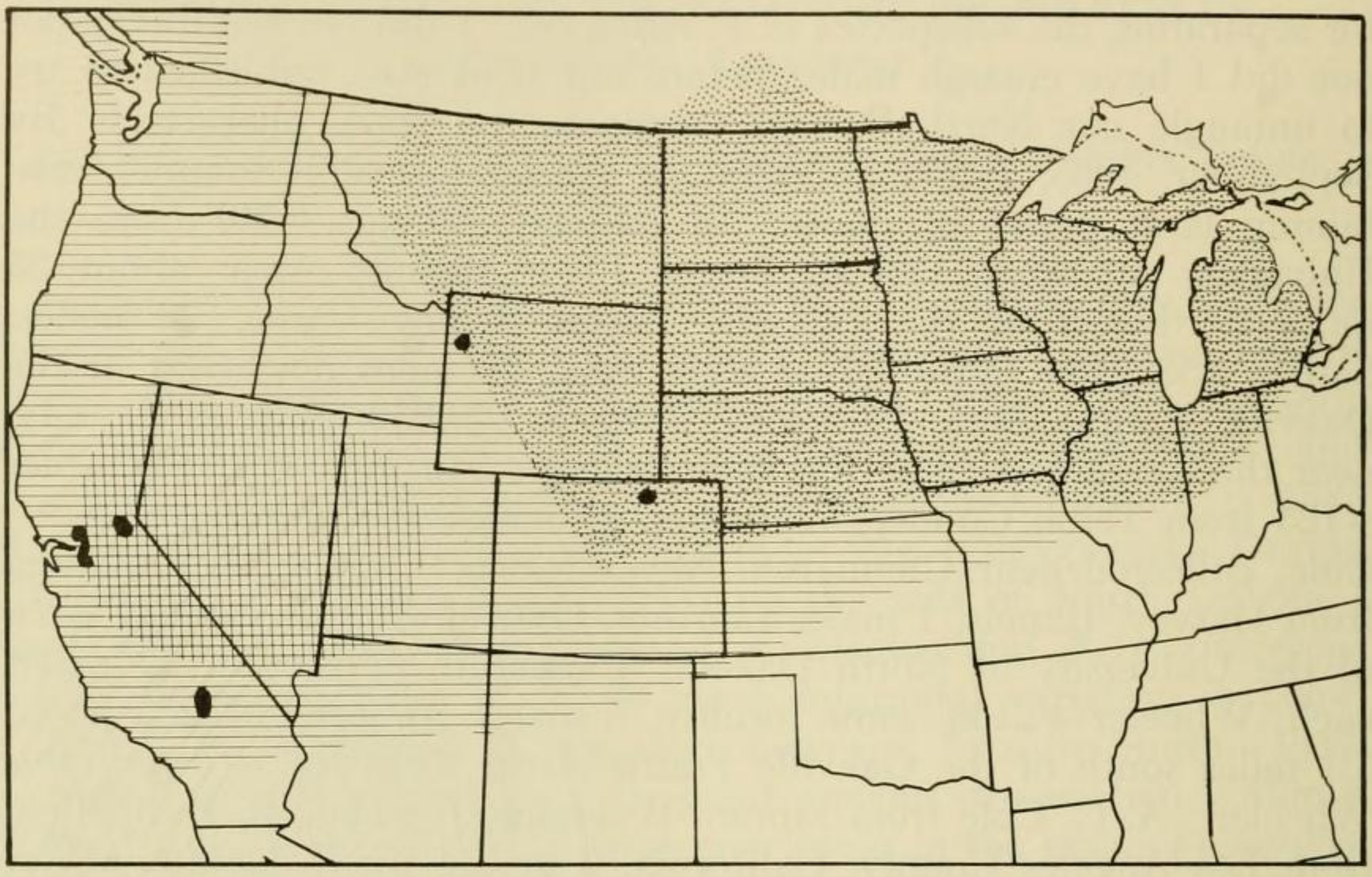

Fig. 1. Reported ranges of the 4 subspecies of *Polyergus rufescens* Lat.

and Hagopian, 1966). Krafchick (1959) did not illustrate any variations for the subgenital plate in *P. lucidus* nor in *P. r. breviceps*. He made one drawing for the "penis valve" (= aedeagus) of *P. lucidus*.

If *P. r. bicolor* and *P. r. breviceps* are subspecies, they should be largely allopatric but with overlapping range-edges. Using the data given by Creighton (1950), Gregg (1963), and Smith (1951, 1959, and 1967) (and adding our own collections from Canada) I have constructed a map, fig. 1, which shows that the subspecies of *P. rufescens* cannot be separated as geographic races and that the range of *P. r. breviceps* includes the ranges of the other 3.

Forbes and Brassel (1962, p. 85) said that the greatest differences between the subspecies in the male genitalia occurred in the length and curvature of the digitus of the middle value (= volsella); but they did not show how to measure that character. Therefore, I have used Clausen's measurement (fig. 2, l. v.) for the base line and added the length of the digitus (l. d.) to the "depth" (d. d.) as a measure of the length and curvature of the digitus combined. It seemed to me that a ratio [l. d. + d.d./l.v] would be meaningful since it relates length and curvature of the digitus to the length of the volsella. While

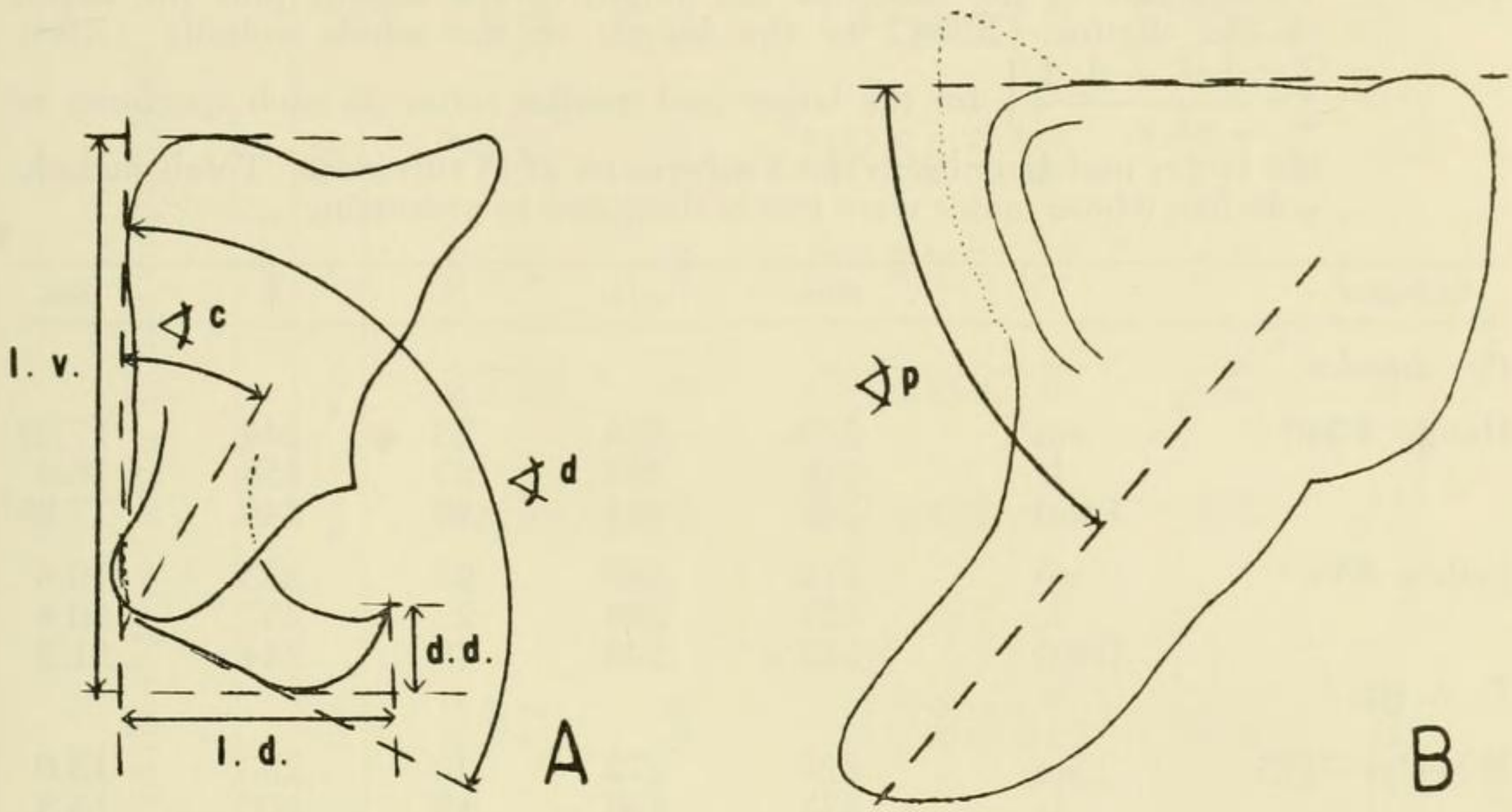

Fig. 2. Orientation for measurements. A, Volsella: angle c = angle between the cuspis and the volsellar dorsum; angle d = angle between the posterior end of the digitus and the volsellar dorsum; d.d. = depth of the digitus; l. d. = length of the digitus; l.v. = length of the volsella. B, Paramere: angle p = angle between the paramere and the basiparamere.

these measurements were being made I was struck by the difference between the two halves on the same individual. Therefore, I calculated the coefficients of regression for the larger nests samples. The results showed that there was no correlation between the ratios of the two valves on the same individual. (Calculations not shown here.)

The means of the ratios for the smaller volsellae and the means for the larger volsellae on the same individual in the subspecies *breviceps* cover nearly the entire range for the means of the ratios for both volsellae in all of the nests in all the taxa considered (see 4th and 5th columns in table 1). The standard deviations show that these differences have no statistical significance. This lack of statistical difference suggests strongly that these characters can have no taxonomic significance.

On first inspection I thought that the angles of the cuspis of the volsella (angle c) which Clausen (1938, p. 294) used and which Forbes and Brassel (1962, p. 83) suggested looked promising as a separatory character for *breviceps* and *bicolor*. I also devised two other angle measurements (angle d and angle p, as shown in fig. 2). These angles were measured on 193 (386 halves) prepared specimens with a mineralogical circular stage microscope. The means (± one standard deviation) of the material from the Oakville Prairie Biology

Table 1. Comparison of the ratios of the length of the digitus plus the depth of the digitus (X384) to the length of the whole volsella (X80) $\left[\frac{=\text{l. d.} + \text{d. d.}}{\text{l. v.}}\right]$ for the larger and smaller ratios on each specimen in the larger nest samples in the 3 subspecies of *P. rufescens*. Totals include volsellae whose mates were lost or damaged in processing.

Collector		min.	max.	N	$\bar{X}$	s.d.
P. r. bicolor						
Hauge #340	sm	206	274	23	244	17.32
	lr	218	284	23	258	16.9
	Total	206	284	49	246	17.65
Sather #58	sm	212	285	22	233	19.6
	lr	221	296	22	257	20.8
	Total	212	296	46	244	21.2
P. r. ssp.?						
Wheeler #125	sm	228	272	18	253	15.0
	lr	235	296	18	266	15.8
	Total	228	296	42	259	16.59
P. r. breviceps						
Limvere #1	sm	204	248	17	230	11.86
	lr	224	269	17	248	12.35
	Total	204	269	41	240	18.38
Limvere #2	sm	208	296	18	233	20.6
	lr	228	300	18	251	20.4
	Total	208	300	42	242	21.3
Limvere #3	sm	204	261	24	239	16.57
	lr	208	284	24	254	19.25
	Total	204	284	48	247	19.22
Wheeler #2522	sm	214	252	12	235	13.8
	lr	216	278	12	251	18.6
	Total	214	278	24	243	18.1
P. r. umbratus						
Cole #163	sm	197	240	6	212	16.4
	lr	202	261	6	223	21.5
	Total	197	261	12	217	18.8

Area include the entire range of the means of all other samples in each of the three measured angles (table 2 c, d, p).

It is obvious that none of these measurements then can be used as key characters. Furthermore the aedeagus is even more variable in length and in number of teeth (even on the two halves of the same individual) and hence obviously cannot be used. In fact, the teeth were so variable in size and so difficult to count that my replicates differ even at a magnification of 384×, therefore the aedeagus measurements are not included in the table.

Forbes and Brassel (1962, p. 85) also said: "Since the subgenital plate differed in all the forms examined, the configuration of this

Table 2. Minimum, maximum, sample size, mean and standard deviation for the angles of the digitus (angle d) and cuspis (angle c) on the volsella, and the angle of the paramere (angle p).

	angle d					angle c					angle p				
Collector	min.	max.	N	$\overline{X}$	s. d.	min.	max.	N	$\overline{X}$	s. d.	min.	max.	N	$\overline{X}$	s. d.
P. r. bicolor															
Hauge #340	107	126	47	116	5.0	24	56	47	36	6.5	54	89	46	70	9.5
Sather #58	106	127	32	118	3.3	18	48	32	36	6.9	52	96	45	71	10.0
Wheeler #2030	110	135	15	122	6.7	28	46	15	38	3.5	66	85	10	72	10.5
P. r. ssp.?															
Wheeler #125	99	183	47	114	11.7	24	65	47	38	8.9	51	92	44	69	10.2
P. r. breviceps															
Cole	123	133	2	128	—	44	49	2	47	—	60	74	2	67	—
Gregg	111	112	2	112	—	40	40	2	40	—	77	82	2	80	—
Limvere #1	100	147	43	118	8.2	25	57	39	41	6.8	51	90	39	65	11.3
Limvere #2	102	128	44	112	6.5	26	55	44	40	6.7	50	88	42	71	9.4
Limvere #3	104	129	36	116	6.8	24	52	36	36	7.7	53	95	39	69	10.5
Wheeler #2166	102	120	5	115	13.2	24	35	5	31	5.7	—	—	—	—	—
Wheeler #2522	110	135	15	122	6.7	28	46	15	38	3.5	50	85	10	72	10.5
P. r. umbratus															
Cole #163	112	131	12	122	4.1	28	48	12	40	6.3	48	81	11	68	10.6
Snelling	125	138	4	132	5.9	30	43	4	36	6.6	48	73	4	64	11.6
P. lucidus															
W. M. Wheeler	106	150	6	123	18.5	24	50	6	33	12.0	47	69	6	61	9.0

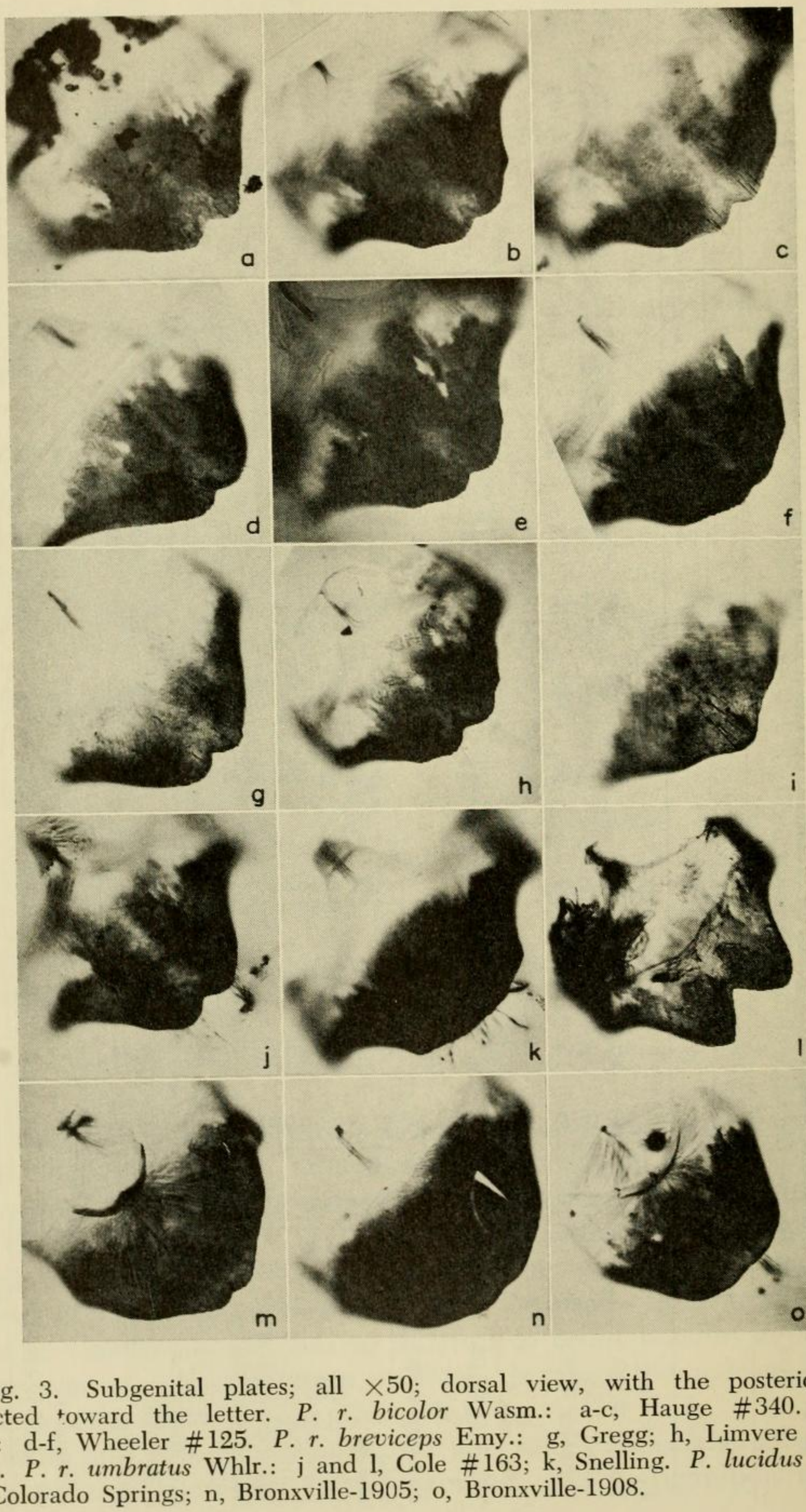

Fig. 3. Subgenital plates; all ×50; dorsal view, with the posterior end directed toward the letter. *P. r. bicolor* Wasm.: a-c, Hauge #340. *P. r.* ssp?: d-f, Wheeler #125. *P. r. breviceps* Emy.: g, Gregg; h, Limvere #1; i, Cole. *P. r. umbratus* Whlr.: j and l, Cole #163; k, Snelling. *P. lucidus* Mayr: m, Colorado Springs; n, Bronxville-1905; o, Bronxville-1908.

segment may be a highly important differentiating aid." I found no constant character within any nest series (see photographs, fig. 3) which I could measure and further more, there was too much variation within each putative taxon (and even in the same nest) to use the subgenital plate as a key character. Referring to my fig. 3: a, d, g, j, and m all have a definite median notch and little or no shoulder, which approaches Forbes and Brassel's fig. 15 (1962, p. 84) for *P. r. bicolor* and Krafchick's fig. 9B (Pl. 12) for *P. r. breviceps*. My fig. 3: b, c, e, f, h, and n have a median notch and more or less distinct shoulders; this is the commonest type in my material but has not been illustrated by any other authors. My fig. 3: i, k, l and o are uniques for my series but i approaches Forbes and Brassel's fig. 11 (p. 84) for *breviceps*; this is the only one in my 93 specimens of *P. breviceps* which looked like this. None of my eight specimens of *P. r. umbratus* resemble Forbes and Brassel's fig. 19 (1962, p. 84). Of my three specimens of *P. lucidus* (fig. 3, m—o) none looked like the drawings made by Forbes and Brassel (1962, p. 82, fig. 4) nor by Krafchick (1959, pl. 12, fig. 9A).

Mr. Roy R. Snelling (*in litt.*) has reported a careful comparison of the external characters of the queen, worker and male of the European *P. rufescens* with our North American material. He concludes that the two are separate but closely related species. Our specimens, therefore, should be called *P. breviceps* Emery.

Conclusions

1. Our North American *Polyergus* should be considered as one species without subspecific designations because:

   a. None of the putative subspecies can be separated as geographic races.

   b. *P. r. bicolor*, *P. r. breviceps*, and *P. r. umbratus* cannot be separated by the characters of the male genitalia.

   c. *P. r. bicolor* and *P. r. breviceps* cannot be separated in many long series on the one accepted criterion of color.

2. Our North American material is a species distinct from the Old World *Polyergus rufescens* (Latr.) and should be called *P. breviceps* Emery.

Acknowledgments

I wish to thank the following myrmecologists for material: A. C. Cole, R. E. Gregg, and R. R. Snelling. Also R. Hauge, E. Limvere, and D. S. Sather, Univ. of North Dakota, collected males at my request. The manuscript was critically reviewed by N. Stark and G. C. Wheeler, Desert Research Institute, Univ. of Nevada.

References

Borgmeier, T. 1950. Estudos sôbre Atta. Mem. Inst. Oswaldo Cruz 48:239–292.

Clausen, R. 1938. Untersuchungen über den männlichen Copulationsapparat der Ameisen, speziell der Formicinae. Mit. Schweiz. Ent. Ges. 17:233–346.

Creighton, W. S. 1950. The ants of North America. Bull. Mus. Comp. Zool. 104:1–585, 57 pl.

Forbes, J. 1954. The anatomy and the histology of the male reproductive system of *Camponotus pennsylvanicus* DeGeer (Formicidae, Hymenoptera). Jour. Morphol. 95:523–555.

———. 1956 (1958). The male reproductive system of the army ant, *Eciton hamatum* Fabricius. Proc. 10th Internat. Cong. Ent. 1:593–596.

——— *and* **R. W. Brassel.** 1962. The male genitalia and terminal segments of some members of the genus *Polyergus* (Hymenoptera: Formicidae). Jour. New York Ent. Soc. 70:79–87.

——— *and* **D. Do-Van-Quy.** 1965. The anatomy and histology of the male reproductive system of the legionary ant, *Neivamyrmex harrisi* (Haldeman) (Hymenoptera: Formicidae). Jour. New York Ent. Soc. 73:95–111.

——— *and* **M. Hagopian.** 1966. The male genitalia and terminal segments of the ponerine ant *Rhytidoponera metallica* F. Smith (Hymenoptera: Formicidae). Jour. New York Ent. Soc. 73:190–194.

Gregg, R. E. 1963. The ants of Colorado. Univ. of Colorado Press, Boulder, 792 p.

Kannowski, P. B. 1956. The ants of Ramsey County, North Dakota. Amer. Midland Natur. 56:168–185.

Krafchick, B. 1959. A comparative study of the male genitalia of North American ants (Formicidae) with emphasis on generic differences. Dissertation, Univ. of Maryland, 78 p. (Univ. Microfilms, Inc., Ann Arbor, Michigan).

Smith, M. R. 1947. A study of *Polyergus* in the United States, based on the workers (Hymenoptera: Formicidae). Amer. Midland Natur. 38:150–161.

———. 1951. *in* Muesebeck *et al.*, Hymenoptera of America North of Mexico, Synoptic Catalog, U. S. Dept. Agr., Agr. Monogr. 2:778–875.

———. 1958. *in* Krombein *et al.*, Hymenoptera of America North of Mexico, Synoptic Catalog, U. S. Dept. Agr., Agr. Monogr. 2(1st suppl.):108–162.

———. 1967. *in* Krombein *et al.*, Hymenoptera of America North of Mexico, Synoptic Catalog, U. S. Dept. Agr., Agr. Monogr. 2(2nd Suppl.): 343–374.

Weber, N. A. 1947. A revision of the North American ants of the genus *Myrmica* Latreille with a synopsis of the Palearctic species. I. Ann. Ent. Soc. Amer. 40:437–474.

———. 1948. A revision of the North American ants of the genus *Myrmica* Latreille with a synopsis of the Palearctic species. II. Ann. Ent. Soc. Amer. 41:267–308.

———. 1950. A revision of the North American ants of the genus *Myrmica* Latreille with a synopsis of the Palearctic species. III. Ann. Ent. Soc. Amer. 43:189–226.

Wheeler, G. C., *and* **Jeanette Wheeler.** 1963. The ants of North Dakota. Univ. of North Dakota Press, Grand Forks, 326 p.