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Doronomyrmex pocahontas: not a workerless parasite but still an enigmatic taxon (Hymenoptera, Formicidae)

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Summary

New data suggest that the North American ant *Doronomyrmex pocahontas* Buschinger 1979, originally described as a workerless inquiline, is not a social parasite. Breeding experiments show a remarkable phenotypic plasticity, which is probably due to hybridization or to intraspecific polymorphism.

Introduction

The ant *Doronomyrmex pocahontas* was described as a workerless social parasite of a host species belonging to the nearctic *Leptothorax* (s. str.) "*muscorum*" complex (not *L. retractus* Francoeur, 1986, not *Leptothorax* sp. A and sp. B, sensu Heinze and Buschinger, 1987; Heinze, 1989 referred to this species as *Leptothorax* C). Three colonies were originally collected in July, 1977 at Maligne Canyon, Jasper National Park, Alberta, Canada. All colonies contained a black, shiny queen with extraordinarily long, tapering hairs and a distinctly trapezoidal postpetiole. It resembled most the European workerless parasite, *Doronomyrmex pacis* Kutter 1950. Workers were morphologically similar to those of the sympatric brownish *Leptothorax* C: they were brownish, with shorter pilosity and a much narrower postpetiole. Hence it was concluded that the black queens belong to a new, workerless *Doronomyrmex* species parasitizing colonies of *Leptothorax* C (Buschinger, 1979).

During the past years, additional material of *D. pocahontas* was collected at the type locality, and laboratory colonies reared offspring for up to eleven breeding cycles (shortened annual cycles). New data suggest that *D. pocahontas* is not a workerless species and probably not a parasitic species at all. We here report observations on the biology of this species and its queen polymorphism and discuss its possible life history.

Material and methods

Ten colonies of *Doronomyrmex pocahontas* were collected in 1977 (A. B.), 1979 (A. B. and K. Fischer), and 1988 (J.H. and S. Kauffmann) at the type locality, Maligne Canyon. Numerous colonies of the presumptive host *Leptothorax* C and of syntopic *L. retractus* were collected at the same site. A large black *Leptothorax* (s. str.) (*Leptothorax* D, Heinze, 1989), which is the host of *L. faberi* Buschinger 1982, was not found at the type locality of *D. pocahontas*, but was collected in areas nearby (Maligne Lake, Mt. Edith Cavell).

Colonies collected in 1979 and 1988 were kept in laboratory conditions according to Buschinger (1974), with shortened annual cycles and daily light and temperature rhythms. Ants were fed three times a week with diluted honey and insect pieces (cockroaches, mealworm pupae).

For mating experiments, sexuals were kept in flight cages of about 15 cm × 20 cm × 30 cm (w × d × h). To study colony founding behavior of *D. pocahontas*, mated gynes were I) placed into small colonies of the presumptive host species, II) put into experimental colonies consisting of four workers from the maternal nest and some larvae and worker pupae of the "host species" ("passive colony founding" of social parasites, Buschinger et al., 1990), and III) returned into a large, queenless fraction of the maternal colony.

Results

Composition of field colonies

Though several hundred colonies of various *Leptothorax* (s. str.) were examined in numerous sites throughout the Rocky Mountains from southern Arizona to central Alaska (S. P. Cover and D. Ortius pers. comm.; A. B. and J. H. unpubl. results; Heinze, 1989), *D. pocahontas* is as yet known only from the type locality. In coniferous forests, colonies of *Leptothorax* (s. str.) typically nest in dead branches or tree stumps, but occasionally nests are found also under flat stones on the layer of pine needles covering the forest floor (Buschinger, 1979). At least seven of ten colonies of *D. pocahontas* were collected from under stones.

Only the three colonies collected on July 28–29, 1977 were directly preserved and thus could be completely censused. They contained a single *D. pocahontas* queen each and 158, 107, 199 workers respectively. Six of the colonies collected in 1979 and 1988 had a typical *D. pocahontas* queen each, one colony was collected without queen but produced *D. pocahontas* sexuals in the laboratory.

D. pocahontas colonies collected in July, 1977 did not contain sexual pupae, but adult males (5, 2, 62 resp.) and winged gynes (79, 2, 39 resp.). The 39 gynes of colony # 3 closely resembled host gynes (see below). In 16 colonies of *Leptothorax* C from the same site, sexual offspring was still in the pupal instar, mostly even not yet pigmented, and very few males and gynes had just eclosed (Buschinger, 1979). *D. pocahontas* colonies collected in August, 1979 and August, 1988 did not contain sexual pupae or winged sexuals. However, winged males and gynes were present in nests of *Leptothorax* C and D, and *L. retractus* from various sites throughout British Columbia and Alberta. It thus appears that sexuals of *D. pocahontas* eclose and mate earlier than those of sympatric *Leptothorax* species.

Results of laboratory rearing

Field colonies # 4 to # 10 were kept in the laboratory for up to 10 breeding cycles within 5 1/2 years. The results are summarized as follows:

4: Collected Aug. 16, 1979. Colony survived for five artificial cycles, the queen died during the third "summer". Workers were reared during the first three cycles, males and workers during the fourth, and only males, probably as worker offspring, during the last cycle. Workers had a comparatively wide postpetiole and dark coloration. They were suspected to be *D. pocahontas* workers.
5: Collected Aug. 16, 1979. The queen died towards the end of the first "summer". During the second cycle, only workers with wide postpetioles, and a single gyne were reared. Worker-laid eggs did not hatch during the third cycle.
6: Collected Aug. 16, 1979. Queen died during the third cycle. Workers were produced during cycles 1 to 4, males during cycles 3–5. One gyne eclosed in cycle 4. During the second cycle, two "intermorphs" were reared, similar to the one described by Buschinger (1979) from a field colony. Each intermorph had six ovarioles (workers have two ovarioles), a receptacle, and three ocelli, similar to gynes, but thoracic sutures were greatly reduced and wings lacked completely.
7: Collected Aug. 17, 1979. Colony survived for ten artificial cycles (from August 1979 to February 1985). The original queen died during the 5th summer, but was replaced by one of her daughters. Male and female sexuals, as well as workers, were reared until the 6th cycle. Though a physogastric queen was observed until the 10th cycle, only males were reared during cycles 7 to 10. Sexual offspring reared in this colony during cycles 3 to 5 were used to study sexual behavior and colony founding. Whereas the old queen was a "typical" shiny *D. pocahontas* queen, many of the produced gynes were intermediate in coloration and sculpture between *D. pocahontas* queens and those of the presumed host species ("dull" phenotype).
8: Collected Aug. 18, 1988. This colony was collected without queen and produced two males, five "dull" gynes and numerous workers in the cycle following collection.
9: Collected Aug. 18, 1988. Colony reared one male, eight "shiny" gynes, and numerous workers during the breeding cycle following collection.
10: Collected Aug. 18, 1988. Colony produced numerous workers for one cycle and was later used for electrophoretic studies. Specimens from this nest were deposited in the ant collection of the Museum of Comparative Zoology, Cambridge, Mass.

Compared to similarly treated laboratory colonies of *Leptothroax* (s. str.), those of *D. pocahontas* were not very productive. In all colonies, in addition to male and female sexuals brown workers with short pilosity and a narrow postpetiole were reared, which closely resembled the presumed "host workers" in the field colonies. At least those workers which eclosed three or four breeding periods after the colony had been transferred into the laboratory evidently were offspring of a *D. pocahontas* queen, hence *D. pocahontas* workers. A close examination of presumed "host workers" in the field colonies of 1977 and 1988 suggested that these also were *D. pocahontas* workers. At least in orphaned colonies, workers appear to be capable of producing males.

Some female sexuals produced by *D. pocahontas* queens were different in coloration, sculpture, hair length, and other morphological characters from their mothers and appeared "intermediate" between typical, shiny *D. pocahontas* queens (Fig. 1) and queens of *Leptothorax* C (Fig. 8 in Buschinger, 1979), i.e., they more

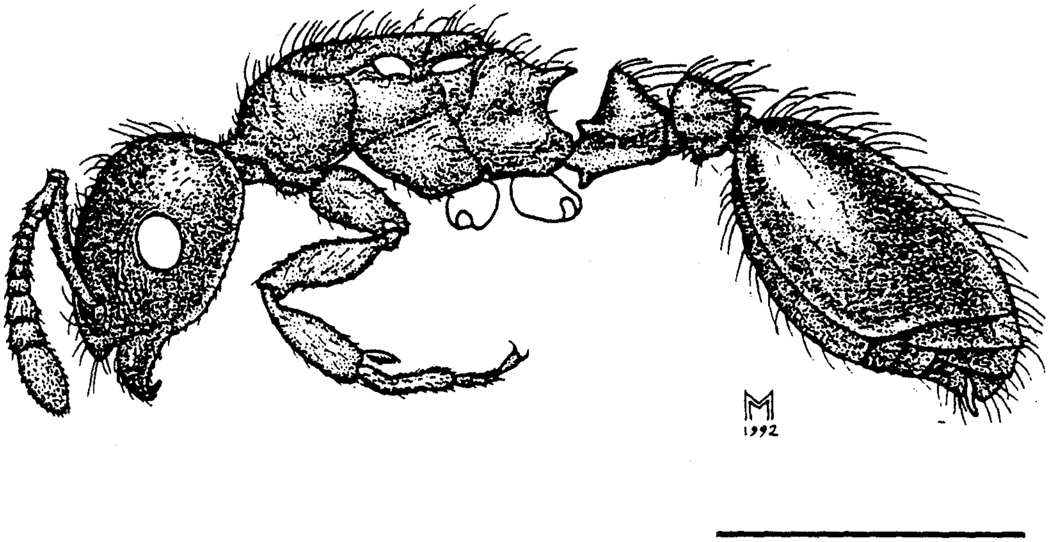

Figure 1. Typical "shiny" *Doronomyrmex pocahontas* queen of field colony # 1 (1977), Scale bar 1 mm

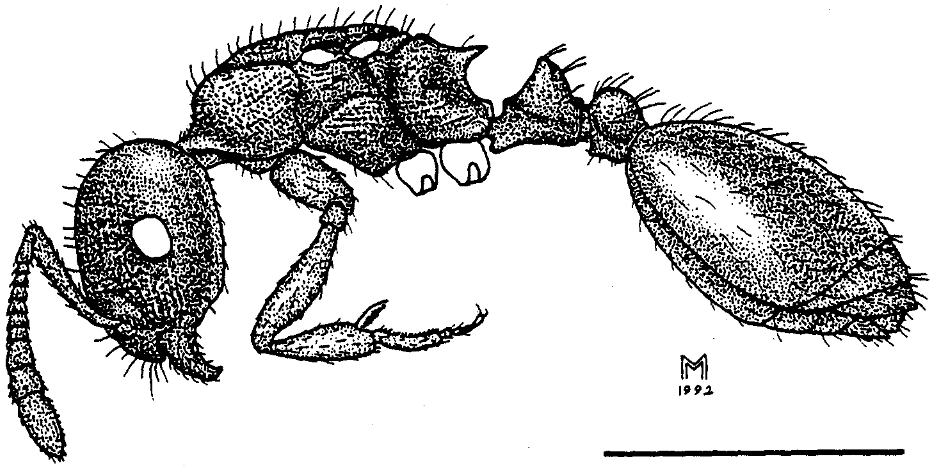

Figure 2. "Dull" gyne from *D. pocahontas* field colony # 3 (1977). "Dull" gynes were originally misidentified as host species gynes (Buschinger 1979), Scale bar 1 mm

closely resembled what one might expect queens of the brownish workers would look like ("dull" phenotype, e.g., the gynes in field colony # 3, Figs. 2, 3).

We must stress here that "dull" gynes respresent a range of phenotypes from such closely resembling the "shiny" specimens (petiole a little less steep, sculpture a bit rougher) to such morphologically similar to gynes of *Leptothorax* C, i.e. strongly sculptured, much smaller and lighter in coloration, and with shorter hairs than the "shiny" gynes.

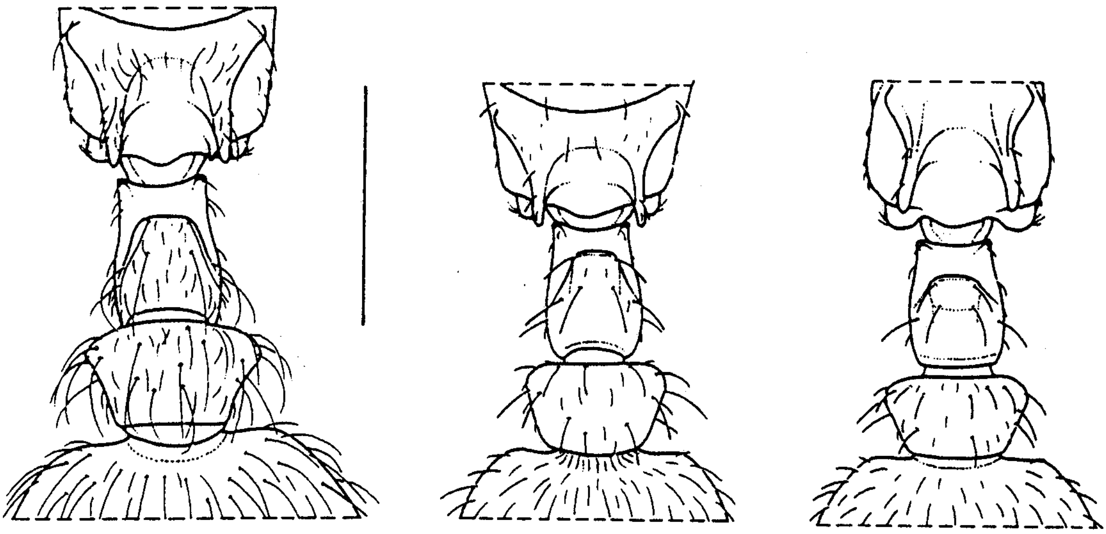

Figure 3. Petioles of (left): *D. pocahontas* "shiny" queen, field colony # 1 (1977); (right): worker of the same colony, which also contained 79 "shiny" gynes; (centre): "dull" gyne of field colony. # 3 (cf. Fig. 2). Scale bar 0.5 mm

Mating and colony founding experiments

Alates of *D. pocahontas* left the nest chambers about one hour after morning temperature increase (during the 15/25 °C summer temperature rhythm). Sexual activity was highest when sunlight was shining into the laboratory. Temperatures in the flight cage raised slowly to 30 °C within two hours. Sexual activity lasted for about one hour. Gynes exhibited sexual calling behavior, similar to gynes of many species of *Leptothorax* (s. str.) and related social parasites (Franks et al. 1991). Copulations lasted typically for less than a minute, but occasionally were continued for up to 35 minutes. Gynes shed their wings between one and several hours after mating. Seven of 21 mated gynes were dissected, some only after colony founding experiments, and all had sperm in their spermathecae.

To study colony founding behavior of *D. pocahontas*, eight mated gynes of colony # 7 were placed into the foraging arenas of formicaries with small natural colonies of *Leptothorax* C. Most gynes were seriously attacked and pulled on legs and antennae by the workers and all died within three to eight days. Nine mated gynes were put into artificial colonies consisting of four workers from their maternal nest, eight *Leptothorax* C pupae, and seven *Leptothorax* C larvae. This "passive colony foundation" has been successfully used in a number of socially parasitic ants (Buschinger et al., 1990) and proved also effective with *D. pocahontas*. Colonies founded in this way survived for up to eleven breeding cycles and produced numerous sexual and worker offspring. Finally, field colony # 7 was split during the first laboratory summer. During the 3rd breeding cycle, a mated daughter was reintroduced into the orphaned branch of the nest, which then survived until the 9th cycle.

Most female sexuals reared in these ten laboratory-founded colonies were more or less "dull" gynes, though some typical "shiny" *D. pocahontas* gynes were also produced. As most field colonies, some laboratory-founded colonies produced predominantly males and workers and only few gynes. No pattern could be recognized in the production of the female phenotypes, some colonies yielding only "dull" gynes, others both "shiny" and "dull" specimens. Since the difference between slightly "dull" and "shiny" gynes was not recognized before the end of the experiments (and because many gynes were lost due to death and dismembering in the colonies), we are unable to provide numerical ratios of the various phenotypes reared. It is also not possible to tell the type of queens used for artificial colony foundation. Only from one experiment we are sure that "dull" gynes were offspring of a "shiny" queen, as in field colony # 3.

Workers and males of Doronomyrmex pocahontas

Workers of *D. pocahontas* (Fig. 4) are easily distinguished from *Leptothorax* (s. str.) *retractus* (compared with specimens from Maligne Canyon, Alta., Jasper, Alta., Kinney Lake, B. C.) and large black *Leptothorax* D (Maligne Lake, Alta.; Lake Edith Cavell, Alta.) by the shape of the petiolar node, which is rounded in lateral view in *D. pacohontas* but sharply angled in *L. retractus* (Francoeur, 1986) and rather flat in *Leptothorax* D. Furthermore, the anterior margin of the clypeus is deeply notched in workers of *L. retractus* but not so in *D. pocahontas*. From *Leptothorax* C (Maligne Canyon, Alta.; Jasper, Alta., Kananaskis, Alta., Manning, B. C.), workers of *D. pocahontas* differ in the shape of their postpetiole, which in dorsal view is markedly trapezoidal. The hairs on petiole, postpetiole and gaster are distinctly longer in *D. pocahontas* (0.06–0.1 mm) than in *Leptothorax* C (0.04–0.06 mm).

As in queens, the sculpture of *D. pocahontas* males (Fig. 5) is highly variable. Nevertheless, at least dorsal and lateral parts of the propodeum were shiny and smooth in most examined individuals. The propodeum of males of all examined *Leptothorax* (s. str.), is opaque, often roughly sculptured or wrinkled.

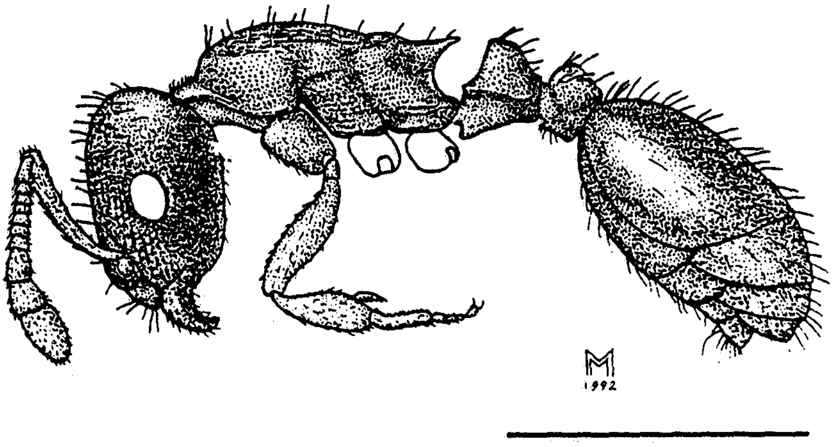

Figure 4. *D. pocahontas* worker from field colony # 1, Scale bar 1 mm

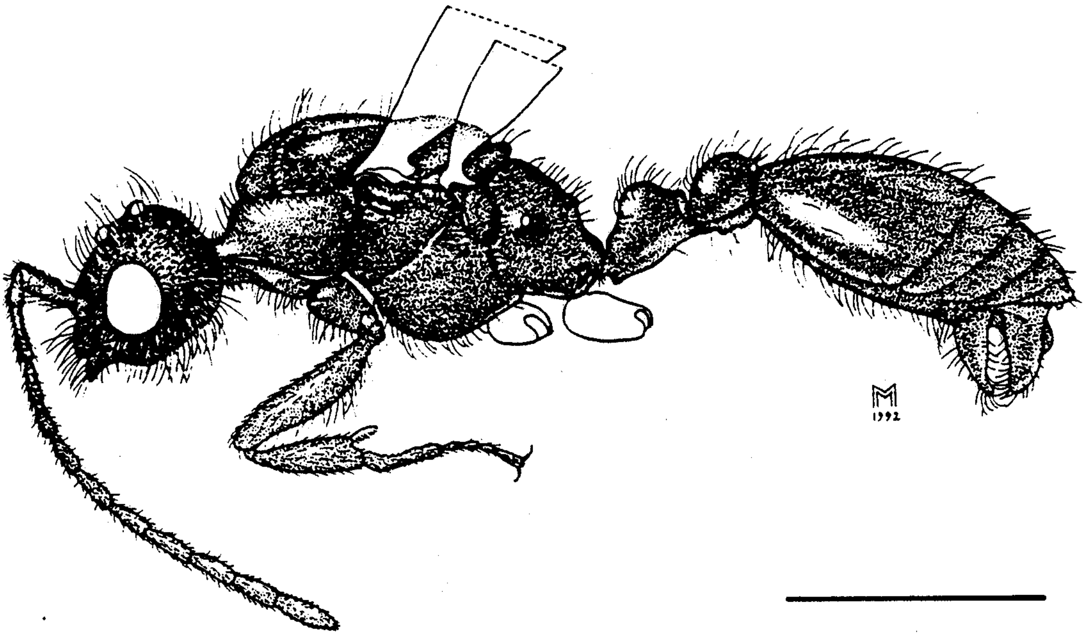

Figure 5. *D. pocahontas* male from field colony # 3, Scale bar 1 mm

Chromosome numbers and allozyme patterns

The chromosome number of *D. pocahontas* ($n = 18$) clearly differs from that of *L. acervorum* and *L. sphagnicolus* ($n = 13$), *L.* sp. A, and the workerless parasites *L. paraxenus* and *L. faberi* ($n = 15$), but is similar to that of *L. retractus*, *Leptothorax* C and D, and palaearctic *L. muscorum* ($n = 17, 18$; Fischer 1987, Loiselle et al., 1990)

In three of four enzyme systems which are of diagnostic value, *D. pocahontas* is indistinguishable from *Leptothorax* C, but differs from large *Leptothorax* D and *L. retractus* (Heinze 1989).

Discussion

The results of this study strongly suggest that *Doronomyrmex pocahontas* is not a workerless parasite. Instead, it produced own workers and pure *D. pocahontas* laboratory colonies were well capable of surviving without any host workers from other ant species. However, the striking variability in size, pilosity, sculpture and coloration of *D. pocahontas* gynes remains to be explained. As mentioned above, some reared gynes were long-haired, black and shiny, while others had shorter hairs, were brownish and roughly sculptured ("dull"), and in these respects resembled the *D. pocahontas* workers and *Leptothorax* C queens. Progeny of the field-collected colony # 3 (1977) were so similar to *Leptothorax* C queens that they were mistaken as gynes of the "host" species. Occasionally individuals were reared which were morphologically intermediate between workers and queens ("intermorphs" sensu

Buschinger and Winter, 1976). It is puzzling that these always had the black coloration and smooth sculpture of the "shiny" phenotype.

It is still unclear what causes phenotypic variation in *D. pocahontas*. In the following, we examine three potential explanations.

1. *D. pocahontas* is a hybrid of two or more *Leptothorax* (s. str.). Hybridization of different species of leptothoracine ants is a well known phenomenon both from the field and laboratory experiments (Buschinger, 1972; Seifert, 1984; Heinze, 1989; Jessen and Klinkicht, 1990; Douwes and Stille, 1991) and might explain the rareness as well as the large morphological variation of *D. pocahontas* adults. The "shiny" phenotype might result from a particular combination of genes from two parental species. Similarly, ordinary queens of *Acanthomyops latipes* (α-females) differ in morphology strongly from β-queens, which are hybrids between *A. latipes* and *A. claviger* (Wing, 1968).

In *Solenopsis* (Hung and Vinson, 1977) and *Leptothorax* (Heinze, 1989; Douwes and Stille, 1991), allozyme studies have been used to detect and analyze interspecific matings: Hybrids of the undescribed nearctic *Leptothorax* (s. str.) species A and B, e.g., are easily recognized by heterozygous enzyme patterns, as the two parental species are fixed for different electromorphs of Malate dehydrogenase, Isocitrate dehydrogenase (IDH), and 6- Phosphogluconate dehydrogenase. With the exception of IDH, which is slightly polymorphic in *Leptothorax* C (Heinze, 1989), these three enzyme systems are monomorphic also in those *Leptothorax* (s. str.), which live sympatrically with *D. pocahontas*, but differ between species. If *Doronomyrmex pocahontas* was a hybrid between these species, it should carry genes for the two enzyme electromorphs of both parental species and might thus exhibit hybrid enzyme phenotypes. Enzyme analyses did not show heterozygous patterns in *D. pocahontas*. However, parental alleles not necessarily are equally expressed in hybrids (e.g., Hung and Vinson, 1977).

2. *D. pocahontas* is a rare, non-parasitic species which hybridizes with *Leptothorax* C. Allozyme analyses cannot rule out this possibility. It would explain why some *D. pocahontas* queens had exclusively "shiny" sexual offspring, while others reared "dull" hybrid progeny.

3. *Doronomyrmex pocahontas* is the rare extreme variant of a non-parasitic species which exhibits a polymorphism of queens, workers, and males. Since *D. pocahontas* workers are morphologically very similar to those of *Leptothorax* C, their karyotypes and enzymes are almost identical, this species might in fact be *Leptothorax* C.

Environmentally or genetically mediated polymorphism is well known from numerous species of ants. Infestation with tapeworm cysticercoids or a fungus (formerly believed to be Haplosporidia, Sánchez-Peña et al., 1993) or different climatic conditions may have strong impact on coloration and also morphology of leptothoracine ants (Plateaux, 1972; Buschinger, 1973; Buschinger and Winter, 1983). A genetical polymorphism affecting queen morphology is known from *Harpagoxenus sublaevis* and *Leptothorax* sp. A (Buschinger, 1978; Heinze and Buschinger, 1989). In *Leptothorax (Myrafant) nylanderi*, pale coloration ("*pallens*"-morph) appears to be caused by a recessive allele (Plateaux, 1981 a, b).

The results of laboratory rearing experiments speak against an environmentally-based modification in the case of *D. pocahontas*, but a genetical mechanism might well be involved. One or several alleles might cause (I) shiny cuticle in female and male sexuals, (II) longer hairs in gynes and workers, (III) wider postpetiole, and (IV), darker coloration. It is puzzling, however, that the "dull" phenotype has never been found as queen of a field colony.

Apparently the hypothetical mechanism underlying the "*pocahontas*" phenotype also accelerates the development of sexual larvae: male and female sexuals eclose several weeks earlier than those of sympatric *Leptothorax*. This might be advantageous in an alpine environment with short summer seasons, as in the type locality. The difference in maturation of the "*pocahontas*" and *Leptothorax* sexuals would ensure a certain reproductive isolation between the genotypes, thus permitting the comparatively frequent occurrence of "*pocahontas*" colonies in the small type area. The local microclimate may fit best their requirements or adaptations.

16th century Indian princess Pocahontas, namesake of the ant from Maligne Canyon, at least temporarily set misconceptions about American natives right when brought to England and charming the court with her gracious manner. Similarly, when transferred from American wilderness to the laboratory, *Doronomyrmex pocahontas* disproved what we thought we knew about its life history. As our study shows it certainly is necessary to reexamine this peculiar ant more closely, and only additional material will help to decide whether *D. pocahontas* is a hybrid, a polymorphic species, or something else. As long as studies on this very species and on the validity of the genus *Doronomyrmex* as a whole are not completed, we suggest to retain the original name *Doronomyrmex pocahontas:* "the playful one".

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