

## A new inquiline ant (Hymenoptera: Formicidae) in *Cataglyphis* and its phylogenetic relationship

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*Cataglyphis hanna*e, a new workerless, putatively inquiline ant species is described and its phylogenetic relationships and biology discussed. *C. hanna*e was collected in two different nests of *C. bicolor* and, based on its smaller size and the delayed production of sexuals in comparison to its host, an inquiline life style is inferred. If correct, this would be the first social parasite within *Cataglyphis*. Cladistic analysis indicates an independent origin of the inquiline with subsequent invasion of its host.

KEYWORDS: Ant, inquiline, *Cataglyphis*, taxonomy, evolution, social parasitism.

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### Introduction

Recently, inquiline ants have been given considerable attention (e.g. Bourke and Franks, 1991; Buschinger, 1990) with a special emphasis on their origin and evolution. Two main hypotheses have been put forward, both originating from Emery's rule (Emery, 1909). The first, the common ancestry hypothesis, stresses the immediate ancestry of host and inquiline and a sympatric mode of speciation, and the second, the social deception hypothesis, a looser relationship with an invasion of the host by the inquiline species. One way to understand the evolution of this behaviour is to study the phylogeny of taxa where this behaviour occurs, and then to superimpose the behavioural data (Bourke and Franks, 1991; Carpenter *et al.*, 1993). In ants, where inquilinism was described and discussed for the first time by Wasmann (1908), none of the genera where inquilinism occurs (Hölldobler and Wilson, 1990), have been cladistically analysed. In wasps, however, Carpenter *et al.* (1993) demonstrated that the inquilines are not sister groups of their respective hosts but rather probably form a monophyletic group whose species later immigrated to several hosts.

In ants, inquilinism occurs in several subfamilies, but mainly in myrmicine ants. In formicine ants, only 10 inquiline species are recognized in the following genera: *Anoplolepis*, *Camponotus*, *Formica*, *Paratrechina*, and *Plagiolepis* (Hölldobler and Wilson, 1990). Among those genera, *Plagiolepis* includes half of the known species, and *Formica* is well known to include many different forms of social parasitism and to be the host for other genera, such as *Polyergus*. It is interesting that, beside this very variable repertoire of social behaviour, the 150 or so *Formica* species show hardly any

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morphological variation. This is in contrast with the other species-rich genus within the Formicini, *Cataglyphis* with some 90 species, which have a great variation in morphological characters, especially male genitalia, but hardly any in social behaviour (Agosti, 1990).

The ant genus *Cataglyphis* currently includes over 100 valid specific and subspecific names, but the identity of hardly any of the names is known. Recently, Tinaut (e.g. 1990, 1991) and Agosti (1990) started to re-analyse this genus, in which some species have become models in fundamental research in orientation behaviour using polarized skylight (Wehner, 1981), path integration (Muller and Wehner, 1988), homing (Wehner, 1992), and thermoregulation (Wehner *et al.*, 1992).

During fieldwork collecting nest series of North African ants of the *Cataglyphis bicolor* species group for a revision of this genus, some 200 nests were at least partially dug out. In 2 nests, small alate females and males were present, but no alate sexuals of the expected size for *bicolor*. The mating flight of *bicolor* must have taken place at an earlier time, as they were present in nests further north, where nuptial flights occur later. After examination of these smaller specimens, especially of the male genitalia, it became obvious that they belong to a new undescribed species. Thus, the occurrence of an inquiline in a genus which has sufficient morphological characters to be used in a cladistic analysis is the ideal case to test hypotheses for the evolution of inquilineism in ants.

In this study, I describe this species (*C. hanna*) and analyse its sister group relationships. This is then used to test the hypotheses of inquiline origin from a common ancestor versus the origin of the inquiline independently with a subsequent invasion of its host.

### Material and method

The specimens were collected alive in 2 separate nests in El Guettar (Tunisia) in an oasis, with the nests being at the edge of irrigated fields. The sexuals of *hanna* were kept alive for three weeks in plastic boxes with a plaster layer together with their host, *C. bicolor*. On several occasions *hanna* males and females were observed being fed by *bicolor* workers, and in no case was any sign of aggression between the 2 species detected. The identity of the host has been confirmed by worker morphology as well as allozyme pattern (Agosti *et al.*, in preparation).

Abbreviations, acronyms of depositories and measurements follow Agosti (1990), and all measurements (mm) are given (e.g. HL 1.40). TAI (Hind tibia-alitrunk index) = Length of hind tibia  $\times$  100/AL. LI (Leg index) = Length of hind tibia  $\times$  100/length of hind femur.

### *Cataglyphis hanna* n. sp.

#### Material examined

HOLOTYPE: ♂, HL 1.40, HW 1.20, EL 0.50, SL 2.18, AL 2.63, CI 86, SI 181, EI 41.7, FI 35.4, LI 100.8, TAI 114.3.

#### Diagnosis of male

Ant of the *Cataglyphis bicolor* species group (Agosti, 1990), with the following diagnostic features:

- (1) Black head and alitrunk.
- (2) Alitrunk length 2.63 mm.

- (3) Subgenital plate distally trilobed with the median process triangular and not digitiform.
- (4) In ventral view, median process with hair-carrying pits to the tip.
- (5) In lateral view, apicolateral appendix of sagitta not overreaching outline of apical, serrated plate.
- (6) Apicolateral appendix of sagitta short and terminally rounded; in ventral view only slightly raised above the plane of the apical, serrated plate.
- (7) Long hind tibiae (TAI 114.3).

PARATYPE: ♂♂ HL 1.30–1.43, HW 1.05–1.19, EL 0.44–0.50, SL 1.98–2.23, AL 2.48–2.73, CI 80.8–86.6, SI 175.5–195.6, EI 41.1–43.0, FI 91.4–103.2, LI 101.7–105.5, TAI 108.3–116.0 ( $n = 8$ ).

There is a slight variation in size, but the extremes of the range of absolute measurements are always far below those of the other males of the *bicolor* species group. Compared with all the other males of the *bicolor* group, *hannae* has the longest hind tibiae (TAI > 108). Head and alitrunk always black in colour.

#### Diagnosis of female

Ant of the *Cataglyphis bicolor* species group with the following diagnostic features (Fig. 1B):

- (1) Small size, alitrunk < 3.2 mm.
- (2) Scape much longer than head length (SI > 120).

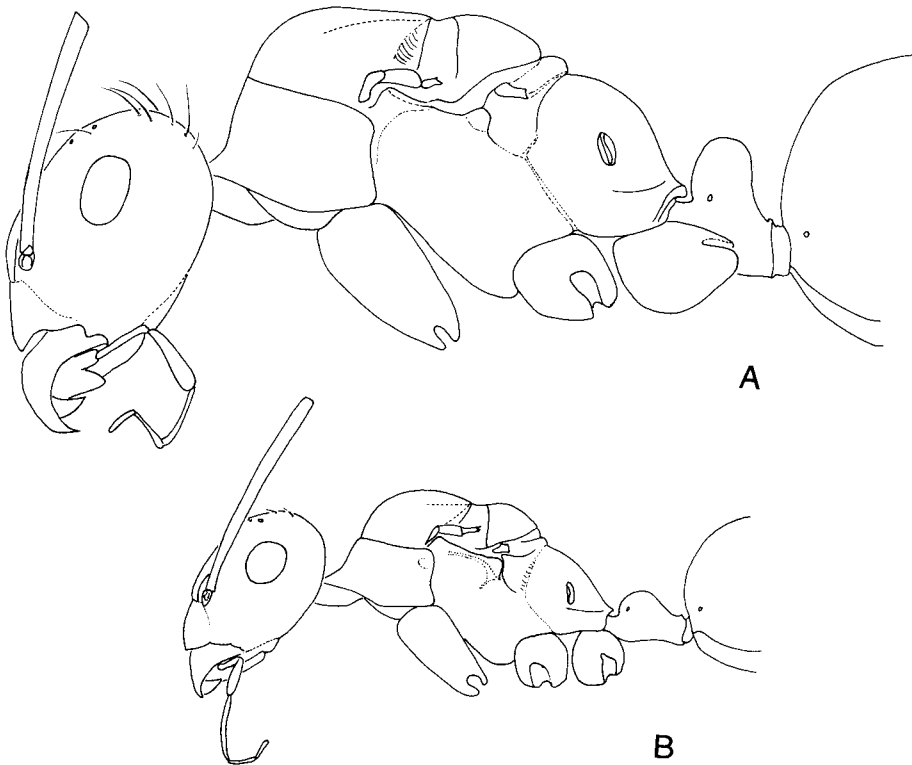


FIG. 1. Lateral view of the females of *C. bicolor* (A) and its inquiline *C. hannae* n.sp. (B). Hairs are only drawn on the occiput.

- (3) Long hind tibiae (TAI > 90).
- (4) Head and alitrunk bright red.
- (5) First funicular segment of intermediate length ( $28 < FI < 35$ ).
- (6) Low rounded petiole in lateral view.

PARATYPES: ♀♀ HL 1.75–1.88, HW 1.65–1.73, EL 0.48–0.50, SL 2.00–2.18, AL 2.95–3.13, CI 90.4–94.3, SI 121.2–129.9, FI 29.0–31.1, EI 28.4–29.0, LI 101.8–107.1, TAI 93.5–100.8 ( $n = 5$ ).

#### *Deposition of type material*

HOLOTYPE: ♂, **Tunisia**, El Guettar, 34.33°N, 8.92°E, 300 m; in Oasis, at the edge of irrigated fields under *Eucalyptus* trees, D. Agosti, 08.06.1992, sample F92039, in nest with *Cataglyphis bicolor* (MHNG).

PARATYPES: 5 ♀♀, (alates) and 14 ♂♂, same as holotype. 7 males, Tunisia, El Guettar, 34.33°N, 8.92°E, 300 m; in Oasis, at the edge of an irrigated lucerne field, D. Agosti, 08.06.1992, sample F92309, in nest with *Cataglyphis bicolor* (BMNH, CDA, CRW, MCZ, MHNG).

*C. hanna* can be separated from all the other known species in the *bicolor* group by the above mentioned diagnostic characters, especially by the body size, the long antennal scape and hind tibiae, the low rounded petiole, and the male genitalia. *C. abyssinicus*, the only species with small females, has a much shorter scape (SI < 113), and shorter hind tibiae (TAI < 85); no males of this species are known. The long black hairs on the occiput of the head as seen in *bicolor* are not present in *hanna*, and thus exclude the possibility of *hanna* being a microgyne of *bicolor*.

Although > 1500 different samples of species of the *bicolor* complex are in our collections, and most of them from Tunisia, no further *hanna* specimens have been collected before. The host of *hanna* is distributed along the southern foothills of the Atlas mountains in the transitional zone from the Mediterranean to the Desert region, not reaching the Atlantic in the West and not extending into Libya (Agosti *et al.*, in preparation). Thus, *hanna* might be more common, certainly if one considers that the southern extension of the Mediterranean vegetation during the Pleistocene reached as far south as the Saharan mountains Tassili and Hoggar (Quezel, 1965). But social parasitic ants tend to have a clumped distribution (Buschinger, 1985) and the restricted collecting area might truly reflect its distribution. Finally, these males and females were collected as alates, during a survey where > 200 nests were at least partially dug up.

The habitat was at the edge of an irrigated *Medicago sativa* field and on a sandy place in the shade of some tall *Eucalyptus* trees on the side of a track within the oasis. In this desert region, the occurrence of species of the *bicolor* group is restricted to oases.

The position of *hanna* within the *bicolor* species group is established by the male genitalia and the funicular index of the female. More problematic, and challenging, is the sister group relationship within the *bicolor* group. A phylogenetic analysis using morphological characters of *nodus* (outgroup), *abyssinicus*, *bicolor*, *savignyi*, *viaticus* (Table 1) and the explicit enumeration procedure from the computer program Hennig86 (Farris, 1988), resulted in 3 most parsimonious trees. Subsequent successive weighting established 2 most parsimonious trees (Fig. 2). Both these trees share the sister group *hanna* + *abyssinicus*, and support a sister group *viaticus* + (*hanna* + *abyssinicus*). The sister group relationship of *hanna* + *abyssinicus* is so far only supported by female characters, as the males of *abyssinicus* are unknown. However, the long antennal scape and the small size of the females of

Table 1. Data matrix. One ♂: SI > 170 (character state 0), SI < 170 (1); 2 Queen: CI > 95 (0), CI < 95 (1); 3 Q: SI < 105 (0); SI > 105 (1); 4 Q, TL < 3.5 mm (0), TL > 3.5 mm (1); 5 Q, TAI < 90 (0), TAI > 90 (1); 6, Q, white hairs on occiput of head (0), black hairs (1); 7, Q, head and alitrunk bright red (0), dark red to black (1); 8 M, lateral apical appendage of subgenital plate digitiforme, parallel sided (0), triangular (1); 9 M, median apical appendage of subgenital plate in crosssection (at midlength) rounded (0), angular (1); 10 M, Sagitta with antero-lateral appendage convergent at base (0), parallel sided at base (1); 11 M, in lateral view, antero-lateral appendage of sagitta crossing outline of apical blade (0), not extended beyond (1); 12 M, median appendage of subgenital plate shorter as lateral appendages (0), of same length (1); 13 M, antero-lateral appendage of sagitta apically pointed (0), rounded (1). (A full discussion of the characters, and coding, based on > 1000 specimens, will be provided elsewhere (Agosti, in preparation).

Species	Characters												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Nodus</i>	1	1	0	0	0	0	0	0	1	0	0	1	1
<i>Hannae</i>	0	1	1	1	1	0	1	1	0	0	1	0	0
<i>Abyssinicus</i>	–	1	1	1	0	0	1	–	–	–	–	–	–
<i>Bicolor</i>	1	0	0	0	0	1	0	0	1	1	0	0	0
<i>Savignyi</i>	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Viaticus</i>	1	0	0	0	0	0	1	0	0	0	0	0	0

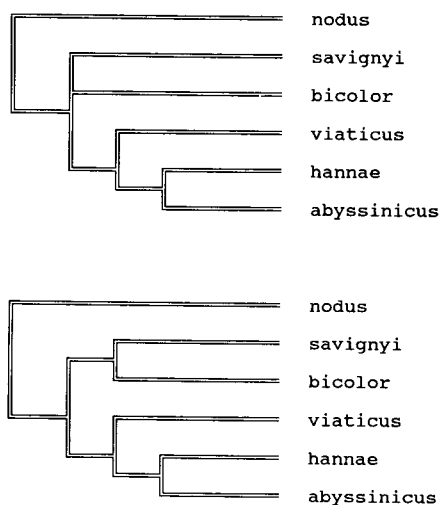


FIG. 2. Phylogenetic relationships of *Cataglyphis hannae* n. sp. Two most parsimonious trees shown with a consistency index (*ci*) of 98 and a retention index (*ri*) of 96. The synapomorphies for the sistergroup *hannae* + *viaticus* are small body size (characters 3 (1) in Table 1), and long antennal scape (4 (1)); for the sistergroup *viaticus* + (*hannae* + *abyssinicus*) the synapomorphies are bright red colour of head and alitrunk (7 (1)) and shape of median appendage of the male subgenital plate (9 (0)).

*abyssinicus*, which is the same as in *hannae* and unique in species of the *bicolor* species group, indicate an inquiline life style for this species too. A more detailed discussion will be provided by Agosti (in preparation).

As all the results are based on morphological characters, it would be interesting to test them using other characters such as DNA sequences, electrophoretic data or the chemical composition of glandular compounds, all of which have already showed their specificity at the species level (Keegans *et al.*, 1992; Agosti *et al.*, in preparation).

## Conclusions

Although the discussion on the origin of inquilinism in ants has lasted at least since Wasmann (1908), it is only recently that Carpenter *et al.* (1993) used cladistic analyses to test the proposed evolutionary hypotheses. They demonstrated by analysing allozyme data, that the social deception hypothesis is the more likely for the evolution of the inquiline wasps *Polistes atrimandibularis* and *P. semenowi*. In none of their trees were these species the sister group of their respective host. The same pattern appeared in a biochemical analysis of leptothoracine social parasitic ants (Heinze, 1991).

In neither of the 2 most parsimonious cladograms is the inquiline *hannae* the sister group of its host *bicolor*. This refutes the common ancestor hypothesis, in which sympatric speciation is involved, and indicates an independent origin of the inquiline with a subsequent invasion of its host. Assuming *abyssinicus* to be an inquiline too, its sister group relationship with *hannae* indicates a common ancestry of the two inquilines, which invaded two independent hosts: *hannae* into *bicolor*, and *abyssinicus* possibly into *savignyi* (the only *bicolor* group species to co-occur in Ethiopia).

This result is also supported by the fact, that in *Cataglyphis* polygynous colonies, requested as a step within the evolutionary scenario proposed by Buschinger (1990) and Bourke and Franks (1991), were extremely rare (D. Agosti, unpublished data).

Finally, the question might be raised, whether the evolution of inquilines can be explained by one general theory or whether inquilines are just one phenomenon. How can inquilines in *Myrmica* species (Bourke and Franks, 1991) possibly explain inquilines in the myrmicine genus *Rhoptromyrmex*, which can be found in different subfamilies such as in the dolichoderine genus *Tapinoma* (Bolton, 1986)?

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