Molecular phylogeny of the desert ant genus *Cataglyphis* (Hymenoptera: Formicidae)

Markus KNADEN, Alberto TINAUT, Johannes STÖKL, Xim CERDÁ & Rüdiger WEHNER

**Abstract**

Since the middle of the 20th century ants of the genus *Cataglyphis* – inhabiting the southern part of the Palearctic region – have become model organisms for insect navigation and various other fields of biological research. Currently ca. 100 *Cataglyphis* species are described. However, although molecular-based phylogenetic analyses are common practice in ant systematics, to date phylogenetic analyses of *Cataglyphis* have been strictly morphology-based. Here we present the first molecular phylogeny based on mitochondrial DNA (754 bp) of 78 *Cataglyphis* specimens collected over a large part of the distributional range of the genus. By examining the same specimens based on morphological characters, we can conclude that major features of the morphology-based species-group phylogenies are supported by our molecular approach.

**Key words:** *Cataglyphis*, phylogeny, mtDNA, morphology, systematics.

**Introduction**

Starting in the late 1960s (WEHNER 1968) desert ants of the genus *Cataglyphis* have become a neuroethological model system for the study of animal navigation, especially of visually guided behaviour such as the use of celestial and terrestrial orientation cues, odometry, and path integration (for reviews, see WEHNER 1982, 2003, 2008; for path integration, see WEHNER & SRINIVASAN 2003; for odometry, see WITTLINGER & al. 2006). In addition, and partly in connection with the studies mentioned above, several species of the genus have attracted the interest of biologists covering as widely a spectrum of research areas as optics (e.g., ZOLLIKOFER & al. 1995), brain research (e.g., WEHNER & al. 2007, SEIDL & WEHNER 2008, STIEB & al. 2010), locomotor physiology (e.g., ZOLLIKOFER 1994, SEIDL & WEHNER 2008), respiratory physiology (e.g., LIGHTON & WEHNER 1993), thermobiology (e.g., WEHNER & al. 1992, GEHRING & WEHNER 1995, CERDÁ & RETANA 1997, 2000, CLEMENCET & al. 2010), ecology (e.g., HARKNESS 1977, WEHNER & al. 1983, HARKNESS & MAROUDAS 1985, LENOIR & al. 1990, CERDÁ & RETANA 1998, CERDÁ & al. 2002, DIETRICH & WEHNER 2003, KNADEN & WEHNER 2006), social behaviour and division of labour (RETANA & CERDÁ 1990, 1991) and various sociobiological aspects such as life history traits, genetic structure, colony reproduction, and sex-ratio determination (e.g., CAGNIANT 1982, 1988, LENOIR & CAGNIANT 1984, LENOIR & al. 1988, BER-
cation of the type specimen of *C. viatica*, which FOREL (1890) placed (erroneously) in the *C. alisquamis* species group – the subgenus *Monocomas* of SANTSCHI (1929) – rather than (correctly) in the *C. bicolor* species group – the subgenus *Cataglyphis* of SANTSCHI (1929). It was only after AGOSTI (1990) and TINAUT (1991) had pointed out FOREL’s error that this major confusion about the *C. viatica-bicolor* assignment has been cleared.

To date the taxonomy of the genus *Cataglyphis* is based on morphological investigations mainly performed by EMERY (1906), FOREL (1908a) and SANTSCHI (1929) between the end of the 19th and the beginning of the 20th century. As all three investigators were elaborate “splitters”, their nomenclatures are fraught with trinominal and tetranominal taxa such as *Cataglyphis viaticus* var. *bunignonii* (FOREL 1908b) or *Cataglyphis adenensis* st. *livida* var. *bunignonii* (SANTSCHI 1929). In fact some 100 subspecies, subtypes, varieties, etc., have been described, most of them representing only four species: *C. albicans* with 27, *C. bicolor* with 19, *C. cursor* with 13 and *C. viatica* with ten subclassifications. This confusion reflects the high intraspecific variability and, hence, the difficulty to identify valid morphological characters that are species- and not just population-specific. Therefore, in recent years the investigations have focused more and more on non-morphological characters. A restricted number of species has been investigated also biochemically (by comparing glandular secretions and cuticular hydrocarbons: e.g., HÉFETZ & ORION 1982, KEEGANS & al. 1992, DAHBI & al. 1996, GÖKÇEN & al. 2002, DAIMI & al. 2008) or molecular phylogenetics (by employing nuclear and mitochondrial DNA: KNADEN & al. 2005).

Here we present a preliminary molecular phylogeny inferred with mitochondrial DNA from 78 *Cataglyphis* worker specimens that were collected over a large part of the distributional range of the genus. The same specimens were also identified based on their worker morphology using not only the classical keys of EMERY (1906) and SANTSCHI (1929) – the subgenus *Cataglyphis* – but also regional keys such as COLLINGWOOD (1978) for the Iberian Peninsula, COLLINGWOOD (1985) and COL-

... continued...
Fig. 1: Locations of the *Cataglyphis* samples used in this study. Numbers depict appearance within the phylogenetic tree (Fig. 2). Colors depict morphologically identified species groups. Red, *C. bicolor* group; blue, *C. albicans* group; green, *C. cursor* group; pink, *C. pallida* group; yellow, *C. altisquamis* group; brown, *C. bombycina* group. Inset figure depicts Tunisia, the country with the highest sample density in this study.

LINGWOOD & AGOSTI (1996) for Saudi Arabia, AGOSTI & COLLINGWOOD (1987) for the Balkan region and CANNANT (2009) for Morocco. For a list of the species names used see appendix (provided as digital supplementary material to this article, at the journal’s web pages). We should mention here, that in some cases different authors use different name variants for the same species (e.g., *Cataglyphis nodus* vs. *C. noda*, *C. viaticus* vs. *C. viatica* (AGOSTI 1990, KNADEN & al. 2005, LENOIR & al. 2009). As the gender of the species name needs to conform to the gender of the genus, which is feminine in case of *Cataglyphis*, we always used the feminized version of the species name. Finally we compared the specimens we included with *Cataglyphis* type specimens in the collections of the museums of Basel, Genève, Paris, and Warsaw.

From the nine species groups described by AGOSTI (1990) we identified six (*Cataglyphis albicans* group, *C. altisquamis* group, *C. bicolor* group, *C. bombycina* group, *C. cursor* group, and *C. pallida* group, with the latter being represented by only one specimen). We then compared whether those specimens that were morphologically determined to belong to the same species group also clustered in the molecular-based phylogenies.

**Results**

Of the analyzed 754 bp 311 sites were variable, and 275 were parsimony informative. The mtDNA analysis resulted in a tree with two well supported clades. Clade one further splits into a *Cataglyphis bicolor* and a *C. albicans* clade, while clade two contains the *C. cursor*, the *C. bombycina*, and the *C. altisquamis* clades, whose separation was supported by BI, but not by NJ or MP. Of the 78 specimens we included, 77 clustered at the level of species groups as predicted by the morphological determination (Fig. 2), while the only representative of the *C. pallida* group appeared within the *C. cursor* clade. However, especially within the *C. bicolor* clade the assemblage of species was quite mixed with, e.g., *C. viatica*, *C. bicolor*, and *C. savignyi* appearing at several statistically well supported positions within the clade. We conclude that for an in-depth analysis across the *Cataglyphis* species groups, the CO1 sequence used in our approach would need to be complemented by additional mtDNA genes and / or nuclear genes.

We next checked whether the 48 specimens from the *Cataglyphis bicolor* group clustered according to their geographical origin. However, this was not the case (Figs. 1, 2). For example, specimens from Greece appeared in the same clade as specimens collected in Yemen, and specimens from Tunisia clustered with those from Burkina Faso.

**Discussion**

Until recently the most thorough classification of ants of the genus *Cataglyphis* was based on the morphology of male genitalia (for a review, see AGOSTI 1990). The majority of ant individuals belongs to the worker caste, while males are rare and can be collected only during the restricted time frame of nuptial flights. We therefore revisited the morphology-based classification of this genus with a mo-
Tab. 1: List of samples used for the molecular analysis. 1st column, position in the phylogenetic tree (Fig. 2); 2nd column, morphology-based assigned species names; 3rd column, collection numbers under which these samples are stored in the Rüdiger and Sibylle Wehner *Cataglyphis* Collection at the Senckenberg Research Institution (Leibniz Institute) in Frankfurt/Main, Germany; 4th column, country of collection; 5th column, sampling site; 6th column, GenBank accession numbers.

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<td>ttgattttttgtatatccagaakt</td>
<td>24 bp</td>
<td>2492</td>
<td>CROZIER &amp; CROZIER (1993)</td>
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<td>COH1</td>
<td>tagggaaatttttgatttagag</td>
<td>24 bp</td>
<td>3376</td>
<td>KNADEN &amp; WEINER (2006)</td>
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<tr>
<td>COH1bic</td>
<td>tggggaaattttgattttggag</td>
<td>24 bp</td>
<td>3376</td>
<td>KNADEN &amp; al. (2005)</td>
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</table>
Fig. 2: A phylogenetic tree of the genus *Cataglyphis* inferred from CO1 data. Topology and branch length were inferred in the Bayesian Inference (BI) framework. Average standard deviation of split frequencies was 0.0082, indicating that the rather low burn-in of only 25% was sufficient. Numbers at nodes are Bayesian posterior probabilities (BI), bootstrap support from Neighbor Joining (NJ) and from Maximum Parsimony (MP) analysis. Alternatively, if space is limited, numbers are given in the order BI / NJ / MP. – indicates a bootstrap value below 50 or a conflict in the topology of the BI tree and the MP / NJ tree. The scale bar gives substitutions per site. *Camponotus conithorax* (Accession no. EF653271.1) and *Formica cunicularia* (Accession no. HQ853323.1) were used as outgroups as both *Camponotus* and *Formica* represent closely related genera of *Cataglyphis* (see AGOSTI 1990). The branch leading to *Camponotus* was shortened for better presentability of the tree. Numbers in brackets correspond to sampling sites in Figure 1. Colors depict morphologically identified species groups (see Fig. 1). B. Cladogram based on male genitalia after AGOSTI (1990). C. Scheme based on a qualitative assessment of worker characters after RADCHENKO (2001).
molecular-based approach. HEBERT & al. (2003) showed that the CO1’s sequence variability allows assigning taxa not only to animal phyla or insect orders, but often to spe-
cific species. Since then the CO1 sequence has been wide-
ly used as a so-called DNA barcode for the identification of
genera, subgenera (ants: MARUYAMA & al. 2008) and spe-
cies (e.g., ants: species-group phylogeny for Pheidole:
MOREAU 2008; moths: BEHERE & al. 2007; snails: KANE &
al. 2008; birds: TAVARES & BAKER 2008). As our study
was initiated before the barcode era, and as we were not
able to amplify the universal primers used for barcoding
(FOLMER & al. 1994) we did not analyze the region of CO1
that is now commonly used as a standard for barcoding.
However, the region of CO1 that we used has also been
used for phylogenetics in ants (BACCI & al. 2009, SEPPÄ
& al. 2011). Furthermore the ratio of parsimonious infor-
mative bp of 36.4% lies well within the ratios described
for the barcoding region of other ant genera (Lasius: 8%,
Therefore this mitochondrial gene seems to be well suited
for comparing morphological and molecular phylogenies
in Cataglyphis. We analyzed 78 specimens that were col-
clected from across the geographical distributional range
of this genus. Unfortunately the CO1 sequences were not
sufficient to resolve the phylogeny in full detail, which
suggests the need to include additional mitochondrial and
/ or nuclear genes in future studies. However, despite the
unresolved base of the tree the analysis of the CO1 se-
quences supports the hitherto existing morphology-based
phylogeny (Fig. 2) with most of the 78 taxa clustering in
species groups as predicted by morphology.

First, at the species-group level the Cataglyphis bicolor
group clusters with the C. albicans group (Fig. 2), which is
in accord with the morphology-based species-group dia-
grams provided by AGOSTI (1990) (Fig. 2b) and RAD-
CHENKO (2001) (Fig. 2c). The resolution of our phylogeny
does not allow us to confirm the monophyletic origin of
the C. altisquamis and the C. cursor group. The only dis-
agreement of our analysis with the previously published
ones (AGOSTI 1990, RADCHENKO 2001) consists in placing
the single C. pallida specimen we were able to include in
our study within the C. cursor group. Based on worker
morphology and the anatomy of the male genitalia it should
have clustered with C. bombycina (see AGOSTI 1990; RAD-
CHENKO 2001). The specimen included here was collected
in Kazakhstan, i.e., within the distributional range of C.
pallida (see KARAVAIEV 1910), together with males and
females from the same nest. We were able to confirm our
identification based on the male genitalia. The latter shared
characters with those of the C. cursor group (stipes and squa-
mula), the C. bombycina group (subgenital plate) and even
the C. altisquamis group (subgenital plate, volsella, and
lacinia). On the basis of C. emeryi male genitalia mor-
phology AGOSTI (1990) placed the C. pallida group close to
the C. emmae group. However, the genitalia of C. emmae
differ significantly from those of C. pallida. Future analyses
will be necessary to determine whether the morphology-
based description of the C. pallida group is valid.

Second, at the species level roughly two scenarios can be
inferred. In scenario one most specimens used in the
present study are grouped in the same clade and belong to
the same geographical area. This is the case for Cataglyphis
longipedem (India), C. noda (Turkey, Greece), C. fortis
(Tunisia), C. cursor (Turkey) as well as C. hispanica, C.
velox and C. humeya from Spain. In scenario two "species"
such as C. bicolor (Morocco, Tunisia, Lebanon) and C.
savigyi (Morocco, Tunisia, Mali) appear to have very wide
graphic ranges. The latter case could be due to (I) in-
trinsic characteristics of the species such as particular dis-
persal abilities, (II) lack of resolution from the molecular
data, (III) or incorrect identification of the specimens. That
species-specific differences can occur with respect to argu-
ment (I) has been shown by KNADEN & WEHNER (2006),
but dispersal performances are unlikely to explain the oc-
currence of, e.g., C. bicolor in Lebanon and Morocco. Due
to the difficulty to access some of the distributional areas
of Cataglyphis the transect includes some sampling gaps.
However, these gaps cannot account for the phylogenetic
clustering of geographically distant samples.

Argument (II) is at least partially supported by the study
of KNADEN & al. (2005), in which Cataglyphis bicolor and
C. viatica could not be separated by the mitochondrial CO1
gene, but could be separated clearly by nuclear microsat-
eellite genes. Another case in point is C. gaetula, which on
the basis of morphological characters is clearly separated
from C. mauritanica, but appears intermixed with the latter
species in the molecular phylogeny. In many cases CO1
data have discrimination potential at the species level (see
below), but this is not true in all cases. Argument (III)
seems to be an inescapable one as worker morphology does
indeed provide only limited identification potential. To be
really certain in this respect we again checked all speci-
mens of the scenario two with the criteria of the published
keys available, and reconfirmed our species level identi-
fications. Given the amount of variability in morphologi-
cal characters of the worker caste, especially in the species
rich C. bicolor and C. albicans species groups, any identi-
fications and phylogenies based on worker characters alone
will suffer from imperfections. Taken together, the appear-
ance of individual "species" at different positions within
the phylogeny seems to be due to species identification
problems based on worker morphology rather than on a
lack of resolution from our molecular data. Note that what
we have labeled, e.g., "C. bicolor" represents what accord-
ing to current taxonomy based on morphological characters
of the worker caste has to be identified as "C. bicolor".
This is not to say that all taxa labeled this way as "C. bi-
color" belong to one species.

The Cataglyphis bicolor species group appears as the
most variable based on morphology, but there is at least one
important conclusion that can be derived from our molecu-
lar phylogenetic analysis. Based on a comparison of gland-
ular secretions of C. viatica and C. bicolor from Morocco
and some Cataglyphis group specimens collected in Bur-
kina Faso, DAHBI & al. (2008) suggested that the C. bicolor-
group species have evolved separately north and south of
the Sahara. However, in our mtDNA analysis the speci-
mens collected in Burkina Faso (Fig. 2A, Nos. 15 and 21)
and in Mali (Fig. 2A, Nos. 16, 17, and 18) clustered within
the specimens collected north of the Sahara. Therefore, our
data do not support the hypothesis raised by DAHBI & al.
(2008). We suggest that the evolution of the C. bicolor
group, and probably of the C. albicans group as well, fol-
lowed a Secular Migration model (see LOMOLINO & al.
2006) in so far as populations might have expanded grad-
ually through the Arabian peninsula and African conti-
nent and by this produced diversification during range expansion.

In conclusion, the molecular approach applied in the present account provides a valuable tool to assist species determination based on worker morphology. For the morphological determination of Cataglyphis ants to the species level, one usually needs access to the male sexual organs (AGOSTI 1990). As most samples of Cataglyphis belong to the worker caste (sexuals can be collected only during the restricted time frame of nuptial flights), the specimens used in our study could often be determined only down to the species-group level. As mentioned above nuclear microsatellite genes might be necessary to separate species if mtDNA analyses do not suffice (KNADEN & al. 2005).

When collecting Cataglyphis noda males during a transect through Greece we found unexpectedly high variability in the males’ genitalia (data not shown). In order to check, whether this variability was due to population-specific differences, we also collected 100 males from a single nest. Again we found striking differences in the shapes of the different parts of the genitalia that resembled the variability of the total Greek population (Fig. 3). The morphological classification of AGOSTI (1990) did not include any intraspecific variability but was based on interspecific variability only. We conclude that although both the anatomy-based and the molecular-based phylogenies yielded comparable results, due to potentially high intraspecific variability identifications based on morphology should be considered with care.

As the main result of the present study we find that the major features of the morphology-based species-group phylogenies as provided by AGOSTI (1990) and RADCHENKO (2001) are supported by our molecular approach, and that the sequence data add phylogenetic resolution to worker-based morphological identification. Furthermore, our study emphasizes the strong need for geographically fine-scale studies on the species and population level in Cataglyphis.

Finally, in studying the evolution of various modes of navigation in different Cataglyphis species we will heavily rely on knowledge of the phylogenetic relationships between the species in question. This comparative approach focuses especially on the salt-pan species C. fortis, which inhabits flat, unstructured environments nearly completely avoid of visual landmarks, and various representatives of the C. bicolor species group, which occur in a variety of habitats cluttered with grass tussocks, shrubs, and / or loosely scattered trees and rocks, and hence of a variety of visual cues. This leads to the question of whether all Cataglyphis species are equipped with the same navigational toolkit (consisting of one or several compasses, odometers, path integrators and landmark-guidance routines), but that the weight that any particular species puts on these particular modes of navigation is adapted to the particular ecological niche occupied by the species in question (see, e.g., the comparative study including C. albicans, C. bicolor, C. fortis, C. noda, and C. rubra on the peripheral olfactory pathway; STIEB & al. 2011). As in all such studies phylogeny-based and experience-based traits must be disentangled (see, e.g., the intergeneric study of the relative importance of different mechanisms of navigation in C. fortis in North Africa and Melophorus bagoti in central Australia; BÜHLMANN & al. 2011), the phylogenetic status of the animals participating in the various experimental programmes must be known in the first place.

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