Patterns of biogeographic distribution within the *bicolor* species group of the North African desert ant, *Cataglyphis* FOERSTER 1850

(Insecta: Hymenoptera: Formicidae)

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With 12 figures and 2 tables

Abstract

On the basis of morphometric, biochemical (pheromone and isozyme) as well as molecular biological (mtDNA) analyses, the species *Cataglyphis bicolor* (sensu SANTSCHI 1929) is divided into three parapatric species: *C. viaticus*, *C. bicolor* and *C. savignyi*. When two species meet in a broad contact zone (*C. viaticus* and *C. bicolor* in the north, *C. bicolor* and *C. savignyi* in the south), interbreeding does not occur.

The geographical distribution of *C. viaticus*, *C. bicolor* and *C. savignyi* in Tunisia is described and mapped by using a rectangular grid (mesh width 20 km). The distributional pattern of these three species of the *bicolor*-species group is compared with that of *C. mauritanicus*, the only Tunisian species of the *altisquamis*-species group. All four large-sized *Cataglyphis* species exhibit a zonal distribution following more or less the gross orographic and climatic divisions of the Maghrebian area. *C. viaticus* inhabits the zone of the Mediterranean sclerophyllous vegetation in the north, *C. bicolor* the lowland and highland steppes in the central parts of Tunisia, and *C. savignyi* the Presaharan semidesert in the south. Along the transitional zone of *C. viaticus* and *C. bicolor*, the range of *C. mauritanicus* overlaps widely with those of the two other species.

In contrast to this zonal pattern of distribution, *C. fortis* and *C. diehlii* are distributed in a patch-like way. While *C. fortis* is confined to the salt-pan areas, the chotts and sebkhas, *C. diehlii* occurs exclusively in the gravel plains, the regs and hamadas.

The two distributional patterns are discussed in terms of both ecological and historical factors. The discussion centres on the question of what factors might have led to the present-day segregation of the three zonal species of the *bicolor* group. Although the distributional ranges of *C. viaticus*, *C. bicolor*, and *C. ʃavignyi* can be correlated quite distinctly with the zonation of environmental factors like mean annual rainfall and type of vegetation, the actual niche preferences of the three species cannot be inferred directly from this large-scale picture — at least as far as the foraging ecology of the species is concerned. In contrast, the disrupted distributional range of *C. fortis* spans the entire aridity gradient from the *viaticus* range in the north to the *savignyi* range in the south; but within this vast area, *fortis* is restricted to a particular, patchily distributed type of habitat, in which no other *Cataglyphis* species occurs.

Kurzfassung

Die nordafrikanische Formicinen-Art *Cataglyphis bicolor* (sensu SANTSCHI 1929) wird aufgrund morphometrischer, biochemischer (Pheromon- und Isozym-) sowie molekularbiologischer (mtDNA-) Analysen in drei parapatrische Arten aufgeteilt, die geographisch längs des in Nord-Süd-Richtung verlaufenden Ariditätsgradienten als *C. viaticus*, *C. bicolor* und *C. savignyi* aufeinander folgen. Morphometrische Merkmale, vor allem aber die auf Isozymvergleichen beruhenden populationsgenetischen Untersuchungen zeigen, daß in den breiten Überlappungsgebieten je zweier Arten keine Hybridisierung stattfindet, *C. viaticus*, *C. bicolor* und *C. savignyi* also als echte Arten zu klassifizieren sind.

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Die geographische Verbreitung der genannten Arten wird beschrieben und in einem ganz Tunesien überspannenden Koordinatennetz von 20 km Maschenweite kartiert. Den Arealen von *C. viaticus*, *C. bicolor* und *C. savignyi*, die zur *bicolor*-Artengruppe zählen, überlagert sich das Areal von *C. mauritanicus*, des einzigen tunesischen Vertreters der *altisquamis*-Artengruppe. Alle vier Arten zeigen ein zonales Verbreitungsmuster. Sie besiedeln bandförmige Zonen, die sich in südwest-nordöstlicher Richtung durch Tunesien ziehen und damit der allgemeinen orographischen, klimatischen und pflanzengeographischen Gliederung des Landes folgen. Dabei besetzt *C. viaticus* die Zone der eumediterranen Sklerophyll-Vegetation im Norden, *C. bicolor* die Hoch- und Tieflandsteppen Zentraltunesiens und *C. savignyi* die Präsaharische Wüstensteppe im Süden. Während sich großräumig die Areale der beiden erstgenannten Arten auf den maghrebinischen Raum beschränken, greift jenes von *C. savignyi* weit nach Osten über Libyen bis nach Ägypten aus. Das Verbreitungsgebiet von *C. mauritanicus* überlagert sich der Transitionszone von *C. viaticus* und *C. bicolor* und folgt damit im wesentlichen der „Grande Dorsale", den westlichen Ausläufern der Atlasketten.

Dieses zonale Verbreitungsmuster von *C. viaticus*, *C. bicolor*, *C. savignyi* und *C. mauritanicus* kontrastiert mit dem disruptiven Verbreitung von *C. fortis* und *C. diehlii*. Während *C. fortis* auf die inselartig verteilten Salztonflächen der Chotts, Sebkhas und Sebkhets beschränkt ist, besiedelt *C. diehlii* die Kiesel-, Schotter- und Steinwüstenflächen der Regs und Hamadas.

Beide Verbreitungsmuster werden im Hinblick auf ökologische Habitatansprüche und historische (verbreitungsgeschichtliche) Prozesse diskutiert. Obwohl sich die Areale der „zonalen Arten" mit großräumig variierenden ariditätsabhängigen ökologischen Faktoren korrelieren lassen, ist eine Abgrenzung nach Nahrungsnischen nicht möglich. Alle *Cataglyphis*-Arten leben als tagaktive, thermophile Saprophagen von weniger hitzeresistenten Arthropoden. Dabei stimmen die vier großen *Cataglyphis*-Arten Tunesiens (*C. viaticus*, *C. bicolor*, *C. savignyi* und *C. mauritanicus*) in Art und Größe der Beutestücke sowie im Zeitpunkt der Beutesuche überein. Die Charakterisierung artabgrenzender Faktoren muß daher verstärkt Bereiche außerhalb des Kontextes der Nahrungssuche einbeziehen.

Mit ihrem inselartigen Verbreitungsmuster besiedelt *C. fortis* die salzhaltigen Inundationsflächen des gesamten tunesischen (und nordostalgerischen) Untersuchungsgebiets, überspannt also das Areal aller zonalen Arten. In ihren durch extrem niedrige Beutedichte charakterisierten Habitatsinseln bildet sie als mittelgroße Art den einzigen Vertreter der Gattung *Cataglyphis*. Im Gegensatz dazu leben in den angrenzenden Gebieten mit höherer Beutedichte die vier großen Arten *C. viaticus*, *C. bicolor*, *C. savignyi* und *C. mauritanicus* stets sympatrisch und syntopisch mit jeweils einer kleinen *Cataglyphis*-Art — meistens mit *C. albicans* — zusammen. Damit zeichnet sich ein generelles Muster ab, nach dem das Beutespektrum bei hoher Beutedichte von jeweils zwei *Cataglyphis*-Arten (einer großen und einer kleinen), bei niedriger Beutedichte von nur einer (dann mittelgroßen) *Cataglyphis*-Art als Konsument genutzt wird.

Wir danken unseren tunesischen Freunden und allen Bewohnern des Landes, die uns mit Gastfreundschaft, Hilfe und Verständnis begegnet sind.

Résumé

Sur la base des données morphométriques et biochimiques (phéromones, isozymes) ainsi que sur des analyses moléculaires (mADN) la fourmi du désert *Cataglyphis bicolor*, (sensu SANTSCHI 1929) comprend en effet les trois espèces parapatriques suivantes: *C. viaticus*, *C. bicolor* et *C. savignyi*. Où les zones de répartition de deux espèces chevauchent (*C. viaticus* et *C. bicolor* au nord, *C. bicolor* et *C. savignyi* au sud) il n'y a pas de croisement entre ces espèces occupant le même territoire.

La distribution de *C. viaticus*, *C. bicolor* et *C. savignyi* en Tunisie est décrite et représentée en forme d'un système de coordonnées rectangulaires dont l'unité couvre 400 km^2 chacune. En plus, la distribution de ces trois espèces appartenant toutes au complexe d'espèces du type *bicolor* est comparée avec celle de *C. mauritanicus* qui, en Tunisie, est la seule espèce qui fait part du groupe d'espèces connu sous le nom *altisquamis*. La distribution de toutes les espèces du genre *Cataglyphis*, qui frappent par leur grande taille, suit plus ou moins la division orographique et climatologique de la région maghrébienne. Au nord, *C. viaticus* occupe la zone de la végétation méditerranéenne du type sclérophylléenne, tandis que *C. bicolor* préfère les plaines basses ainsi que les steppes élevées dans la partie centrale de la Tunisie. L'aire de distribution de *C. savignyi* est plus méridionale et coincide avec la région semidésertique présaharienne. Tout le long de la zone de transition qui sépare *C. viaticus* de *C. bicolor*, l'aire de distribution de *C. mauritanicus* chevauche amplement celles de deux autres espèces.

Contrairement à cette catégorie de distribution en forme de régions étendues, les deux espèces *C. fortis* et *C. diehlii* fréquentent plutôt des aires qui sont isolées l'une de l'autre. Tandis que *C. fortis* occupe les dépressions de terrain salé nommées «chotts» et «sebhas», *C. diehlii* préfère les plaines pierreuses («regs», «hamadas»).

Les deux modes différents de distribution sont l'objet d'une discussion qui respecte les données écologiques et historiques tout en examinant plusieurs facteurs, qui auraient pu être le cause de la segrégation et répartition actuelles des aires de distribution des espèces du groupe *bicolor*. Malgré le fait que les aires de répartition des espèces *C. variatus*, *C. bicolor* et *C. savignyi* puissent être corrélées assez nettement avec la zonation des facteurs écologiques tel que les types de végétation, les quantités de précipitations, les préférences des trois espèces ne semblent pas être la conséquence

directe de ces facteurs, en tout cas pas lorsqu'on prend en considération les habitudes des trois espè-
ces relatives aux modes de se procurer leur nourriture. D'autre part les aires de distribution de
C. fortis isolées l'une de l'autre s'étendent tout le long du gradient d'aridité, soit à partir de l'aire
de distribution de *C. viaticus* dans le nord jusqu'à celle de *C. savignyi* au sud. Pourtant, au sein
de cette région *C. fortis* occupe des habitats isolés ou l'on ne rencontre pas d'autres espèces du
genre *Cataglyphis*.

Nous remercions les citoyens tunésiens de leur hospitalité, leur amitié et leur compréhension.

خلاصة

نماذج للوازع البيوجغرافي ضمن مجموعة صنف نمل الصحراء الثنائيّ اللون

Cataglyphis FORSTER 1850 (Insecta: Hymenoptera: Formicidae)

بناء على تحليل مقاسات الأطراف والتحليلات البيوكيميائيّة (-pheromone- and isozyme) بالإضافة إلى التحليلات البيوجزيئيّة (مثل العوامل الوراثيّة mtDNA) فإنّ الصنف -Cataglyphis bi color (sensu SANTSCHI 1929) يقسم إلى ثلاثة أصناف شبه صخريّة وهي C. viaticus، و C. و bicolor و C. savignyi. وعندما يلتقي نوعان في مناطق تماس واسعة (في الشمال C. viaticus، و C. bicolor وفي الجنوب C. bicolor، و C. savignyi) فإنّه لا يحدث أيّ تهاجن.

إنّ التوزيع الجغرافي لـ C. savignyi, C. bicolor, C. viaticus في البلاد التونسيّة مشروح ورسمت له خرائط عن طريق استعمال الشبكة المتساهمة ذات الوحدات المستطيلة الشكل (عرض كلّ شرك ٢٠ كيلومترا). وبالإضافة إلى ذلك، فإنّ نموذج التوزيع لهذه الأصناف الثلاثة من مجموعة النمل الثنائيّ اللون تقارن مع النوع المسمّى C. mauritanicus وهو الصنف التونسيّ الوحيد من مجموعة صنف altisquamis. ثمّ إنّ جميع الأصناف الأربعة الكبيرة الحجم من نوع Cataglyphis تظهر وازعاً منطقيّاً يتبع بشكل أو بآخر التقسيم الجبلي والمناخي للمنطقة المغاربيّة. C. viaticus يسكن في الشمال في منطقة حوض المتوسّط المكسوّة بالأعشاب الدائمة الخضرة ذات الورق القاسي. C. bicolor يقطن السهول المنخفضة والمرتفعات الجافة في أواسط الأراضي التونسيّة. أمّا C. savignyi فتعيش في المناطق الشبه صحراويّة في الجنوب. وعلى طول المنطقة الانتقاليّة لـ C. bicolor, C. viaticus فإنّ مجال الـ C. mauritanicus يتداخل بشكل واسع مع مجالات الأصناف الأخرى.

وبالمقارنة مع نماذج التوزيع لـ C. diehlii, C. fortis فإنّ هذه موزّعة بشكل رُقعيّ. فبينما ينحصر صنف الـ C. fortis في المناطق الملحيّة و"الشطّ" والسبخات، فإن الـ C. diehlii يتواجد في مناطق الحصباء والصحاري الحجريّة والصحاري الصخريّة فقط.

إن كلا نوعي نماذج التوزيع يبحثان هنا من حيث عوامل الترابط البيئي بالإضافة إلى العوامل التاريخيّة. والنقاش يدور خصوصاً حول السؤال: ما هي العوامل التي يمكن أن تكون قد تسبّبت في الوضع الحالي للعزلة بين المناطق الثلاثة للأصناف الثلاثة للمجموعة الثنائيّة اللون؟ بالرغم من أن مدى كلّ من هذه التوزيعات لـ C. savignyi, C. bicolor, C. viaticus قد يرتبط بالعوامل البيئيّة التي تنقسم إلى مناطق مثل المتوسّط السنويّ لهطول المطر وأنواع ما ينمو من الأعشاب، إلاّ أنّ اختيار البيئة الملائمة وتفضيلها بالنسبة إلى كلّ من هذه الأصناف لا يمكن أن يستدلّ عليه مباشرة من هذا الصورة ذات مقياس الرسم الكبير – وعلى الأقلّ بالنسبة لعوامل البيئيّة المؤثّرة على تخزين العلف والمؤن من قبل هذه الأصناف. ومن جهة أخرى فإنّ مجالات التوزيع الممزّقة بعضها عن بعض لـ C. for- tis تغطي مختلف المناطق الجافة من مجال viaticus في الشمال إلى مجال savignyi في الجنوب، ولكن ضمن هذه المنطقة الشاسعة تنحصر مواطن الـ fortis في مناطق موزعة كالرُقع، لا يظهر فيها أيّ صنف آخر من الـ Cataglyphis.

نود هنا أن نعبر عن صادق امتناننا للشعب التونسي لما أبداه تجاهنا من كرم وصداقة وتفهم

Introduction

In the history of the biological sciences comparative methods have given way to experimental ones, but in the present study, we have taken the reverse course.

For more than two decades (starting with WEHNER 1970) the North African thermophilic desert-dwelling ants of the genus *Cataglyphis* have been the subject of intensive research in neuroethology (rev. WEHNER 1994) and, more recently, in physiology (energy metabolism: LIGHTON & WEHNER 1993) and biochemistry (heat shock proteins: GEHRING & WEHNER in prep.). The intuitive reasons for selecting *Cataglyphis* as the subject of multidisciplinary research in functional biology have been twofold. They might be illustrated best by referring to the two attributes associated above with the genus *Cataglyphis:* "thermophilic" and "desert-dwelling".

As regards the latter aspect, *Cataglyphis* inhabits the food-impoverished areas of the Old World deserts including the Sahara, the Near and Middle East, the Arabian peninsula and central Asia. In evolutionary terms, the low prey density of these habitats has placed a high premium on large foraging distances and hence superior navigational abilities. As *Cataglyphis* navigates by means of visual rather than chemical cues, the mechanisms of visually guided behaviour have become the main focus of our research in this genus of ants, and have led to general insights in how sensory data are processed by neural systems (WEHNER 1989a, 1994).

From an ecological viewpoint, *Cataglyphis* is a central-place forager and single-prey loader; each individual must frequently survey a large foraging area and routinely return, by whatever navigational means, to the start of its foraging excursion (WEHNER 1987a). The fact that this task must be accomplished by processing visual rather than chemical (pheromone) information, is due to the second attribute mentioned above, namely the ant's thermophilic behaviour. All members of the genus are temporally out of phase — with respect to both their circadian and their circannual activity patterns — with the other species of desert ants with which they occur sympatricly. During the summer months they are the only ants foraging diurnally, especially under the hot midday sun (WEHNER et al. 1992), while in winter, when ants of many other genera have shifted their foraging activities from night or crepuscular times to day-time hours, they hibernate under ground. This thermophilic behaviour is correlated with the trophic role *Cataglyphis* plays in its desert environment. *Cataglyphis* species are neither harvesters (like the sympatric *Messor* species) nor predators (like the sympatric dorylines), but scavengers (WEHNER et al. 1983, SCHMID-HEMPEL 1983, WEHNER 1987a). They forage for arthropods that have presumably succumbed to the heat stress, which they themselves are able to withstand more effectively (DELYE 1967, WEHNER 1989b, HEATWOLE & HARRINGTON 1989,

CERDA et al. 1989, WEHNER et al. 1992). This mode of foraging behaviour implies that *Cataglyphis* workers forage individually, do not become engaged in any kind of chemical recruitment or reorientation, and hence must rely almost entirely on visual mechanisms of navigation.

Most of our behavioural and physiological work was carried out on what at that time had been classified as *Cataglyphis bicolor* (SANTSCHI 1929). However, during our studies on these large-sized members of the genus, it soon became apparent that "*Cataglyphis bicolor*" included three separate species in our North African study area. They were tentatively referred to as forms *a, b,* and *c* in WEHNER et al. (1983: map 2). According to the rules of taxonomic nomenclature they must now be named *C. viaticus, C. bicolor* and *C. savignyi,* respectively. A full synonymy is given by AGOSTI (in prep.). For diagnostic characters see Table 2.

Although the myrmecologist FELIX SANTSCHI spent nearly four decades of his life in Tunisia and concentrated his untiring collecting activities especially on *Cataglyphis* (SANTSCHI 1929), there is still need for a taxonomic revision of this genus. In fact, SANTSCHI — a driven man, who could do nothing by half — amassed a great collection; and can be considered one of the most important unsung collectors and describers in the history of ant systematics. But, due to his profligate naming of an abundance of new species, subspecies (or "stirpes" in his terminology) and varieties, based mainly on slight differences in colour and pubescence of a few individual specimens, his taxonomy must be regarded as erroneous and outdated (BROWN 1955). One example might suffice to support this argument. It illustrates the uncanny "splitting" character of SANTSCHI's taxonomic endeavours and his unwieldy use of tri- and tetranomial nomenclature. In his 1929 monograph on *Cataglyphis* the three species mentioned above (*viaticus, bicolor, savignyi*) are found under different designations[1].

C. viaticus: *Cataglyphis (Cataglyphis) bicolor* st. *nodus* var. *desertorum*
               Cataglyphis (Cataglyphis) bicolor var. *pubescens*
               Cataglyphis (Cataglyphis) bicolor var. *basalis*
               Cataglyphis (Cataglyphis) bicolor var. *adusta*

C. bicolor: *Cataglyphis (Cataglyphis) bicolor* sp. *megalocola*
               Cataglyphis (Cataglyphis) bicolor st. *saharae* var. *bucculenta*

C. savignyi: *Cataglyphis (Cataglyphis) bicolor* st. *nodus* var. *oasium*
               Cataglyphis (Cataglyphis) bicolor st. *nodus* var. *savignyi*

Certainly, SANTSCHI was one of those who at the beginning of this century "brought discredit to the field [of taxonomy] by the creation of numerous synonyms and an excessive splitting of families and genera" (MAYR & ASHLOCK

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[1] SANTSCHI did not even detect the error made by FOREL (1890) and continued by EMERY (1906, 1925) in assigning *viaticus* to the *altisquamis* group (see e.g. Figs. 18, 19 and 34 in SANTSCHI 1929). Ever since, this misidentification, which was first pointed out by AGOSTI (1990) and TINAUT (1990), has led to a state of severe confusion: in Tunisia and eastern Algeria, for example, SANTSCHI's *viaticus* is actually *mauritanicus,* and the nomen *viaticus* must be reserved for what later had been called the "light form" of *bicolor* (WEHNER et al. 1983: map 2, form *a*; in the worker caste, this form, i.e. the present *viaticus,* is indistinguishable from *nodus* described in WEHNER et al. 1983 for Greece).

1991: 12) — and species. One reason for this "excessive splitting" was that SANTSCHI adhered to a nominalistic-typological concept of taxonomy; another might have been — though surprisingly at first glance — that he was a gifted experimentalist. Indeed, as SANTSCHI's taxonomic conclusions and inferences became more and more irrelevant, the originality and the permanence of his work on the sensory performances of ants increased substantially (WEHNER 1990). SANTSCHI was interested much more in functional rather than evolutionary aspects of life — or, in modern parlance — in the biology of proximate rather than ultimate causation. His focus on the functional design of the organism under investigation (ants of the genera *Messor, Monomorium, Aphaenogaster, Pheidole, Cataglyphis*) seems to have prevented him from regarding his experimental animals as the result of opportunistic, vicissitudinous historical processes. Obviously, population thinking was alien to his physiologist's mind, and so he never entered what came to be called, in the year of his death, the "new systematics" (HUXLEY 1940).

The foregoing remarks are intended to serve a twofold function: to demonstrate first that a taxonomic revision of *Cataglyphis* is much in need, and second that this need is not only to satisfy the systematist's demands, but also to encourage what could be dubbed, analogous to HUXLEY's connotation, the "new physiology". The intensive physiological work done on some members of the genus *Cataglyphis* (lit. cit.) revealed the not-so-obvious, namely that physiological mechanisms have not been designed from first principles, but bear the signs of their intricate evolutionary past as much as morphological traits do (WEHNER 1987b). For this reason, the physiologist should not be preoccupied completely with the experimental paradigm, but must turn, for his own sake, to the comparative approach as well. The present account is a first cautious step along that road.

Taxonomy:
Reclassifications and species-level distinctions

We must consider taxonomical aspects before delving into our subject proper, namely biogeography.

Cataglyphis ants were first described by the Danish entomologist (and economist) JOHANN CHRISTIAN FABRICIUS on the basis of worker specimens (*Formica viatica* FABRICIUS 1787, *Monocombus viaticus* MAYR 1855, *Cataglyphis viatica* MAYR 1861): "Caput magnum fer-

rugineum ... postici elongati tibiis fuscis ... velocissime cursitans."

More than half a century later, the morphology of the male genitalia was used to define a new genus, *Cataglyphis* (FOERSTER 1850)[2]: *Cataglyphis fairmairei* FOERSTER 1850, *Cataglyphis viaticus* SMITH 1861. Although the genus *Cataglyphis* (subfamily Formicinae, tribe Formicini) is a

Tab. 1. Inventory of the Tunisian *Cataglyphis* species.

Species group	Species	Size class	Alitrunk length (mm)	
bombycinus group	*bombycinus*	M	2.76,	2.54–3.00
altisquamis group	*mauritanicus*	L	4.16,	3.76–4.24
bicolor group	*viaticus*	L	3.66,	3.49–3.92
	bicolor	L	4.16,	4.00–4.40
	savignyi	L	4.32,	4.23–4.48
	diehlii	L*	3.60,	3.35–3.84
albicans group	*albicans*	S	1.94,	1.80–2.24
	ruber	S	2.08,	1.98–2.26
	fortis	M	2.84,	2.59–3.21

L, large-sized; M, middle-sized; S, small-sized. For alitrunk length medians as well as first and third quartiles are given (n = 20 in each case). All members of any particular size-class (L, M, or S) vary significantly from all members of the other two classes (p < 0.01; Kolmogorov-Smirnov-test). * Within the L class, *diehlii* is significantly smaller than *bicolor, savignyi,* and *mauritanicus*. Therefore in the text we sometimes refer to only 4 large-sized species.

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[2]) The Greek name *Cataglyphis* (*kata* – in; *glýpho* – to constrict) refers to the marked segmental constrictions identing the male's gaster: "abdomine segmentis omnibus apice transversim impressis" (FOERSTER 1850: 493).

distinct and most probably monophyletic taxon, diagnosed unambiguously by both male and female characters, the species-level taxonomy is in a state of bewildering complexity and confusion. As mentioned previously, the last comprehensive treatise on the systematics of *Cataglyphis* (SANTSCHI 1929) has left us with a tangle of specific and subspecific names and synonyms. Since then, *Cataglyphis* has received the taxonomist's attention only sporadically

(e.g. ARNOLDI 1964, BARONI URBANI 1969, KUGLER 1981, WEHNER 1983, 1986, COLLINGWOOD 1985, TINAUT & PLAZA 1989, TINAUT 1990, 1993), until AGOSTI (1990, 1993) made full use of the highly diversified sexual armature of *Cataglyphis* males, and provided a reclassification of the species groups of the genus. Based on this work, and on the current results of our multidisciplinary microtaxonomical programme described below, four species groups,

Tab. 2. Diagnostic morphological characters of workers (☿) and males (♂) of the four L-sized Tunisian *Cataglyphis* species whose zonal distributional ranges are given in Figs. 7–10.
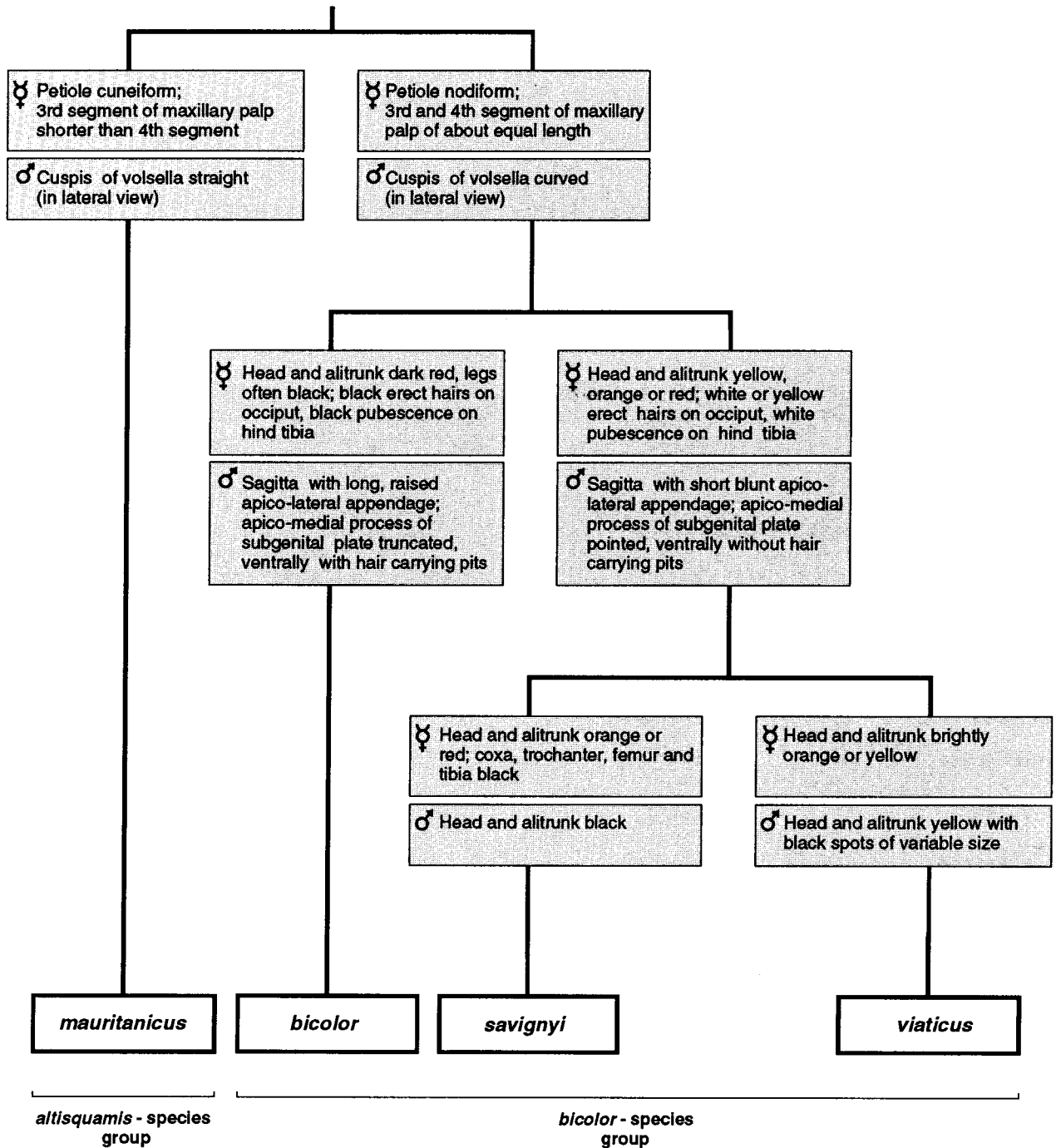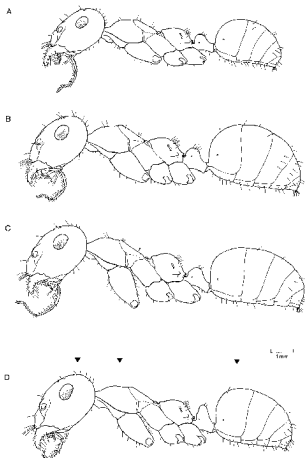
Fig. 1. Cataglyphis savignyi, ♀

A

B

C

D

Fig. 2. Line drawings and colour portraits of the four large Asrican Crematogaster species (worker caste). (A) C. mimosae. (B) C. nigriceps. (C) C. sjostedti. (D) C. ancanancanus. The arrow heads in the lower left figure mark the locations for which cuticular structures are shown in Fig. 3.

including in total nine species of *Cataglyphis*, occur in Tunisia (Table 1). In the present account, we have focused on the large-sized species labeled L in Table 1, especially on the members of the *bicolor*-species group. With their long legs and high running speeds they are among the most conspicuous — and certainly the most elegant — representatives of the insect fauna inhabiting the North African soil surfaces.

Our study in microtaxonomy is a joint venture, in which morphometric, biochemical and molecular biological methods are combined, to unravel the phylogenetic relations among the species treated here. The whole project has been carried out under the auspices of the Swiss National Science Foundation (principal investigators: R. WEHNER and D. AGOSTI). Apart from our Zürich group (for morphometrics see AGOSTI, in prep.) two other laboratories are involved: E. D. MORGAN and associates at the Department of Chemistry, University of Keele, U.K. (biochemical analyses of pheromones from exocrine glands, especially secretions from mandibular and Dufour's glands; see KEEGANS et al. 1992; work continued) and P. READY and D. AGOSTI at the Natural History Museum (BMNH), London, U.K. (isozyme and mtDNA analyses; see READY et al., in prep.; work continued).

In the present publication we present and discuss the biogeographical data that were collected during a 20-year period. Although our collecting tours covered all North African countries (Egypt, Libya, Tunisia, Algeria, Morocco), we concentrate here on the most heavily surveyed geographical area, Tunisia, which provided 80.3 per cent of the 1396 North African sampling sites.

In morphometric terms the Tunisian L-species can be discriminated on the basis of both male and female characters (Table 2). The typical colouration patterns are depicted in Fig. 2 (right figures). As far as the colour of head and alitrunk is concerned, the most variable species is *savignyi*. The specimen shown in Fig. 2C is representative for the most southern parts of Tunisia (see WEHNER et al. 1983: map 2, form c). Note also the differences in the fine structure of the cuticular surface. The shiny and mat appearance of the body surface in the three *bicolor*-group species and in *mauritanicus*, respectively, is obvious even to the unaided eye (compare the colour portraits in Fig. 2). Scanning electron microscopy (Fig. 3) has revealed that this difference is due to the presence (in *mauritanicus*) or absence (in the *bicolor*-group species) of marked second-order arrays of microsculptures (networks of ridges).

Furthermore, the isozyme patterns of the three parapatric Tunisian L-species of the *bicolor* group, namely of *viaticus*, *bicolor*, and *savignyi*, indicate absence of gene flow between adjacent populations. This is inferred from the fixed polymorphisms of allele frequencies in the populations studied: *viaticus* can be diagnosed by the unique presence of the allele *a* of 6GPDH (glucose-6-P-dehydrogenase), allele *a* of PGM (phosphoglucomutase), alleles *b* and *c* of XDH (xanthine dehydrogenase) and PGI (phosphoglucose isomerase); *bicolor* by allele *b* of 6GPDH, allele *b* of PMG, alleles *b* and *c* of XDH and PGI; and *savignyi* by allele *b* of 6GPDH, allele *b* of PGM, allele *a* of XDH and PGI (AGOSTI et al., in prep.).

DNA-sequence comparisons of a fragment of the small subunit ribosomal mtDNA provide additional evidence for the species status of the Tunisian L-species of the *bicolor* group (READY et al., in prep.).

Finally, all Tunisian species of the *bicolor* group can be separated distinctly by the composition of the secretions of their exocrine glands. The Dufour glands of these species contain straight-chain and branched alkanes, alkenes, ketones, acetates, aldehydes and esters in species-specific combinations and amounts. For example, *bicolor* can be distinguished from *savignyi* by its higher percentage of esters. In *viaticus*, the major component of the Dufour glands is tridecane, in contrast to the other species in which this component is displaced by pentadecane. Moreover, the mandibular gland secretions of all species of the *bicolor* group are characterized by the primary alcohol 2-methyl-1-hexanol, which sets them apart from other *Cataglyphis* species which do not contain this substance (MORGAN et al., in prep.).

For comparison, additional biogeographical information is given for *diehlii* and *fortis*, whose patterns of geographical distribution are distinctly different from those of the former species. When first described by FOREL in 1902, both species had been given subspecies rank, and this designation was later accepted by SANTSCHI (1929) in his final work on *Cataglyphis*:

Myrmecocystus albicans var. *fortis* (FOREL 1902a),
Cataglyphis (*Cataglyphis*) *albicans* st. *fortis* (SANTSCHI 1929).
Myrmecocystus viaticus var. *diehlii* (FOREL 1902b),
Cataglyphis (*Cataglyphis*) *bicolor* st. *diehlii* (SANTSCHI 1929).

When the genitalia of the males were described, and the morphology of the workers was analysed in more detail, *fortis* and *diehlii* had to be raised to species rank (WEHNER 1983, 1986)[3].

Another species of the M-size range, *bombycinus*, is restricted to the sand-dune areas in the southernmost parts of Tunisia (Grand Erg Oriental). This geographical area is not included in the present investigation.

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[3]) See also COLLINGWOOD (1985): *Cataglyphis diehlii* stat. nov. (designation based on the characteristics of workers that had been collected in the Arabian peninsula).

▶

Fig. 3. Cuticular microstructures of head (occiput: left row), alitrunk (pronotum: middle row) and gaster (first segment: right row) of the four large Tunisian *Cataglyphis* species. Dorsal views. For exact location of the body areas of which the pictures were taken see arrow heads in Fig. 2. — Scale mark 20 μm.
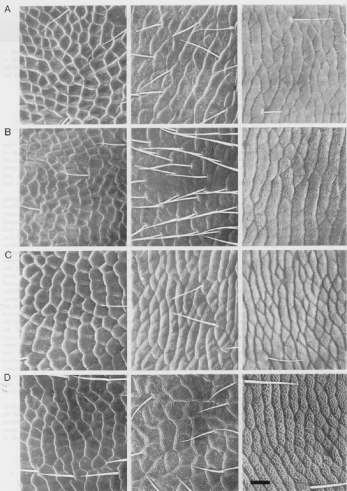
Biogeography:
Parapatric zones and distributional patches

Methods

The biogeographical study presented here is based on 20 years of field work (1973–1993) carried out largely by R. W. and S. W. joined, since 1985, by D. A. During that period *Cataglyphis* specimens were collected at 1121 Tunisian sites. Each sampling exercise lasted ca. 15 min (collecting time excluded) and consisted of surveying an area in which the relevant species was most likely to occur. The sampling areas were selected on the basis of our previous knowledge of the specific habitat preferences of *Cataglyphis*. During most surveys we succeeded in locating the entrances to *Cataglyphis* colonies, so that we could collect the ants directly at their nesting sites. Some of the specimens were later mounted on pins, the others were preserved in alcohol. All sampled ants are available for future inspection in the collection of R. W. at the Department of Zoology, University of Zürich, Switzerland. Notes on the ecological characteristics of the relevant habitat were taken at each site.

For cartographic analysis Tunisia was subdivided into $20 \times 20 \text{ km}^2$ sampling areas (test squares). As all finds were summed up within each sampling area, the mesh width of the gridwork shown in Fig. 4 defines the spatial resolution of the present investigation (Figs. 7–9). Note that this method of spatial averaging within pixel-like test areas was not applied in *fortis* and *diehlii*, which were more geographically restricted (Fig. 11).

The frequency distribution of the sampling densities is given in Fig. 5 and mapped out in Fig. 6. The latter figure shows that the northern part of the study area, which is inhabited by three of the large-sized species, either parapatricly or sympatricly, is sampled with a slightly higher density than the southern part, in which maximally two of the four species occur in any particular test area. Furthermore, the largest uninterrupted part of unsampled area is confined to the fields of sand dunes in the most southern and south-western parts of Tunisia, i.e. to the Grand Erg Oriental. This habitat is occupied only by *bombycinus*, but by none of the species considered here.

In 1992 we started a long-term project on the spatial and temporal (seasonal) variation of colony size, worker-size distribution and worker morphometrics in the four zonal L-species. Some preliminary results of this work, which is still in progress, are included.

To test the hypotheses whether the three *bicolor* forms *a*, *b* and *c* as described by WEHNER et al. (1983) were three species or belonged to one species, we chose four transects through areas in which sympatric populations of forms *a* and *b* or forms *b* and *c* were known to occur. T1: Tabarka – Kasserine – Gafsa – Kebili; T2: routes P12 and C77

north and south of Maktar; T3: Bizerte – Teboursouk – Kairouan – Maharès – Gabès; T4: Soliman – Korba – Nabeul. The phenotypic variation within and between the populations (isozyme studies) was then used to decide between the two hypotheses.

Results

The zonal distribution of *C. viaticus*, *C. bicolor*, *C. savignyi* and *C. mauritanicus*

The most striking result that can be read off the maps shown in Figs. 7–9 is the band-like, zonal distribution of the four largest Tunisian *Cataglyphis* species. In general, all distributional ranges run in a south-westward, north-eastward direction. They clearly follow the orographic and climatic structure, as defined by the anticlinal ridges and foot-hills of the Atlas mountain-chains (see Fig. 4).

Let us first turn to the three species of the *bicolor* group (Fig. 7). The distributional range of the most northern species, the truly bicoloured *viaticus*, covers the mountainous regions of the Riff Tell (Kroumerie and Mogod) and the Haut Tell (High Plateau), including the plain and delta of the Medjerda river as well as the peninsula of Cap Bon[4]. Its rather sharp southern border coincides almost exactly with the southern fringe of the Grande Dorsale, the core region of the Tunisian Atlas mountains, which traverses the country diagonally and tapers off in the Cap Bon peninsula. Along this line, which runs from Masmoura at the southeast corner of Cap Bon to Saouaf (south of Zaghouan), Ksar Lamsa, Kef-el-Gafia to Sbiba, and finally reaches the Algerian border west of Foussana, the mean annual rainfall drops sharply from 500 mm in the north-west to less than 300 mm in the south-east (GOUDIE & WILKONSON 1977); the number of humid months (in which precipitation exceeds potential evaporation) decreases abruptly from 7 to less than 3 per year (LAUER 1952); and the gradient representing the variability of rainfall within consecutive years exhibits its steepest rise (ISNARD 1952)[5]. In bioclimatologic terms, this cardinal geographic line separates the Mediterranean-semihumid from the Mediterranean-semiarid regime (BORTOLI et al. 1969, HOUEROU 1969, GIESSNER 1979) and forms the southern border of the original Mediterranean sclerophyllous forest (WHITE 1983).

It is along the latter line that *viaticus* is replaced, rather sharply, by *bicolor*. Although the transitional zone of the two species is fairly narrow, especially along the southern foot-hills of the Dorsale, *viaticus* and *bicolor* often occur side by side, e.g. at Testour (test square I7), Beni Khiar 12

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[4]) For definition and demarcation of geographical regions in Tunisia see DESPOIS (1955), GIESSNER (1964), MENSCHING (1979).

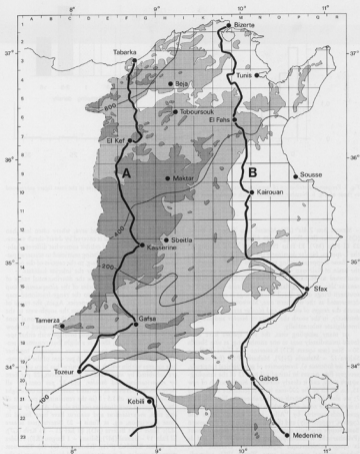[5]) With respect to the latter argument see also MENSCHING et al. (1970), WINSTANLEY (1972), GIESSNER (1977).

Fig. 4. Map of study area: Tunisia, North Africa. Isolines are given for altitudes of 150 m (separating white and light-grey areas) and 600 m (separating light-grey and dark-grey areas). Isohyets (blue lines) indicate 100, 200, 400, and 800 mm mean annual rainfall. Geographical coordinates: degrees of eastern longitude and northern latitude. The 20 × 20 km² sampling areas are defined by a rectangular system of coordinates (abscissa, longitude: A–R; ordinate, latitude: 1–23). The same system of coordinates is used in designing transects A and B. For the distribution of species along the two transects A and B see Fig. 10.
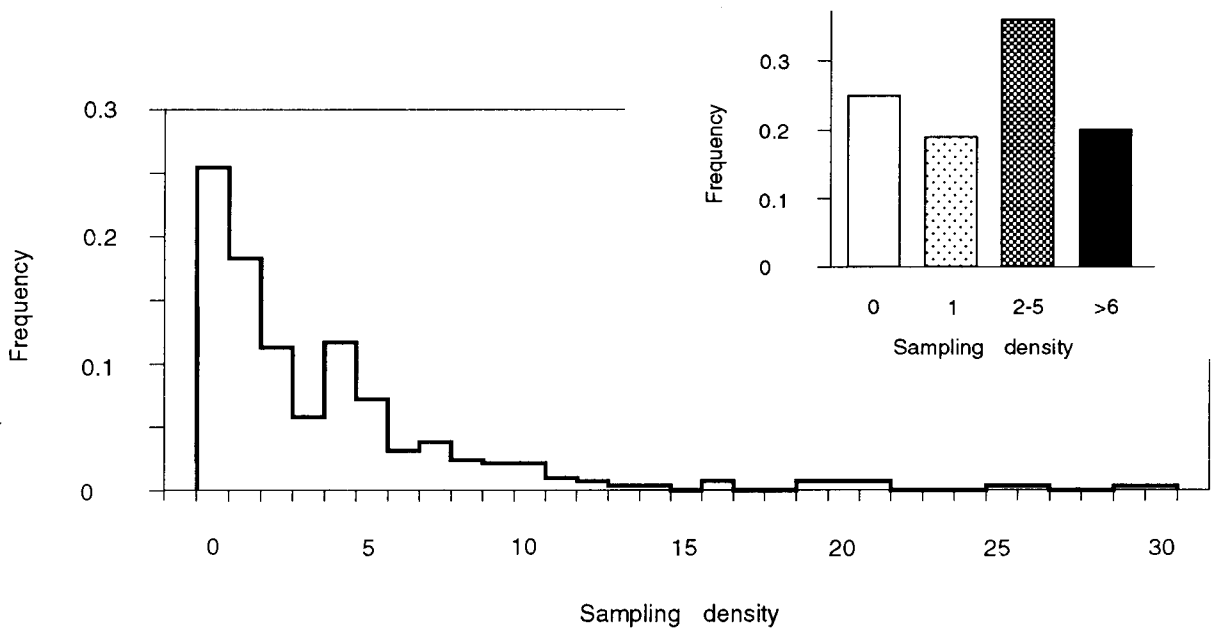
Fig. 5. Frequency distribution of sampling densities within the 20 × 20 km² test squares. The signatures in the inset figure correspond to those of Fig. 6. Number of sites at which samples were taken: N = 1121.

– Menzel Bou Zelfa[6] (P5), Menzel Bou Zelfa – 8 Korba (Q5), Gafour (I6), Dougga – 25 Siliana (I7), Kairouan – 23 El Fahs (M7), El Fahs 19 – Saouaf (M7). Among all the L-species, *bicolor* dominates the Tunisian lowland steppes (Basse Steppe according to DESPOIS 1942) — especially the basin of Kairouan — and the Tunisian sahel extending southward to Mahares, but occurs together with *mauritanicus* also in the highland steppes (Haute Steppe). The southern fringe of its distributional range is not as clearly demarcated as the northern one. Moreover, while in the north the ranges of *viaticus* and *bicolor* are separated quite distinctly, in the south the ranges of *bicolor* and *savignyi* interdigitate substantially.

At many sampling sites, the two species have been found immediately next to one another, e.g. at sites Sbeitla 50 – Sfax (test square K13) Kasserine – 31 Gafsa (E15), La Skhira 12 – Mahares (N17), Mahares (P16) (for conventions see footnote 6). Irrespective of geographical longitude, *savignyi* first occurs in latitudinal row 13 of the sampling-square array, and it clearly outweighs *bicolor* south of row 15, i.e. south of the 200-mm isohyet (compare Figs. 4 and 7; see also the two north-south transects in Fig. 10). This is roughly the zone, along which the western Haute Steppe grasslands covered by "Alfa" and "Sparte" (*Stipa* and *Lygeum,* respectively) and the low-shrub area of the eastern Basse Steppe gradually turn into the presaharan semi-desert (Präsaharische Wüstensteppe, MENSCHING 1974; le sud de la marge subdésertique septentrionale, OZENDA 1977; Sahara regional transition zone, WHITE 1983; submediterranean regional transition zone, WICKENS 1984). In this extremely food-impoverished area, where often less than 20 per cent of the ground is covered by dwarf-shrub vegetation, *bicolor* and *savignyi* exhibit somewhat different habitat preferences: the former being restricted to scattered patches of richer environment (e.g. to the centres of the oases), the latter ranging widely over the inferior habitats.

Finally, let us superimpose the distributional range of *mauritanicus* — the only species of the *altisquamis* group that occurs in Tunisia — on to the range-fractioned map of the former (*bicolor* group) species. Again, the range of *mauritanicus* traverses Tunisia from the south-west to the north-east (Fig. 8), and does so along the transitional zone of *viaticus* and *bicolor.* Fig. 9 has been designed to show the degree to which *mauritanicus* overlaps with either species. On a large scale, there is a slight but consistent tendency of *mauritanicus* to occur more frequently together with *viaticus* than with *bicolor:* 36 per cent of the 56 sampling squares within which *mauritanicus* has been observed, are inhabited by *mauritanicus* and *viaticus,* 28 per cent by *mauritanicus* and *bicolor,* and 32 per cent by all three species; but even in the latter case, *viaticus* outweighs *bicolor* by a ratio of 1.5 : 1 (in the remaining 4 per cent of the test squares *mauritanicus* occurs alone). At many sampling sites, *mauritanicus* and *viaticus* have been found in close association, e.g. at Tunis – 23 Bizerte (test square M2); Tunis – 44 Bizerte (M3); El Kef 21 – El Krib (G7); El Fahs 19 – Saouaf (M7); Siliana – 1 Bargou (K8); Haidra 5 – Kalaat Kashbah (F11); Teboursouk (H/I6). The most extensive overlap of *mauritanicus* and *bicolor* occurs in the north-east and the south-west, i.e. in the alluvial plains of

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[6]) "A 12–B" means that the sampling site is located between sites A and B; more specifically, 12 km apart from A in the direction of B.
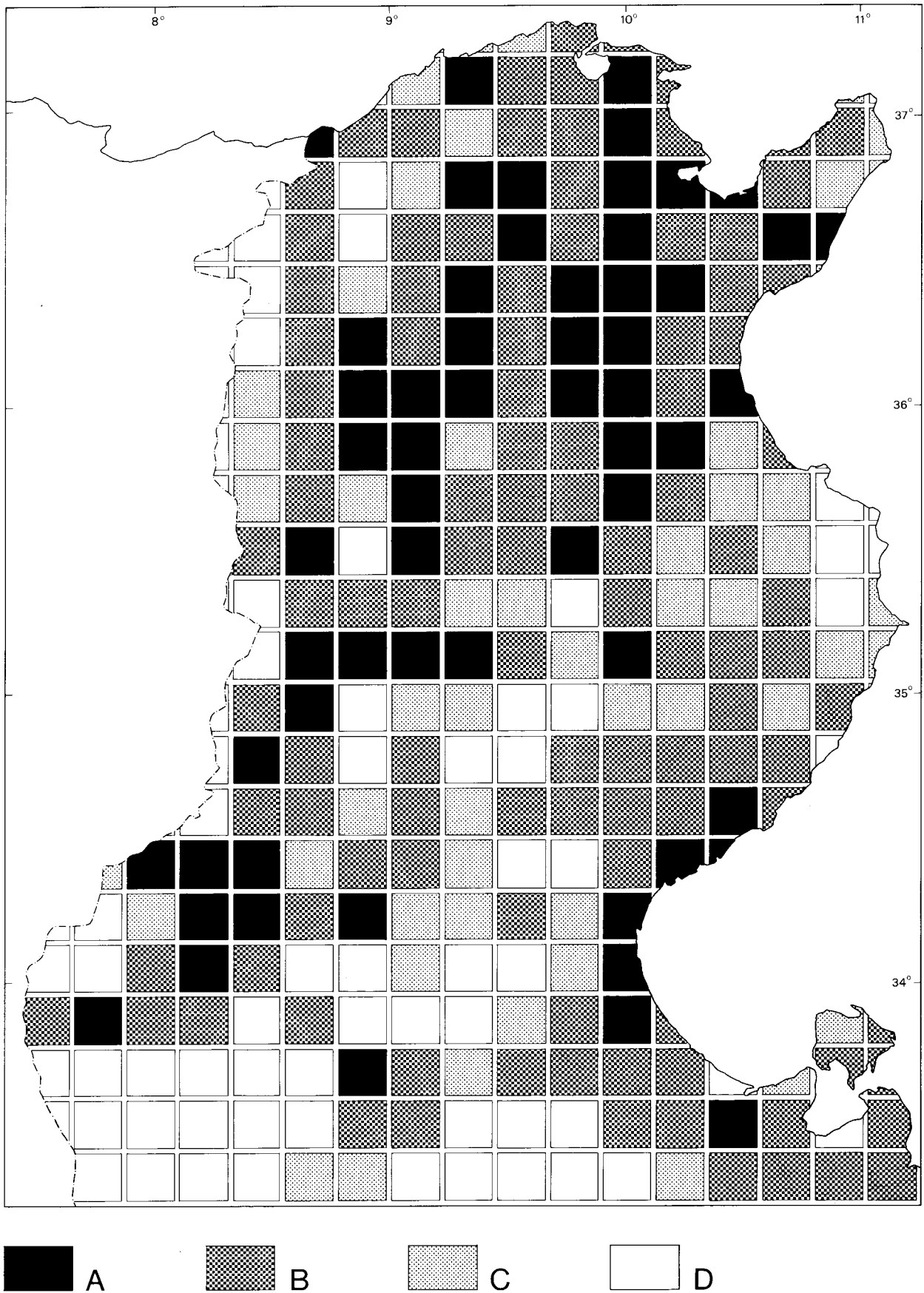
Fig. 6. Spatial distribution of sampling frequencies within the study area (Fig. 4). **A**: ≧ 6 samples, **B**: 2–5 samples, **C**: 1 sample, **D**: area not sampled. See also Fig. 5.
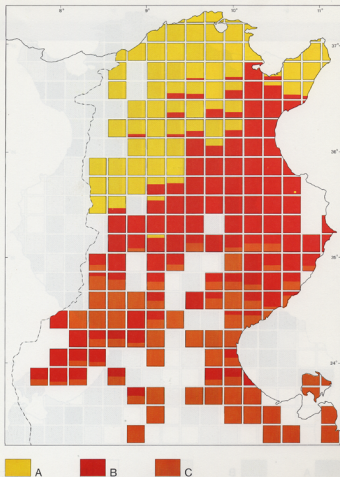
Fig. 7. Distributional ranges of (A) *Cataglyphis viaticus*; (B) *C. bicolor*; and (C) *C. savignyi*. Within any particular sampling square, the ratio of areas A, B and C depicts the relative abundance of the three species.
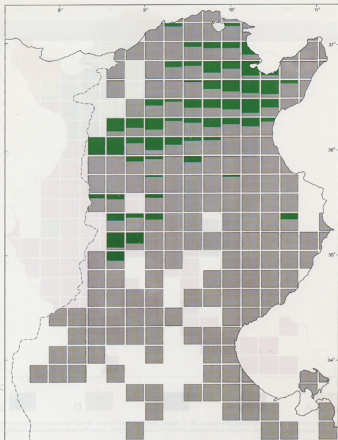
Fig. 8. Distributional ranges of (A) the three large Cataglyphis species belonging to the *bicolor*-species group (C. *viaticus*, C. *bicolor*, C. *savignyi*; see Fig. 7) and (B) C. *mauritanicus* (*altisquamis*-species group). For further explanations see Fig. 7.
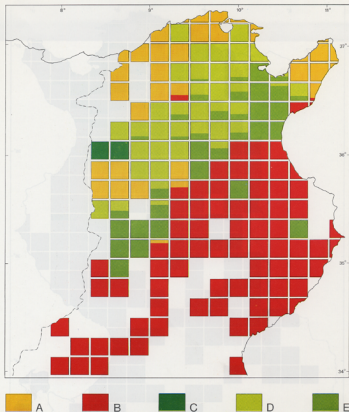
Fig. 9. Distributional ranges of (A) *Cataglyphis viaticus*, (B) *C. bicolor*, and (C) *C. mauritanicus*. Special signatures are used wherever *C. mauritanicus* concurs in the same sampling square together with (D) *C. viaticus* and (B) *C. bicolor*. For further explanations see Fig. 7.

A ▮   B ▮   C ▮   D ▮   E ▮

Fig. 10. Geographical distribution of *Cataglyphis viaticus* (yellow), *C. bicolor* (red), *C. savignyi* (orange), and *C. mauritanicus* (green) along two north-south transects (A, B). For topographic locations of the two transects see Fig. 4. Ordinate: altitude [m]; abscissa: path length [km] and number of latitudinal rows as defined by the system of coordinates depicted in Fig. 4. Locations: Bī = Bizerte, EF = El Fahs, EK = El Kef, GA = Gabès, GF = Gafsa, KA = Kairouan, KE = Kebili, KS = Kasserine, ME = Medenine, SF = Sfax, TA = Tataouine, TH = Thala, TO = Tozeur.

A

B
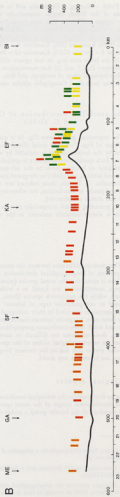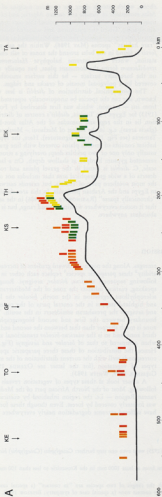
Bou Ficha – Mornag – Grombalia and in the highland plateau of the Haute Steppe, respectively. Colonies of *mauritanicus* and *bicolor* have been located close to each other, for example at Soliman 4 – Hamman Lif (test square O4); El Fahs 19 – Saouaf (M7); Kasserine 35 – Thala (F11); Kasserine (B2); Kasserine 4 – Feriana (G13); Kasserine 5 – Feriana (G13); Kasserine 10 – Feriana (F14). It is in the latter area (e.g. in test square 13G, see Fig. 9 and compare Figs. 7 and 10) that *mauritanicus* just reaches the distributional range of *savignyi*, and that, consequently, all four large-sized *Cataglyphis* species meet.

The patch-like distribution of *C. fortis* and *C. diehlii*

The impression gained from Fig. 11 is quite different from that of Figs. 7–9. The zonal distributional pattern shown by the former species is replaced by a patchwork pattern. Each species considered here is specialized to a particular kind of habitat: *fortis* to the salt-pan areas, the chotts and sebkhas, and *diehlii* to the gravel plains, the regs and hamadas. In Tunisia, these habitats are restricted in range and patchy in distribution, but wherever they occur, *fortis* and *diehlii* are observed.

The preceding remark is especially true for *fortis*. This species is almost certainly endemic to the zone of the chotts, which extends along the southern margins of the Atlas mountains in Tunisia and eastern Algeria; and of the numerous small sebkhas scattered around this core area of distribution. Given the patchiness and scattered distribution of this type of habitat, *fortis* can be classified as a truly "rare habitat" species (MAY 1988). Within the salt-pans *fortis* is found in the belts around the zones of salt encrustation, where the extreme halophyte *Halocnemum strobilaceum* forms the dominant plant, but equally well on the bare salty surface — be this surface smooth or covered by a polygonal mosaic of cracks and ridges.

The geographical distribution of *diehlii* is less well known, nor can the species be unequivocally separated yet from *isis* — a taxon, which was first described by FOREL (1913) for Egypt[7]. In Tunisia, *diehlii*'s centres of distribution lie in the regs and hamadas of the Atlas foot-hills (glacis areas), e.g. in the region of Metlaoui – Moulares – Tamerza (see Fig. 11, square signatures). Here, the typical habitat consists of smooth plains covered with fine gravel, usually only one or two pebbles deep; overlying a strongly cemented gypsum hardpan at shallow depth. On a larger scale, *C. diehlii* is found in the gravel plains and rocky deserts of a wide geographical area that includes not only the most southern parts of Tunisia, but extends eastwards to Egypt and the Arabian peninsula. In this area *diehlii* is "chronically sparse" (RABINOWITZ et al. 1986) in the sense that it occurs everywhere within its broad range, but is not abundant anywhere.

Discussion

What does the difference between the zonal and patch-like patterns of biogeographical distribution actually tell us? Does it mean that the zonal species (*viaticus, bicolor, savignyi, mauritanicus*) are found in a wide variety of habitats, while the patchwork species (*fortis, diehlii*) are confined to one particular type of habitat? Or are the former species as restricted in their ecological preferences as the latter ones, but prefer habitats that extend over much wider and much more continuous geographical ranges? At present, these questions are difficult to answer, because neither the ecophysiological niches of the species nor the historical events that led to the current biogeographical picture are known in any detail.

Ecological aspects

Let us first consider the ecological conditions prevailing in the distributional ranges of the zonal species. For the three members of the *bicolor* group a rather clear picture emerges. Along the north-southward gradient of increasing aridity[8] these parapatric species[9] replace each other in the following sequence: *viaticus, bicolor, savignyi*. Roughly speaking, *viaticus* inhabits the zone of the Mediterranean sclerophyllous vegetation in the north, *bicolor* the low- and highland steppes in the central parts of the country, and *savignyi* the presaharan semidesert in the south. The boundary between the first and second biogeographical zone is much sharper than that between the second and the third zone, and so is the *viaticus-bicolor* transitional zone when compared to that of *bicolor* and *savignyi* (Fig. 7). Hence, the distribution of these three parapatric species corresponds well with the current distribution of the main types of vegetation (for the latter see OZENDA 1977, GIESSNER 1979, WHITE 1983).

A closer look at these types of vegetation reveals the following. Most of the North African part of the Mediterranean Region — i.e. the region inhabited by *viaticus* — was formerly covered by forest. Even though these forests have suffered extreme degradation nearly everywhere and

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[7]) In fact, FOREL (1913) made *isis* a subspecies of *diehlii*. EMERY (1925) went even one step further: *Cataglyphis (Cataglyphis) bicolor* ssp. *diehlii* var. *isis*.

[8]) Mean annual rainfall decreases over a distance of only 300 km from at least 1000 mm in the Kroumirie to less than 100 mm in the Chott-el-Djerid.

[9]) Parapatry describes the biogeographical situation, in which the ranges of two species are "in contact" (a special case of allopatry; SMITH 1955) or overlap, at least to some extent, along the contact zone (a special case of sympatry; BIGELOW 1965).
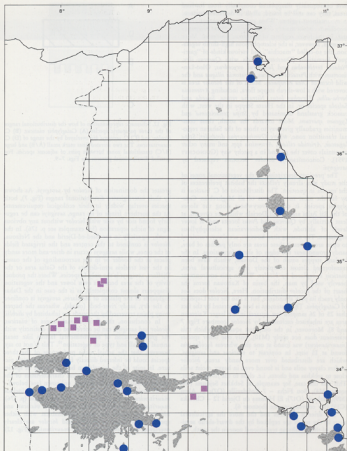
Fig. 11. Geographical distribution of *Cataglyphis fortis* (●, blue) and *C. diehlii* (■, pink). Stippled areas indicate salt-pan flats (sebkhas and chotts).

have consequently disappeared completely from lowland areas, they can still be found, albeit in degraded versions, in mountainous regions. When present in remnant areas, woodlands consist mainly of *Quercus ilex, Pinus halepensis* and, in the lower regions, of *Juniperus phoenicea*. More common, however, is the sclerophyllous high-shrub vegetation, the so-called "macchia", and various kinds of "garrique" formations (Quercetum ilicis with *Quercus ilex, Pistacia terebinthus* and *Juniperus oxycedrus;* Oleo-Lentiscetum with *Pistacia lentiscus, Ceratonia siliqua* and the wild form of *Olea europaea*). Much of the *bicolor* area is covered with a low-shrub steppe flora, including *Artemisia herba-alba, Zizyphus lotus, Nitraria retusa, Suaeda* and *Salsola* species or, in the Haute Steppe in the west, with tussock grassland dominated by *Stipa tenacissima* and *Lygeum spartum*. More towards the south, these communities gradually give way to those of the Saharan regional transition zone, where *Gymnocarpus decander, Stipa lagascae, Aristida ciliata, Artemisia* spp. and many other perennials cover the ground in a patchy way (GUINOCHET 1951). Concomitantly, *bicolor* becomes replaced by *savignyi*.

The previous description of the vegetational zones of the study area already reflects the habitat preferences of the species in question. The distribution of C. *viaticus* is by far the most mountainous of all Maghrebian *Cataglyphis* species. It occurs everywhere along the slopes of the Rif Atlas and Grand Dorsale which are covered, at least partially, by *Quercus* and *Pinus* forests and, at lower levels of altitude, with Mediterranean sclerophyllous vegetation. The nesting sites, however, are always restricted to open areas, even if these areas are only patches of bare, sandy ground near the edges of shrub formations. In the lowland steppes south of the Dorsale, which have been transformed almost completely into agricultural areas, *viaticus* is replaced by *bicolor*. Within this environment heavily used by man, the basin of Kairouan forms the heart of the *bicolor* distribution. Here, *bicolor* does not only reach its peak abundance, but is also the sole L-species of *Cataglyphis*. This statement is best illustrated by the fact that 25 of 26 sampled test squares in the larger Kairouan area are inhabited exclusively by *bicolor* (compare Figs. 7 and 8). Moreover, in the only test square to which this statement does not apply (M10), only one other species (*mauritanicus*) was found at one site, whereas *bicolor* was found at 15 sites. In contrast to *viaticus* and *savignyi*, which are distributed over more sandy areas, *bicolor* prefers clayey soils and is found even in heavy, moist soils close to sebkhas and chotts, i.e. close to the *fortis* habitat. This was the case, for example, at Sebkhet Sejoumi (test square M4); Bou Ficha – 7 Enfidaville (O7); El Alem (M9); Maharès (O17); El Hamma du Djerid 12 – Chebika (C19) (for conventions see footnote 6).

The drier it becomes and the more the agricultural areas in the north are replaced by the dwarf-shrub semidesert of the presaharan transitional zone in the south, the
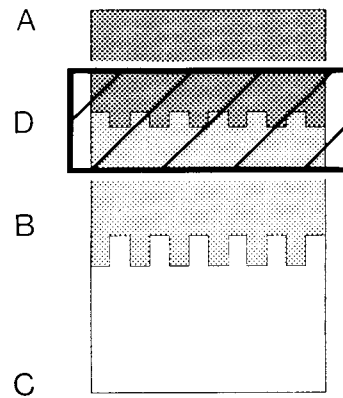

Fig. 12. Schematic representation of how the distributional ranges of the three parapatric species (A) *Cataglyphis viaticus*, (B) C. *bicolor*, and (C) C. *savignyi* are overlayed by the range of (D) C. *mauritanicus*. The two serrated lines mark small (A/B) and large (B/C) transitional zones between pairs of adjacent species. For detailed distributional patterns see Figs. 7–9.

greater the domination of *bicolor* by *savignyi*. As shown by their interdigitated distributional ranges (Fig. 7), both species overlap widely in their ecological requirements. At the northern fringe of its range, *savignyi* can be regularly found side by side with *bicolor* without any obvious signs of niche separation (for examples see p. 176). In the south, especially in the Bled-ed-Djerid and the Nefzoua, *bicolor* is confined to the centres and the irrigated fields of the oases, while *savignyi* occurs in drier and more sandy places at the border or in the surroundings of the oases. In the vast treeless semi-deserts of the Gafsa area or the Djeffara, *savignyi* is the only L-species. Where the productivity of the area becomes even lower and the vegetation disappears almost completely, as is the case in the Dahar highlands or the plateau of Moulares, *savignyi* is confined to the dry, sandy river-beds (oueds), whereas the barren stony plains traversed by the oueds are inhabited by *diehlii*.

In conclusion, the distributional ranges of *viaticus, bicolor* and *savignyi* can be correlated quite distinctly with the gross zonation of environmental factors like mean annual rainfall and type of vegetation[10]. This is not to say, however, that the actual niche preferences of the three species could be inferred directly from this large-scale picture. In spite of the correlation between range of species and type of habitat, the ecological characteristics of the species-specific niches are largely unknown (see below).

We reach a higher level of complexity when we include *mauritanicus* in the picture. As mentioned above (p. 176), *mauritanicus* overlaps widely with both *viaticus* and *bicolor*, and shares the same microhabitat with either species. The ranges of *viaticus* and *bicolor* are clearly overlayed, so to speak, by that of *mauritanicus* (Fig. 12).

This pattern of distribution might call for explanations that predate present-day ecological conditions. But before we take such historical processes into account, let us first obtain a broader perspective of the ecological role, that the *Cataglyphis* species play in their desert environment. This role might shed some light on interspecific competition and species packing.

All *Cataglyphis* ants are scavengers[11], combining solitary hunting with solitary retrieval. They forage at about the same time of day and year for similar arthropod carrion. In terms of diet niche breadth and overlap there seem to be only two parameters that vary between *Cataglyphis* species. The most obvious one is the size of the food particles utilized. It has generally been found that in single-prey loaders, prey size is correlated with the body size of the loader. This is true for the harvesting ants of North America [*Pogonomyrmex* spp.: HÖLLDOBLER 1976, HANSEN 1978, CHEW & DE VITA 1980; *Messor* (= *Veromessor) pergandei:* DAVIDSON 1978; *Pheidole* spp.: CHEW & DE VITA 1980] as well as North Africa (*Messor arenarius:* NEUMEYER & WEHNER 1994)[12]; and it also holds for the scavenging *Cataglyphis* species. Within their entire distributional ranges, the large-sized species *viaticus, bicolor, savignyi* and *mauritanicus* concur with the small-sized species *albicans*. For example, among the foragers of *bicolor* and *albicans* body size ranges from 15 to 40 mg and 3 to 9 mg, respectively, and the sizes of the food items retrieved by these foragers differ accordingly (39.6 ± 4.3 mg and 4.2 ± 2.2 mg, respectively[13]; t-test, p < 0.001). Clearly, the range of food sizes is exploited differentially by the small and large *Cataglyphis* species. Where food becomes sparse — e.g. in the "zone abiotique" (OZENDA 1977: 82) of the chotts and sebkhas — only one species of *Cataglyphis* prevails, and this species, namely *fortis*, is of medium size (see Fig. 11 in WEHNER 1983).

Another ecological factor that varies among *Cataglyphis* species — even among species of the same size class — is food abundance. Productivity in deserts is largely dependent on precipitation, so that mean annual rainfall (MAR) turns out to be a sufficiently precise indicator of net primary production (ROSENZWEIG 1968, NOY-MEIR 1973, SEELY 1978) and, consequently, of higher-order levels of production as well. Along a 100-km transect traversing the flat gravel plains of the central Namib desert, ant species richness is strongly correlated with MAR: it varies from 4–6 to 20–25 species for areas receiving 20 to 100 mm MAR, respectively (MARSH 1986). A similar correlation has been found in Australian and North American deserts, which are characterized by less extreme levels of aridity (100–300 mm MAR) and higher productivity (DAVIDSON 1977a, GREENSLADE & HALLIDAY 1983). It also

applies to *Cataglyphis* in North Africa. Only 2 L-species (*savignyi* and *bicolor*) are found in areas of less than 200 mm MAR, whereas 3–4 L-species concur north of the 200 mm isohyet. Nevertheless, it is by no means clear whether higher levels of productivity and, hence, higher densities of food particles are the immediate cause for the increase in species diversity one observes concomitantly. All other things being equal, density specialization (HÖLLDOBLER & WILSON 1990: 427) requires a non-homogeneous spatial distribution of food items within the sympatric range of the species under consideration. This is certainly true for *bicolor* and *savignyi*, wherever they occur sympatricly in the Saharan regional transition zone at sites of high and low productivity, respectively (see p. 176). But many other ecological factors, such as the structural complexity of the habitat or the temperature-humidity relations, are correlated with productivity and hence could also act as the prime agents of niche separation — not to speak of subtle differences in microhabitat. However, from prior experience, any such differences among *savignyi, bicolor, viaticus* and *mauritanicus* will be difficult to detect. For example, SCHMID-HEMPEL (1983) devoted a two-year project to the foraging behaviour and ecology of (what was then) "*bicolor*". In his study area, the Tunisian sahel, *bicolor* and *savignyi* occur sympatricly at the very same site, but he did not detect any ecological differences between the two species, nor did he actually realize that he had two rather than only one species under investigation.

Finally, let us have a closer look at the hypothesis of density specialization. The hypothesis was originally proposed by DAVIDSON (1977b) in her studies on harvester-ant communities. As the argument goes, trunk-trail and solitary foraging are most efficient in exploiting high and low food densities, respectively. The hypothesis further assumes that high food densities are correlated with patch-like food distributions, which in turn favour competitive group-foraging techniques, whereas under conditions of low food density, the food particles are more evenly dispersed. Consequently, niche separation based on differences in foraging strategy should increase when food becomes more abundant. Although recent work has shown that granivorous desert ants are much more opportunistic in switching from solitary to group foraging, and vice versa (NEUMEYER & WEHNER 1993), density specialization might occur much more readily in seed harvesters than in arthropod scavengers.

First, desert-ant communities are dominated in terms of number of species, forager abundance and biomass by the primary consumers, the seed-harvesting ants (CHEW 1977, BRIESE 1982, MARSH 1985). This also holds true for our study site near Maharès in central Tunisia. If one further

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[11]) Live prey (e.g. harvester termites: WEHNER 1987a) is taken only occasionally. Besides foraging for dead arthropods, *Cataglyphis* ants often lick plant exudates and collect succulent leaves and berries when available during certain times of the year (WEHNER et al. 1983, SCHMID-HEMPEL 1983).

[12]) In some cases, a consistent relationship between the body size of the harvesting ant and the size of the food particle utilized has not been found (e.g. in MORTON 1982, RISSING & POLLOCK 1984, MARSH 1985), but in most of these cases the range of body sizes of the species compared within an ant community was restricted.

[13]) Means and standard errors are given for data acquired in two consecutive years during the month of August (data taken from SCHMID-HEMPEL 1983). Carcasses of ants account for about half of the food items taken by *bicolor* in the shrub steppe near Maharès (test square P16).

assumes — as Brown et al. (1979) do — that due to their high abundance granivorous ants in desert habitats are food-limited, interspecific foraging specializations are more likely to occur in harvesters than in scavengers. Nevertheless, substantial evidence now suggests that harvester ants are by no means "supreme specialists"[14], but exhibit rather high degrees of dietary flexibility, and are therefore not necessarily subject to severe interspecific competition for food (Whitford 1978, Briese & Macauley 1981, Marsh 1985, 1987). In the extremely unpredictable, arid environment of the gravel plains of the Namib desert, such competition does not occur in all but the most arid and hence food-impoverished years.

Secondly, spatial segregation of foraging areas is apparent among harvester ants (rev. Brown et al. 1979), but not in the scavenging Cataglyphis, in which scramble rather than interference competition prevails. It seems that in the sympatric L-species of Cataglyphis, interspecific competition for food has not led to any obvious sign of trophic specialization and food-niche separation. In any case, a fine-grain analysis of the foraging characteristics of the four L-species is much in need.

On the other hand, the ecological relations between distributional range and type of habitat are extremely tight in the two "patchwork species". For example, the halophilous fortis is strictly bound to the salt-pan areas, and can regularly be found from the very north to the very south of the country, wherever chotts, sebkhas or sebkhets occur. Hence, it spans the entire latitudinal range of the four zonal L-species. Clearly, in the case of fortis edaphic factors have proven to be much more important than global climatological conditions, and such factors might finally turn out to be decisive also in the zonal species considered here. Having observed in the field how inseminated Cataglyphis females painstakingly select their future nesting sites, this hypothesis is worth pursuing.

Historical aspects

To understand the origin of the distributional patterns unraveled in the present investigation, we must widen our geographical horizon and survey the entire distributional ranges of the species in question. As far as the "zonal species" are concerned, viaticus and bicolor can be considered as truly Maghrebian forms, distributed from Morocco in the west to Tunisia in the east. Within this region spanning 20° of geographical longitude viaticus occurs in the Mediterranean north, and bicolor in the south, in a belt-like zone directly adjacent to the viaticus range. While in the west viaticus reaches the Atlantic coast, it is not clear yet whether the same holds true for bicolor, or whether the geographical range of the latter species thins out, as one proceeds westward from Tunisia to Morocco.

In contrast to these two species, savignyi is distributed over a wide geographical area ranging from the Atlantic coast to the Near East, and from the southern foot-hills of the Atlas chains and the Mediterranean coast of Libya and Egypt in the north to the Sahel in the south. Within major portions of this vast area, the species is divided into separate, largely isolated populations residing in the Saharan oases. Further detailed studies are required to determine if the observed variation in colour and other morphometric characters follow a grade-like geographical pattern, whether they indicate events of speciation, or whether they are just chance variations. Biochemically, at least, all populations studied so far (including samples from Egypt and Libya) can be regarded as belonging to one species.

The members of either pair of species (viaticus/bicolor on the one hand and bicolor/savignyi on the other) meet in a zone of contact, but do not interbreed (type-4 kind of parapatric contact, see Mayr & Ashlock 1991: 101; normal geographical intergradation, Key 1981: 431). Furthermore, superimposed on this parapatric three-species pattern is the range of mauritanicus (Figs. 8, 9 and 12). This result is somewhat perplexing not only ecologically (see p. 185), but also biogeographically, because other species of the altisquamis group, to which mauritanicus belongs, occur in areas that are completely disconnected from the mauritanicus range: in southern Spain, the Levant, Yemen, and Iran. This discontinuous distribution of the altisquamis-group species suggests that the whole group had once been distributed continuously over a larger area, and had then got split up into geographically isolated species.

We cannot speculate about the nature of such splitting events without considering the evolutionary biogeography of the genus Cataglyphis as a whole. This is the topic we shall consider next. For example, phylogenetically closely related to Cataglyphis is Formica, a genus comprising the holarctic wood ants. Formica is distributed north of the Cataglyphis range. According to a hypothesis put forward by Emery (1912, 1920) Cataglyphis originated in the arid regions of central Asia. This hypothesis is based on the assumptions (i) that Cataglyphis is closely related to Proformica, and (ii) that C. cursor, the most original and Proformica-like species of Cataglyphis, shows a completely Eurasian (primarily Asian, secondarily European, but not African) distribution.

If one accepts this hypothesis, one could surmise that the forms that gave rise to the cursor group spread westward along a northern route (across the Balkan peninsula and north of the Alps into southern France), while the predecessors of what now forms the bicolor group proper (bicolor and niger complexes including savignyi, bicolor and viaticus) moved along a southerly route into North Africa. A similar route might have been taken by early forms of the altisquamis (and emmae) group, which even colonized southern Spain — an area never reached by any member of the bicolor group (Tinaut 1990, 1993).

Large-scale movements, as proposed above for cataglyphid ants, have been documented for vertebrates and plants (members of the Aral-Caspian fauna and Irano-Turanian flora in North Africa; e.g. Frankenberg 1977, Tchernov 1992). When did such movements occur? At the latest about 12 Myr ago, the Asian and Indian plates had joined in the Middle Miocene; and the fusion of Eurasia and Africa had raised the Taurides, Hellenides, Dinarides and the Alps. At that time, the open seaway between the

[14]) Based on work by Davidson (1977a, b, 1978), the term "supreme specialist" was coined for Messor (= Veromessor) pergandei by Hölldobler & Wilson (1990: 427, 610).

Atlantic and the Indian Ocean was finally closed. Concomitantly, warm, subtropical forests gave way to temperate and dry grasslands in the Middle East. In Messinian times (Late Miocene), when the desiccation of the Mediterranean Sea was supposed to have occurred (HsÜ et al. 1977), savannah covered the Vienna Basin. Therefore, during that late Tertiary epoch *Cataglyphis* might have moved out of central Asia, which had been a desert for a long time, into the Near East and North Africa[15].

As can be inferred from the absence of any species of the genus in Sicily (BARONI URBANI 1971), *Cataglyphis* did not cross what is now the Sicilian channel between the Cap Bon peninsula and Sicily. However, it did enter southern Spain. During the late Miocene desiccation period there was a land connection between North Africa and the Iberian peninsula, but such a connection also existed between North Africa and Italy. The latter, however, might have been a salt-lake area hostile to faunal exchanges (HsÜ, in litt.). Both connections broke down at the end of the Messinian, when the flooding of the Mediterranean occurred about 5.5 Myr ago.

Apart from these geological events, *Cataglyphis* might have colonized southern Spain during Pliocene times. At present, the Strait of Gibraltar is only 13 km wide, whereas the Sicilian Channel has more than ten times that width. In this respect, it is interesting to note that species of the *altisquamis* group, but not of the *bicolor* group, have moved from North Africa to Spain, so that the latter group has colonized the Maghrebian area most likely at a later period.

Regardless of when these colonizing movements finally occurred — but assuming that they had in fact occurred — one can propose two hypotheses about the origin of the present-day distributional pattern of the large North African *Cataglyphis* species. Either the species evolved in the east and later moved into their appropriate ecological niches in the west (H1), or the speciation events happened in the west (H2). H1 is unlikely for a number of reasons. For example, in the Levant a parapatric zonation of L-type *Cataglyphis* species is found similar to the one described here for North Africa: an unnamed species near *drusa* (*nodus* complex, *bicolor* group) in the north is followed by a new species of the *bicolor* group (near *savignyi*) and finally by *niger* and *savignyi* in the south. Furthermore, members of the *altisquamis* group are distributed within the ranges of these (*bicolor* group) species in the very same way that we have uncovered in North Africa. These analogous distributional patterns suggest that speciation events have taken place independently in the eastern and southern Mediterranean Region (H2), while H1 would lead one to assume that, at present, either area is inhabited by about the same *Cataglyphis* community. Furthermore, H2 leaves us in the favourable position that we need not necessarily subscribe to an out-of-Asia explanation for the

genus. Of course, the "superimposition" of the *mauritanicus* range on the ranges of the *bicolor*-group species can be explained best by assuming that two colonization waves have reached North Africa (see above), but *savignyi, bicolor* and *viaticus* could well have evolved out of an autochthonous pre-*bicolor* stock.

In any event, the final question is: What are the selective forces that have led to the evolution of the North African L-type species of the *bicolor* group? The question is more readily posed than answered. The parapatric zonation of *viaticus, bicolor* and *savignyi,* and the rather clear-cut correlation of the ranges of the species with present-day large-scale ecological factors, seem to call for a causative effect of the environmental aridity gradient — however indirect this effect actually might have been. If such a tight coupling of species ranges and environmental characteristics had indeed existed over long periods of evolutionary history, the distributional ranges of the three species must have undergone substantial north-south displacements even in more recent (late Pleistocene and early Holocene) times. Research done by the PALHYDAF (Palaeohydrology of Africa) group in southern Tunisia, Algeria, Niger and Mali indicates that one or several wet periods have occurred in the Sahara between c. 150'000 and 75'000 yrs ago (FONTES & GASSE 1991); and the radiocarbon measured ages of the fossil ground-water in the Sahara suggest that a long humid period ended just 20'000 yrs B.P. (SONNTAG et al. 1980). The last wet period occurred at about 5'000 yrs. B.P., when in the Maghreb the 100-mm isohyet extended 200 km farther south than it does today. Then, *Acacia* savannahs reached the southern foot-hills of the Atlas mountains, and high-shrub steppe vegetation covered the present-day presaharan semi-desert northward up to the latitude of Gafsa (LAUER & FRANKENBERG 1979). Alternatively, it might have been these recent climatological events *per se* that provided the selective forces for the speciation processes, and that have led to the evolution of one or the other species of the *bicolor* group. Seen in this light, at least *bicolor* and/or *viaticus* might be of quite recent origin[16].

A similar hypothesis was proposed for *fortis* (for details see WEHNER 1983). As the species is adapted to wet-soil habitats, it might have had a much wider geographical distribution during the last (neolithic) humid period mentioned above, or during any other wet period dating back further. The patchwork pattern of distribution found today would then reflect nothing but the scattered array of relict areas to which *fortis* is now confined. Interestingly, a *fortis*-like species of the *albicans* group occurs in the same type of habitat, but is spatially completely disconnected from the North-West African populations, 3000 km farther east in Syria.

Nevertheless, the principal question posed above still remains. What ecological factors, or combination of fac-

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[15]) POINARD (1992) has listed the genus *Cataglyphis* among the fossil insects of the Baltic amber, which dates back to Eocene-Oligocene times. This remark, however, is certainly false. Neither MAYR (1868) nor WHEELER (1915) mention *Cataglyphis* in their substantial monographs on the ants of the Baltic amber, nor is there any reference to *Cataglyphis* in more recent publications on this subject (LARSSON 1978; KRZEMINSKA et al. 1992).

[16]) Our mtDNA analyses give only relative times of divergence. If, however, the small subunit ribosomal mtDNA gene has a similar clock in *Cataglyphis* and *Drosophila*, then *C. bicolor* and *C. viaticus* diverged at least 1 Myr ago (P. READY, in litt.). Is it possible that the extreme thermal habitat of *Cataglyphis* could lead to a faster mtDNA clock? See RAND (1994).

tors, have finally resulted in the present-day zonation of the L-species of the *bicolor* group? Has it been the marked aridity gradient that, directly or indirectly, acted as the prime mover of the speciation process? We should be careful not to lay our bets exclusively on behavioural and ecological adaptations of the worker caste. As shown for many species of morabine grasshoppers in Australia (KEY 1981), the parapatric distributional pattern of the *Cataglyphis* species might have resulted primarily from reproductive rather than behavioural isolation[17]. In any event, there is one point we must not overlook in the study of *Cataglyphis* evolution, and in the evolution of any other group of organisms as well: namely that adaptation of function — e.g. ecophysiological adaptations of the *Cataglyphis* foragers — may obscure the origin of structure — e.g. differences in the morphology of the male's genital armature, which are so pronounced in the genus *Cataglyphis*.

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[17]) For example, in contrast to the monogynous members of the *bicolor* species group, *mauritanicus* (*altisquamis*-species group) is polygynous. The maximal number of queens per colony recorded until now is 33 (site: Grombalia; test square O5).

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