

## Review and reclassification of *Cataglyphis* (Hymenoptera, Formicidae)

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Exactly 100 years ago Forel made a misidentification of *Cataglyphis viaticus* as *C. megalocolus*, one of the most characteristic insects of North Africa. This far-reaching error has influenced the systematics of the genus ever since. What really are the species of *Cataglyphis*? *Cataglyphis* is unique among formicine ants in that the morphology of the male genitalia is highly diverse: their characteristics are used for the differentiation of species groups and as a basis for postulated phylogenetic relationships within the genus. A synopsis, a key to the species-groups, and a full catalogue of all the available names are given. Of the 104 taxa currently recognized as valid, *Cataglyphis albicans* var. *mixtus* is a new combination, *Cataglyphis cursor* ssp. *flavicornis* is transferred to *Alloformica*, and *Cataglyphis mauritanicus* and *Cataglyphis nigripes* are given a new status. *Camponotus phaenogaster* is a new synonym, and *Cataglyphis hispidus* is a nomen nudum. A lectotype has been fixed for *Cataglyphis savignyi*.

KEYWORDS: Formicidae, *Cataglyphis*, key, catalogue, phylogeny.

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### Introduction and history

This survey began as a systematic revision of the Formicini genera (Agosti, in preparation). However, whilst revising the genera it became apparent that much remained to be done, both at species and at species-group level, and that within the Formicini genera there is a striking contrast between *Formica* and *Cataglyphis*. Whereas in *Formica* the male genitalia are uniform and the behaviour of the species very diverse, in *Cataglyphis* the male genitalia are extremely diverse but the behaviour is quite uniform. It is hoped that the results discussed here will help to dispel at least a little of the taxonomic and nomenclatural fog which still surrounds the species-groups and species of *Cataglyphis*, and perhaps clear the way for further detailed taxonomic or phylogenetic work and comparative studies such as sexual selection (see Eberhard, 1985) within *Formica* and *Cataglyphis*.

The study presented here gives an historical review of the subgenus-level and species-group-level taxonomy. A phylogeny is presented together with a redefinition of the species-groups based on male genitalia characters and a full catalogue.

The genus *Cataglyphis* was defined by Foerster (1850), based on a male of *C. fairmairei*. 'Einschnürungen am Hinterleib' was given as the character to separate *Cataglyphis* from *Formica*. He stressed that unless workers were found, this genus had to be given provisional status. At that time he did not realize that his description of the

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worker of *Formica megalocola*, four pages earlier in the same publication, was the one he was looking for, or that this name might be already a synonym of *Formica viatica* Fabricius. Nevertheless, the description of the male and female are accurate enough to relate both of them to the *bicolor* group (see below). Species-specific characters of genitalia or colour pattern on the promesonotum were not provided.

In 1855 Mayr described the genus *Monocombus* based on the worker of *Formica viatica* Fabricius. Again the description is accurate enough to relate it to the *bicolor* group: the first four maxillary palp segments become larger distally and the fifth is the same size as the first; small compound eyes and ocelli; petiole nodiform (Mayr, 1855). Only 6 years later Mayr realized, obviously after he had obtained complete series including workers, females and males, that his genus had already been described by Foerster (1850) and therefore had to be synonymized (Mayr, 1861). Additionally in this paper Mayr gave the first diagnosis of all three castes of *viatica* and *cursor*, which earlier had been given by Nylander (1849) for *aenescens*.

In a synopsis of the ant genera of the world, Forel (1878) treated *Cataglyphis* as junior synonym of *Myrmecocystus* Wesmael, obviously misled by the convergences that both genera share, and failing to mention any of the characters relating them to two different tribes within the Formicinae (Formicini and Lasiini respectively: see Agosti and Bolton, 1990).

The classification of *Myrmecocystus* remained unchanged until Santschi (1911) and Forel (1913) re-used *Cataglyphis* as a subgeneric name for *C. isis*. Later Santschi (1912) re-used *Cataglyphis* as a generic name, as earlier proposed by Wheeler (1908), for the old world species diagnosed by the large genitalia of the male and the long erect hairs on the stipes of the maxillae. This made *Myrmecocystus* an exclusively nearctic genus and *Cataglyphis* an old world genus. This change had been considered for a long time, for Forel (1886b) pointed out that *Myrmecocystus* eventually might have to be separated into *Cataglyphis* and *Myrmecocystus*, after the inclusion of male characters in the analysis. Wheeler (1908) pointed out that the male genitalia of *Cataglyphis* are more similar to those of *Formica*, whereas those of *Myrmecocystus* species resemble those of *Lasius* (*M. aenovirens* at this time had already been transferred into *Melphorus* (Forel, 1902c)) and that therefore *Cataglyphis* should be given at least subgeneric status.

Emery (1906) and Forel (1908b) did not disagree about the position of most of the species, except as concerns the status of *altisquamis*, *bicolor* and *viaticus*. Emery's position was to split this assemblage into two groups, which are mainly separated by the nodiform (*bicolor*) and squamiform petiole (*altisquamis* and *viaticus*) respectively. Forel agreed in this last point but stressed that there is a morphocline, which includes Emery's species *altisquamis*, *viaticus* and *bicolor*, and therefore by comparison with all the other species of the genus, the whole group can properly only be recognized as one species, *viaticus*, with many subspecies and infrasubspecific taxa. In a following publication, Emery (1908) brought up the relative length of the maxillary palpi of the workers, which supported his earlier division (Emery, 1906). Forel (1908b) commented that the result of using this character was that instead of *niger* it was now *altisquamis* that showed an intermediate grade between Emery's groups, *altisquamis*, *viaticus* and *bicolor* respectively.

Within his revision of *Cataglyphis*, Santschi (1929a) proposed a classification with four subgenera, *Cataglyphis* s. str., *Monocombus*, *Machaeromyrma*, and *Paraformica*, based on worker characters. Unfortunately Santschi had designated *viaticus* as the type-species of *Monocombus*, which in fact should be included in *Cataglyphis* s. str.

This was based on a misidentification by Forel (1890a, b), who obviously read only the description but never checked the Fabricius types, otherwise he would have been aware that the type has a nodiform petiole and elongated maxillary palpal segments. Further this taxon does not inhabit the Iberian peninsula but North Africa (see note 1 below *viaticus*). Therefore *Monocombus* is a junior synonym of *Cataglyphis*. This situation has also been noted by Tinaut (in preparation) in the course of his revision of the Iberian species of *Cataglyphis*.

The subgenus *Paraformica* was erected by Forel (1915) within a footnote in a treatise on Australian ants. In the diagnosis he uses the length of the middle segments of the maxillary palpi and the saddle-shaped mesonotum as characters. Earlier he had criticized Emery's separation of *altisquamis*, *viaticus* and *bicolor* for just this reason, that Emery used those characters which, according to Forel, form transformation series. The real reason for separating *Cataglyphis emmae* from all the other *Cataglyphis* spp. was the very slow locomotion of this species (Forel, 1915).

The subgenus *Machaeromyrma* was introduced by Forel (1916), based on the distinct dimorphism in the worker caste, with larger workers with falcate mandibles. He also used the peculiar nesting habits of this species as a differentiating character. Urbani (1969) synonymized this subgenus with *Cataglyphis* (*Cataglyphis*) based on the discovery of *C. lunatica* in Anatolia, which he interpreted as a link in a transformation series *albicans* (*C. Cataglyphis*) → *bombycina* (*C. Machaeromyrma*). Examination of male genitalia characters indicate that the characters previously used (presence of dimorphic workers, maxillary palpi, proventriculus shape and coloration) might be homoplasies (Agosti, unpublished).

Finally *Eomonocombus* has been treated as junior synonym of *Cataglyphis* by Hölldobler and Wilson (1990), without giving reasons. This synonymy might be justified because of the intermediate status of *Eomonocombus* between *Monocombus* and *Cataglyphis*, a feature used to erect it (Arnoldi, 1968); the lack of autapomorphies makes this subgenus a paraphyletic group.

The characters used to separate the subgenera were disputed for a while (e.g. Emery, 1906, 1908; Forel, 1908a, b) but settled down when Santschi (1929a) wrote his revision of *Cataglyphis*, after which his definitions of the subgenera were widely accepted. Only recently have authors such as Urbani (1969) and Collingwood (1985) started to question and abandon his classification.

Male characters have hardly been used in the higher classification although Emery (1906) used them extensively at species level. In later publications (e.g. Karavaiev, 1911, 1912a, b; Arnoldi 1964) male genitalia of further species have been described but have never been used as characters in systematic studies.

Study of the chemical compounds of the Dufour's and mandibular gland revealed differences between species of different species-groups (*cursor*, *bombycinus* and *bicolor* species-group) and between different species of the *bicolor* species-group (Hevetz and Orion, 1982; Hevetz and Lloyd, 1985; Morgan *et al.*, 1990). It is yet not understood at which taxonomic level the chemical compounds and their blends are specific (Morgan *et al.*, 1990 and personal communication).

Analysis of the cuticular hydrocarbon pattern in combination with behavioural tests of ants from the *cursor*-group (Nowbahari *et al.*, 1990) support the morphological pattern.

The genus *Cataglyphis* is characterized by well-diagnosed monophyletic groups within the genus based on male genitalia characters (see below) but the species-level taxonomy is hardly understood. Until a full-scale revision of the genus at species level

can be done, including material from the whole distribution range and all three castes, it does not seem reasonable to re-erect synonymized subgenera, although some of them might easily turn out to be monophyletic groups. The level of the informal species-group is chosen arbitrarily but it is consistent within this genus and does not include paraphyletic taxa.

The problematic nature of the diagnosis of individual species is, on the one hand, based on the lack of adequate species descriptions. This is in itself due to the practice of describing new species based on few specimens, and a poor understanding of the whole genus. On the other hand it is based on a misinterpretation of the early types such as *C. viaticus*, *C. bicolor* and *C. megalocolus* (see notes under *viaticus*), and a failure to appreciate the subtle differences which occur at species level.

The aim of this study is to make a first step towards solving the species-level problems in the taxonomy and systematics of *Cataglyphis* by describing the genus *Cataglyphis*, its species-groups and their phylogenetic relationships, by providing a key to the species-groups, and by giving a catalogue of all available names within the genus.

### Measurements and indices

*Alitrunk length (AL)*: The diagonal length of the alitrunk in profile from the point at which the pronotum meets the cervical shield to the posterior base of the metapleuron.

*Cephalic index (CI)*:  $HW \times 100/HL$ .

*Eye index (EI)*:  $EL \times 100/HW$ .

*Eye length (EL)*: The maximum diameter of the eye.

*Funicular index (FI)*: Length of first funiculus segment  $\times 100$ /Length of second funiculus segment.

*Head length (HL)*: The length of the head proper, excluding the mandibles, measured from the mid-point of the anterior clypeal margin to the mid-point of the occipital margin, in full-face view.

*Head width (HW)*: The maximum width of the head in full-face view, measured below the eyes.

*Metanotum height (MH)*: The maximum distance from the line spanned between the anteriormost and posteriormost part of the alitrunk and the lowest part of the metanotum, measured at a right angle to this line (Figs 11, 12).

*Maxillary palp index (MPI)*: Length of fourth maxillary palp segment  $\times 100$ /Length of fifth.

*Propodeum height (PH)*: the maximum distance from the line spanned between the anteriormost and posteriormost part of the alitrunk and the most raised part of the propodeum, measured at a right angle to this line (Figs 11, 12).

*Propodeum index (PI)*:  $PH \times 100/MH$ .

*Scape index (SI)*:  $SL \times 100/HW$ .

*Scape length (SL)*: The maximum straight line length of the antennal scape excluding the basal constriction or neck to the condylar bulb.

*Subgenital plate index (SPI)*:  $SPL \times 100/SPW$ .

*Subgenital plate length (SPL)*: Measured as a line spanned between the most cranial, median point and the median point of a line between the two most distal points of the two most distal processes of the subgenital plate.

*Subgenital plate width (SPW)*: Measured between the two most basal, sclerotized points of the distal outline of the subgenital plate in dorsal view.

*Wing index (WI)*:  $AL \times 100/WL$ .

*Wing length (WL)*: the maximum length of the front wing from the distalmost point on the tegulae to the distalmost point of the wing.

### Depositories

BMNH	British Museum (Natural History), London, UK.
CAF	Collection of A. Francoeur, Département des Sciences fondamentales, Université de Québec, Chicoutimi, Canada.
CBP	Collection of B. Poldi, Pavia, Italy.
CCAC	Collection of C. A. Collingwood, Skipton, UK.
CDA	Collection of D. Agosti, Uster, Switzerland.
CRW	Collection of R. Wehner, Zoologisches Institut, Universität Zürich, Zürich, Switzerland.
CXE	Collection of X. Espadaler, Departamento de Biología, Universidad autonoma, Bellaterra, Spain.
DBAUG	Departamento de Biología Animal, Universidad de Granada, Spain.
ETHZ	Entomologisches Institut, ETHZ, Zürich, Switzerland.
INER	Istituto Nazionale di Entomologia, Roma, Italy.
IZPAN	Instytut Zoologiczny, Polska Akademia Nauk, Warszawa, Poland.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA.
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland.
MNB	Musée National, Budapest, Hungary.
MNHP	Muséum Nationale d'Histoire Naturelle, Paris, France.
MZL	Musée Zoologique, Lausanne, Switzerland.
NHMB	Naturhistorisches Museum, Basel, Switzerland.
NHMS	National Natural History Museum, Sofia, Bulgaria.
TAU	Zoological Museum, Tel-Aviv University, Tel-Aviv, Israel.
ZIL	Zoological Institute, Academy of Sciences of the USSR, Leningrad, USSR.
ZMH	Zoological Museum of the University, Helsinki, Finland.
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, East Germany.
ZMK	Zoological Museum, Kiev, USSR.
ZMUC	Zoologisk Museum, Universitets Copenhagen, Denmark.
ZMMSU	Zoological Museum, Moscow State University, Moscow, USSR.

### Material

This study has been based primarily on *Cataglyphis* specimens from the following collections: BMNH, CCAC, CDA, MHNG, MNHP, NHMB, ZIL, ZMMSU. Where primary type material has been examined, this is mentioned under the respective taxon. In addition, some material from each of the remaining institutions listed above has also been examined. A total of approximately 2500 specimens (including approximately 230 males) have been studied. A detailed list of material examined will be included in the forthcoming revision of this genus (Agosti, in preparation).

### *Cataglyphis* Foerster

*Cataglyphis* Foerster, 1850: 493. Type-species: *Cataglyphis fairmairei* Foerster, 1850: 493 [Junior synonym of *Formica bicolor* Fabricius, 1793: 356; by monotypy.

*Monocombus* Mayr, 1855: 493. Type-species: *Formica viatica* Fabricius, 1787: 308; by monotypy. [Synonymized by Mayr, 1861: 44; re-erected as subgenus *Cataglyphis* (*Monocombus*) by Santschi, 1929a: 30.] Synonymy here reconfirmed.

*Formica subdiviso* 3 Nylander, 1856: 59 [see note 1 below].

*Myrmecocystus* Wesmael, 1838 sensu Forel, 1878: 372, p.p [see note 2 below]; *Myrmecocystus*, Lomnicki, 1925: 164, misapplication of name.

*Paraformica* Forel, 1915: 95 (footnote). [As subgenus of *Formica*.] Type-species: *Formica* (*Proformica*) *emmae* Forel, 1909: 381; by monotypy [raised to genus by Emery, 1925: 260]; new combination and new status as subgenus of *Cataglyphis* (*Paraformica*) by Santschi, 1929a: 30. Syn. nov.

*Machaeromyrma* Forel, 1916: 441 [as subgenus of *Cataglyphis*]. Type-species: *Formica bombycina* Roger, 1859: 232; by original designation. [Synonymy by Urbani, 1969: 218.]

*Eomonocombus* Arnoldi, 1968: 1815 [as subgenus of *Cataglyphis*]. Type-species: *Myrmecocystus albicans* st. *cinnamomea* Santschi, 1929a: 61; by original designation. [Synonymy by Hölldobler and Wilson, 1990: 18.]

Note 1: Nylander (1856: 59) synonymized *Cataglyphis* and *Monocombus* with *Formica*, but the proposed name, *subdiviso* 3, is unavailable. Nevertheless, the diagnosis he gave is accurate and corresponds with the actual diagnosis of *Cataglyphis*

Note 2. Emery and Forel (1879) made this synonymy without explanations; possibly because Roger (1862: 254) stated that *Myrmecocystus melligerus* 'zeigt, mit Ausnahme des, bis zur Stärke einer grossen Erbse aufgetriebenen Hinterleibes, vollkommene generische Uebereinstimmung mit *Cataglyphis viatica*'. Curiously enough, 1 year later Roger (1863: 12) synonymized the older genus *Myrmecocystus* with the later published *Cataglyphis* (and therefore a junior synonym of *Myrmecocystus*), a situation that was cleared up by Emery and Forel (1878: 372).

### Diagnosis

Workers and females: Formicine ants with the following diagnostic characters.

1. Mandibles large triangular, a row of five teeth which become smaller from apical to basal (Fig. 6). In the *bombycinus* group sometimes up to seven teeth and large workers with a falcate mandible (Figs 4 and 5); in *kurdistanicus* large workers with an elongate mandible with a row of denticles; longitudinally striate.
2. Macrochaetae on the stipes of the maxilla.
3. Often a distinct psammophore formed at least by the macrochaetae on the stipes of the maxillae and on the inner apical margin of the mandibles; sometimes with long curved hairs on the third to fifth segment of the maxillary palps.
4. First maxillary palp segment flat.
5. Eyes located distinctly behind the midlength of the head.
6. Propodeal spiracles slit-shaped.
7. Wings (female caste) with a straight frontal side and very sparse, short pubescence (length of the hairs  $\ll$  space between the hairs).

Males: Formicine ants with the following diagnostic characters.

1. Body of the same size as the females.
2. Ocelli and eyes only slightly enlarged in comparison to those in the female caste.
3. Stipes with a median appendage (Fig. 28).
4. The toothless zone on the sagittated side ventral of the ergot stretched (Fig. 63).
5. Front wing short in comparison to the alitrunk ( $WI > 50$ ).
6. Dorsum of alitrunk black or bicoloured with two lateral bands and a semicircular spot cranially.

*Distribution and biology*

*Cataglyphis* species are distributed exclusively in the palaearctic realm, from Portugal to Mongolia and the Ganges valley in the East, from the Coté d'Ivoire and southern Sudan to Czechoslovakia, from sea level to over 3000 m. They avoid the forests, but live within the gaps of forested areas in Rosaceae forest of central Asia or the steppic forests, and can be found between sand dunes of the Sahara or the Chotts. Most species are found in steppic or Mediterranean-type habitats.

Summaries of the biology and physiology are to be found in Dlussky (1981), Wehner (1982, 1987), and Wehner *et al.* (1983).

**Phylogeny of *Cataglyphis***

The taxonomic and systematic problems in *Cataglyphis* are mainly to be found at species level. Thus it is easier to place specimens in a species-group or complex than a species. Species-groups, as they are defined here, are taxa for which at least one autapomorphy can be found which is not merely a change in length or width.

The character states of male genitalia characters which are included in the analysis (Table 1) are the following:

1. Subgenital plate short, SPI < 125 (0); long, SPI > 125 (1).
2. Subgenital plate bilobed, sometimes with an emarginate median part (0) (Figs 13, 18, 19, 25–27); distally emarginate, without lateral lobes (1) (Fig. 17); trilobed (2) (Figs 14–16, 20–24).
3. Squamula and stipes confluent (0) (Figs 33–39); squamula overlapping stipes caudally (1) (Figs 28–30, 32, 40–42).
4. Stipes without a mediobasal appendage (0) (Figs 29, 30, 40–42); with a mediobasal appendage, separated from the stipes by a carinae (1) (Figs 28, 33–39); or confluent (2) (Figs 31, 32).
5. Volsella straight (0) (Figs 48–52); volsella curved (1) (Figs 53–62).
6. Sagitta with serrated face ventrally [if not serrated, then ventral face simple] (0) (Figs 64, 66–74); sagitta with serrated face laterally (1) (Figs 63, 65).
7. Median fold pointing towards the basal end of the ventral face (0) (Figs 63–65); towards anterior edge of the ventral face (1) (Figs 66, 67); towards the anterodorsal appendage (2) (Figs 68–77).
8. Anterodorsal appendage absent (0) (Figs 63–67); present (1) (Figs 68–77).

Table 1. Data matrix for male genitalia characters of *Cataglyphis*

Characters	123456789
<i>Proformica</i>	000000000
<i>urens</i> group	000100212
<i>nigripes</i> group	000100212
<i>bicolor</i> group	120100212
<i>albicans</i> group	101100212
<i>cursor</i> group	001011000
<i>altisquamis</i> group	021011000
<i>pallidus</i> group	021010101
<i>bombycinus</i> group	020210101
<i>emmae</i> group	011210101

Only characters indicating relationships are presented. Synapomorphies and autapomorphies are given in Fig. 1. The characters are explained in the text.

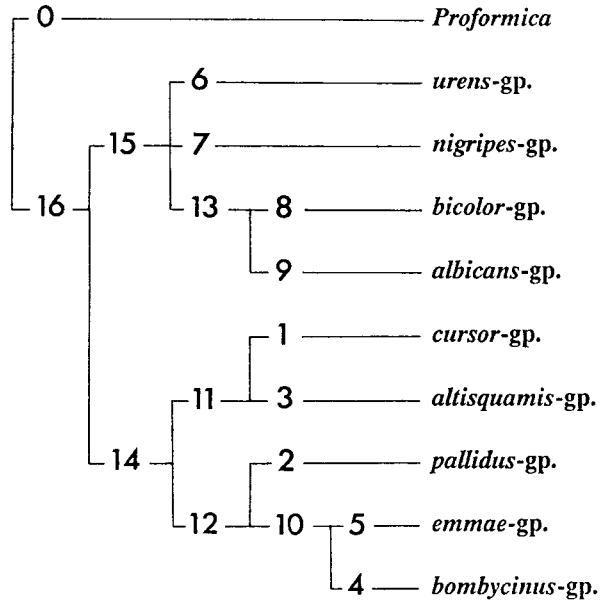


FIG. 1. Cladogram of the species groups of *Cataglyphis*. 0–9: Autapomorphies, 10–16 Synapomorphies (Plesiomorphic states in brackets). 0: Median lobe between stipes and volsella (not present); 1: stipes with a mediobasal lobe (not present); 2: cuspis with an apical extension (acute); 3: cuspis with a medioventral extension (straight); 4: lateral lobes of subgenital plate triangular, acute (bilobed with a median part); 5: subgenital plate distally completely emarginate (bilobed with a median part); 6: subgenital plate with diverging lateral lobes (parallel); 7: subgenital plate with a deeply emarginate median part (median part simple); 8: trilobed subgenital plate (bilobed), squamula and stipes confluent; 9: sagitta with a blunt dorsal process (acute); sagitta without a serrated ventral face (serrated); 10: stipes with a confluent median appendage (no appendage present); 11: sagitta with serrated face laterally (ventrally); 12: sagitta anteriorly (ventrally) rectangular (depressed); 13: subgenital plate long, SPI > 125 (short SPI < 125); 14: squamula and stipes confluent (overlapping), volsella straight (cuspis bent); subgenital plate anteriorly trilobed (bilobed); 15: sagitta elongated (Figs 68–77), stipes with a mediobasal appendage, separated by a carina (no appendage present); 16: laterally, stipes separated from squamula by a membranous part (stipes and squamula confluent), squamula overlapping stipes caudally (confluent).

9. Sagitta with anterior (ventral) part depressed (0) (Figs 63 and 64); a quadrangular to rectangular shield (1) (Figs 64, 66, 67); elongated (2) (Figs 68–77).

The analysis of the data, using mhennig\* of *hennig86* and unordered, unweighted characters, revealed two equally parsimonious trees (17 steps; ci = 76, ri = 85), of which the one chosen matched best with characters of the female castes (Fig. 1). *Proformica*, as the supposed sister-group of *Cataglyphis* (Agosti, in preparation) has been chosen as the outgroup. All trees showed the main division at node 16, which is also supported by the appearance of a squamiform petiole in clade 14 and a nodiform petiole and elongated third and fourth maxillary palp segment in clade 15. Clade 15 corresponds with the former subgenus *Cataglyphis* sensu strictu.

Within clade 14 the *emmae* group and the *bombycinus* group are always sister-groups and together they are the sister-group of the *pallidus* group.

Finally the sister-group relation *altisquamis* group/*cursor* group has been favoured



because otherwise the autapomorphies of the *altisquamis* group are two reversals (characters 7 and 9) and the lateral serrated face of the sagitta (character 6), which is the autapomorphy of the sister-group *altisquamis* group/*cursor* group in the proposed tree, is a homoplasy. This treatment best matches the assumed relationship based on female castes.

The sister-group of the *pallidus* group has always been *bombycinus* group and *emmae* group.

This system does not support Santschi's subgenera (Santschi, 1929a), because his subgenus *Monocombus* (= *altisquamis*, *cursor* and *pallidus* groups) is polyphyletic.

It is hoped that further analysis, including characters of the female castes and species as terminal taxa, will reduce the number of trees (Agosti, unpublished) and furthermore make *Cataglyphis* available for zoogeographic studies.

### Key to the species-groups

The classification of the species-groups of *Cataglyphis* is based on male genitalia characters. It is not possible to key out all the species groups thus defined within the worker and the female castes. Furthermore, series of workers have to be included in the determination of the species-groups to see variation, and also because the indices given below apply strictly only to the larger workers.

#### Workers and females

- |   |   |                               |
|---|---|-------------------------------|
| 1 | Petiole squamiform (Figs 7, 10) . . . . .   | 2                             |
| – | Petiole nodiform (Figs 8, 9) . . . . .  | 6                             |
| 2 | Mandible with six or more teeth, without postbasal (Fig. 4) or falcate with a cleft posterior the apical tooth (Fig. 5). Third maxillary palp segment flat with erect hairs longer than twice their maximum diameter. Gaster usually covered with thick, silvery shining pubescence, except <i>lucasi</i> . . . . .   | <i>bombycinus</i> group       |
| – | Mandible with five teeth, without postbasal, sometimes with six or seven teeth by splitting off of the median and the premedian teeth into two denticles or four teeth by fusion of the prebasals, but then workers with five teeth always present in the same series (Fig. 6); if with a falcate mandible then denticles always indicated. Third maxillary palp segment never flattened and with erect hairs shorter than 1.5 × maximum diameter of the segment. Gaster with widely set pubescence . . . . . | 3                             |
| 3 | Petiole cuneiform (Fig. 10); frons reticulate and sometimes with an additional punctuation; AL > 4.2 mm . . . . .   | <i>altisquamis</i> group p.p. |
| – | Petiole an upright or slightly inclined scale (Fig. 7); frons longitudinally striate or reticulate; AL < 4 mm . . . . .   | 4                             |
| 4 | Body colour chestnut brown or yellow, shining; AL < 2.5 mm . . . . .  | <i>pallidus</i> group         |
| – | Body colour brownish-black to black, matt or silky lustre; if shining then whole body jet black ( <i>frigidus</i> complex); AL > 3.0 mm . . . . .   | 5                             |
| 5 | FI > 190; unicolorous dull brownish black; distinct allometric growth with almost dimorphic workers . . . . .   | <i>emmae</i> group            |
| – | FI < 180; monophasic size variation in the worker caste . . . . .   | <i>cursor</i> group           |
| 6 | EI > 35; gaster not raised in locomotion . . . . .  | <i>altisquamis</i> group p.p. |
| – | EI < 35; Gaster raised in locomotion . . . . .  | 7                             |
| 7 | Petiole anterodorsal straight, in lateral view anterior and posterior surface meeting at an angle (Fig. 8). In locomotion, an acute angle between the ventral surface of the gaster and a line spanned between the anterior- and posteriormost point of the alitrunk (Fig. 2). EI > 27, CI > 96 (measured by the largest workers of a nest-series; an overlap of the EI and CI can exist with those of the <i>bicolor</i> group and has to be taken into consideration.) . . . . .                            | <i>albicans</i> group         |

- Petiole anterodorsal domed, in lateral view whole dorsum of petiole rounded (Fig. 9). In locomotion obtuse angle between the ventral surface of the gaster and a line spanned between the anteriormost and the posteriormost point of the alitrunk (Fig. 3).  
EI < 28; CI < 97 . . . . . 8
- 8 Propodeum raised, PI > 300 (Fig. 12) . . . . . *urens* group
- Propodeum arched, PI < 200 (Fig. 11). . . . . *bicolor* group, *nigripes* group

### Males

- 1 In lateral view, volsella straight (Figs 48–52). . . . . 2
- In lateral view, volsella curved (Figs 53–62). . . . . 6
- 2 In lateral view, sagitta with the distal part rectangular (Fig. 64) or quadrangular (Figs 66, 67) . . . . . 3
- In lateral view, sagitta with the distal part depressed (Figs 63, 65) . . . . . 5
- 3 The overlapping part of the squamula of almost the same length as stipes, distally truncated (Fig. 29); Volsella with cuspis distally extended, pediform (Fig. 49) . . . . . *pallidus* group
- The overlapping part of the squamula shorter or at least distally acute . . . . . 4
- 4 Subgenital plate distally emarginate (Fig. 17) . . . . . *emmae* group
- Subgenital plate distally with at least two truncated, lateral projections (Fig. 16); distally never emarginate over the entire width . . . . . *bombycinus* group
- 5 Stipes with a large, round median appendix with a diameter of almost half the length of the stipes (Fig. 28). . . . . *cursor* group
- Stipes without a median appendix (Fig. 30); Volsella most extended at half length (Fig. 50) . . . . . *altisquamis* group
- 6 Sagitta with an anteromedian appendix which does not overlap the outline of the sagitta in lateral view (Fig 68). The two rounded distal processes of the subgenital plate divergent (Fig. 18). . . . . *urens* group
- Sagitta with an anteromedian appendix projecting over the outline of the sagitta in lateral view (Figs 69–77). If only two distal processes of the subgenital plate are present then they are never divergent (Figs 19–27) . . . . . 7
- 7 Subgenital plate short (SPI < 125) with two distal processes and a deep median emargination distally (Fig. 19) . . . . . *nigripes* group
- Subgenital plate long (SPI > 125), either with three distinct distal processes (Figs 20–24) or narrowed distally, often with the lateral margins turned upwards (Figs 25–27) . . . . . 8
- 8 Subgenital plate with three distinct distal finger-shaped teeth (Figs 20–24; stipes with a basal, median appendix, squamula and stipes confluent (Figs 33–39); sagitta with the ventral side serrated (Figs 70–74) . . . . . *bicolor* group
- Subgenital plate without three distinct finger-shaped teeth, at most the lateral parts forming bulges or fingershaped (Figs 25–27); stipes without a basal median appendix or only indicated by a minute protuberance, squamula overlapping stipes (Figs 40–42); sagitta with the ventral side smooth (Figs 75–77) . . . . . *albicans* group

### Synopsis of the species-groups and -complexes of *Cataglyphis*

#### *cursor* group

##### *cursor* complex

##### *aenescens*

##### *cursor* var. *caspius* (synonym)

##### *aenescens* spp. *chatkalensis*

##### *aenescens* spp. *georgicus*

##### *aenescens* spp. *jakobsoni*

##### *aenescens* spp. *tancrei*

*cursor* spp. *aenescens* var. *kuenlunensis* (unavailable)

*cursor* spp. *aenescens* var. *flavigastra* (unavailable)

*cursor* spp. *aenescens* var. *maeotica* (unavailable)

*cugiai*

*cursor*

*cursor* spp. *aterrimus*

*cursor* var. *creticus*

*cursor* spp. *rockingeri*

*cursor* spp. *tancrei*

*hellenicus*

*cursor* st. *hellenica* var. *dorica* (unavailable)

*hispidus* (unavailable)

*italicus*

*piliscapus*

*tibialis* (synonym)

*frigidus* complex

*frigidus*

*frigidus* spp. *persicus*

*altisquamis* group

*altisquamis* complex

*altisquamis*

*altisquamis* var. *bucharicus*

*asiriensis*

*foreli* complex

*foreli*

*foreli* ssp. *oxianus*

*foreli* ssp. *piligerus*

*gracilens*

*hispanicus* complex

*foreli* ssp. *murgabicus*

*hispanicus*

*hispanicus* var. *nigroides*

*kurdistanicus*

*kurdistanicus*

*mauritanicus* complex

*gaetulus*

*gaetulus* var. *pilisquamis*

*mauritanicus* stat. nov.

*viaticus* st. *mauritanicus* var. *occidentalis* (unavailable)

*viaticus* st. *mauritanicus* var. *opaciventris* (unavailable)

*viaticus* var. *tonsilis*

*viaticus* var. *velox*

*pallidus* group

*emeryi*

*emeryi* var. *abdominalis*

*emeryi* st. *karawaiewi*

*pallidus*

*pilosulus*

*bombycinus* group*bombycinus* complex*bombycinus**phaenogaster* syn. nov.*bombycinus* var. *bruneipes**bombycinus* var. *sinaiticus**lucasi**phaenogaster**sabulosus* complex*sabulosus**emmae* group*emmae**emmae* var. *hoggarensis**urens* group*urens**nigripes* group*nigripes* stat. nov.*bicolor* group*abyssinicus* complex*abyssinicus**bicolor* complex*bicolor**megalocolus* (synonym)*fairmairei* (synonym)*albicans* ssp. *rotundinodis* (synonym)*bicolor* var. *adustus**bicolor* var. *basalis**bicolor* var. *oasium**bicolor* var. *pubens**bicolor* st. *seticornis**saharae**bicolor* st. *saharae* var. *bucculentus* (unavailable)*viaticus**desertorum* (synonym)*diehlii* complex*adenensis**adenensis* var. *bugnioni**diehlii**isis**laevior**bicolor* st. *laevior* var. *rufidens* (unavailable)*niger* complex*bicolor* var. *sudanicus**niger**bicolor* st. *nodus* var. *caerulescens* (unavailable)*bicolor* st. *niger* var. *pharao* (unavailable)

*savignyi*

*nodus* complex

*bicolor* ssp. *bellicosus*

*bicolor* st. *nodus* var. *assyrius* (unavailable)

*bicolor* st. *nodus* var. *drusus* (unavailable)

*bicolor* st. *nodus* var. *helladicus* (unavailable)

*bicolor* st. *protuberatus*

*bicolor* var. *rufiventris*

*lunaticus*

*nodus*

*viaticus* var. *orientalis* (synonym)

*nodus* spp. *caucasicolus*

*nodus* spp. *mesasiaticus*

*setipes* complex

*bicolor* var. *congolensis*

*indicus*

*setipes*

*setipes* spp. *bergianus*

*setipes* spp. *dschambulicus*

*setipes* spp. *karakalensis*

*turcomanicus*

*viaticus* ssp. *setipes* var. *setipedesertorum* (unavailable)

*longipedum* (synonym)

*albicans* group

*albicans* complex

*alibabae*

*albicans*

*albicans* ssp. *armenus*

*albicans* r. *cubicus*

*albicans* ssp. *franchettii*

*albicans* var. *kairuanus*

*albicans* var. *opacus*

*albicans* var. *targuius*

*albicans* var. *vaucheri*

*canus*

*ibericus*

*lividus* ssp. *bulgaricus*

*minimus*

*otini*

*rosenhaueri*

*ruber*

*albicans* st. *ruber* var. *agilis* (unavailable)

*semitonsus*

*theryi*

*viaticoides* ssp. *cuneinodis*

*cinnamomeus* complex

*cinnamomeus*

*elegantissimus*

*fortis* complex

*fortis*

*halophilus* (Synonym)

*lividus* complex

*albicans* var. *auratus*

*albicans* var. *fezzanensis*

*albicans* var. *mixtus*

*argentatus*

*lividus*

*lividus* ssp. *luteus*

*albicans* st. *lividus* var. *agnatus* (unavailable)

*albicans* st. *lividus* var. *ambiguus* (unavailable)

*albicans* ssp. *livida* var. *arabica* (unavailable)

*albicans* ssp. *lividus* var. *arenaria* (unavailable)

*viaticoides*

#### ***cursor*** group

##### *Diagnosis*

Workers and females: *Cataglyphis* ants with the following diagnostic characters:

1. Petiole squamiform, the anterior and the posterior surface meeting at an angle but only partially forming a crest (Fig. 7).
2. Third and fourth maxillary palp segments shorter than fifth and sixth together, MPI < 90; third segment round in cross-section.
3. Uniform black, exceptionally with dark reddish-brown spots on the head, mainly dull, rarely shining, surface.
4. Head finely, longitudinally striate on frons; if reticulate then dorsum of alitrunk without pilosity.
5. Alitrunk length of large workers < 3.4 mm.

Males: *Cataglyphis* ants with the following diagnostic characters:

1. Uniform black or with a reddish or yellow gaster.
2. Subgenital plate short (SPI < 125; Fig. 13); with two distal, lateral rounded processes and a median part which is variable but always present.
3. Squamula caudally always projecting over the stipes, sometimes forming a distinct process pointing ventrally (Fig. 28).
4. Stipes with a large, simple, median appendix with its largest diameter longer than half the length of the stipes (Fig. 28).
5. Volsella straight; in lateral view the sides of the volsella subparallel at most, distally truncated or pointed, never pediform (Fig. 48).
6. Sagitta with a depressed shield (Fig. 63); at least distal part of the serrated face curved laterally.

##### *Distribution*

The species of the *cursor* group are found in the gaps of steppe and Mediterranean forest up to dry forest, discontinuously distributed from central Spain to Mongolia, but are not present in North Africa or the semideserts of the Middle East. They have a local distribution; thus if present they may be very common. No species are present in the lowland deserts of the palaearctic and they are always found at high altitude along their southern distribution limit in mountains; Antilebanon higher than 2000 m,

above 2000 m (Menozzi, 1939). A doubtful record of one female from the Côte d'Ivoire was published by Emery, 1898: 147 (footnote).

### Comments

As previously stated, the *cursor* species-group consists mainly of taxa with a rather isolated, limited and allopatric distribution with the exception of *aenescens*, spread over the steppe parts of eastern Europe, the higher parts of Anatolia and the Caucasus. Differences at species level are to be found in the chaetotaxy of the head and dorsum of alitrunk and the sculpturing of the head of the worker caste, and in the genitalia of the male caste. But a study of variation in these characters needs to be undertaken. The preliminary morphological analysis of Mediterranean species is supported for the west Mediterranean species by an analysis of cuticular hydrocarbons of the workers (Nowbahari *et al.*, 1990).

The *cursor* species-group currently includes 15 taxa which can be split into two species-complexes:

- (i) *frigidus* complex: with workers with a shining and smooth head and males with an apically rounded sagitta;
- (ii) *cursor* complex: with workers with matt heads, a distinctly striate or reticulate frons and males with an apically pointed sagitta (for the species see synopsis above).

The affinities of *cugiai* remain unresolved. It might belong to the *pallidus* species-group (Menozzi, 1939) or to the *frigidus* complex. The study of recently collected material from Afghanistan and Pakistan reveals some common but yet undescribed species (CCAC, CDA).

### *altisquamis* group

#### Diagnosis

Workers and females: *Cataglyphis* ants with the following diagnostic characters:

1. Petiole cuneiform (Fig. 10), if very low and pseudo-nodiform (Fig. 9) than  $EI > 35$  (*C. foreli*, *C. foreli* ssp. *oxianus*).
2.  $MPI < 80$ ; third maxillary palp-segment often distally thickened, clavate.
3. Body uniform black to bicoloured with gaster blackish but head and alitrunk from black to bright red or whole body yellowish-brown; body surface never shining.
4. Head sculpture finely reticulate, sometimes with punctuation on the frons.
5. Alitrunk length of large workers up to 5 mm.

Males: *Cataglyphis* ants with the following diagnostic characters:

1. Uniform black or with at least the apex of the gaster reddish or yellow.
2. Subgenital plate short ( $SPI < 125$ ); with two distal, lateral rounded processes and a median part which is variable but always present (Fig. 15).
3. Squamula caudally always projecting over the stipes, sometimes forming a distinct process pointing ventrally (Fig. 30).
4. Stipes without a basal median appendix (Fig. 30).
5. Volsella straight, broadest before midlength, distally divergent, truncated or pointed, never pediform (Fig. 50).
6. Sagitta apically with a depressed shield (Fig. 65); at least distal part of the serrated face curved laterally.

### Distribution

The *altisquamis* species-group almost replaces the *cursor* species-group in the adjacent southern and drier parts of the palaeartic. No species of one species-group is known to be found in the same habitat as any species of the other. The range of this group is from Portugal and Morocco in the west to central Asia in the East. They are not recorded from north of the Mediterranean Sea, the North African deserts, Anatolia, Iran and along the southern and eastern borders of the central asiatic deserts. The species are present in hilly terrain or along the foothills and share the patchy distribution of those particular habitats. The southernmost limit of distribution of the group is the Assir mountains in Saudi Arabia where *assirensis* has been collected at 3000 m (Collingwood, 1985).

### Comments

The taxonomy of the *altisquamis* species-group is hardly known, and only recently have some efforts been made to clear the situation (Collingwood, 1985; Tinaut, 1990; Agosti (unpublished). The male genitalia of all the species-complexes are very uniform and show only slight variation in shapes. The species complexes are based on worker morphology.

- (i) *altisquamis* complex: uniform black workers with casual reddish-black spots on the head, occasional erect hairs on the alitrunk. Distribution: Middle East and Arabian peninsula.
- (ii) *foreli* complex: workers with an EI < 35, dull, almost uniform dark reddish-black to black, petiole low and nearly nodiform. Distribution: Central Asia.
- (iii) *hispanicus* complex: workers having long erect hairs all over the body and round pits in the otherwise reticulate sculpture of the frons, dull and often uniform dark reddish black; petiole cuneiform with the caudal face concave. There is a wide range of variation in pilosity and pubescence: from entirely pilose frontal femora to very sparse short pilosity of the ventral face; from a long thick pubescence on the gaster to a sparse, sometimes partitioned pubescence. There seems to be a morphocline from east to west within the Iberian peninsula, the Sierra Nevada populations including the least pilose specimen. Distribution: Iberian peninsula and Central Asia.
- (iv) *kurdistanicus* complex: workers uniform yellowish-brown, sometimes the apex of the gaster darker; large workers with an elongate mandible but still with a row of denticles present. Distribution: Iraq.
- (v) *mauritanicus* complex: bicoloured workers with a red head and alitrunk and a black gaster, without or only with occasional erect hairs on the dorsum of the alitrunk, and at least short bristles on the ventral surface of the frontal femora; petiole always cuneiform. These species are rarely collected except *velox* (which varies in head coloration from bright red (above 1000 m altitude) to dull red (usually below 800 m) and in pilosity (Tinaut, 1990) and *mauritanicus* in northern Africa. Distribution: Lebanon mountains, North Africa, Iberian peninsula.

The biology of the ants of this species group is virtually unknown. In Tunisia they sometimes occur in the same habitats as species of the *bicolor* group (Wehner, personal communication). Observations of *altisquamis* in Suweida (Syria), showed that this species is fast-running in columns of ten and more workers.



***pallidus* group***Diagnosis*

Workers and females: *Cataglyphis* ants with the following diagnostic characters:

1. Petiole squamiform, the anterior and the posterior surface meeting at an angle but only partially forming a crest (Fig. 7).
2. MPI < 80; third segment round in cross-section; erect hairs on third segment not longer than 1.5 × maximum diameter of third segment, pilosity all over the surface.
3. Uniform coloured either yellow or a dark chestnut-brown.
4. Head smooth and shining.
5. Alitrunk length of large workers < 2 mm.

Males: *Cataglyphis* ants with the following diagnostic characters:

1. Uniform brownish-black or with a reddish or yellow gaster.
2. Subgenital plate short (SPI < 125); with two distal, lateral finger-shaped processes and a median part which is variable but always present (Fig. 14).
3. Squamula caudally always projecting over the stipes and forming a distinct, pediform process pointing ventrally (Fig. 29).
4. Volsella straight, divergent and distally pediform (Fig. 49).
5. Sagitta with a rectangular shield (Fig. 64).

*Distribution*

The *pallidus* species-group includes three species all described from the vicinity of Ashkhabad and living in the central asiatic desert and semidesert biotopes, such as the Kara Kумы. *C. emeryi* lives in the *Saxaul* desert, and *pallidus* constructs its nests in the sand dunes. A detailed study of the behaviour of the ants of the *pallidus* group has been undertaken by Dlussky (1981).

*Comments*

*Pallidus* and *emeryi* are valid species. The infraspecific taxa of *emeryi* and *pilosulus* remain doubtful as no new material is available.

***bombycinus* group***Diagnosis*

Workers and females: *Cataglyphis* ants with the following diagnostic characters:

1. Petiole squamiform, the anterior and the posterior surface laterally confluent.
2. MPI < 85; third maxillary palp segment compressed in cross-section, with long erect hairs along the margins and the outer surface, forming a part of the psammophore.
3. Uniform brownish or yellowish, sometimes rather dark and with a gaster darker than the remaining body parts; a thick, long pubescence causes the silvery appearance of the ants.
4. Head sculpture finely reticulate.
5. Alitrunk length of large workers variable, in *sabulosus* < 2.5 mm, in the remaining species up to 5 mm.
6. Mandible with more than five teeth, without the postbasal (Fig. 4); in small workers of *sabulosus* occasionally only five teeth present.

Males: *Cataglyphis* ants with the following diagnostic characters:

1. Body colour variable, yellowish to black, unicolourous to bicoloured.
2. Subgenital plate short (SPI < 125); with two distal lateral depressed processes and a median part which is variable only a cleft or a third but much shorter process (Fig. 16).
3. Squamula and stipes caudally almost confluent (Fig. 31).
4. Stipes with or without a median appendix which is confluent with the stipes.
5. Volsella straight, the sides subparallel, distally diverging and truncated (Fig. 51).
6. Sagitta with a quadrangular shield (Fig. 66); the teeth of the serrated side extended over the whole face, not curved laterally.

#### *Distribution*

The *bombycinus* species-group is distributed from western Morocco to the Sinai peninsula, at least following the northern side of the Sahara up to Sinai and down to Saudi Arabia. This species group includes the ants living in the most arid habitats, between the sand dunes of the deserts where *Aristida* spp. occur. This group is an ecological equivalent to *pallidus* from the Kara Kумы of Turkmeniya.

#### *Comments*

The species of the *bombycinus* species-group show the most elaborate dimorphism within *Cataglyphis* and a unique biology. Although they are individual foragers, they tend to leave the nest in groups soon after dawn and before dusk, and are rarely seen foraging in the heat of the day (Wehner, personal communication). The *bombycinus* species-group includes two species-complexes:

- (i) *bombycinus* complex: diagnosed by the male genitalia with a trilobed subgenital plate (Fig. 16), the presence of a median appendix of the stipes which is not separated basally by a carinae, and large (AL > 5 mm) dimorphic workers with a soldier caste with falcate mandibles (Fig. 5) and workers with always six or more teeth on the mandible. The worker castes are characterized by an astonishingly high variation in coloration and the whole *bombycinus* complex nevertheless may consist of only two species: *bombycinus* with workers with a thick, silvery pubescence on the gaster and *lucasi* with a sparse pubescence with hairs shorter than the distance between them. Distribution: deserts of North Africa and Sinai.
- (ii) *sabulosus* complex: diagnosed by the truncated lateral appendices of the subgenital plate, a large, simple, median appendix of the stipes of about half the length of the stipes and smaller, monomorphic, workers (AL < 2.5 mm), with sometimes small teeth on the mandibles which have almost been reduced to five teeth. The complex includes one species (*sabulosus*) and a second species has to be described (CCAC). Further analysis is needed to prove whether the *sabulosus* complex is the sister group of the *bombycinus* complex or of the *emmae* complex, with which it shares the long median appendix of the stipes and the truncated subgenital plate. Distribution: Sinai, Oman.

#### *emmae* group

#### *Diagnosis*

Workers and females: *Cataglyphis* ants with the following diagnostic characters:

1. Petiole squamiform, the anterior and the posterior surface meeting at an angle but only partially forming a crest (Fig. 7).

2. Third and fourth maxillary palp segments shorter than fifth and sixth together; third segment round in cross-section.
3. Uniform black to brownish-black, mainly dull surface.
4. Mandible with a large apical and subapical tooth followed by two or three denticles so that occasionally only four teeth are present.
5. Distinct dimorphism in the worker caste; alitrunk length of large workers 2.0 mm, of soldiers 2.8 mm.

Males: *Cataglyphis*-ants with the following diagnostic characters:

1. Uniform brownish-black.
2. Subgenital plate short (SPI < 125); with two distal, lateral pointed processes and a median part which is emarginate over the whole width (Fig. 17).
3. Squamula caudally always projecting over the stipes, forming a short but distinct, acute process pointing ventrally (Fig. 32).
4. Stipes with a finger-like simple median appendix with its largest diameter shorter than half the length of the stipes (Fig. 32).
5. Volsella straight, with a wider basal part up to midlength, afterwards confluent (Fig. 52).
6. Sagitta with a rectangular shield (Fig. 67); the teeth of the serrated side extended over the whole face, not curved laterally.

#### *Distribution*

The species of the *emmae* species-group are distributed south of the Atlas mountains in North Africa and have recently been discovered in Saudi Arabia (Zahran; Collingwood, 1985). A new collection is recorded here from Quetta (Baluchistan; CDA). It does not live in the plain deserts but along wadis among trees of *Acacia raddiana* and tussocks of *Panicum turgidum* (Delye, 1965). *C. emmae* is infrequently collected and further collecting will show whether there is a disjunct or a continuous distribution along the north side of the Sahara. An undescribed species from Quetta (Pakistan) lives in the steppe with occasional trees of Rosaceae and *Pistacia* spp. at 1600 m.

#### *Comments*

*C. emmae* is characterized by a small morphological variation within its distribution and by its peculiar, slow locomotion (Delye, 1965).

#### *urens* group

#### *Diagnosis*

Workers and females: *Cataglyphis* ants with the following diagnostic characters:

1. Petiole nodiform (Fig. 9).
2. MPI > 100; third segment compressed in cross-section.
3. Bicoloured with a red head and alitrunk and a black gaster, matt.
4. Propodeum raised, PI > 300 (Fig. 12).
5. Alitrunk length of large workers < 5.5 mm.

Males: *Cataglyphis* ants with the following diagnostic characters:

1. Uniform black or with a reddish or yellowish apex of the gaster.

2. Subgenital plate short (SPI < 125); with two distal, lateral rounded processes pointing laterally and a median part which is bipartite (Fig. 18).
3. Stipes with a median appendix with a modified topology; the longest diameter never longer than half the length of the stipes (Fig. 33).
4. Volsella curved, distally truncated (Fig. 53).
5. Sagitta without an apicomedian appendix which is overlapping the outline of the sagitta, seen in lateral view; serrated face curved with the denticles anterior of the turning-point (Fig. 68).

#### *Distribution*

The *urens* species-group is distributed in Oman and southern Saudi Arabia in sandy deserts (Collingwood, 1985).

#### *Comments*

The *urens* complex is monotypic and is the sister-group of all *bombycinus* group + *albicans* group + *nigripes* group. *C. urens* lives in the plain sandy deserts (Collingwood, 1985), in this it differs from all the other bicoloured species of the *bicolor* group. The very strongly raised propodeum is also found in a yet undescribed black species from Saudi Arabia (BMNH, CCAC) of which the males are unknown.

#### ***nigripes* group**

#### *Diagnosis*

Workers and females: *Cataglyphis* ants with the following diagnostic characters:

1. Petiole nodiform (Fig. 9).
2. MPI > 90; third segment compressed in cross-section.
3. Bicoloured with a red head and alitrunk and a black gaster, matt.
4. FI > 160.
5. Alitrunk length of large workers < 5.0 mm.
6. Erect hairs on the body black.

Males: *Cataglyphis* ants with the following diagnostic characters:

1. Uniform black or with a reddish or yellow gaster.
2. Subgenital plate short (SPI < 125); with two distal, lateral, short rounded processes and a median part which is medially deeply emarginate (Fig. 19).
3. Squamula caudally not projecting over the stipes (Fig. 34).
4. Stipes with a simple, median appendix with its largest diameter shorter than half the length of the stipes (Fig. 34).
5. Volsella curved, distally truncated (Fig. 54).
6. Sagitta with a large apical tooth and a prominent, blunt medioapical appendix (Fig. 69).

#### *Distribution*

The *nigripes* species-group is monotypic and the single species is distributed in northwestern Iran up to 1500 m in semideserts and in the foothills of the Transcaucasus (Arnoldi, 1964).

#### ***bicolor* group**

#### *Diagnosis*

Workers and females: *Cataglyphis* ants with the following diagnostic characters:

1. Petiole nodiform, in lateral view rounded dorsally (Fig. 9). In locomotion with the gaster bent dorsally, forming an acute angle between the ventral surface of the gaster and a line spanned between the anteriormost and posteriormost point of the alitrunk (Fig. 3).
2. MPI > 90; third segment compressed in cross-section, with long erect hairs on the margins and the outer surface.
3. Uniform black to bicoloured, with head and parts or entire alitrunk red and gaster black, surface dull or shining.
4. Head finely reticulate sculptured.
5. Striking monophasic variation in body size of workers; alitrunk length of large workers < 5 mm, of small workers < 2 mm.
6. Petiole of female nodiform as in workers.

Males: *Cataglyphis* ants with the following diagnostic characters:

1. Uniform black to complete yellow body, whereby the three bands on the dorsum of the alitrunk are only weakly present.
2. Subgenital plate long (SPI > 125); with two distal, lateral, finger-shaped processes and a median part which is also finger-shaped but variable in length (Figs 20–24).
3. Squamula and stipes caudally always confluent (Figs 35–39).
4. Stipes with a large median appendix with a modified topology, its largest diameter is about half the length of the stipes or less (Figs 35–39).
5. Volsella curved, distally truncated or acute (Figs 55–59).
6. Sagitta with a medioapical appendix; the serrated face always developed and a row of teeth present; the median carinae leading to the medioapical appendix (Figs 70–74).

### *Distribution*

The distribution of the *bicolor* species-group is almost identical with that of the whole genus; it is not present in the Iberian peninsula, the northwestern Mediterranean or southern Italy. It is also absent from the higher altitudes of the mountains (almost always occurring below 1500 m) and in desert habitats. The distribution map given by Wehner *et al.* (1983) for *bicolor* includes references to all the bicoloured species of the *bicolor* species-group, including some doubtful unconfirmed records from the Iberian peninsula, but not those of the *niger* complex. The ants of the *bicolor* species-group can be active at temperatures of 45°C but then it is always near trees or shrubs, e.g. on the edges of the oases or wadis. Most of the species are to be found in open spots in the Mediterranean and steppe habitats of North Africa and the Middle East, or along roads and on the beach in the tropics (Côte d'Ivoire and southern India). An exceptional range of behaviour is shown by the *diehlii* complex with *isis*, which can be found foraging in full sunshine in Chotts of the Middle East or in the deserts north of Basrah (Iraq) and *diehlii*, living in stony deserts at higher altitudes of North Africa (Wehner, 1986).

### *Comments*

The *bicolor* species-group includes the very obvious, large, generally red–black bicoloured ants in the southwestern parts of the palaeartic, which run individually in full sunshine in open spots. Workers have been extensively collected and are present in all ant collections. The first description dates from 1787 and since then many new names have been added. The workers are rather variable and most of the characters are

number of hairs, shape of petiole or colour, which have rarely been assessed but in which the ranges of variation seem to be overlapping between the individual species. Nevertheless, large samples might provide information on the variation of populations and the distribution of particular characters, such as the coloration (Wehner *et al.*, 1983, map 2) or the variation of the shape of the petiole (Wehner, 1983) and so lead to a better understanding and diagnosis of species. Analysis of the secretions of the mandibular and the Dufour's gland within the *bicolor* species-group support the existing morphologically based system (Morgan *et al.*, 1990, and personal communication).

Our current understanding of the *bicolor* species-group is based on male genitalia characters. The proposed system allows at least the recognition of the following species-complexes but more detailed studies are needed to investigate the limits of the male genitalia characters at species level (Agosti, unpublished). In due course it will be possible to discover the identity and variation of the characters of the workers from series with associated males. *C. lunaticus*, known only from two workers, is included in this species-group, as the characters mentioned, such as relative length of the maxillary palp segments, structure of the proventriculus, presence of a particular setae pattern on the hypopygium, fall within the limits of variation of the *bicolor* species-group presented here (Agosti, unpublished). The nocturnal habit, inferred from the yellowish colour, which would make this species unique within the genus (Urbani, 1969), is rather doubtful as the yellow species of the *lividus* species-complex are among the most heliophilous species and more material from Anatolia with rather uniform red-yellowish workers and females is available in CCAC, CDA and BMNH.

The following species-complexes are either diagnosed by characters based on workers or in their absence by male genitalia characters. At least in the latter, a species-complex might be a species. As not all males are known, the proposed species-complexes might be arbitrary.

The species-complexes are diagnosable as follows:

- (i) *abyssinicus* complex: monotypic with bicoloured workers with a low and elongate petiole. Males unknown. Distribution: southern Arabian peninsula, Ethiopia.
- (ii) *bicolor* complex: bicoloured workers which have apressed white to yellow pubescence on the hind tibiae; the male genitalia with the stipes in lateral view convergent (Fig. 44) and with subequal distal appendices of the subgenital plate, a curved serrated face of the sagitta (Fig. 71) and its pointed median appendix. Distribution: North Africa to Côte d'Ivoire, eastern limit probably Libya.
- (iii) *diehlii* complex: male genitalia having the stipes in lateral view apically subparallel (Fig. 43) and with a z-shaped sagitta (Fig. 70), the same as in the *niger* complex but with smaller large worker (AL < 4 mm; AL < 5 mm in the *niger* complex), and a shorter first funiculus segment (FI < 150; FI > 160), the workers are jet black, bicoloured to bright yellow (undescribed species from Oman, CCAC) often variable in behaviour and coloration within the same locality. Distribution: Middle East, including the Arabian peninsula and North Africa, usually on hard dry soils or in chotts.
- (iv) *niger* complex: dark red to black workers, sometimes with a dark red patch on head and pronotum (see also above); petiole anterodorsally flattened; male genitalia with the stipes in lateral view subparallel (Fig. 45) and with a curved serrated face of the sagitta and a blunt median appendage (Fig. 72). Distribution: Egypt and Middle East, Saudi Arabia.

- (v) *nodus* complex: male genitalia having the stipes convergent (Fig. 46) and with three distal appendices of the subgenital plate which are of equal length, a straight serrated face of the sagitta and an apically rounded median appendix of the sagitta (Fig. 73); workers bicoloured and large (AL < 5 mm). Distribution: in the steppe habitats of eastern Europe, Greece, Anatolia and Caucasus to the Kopet dag, Turkmeniya, southern India (Cape Comorin, BMNH).
- (vi) *setipes* complex: males with subequal distal processes of the subgenital plate with the median shortest (Fig. 24), a parallel sided, elongate stipes (Fig. 47) in lateral view, smoothly curved serrated face of the sagitta and a short, apically rounded median appendix of the sagitta (Fig. 74); large workers large (AL < 5 mm); bicoloured with thick, bristle-like black pubescence on the hind tibiae. Distribution: Morocco and Ghana to Central Asia and the Ganges river.

### *albicans* group

#### Diagnosis

Workers and females: *Cataglyphis* ants with the following diagnostic characters:

1. Petiole nodiform, with the anterior dorsal face plane; in lateral view the dorsal outline is angled (Fig. 8). During locomotion the gaster is bent backwards, forming almost a right or blunt angle between the ventral surface of the gaster and a line spanned between the anteriormost and posteriormost point of the alitrunk (Fig. 2).
2. MPI > 90; third segment of the maxillary palps compressed in cross-section (with the exception of *cinnamomeus*) with the fourth segment of the same length or shorter than the fifth and the sixth together.
3. Uniform black and shining to bright yellow and shining, sometimes bicoloured with the gaster darker than the remaining parts of the body.
4. Fringe of hairs on the margins of the propodeum.
5. Alitrunk length of large workers up to 3.2 mm, rather uniform in size.
6. Females with a high scale-like petiole.

Males: *Cataglyphis* ants with the following diagnostic characters:

1. Uniform black to bicoloured with a reddish alitrunk and a darker gaster.
2. Subgenital plate long (SPI > 125); the apex variable, from two distal, lateral processes and a median part which is variable but always present to a truncated apex which is in cross-section a simple plate with the lateral parts bent dorsally (Figs 25–27).
3. Squamula caudally always projecting over the stipes, sometimes forming a distinct process pointing ventrally (Figs 40–42).
4. Stipes without a median appendix, at most indicated by a minute bulge.
5. Volsella curved, distally convergent and pointed (Figs 60–62).
6. Sagitta elongated apically (Figs 75–77) or not, but then the anteromedian appendix and the anterior teeth very prominent (Fig. 75); the dorsocranial appendix wide and truncated (Figs 75–77); the ventral (serrated) surface toothless.

#### Distribution

The *albicans* species-group is distributed from Spain through North Africa and the Middle East to the northern territories of Pakistan, from Bulgaria to the Sudan and the southern Arabian peninsula. Ecologically, the *albicans* and the *bicolor* species-groups are similar but the former is to be found in hotter places (especially ants of the *lividus*

complex) and higher up in the Karakorum. Analogous to *diehlii* in the *bicolor* species-group there is *fortis* in the *albicans* groups, which lives in Chotts of northern Africa.

### Comments

Within the *albicans* species-group is a cline from uniform black to reddish and bright yellow body colour, which corresponds to some extent with a temperature gradient, the brightest yellow to be found in the hottest sand deserts.

Four species complexes are differentiated, of which only the males of the *albicans* and the *fortis* complex are known. The proposed grouping into a *fortis* and an *albicans* complex, based on male genitalia characters, is tentative because the Iberian *albicans* and some of the bicoloured Middle Eastern forms fall within the *fortis* complex rather than the *albicans* complex centred around the North African *albicans* (Tinaut and Plaza, 1989; Agosti, unpublished; see also *albicans*, note 1; Wehner, 1983 and Martinez, 1987).

The four arbitrary species-complexes, based on worker characters, are diagnosed by the following characters:

- (i) *albicans* complex: workers with black to bright red or orange head and alitrunk, gaster in bicoloured species always distinctly darker, large workers up to AL = 3.2 mm, MPI > 90, second funicular segment much shorter than previous (FI > 150); if nearly uniform yellowish then SI < 110 (> 110 in *lividus*) and CI < 96 (> 96). Distribution: over the whole range of the *albicans* species-group except the southernmost parts in deserts and semidesert habitats.
- (ii) *cinnamomeus* complex: workers brownish black, shining with MPI < 90 and FI > 150. Distribution: from the Crimea through Central Asia to Baluchistan.
- (iii) *fortis* complex: jet black workers, AL < 3.6 mm, the second funiculus segment slightly longer than the previous (FI < 130). Distribution: Chotts of North Africa.
- (iv) *lividus* complex: uniform, bright yellow species, AL < 3 mm, FI < 150. Distribution: from Morocco to the Indus river including the Arabian peninsula, in semideserts to deserts.

### Catalogue of the available names in *Cataglyphis*

#### *Cataglyphis cursor* group

##### *Cataglyphis aenescens* (Nylander)

*Formica aenescens* Nylander, 1849: 37. Syntypes workers, females, males, USSR (Rossia meridionale), ZMH [examined]. [Later changes: *Tapinoma aenescens*, F. Smith, 1858: 56; Synonymized with *Cataglyphis cursor*, Mayr, 1861: 45; *Myrmecocystus aenescens*, Emery and Forel, 1879: 449; *Myrmecocystus cursor* ssp. *aenescens*, Emery, 1906: 48; *Cataglyphis cursor* ssp. *aenescens*, Wheeler & Mann, 1916: 173; *Cataglyphis cursor* st. *aenescens*, Santschi, 1921b: 116; *Myrmecocystus (Cataglyphis) cursor* ssp. *aenescens*, Karavaiev, 1924: 301; *Cataglyphis (Cataglyphis) cursor* ssp. *aenescens*, Emery, 1925: 263; *Cataglyphis (Monocombus) cursor* st. *aenescens*, Santschi, 1929a: 35; *Cataglyphis aenescens*, Pisarski, 1967: 416.] (Biology: Karavajev, 1924: 301; description of male and female: Karavajev, 1924: 302.)  
*Myrmecocystus cursor* var. *caspius* Ruzsky, 1903a: 470. Syntypes workers, females, males, USSR (Lake Aral, Kysil-djar, 26 May 1901, leg. L. Berg). [Synonymy by Emery, 1906: 174.]

##### *Cataglyphis aenescens* ssp. *chatkalensis* Tarbinskii

*Cataglyphis aenescens* ssp. *chatkalensis* Tarbinskii, 1976: 202. Holotype female, USSR (Kirgizia, Tyan' Shan', Chatkalskaya Dolina, ur. Ak-Kul', 13 June 1968, leg. Tarbinskii; Paratype 3 females, 8 workers, same locality).

##### *Cataglyphis aenescens* ssp. *georgicus* Arnoldi

*Cataglyphis (Monocombus) aenescens* ssp. *georgica* Arnoldi, 1968: 1816. Holotype male, USSR (East



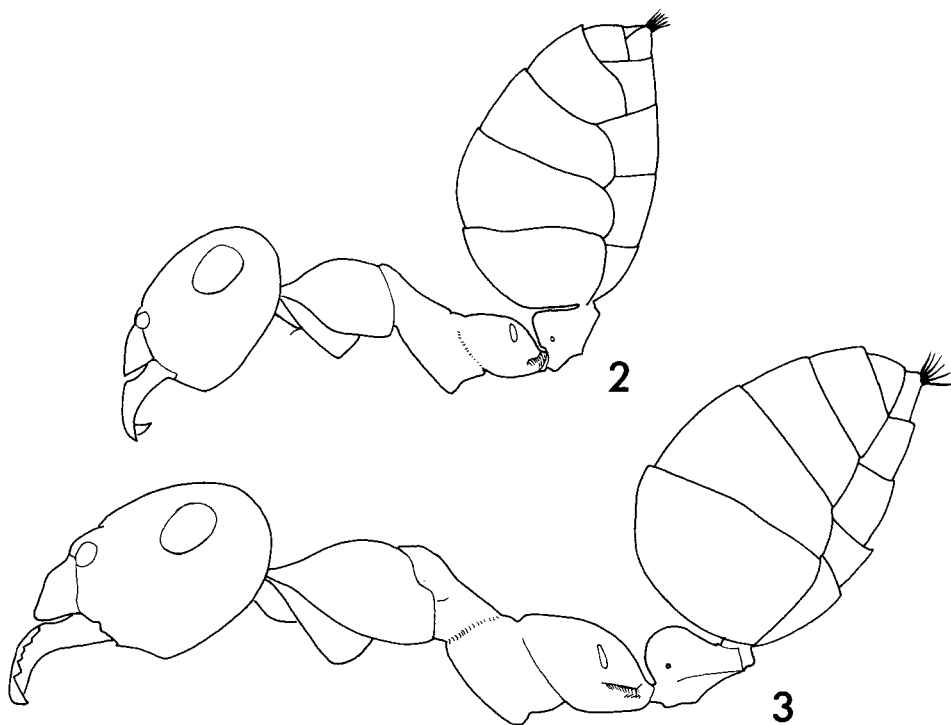


FIG. 2, 3. Lateral view of *Cataglyphis* spp. with raised gaster in locomotion. 2: *C. albicans* with the gaster raised to almost a right angle to the longitudinal axis of the alitrunk; 3: *C. nodus* with the gaster never at more than an acute angle to the longitudinal axis of the alitrunk.

Georgia, Magaro, 26 May 1961, leg. Shshilashwili, No. 533), ZIL; paratypes 8 males, 15 workers from the same nest; 1 paratype female from sample No. 520, same date and locality.).

*Cataglyphis aenescens* ssp. *jakobsoni* (Ruzsky)

*Myrmecocystus altisquamis* var. *jakobsoni* Ruzsky, 1905: 436. Syntypes workers, USSR (Turkestan). [Later changes: *Cataglyphis (Cataglyphis) cursor* ssp. *jakobsoni*, Emery, 1925: 264; *Cataglyphis (Monocombus) cursor* st. *jackobsoni* [misspelling], Santschi, 1929a: 58; *Cataglyphis cursor* ssp. *jakobsoni* [misspelling], Stärke, 1935: 269; *Cataglyphis aenescens* ssp. *jakobsoni* [misspelling], Pisarski, 1967: 417.]

*Cataglyphis aenescens* ssp. *tancrei* (Forel)

*Myrmecocystus cursor* r. *tancrei* Forel, 1901: 66. Syntypes workers, Sinkiang (Kashgar Darja, Maralbaschi, leg. Tancre, 6 December 1894), MHNG [examined]. [Later changes: *Myrmecocystus cursor* r. *tancrei*, Forel, 1904: 383; *Myrmecocystus cursor* ssp. *tancrei*, Ruzsky, 1905: 445; *Myrmecocystus (Cataglyphis) cursor* ssp. *tancrei*, Karavajev, 1924: 301; *Cataglyphis (Cataglyphis) cursor* ssp. *aenescens* var. *tancrei*, Emery, 1925: 263 [name not available]; *Cataglyphis (Monocombus) aenescens* var. *tancrei*, Santschi, 1929a: 58; *Cataglyphis aenescens* ssp. *tancrei*, Tarbinskii, 1976: 201.] (Description of male: Forel, 1904: 383.)

*Cataglyphis cugiai* Menozzi

*Cataglyphis (Monocombus) cugiai* Menozzi, 1939: 323, figs 13–15. Syntypes worker, female, India (Karakorum, Paju, 3500–3600 m, in oasis with *Salix* sp. and *Tamarix* sp.).

*Cataglyphis cursor* (Fonscolombe)

*Formica cursor* Fonscolombe, 1846: 41. Syntypes workers, males, females, France (Aix-en-Provence, leg. Fonscolombe). [Later changes: *Cataglyphis cursor*, Mayr, 1861: 45; *Myrmecocystus cursor*, Emery and Forel, 1879: 449; *Myrmecocystus cursor* ssp. *cursor*, Emery, 1906: 48; *Cataglyphis cursor*, Emery, 1914: 2; *Myrmecocystus (Cataglyphis) cursor*, Karavaiev, 1924: 301; *Cataglyphis (Cataglyphis) cursor*, Emery 1925: 263; *Cataglyphis (Monocombus) cursor*, Santschi, 1929a: 29].

*Cataglyphis cursor* ssp. *aterrimus* Pisarski

*Cataglyphis cursor* ssp. *aterrima*, Pisarski, 1967: 417. Syntypes workers, USSR (Fergana district, 8 July 1914, leg. Zvartsesky). [*Myrmecocystus* (*Cataglyphis*) *cursor* ssp. *aenescens* var. *aterrima* Karavaiev, 1916: 507; *Myrmecocystus* (*Cataglyphis*) *cursor* ssp. *aenescens* var. *aterrima*, Karavaiev, 1924: 304; *Cataglyphis* (*Monocombus*) *cursor* st. *aenescens* var. *aterrima* Santschi, 1929a: 53; names not available.]

*Cataglyphis cursor* var. *creticus* (Forel)

*Myrmecocystus cursor* var. *cretica* Forel, 1910: 23. Syntypes workers, male, Greece (Crete, Candia), MHNG [examined]. [*Myrmecocystus cursor* ssp. *hellenicus* var. *cretica* Emery, 1906: 174; *Cataglyphis cursor* ssp. *hellenica* var. *cretica*, Emery, 1925: 264; names not available.]

*Cataglyphis cursor* ssp. *rockingeri* (Forel)

*Myrmecocystus* (*Cataglyphis*) *cursor* ssp. *rockingeri* Forel, 1911a: 287. Syntypes workers, USSR (Tianshan, left Illi river bank, leg. Rockinger), MHNG [examined]. [Later changes: *Cataglyphis* (*Cataglyphis*) *cursor* ssp. *rockingeri*, Emery, 1925: 264; *Cataglyphis* (*Monocombus*) *cursor* st. *rockingeri*, Santschi, 1929a: 36; *Cataglyphis aenescens* ssp. *rockingeri*, Pisarski, 1969: 315.]

*Cataglyphis frigidus* (E. André)

*Myrmecocystus cursor* var. *frigidus* E. André 1881: 59. Syntypes workers, Syria (Bloudan) MHNG, MNHP [examined]. [Later changes: *Myrmecocystus frigidus*, Emery, 1906: 49; *Cataglyphis* (*Cataglyphis*) *frigida*, Emery, 1925: 264; *Cataglyphis* (*Monocombus*) *frigidus*, Santschi, 1929a: 29.] (Description of female, male, male genitalia, larval stages and biology: Thomé and Thomé, 1985: 84, figs 1–12.)

*Cataglyphis frigidus* ssp. *persicus* (Emery)

*Myrmecocystus frigida* var. *persica* Emery, 1906: 50. Syntypes workers, Iran (Sciraz?). [Later changes: *Cataglyphis* (*Cataglyphis*) *frigida* var. *persica*, Emery, 1925: 264; *Cataglyphis* (*Monocombus*) *frigida* var. *persica*, Santschi, 1929a: 53.]

*Cataglyphis hellenicus* (Forel)

*Myrmecocystus cursor* var. *hellenicus* Forel, 1886b: 204. Syntypes workers, Greece (Elide, Pyrgos, leg. M. von Oertzen), MHNG [examined]. [Later changes: *Myrmecocystus cursor* ssp. *hellenicus*, Emery, 1906: 48; *Cataglyphis* (*Cataglyphis*) *cursor* ssp. *hellenica*, Emery, 1925: 263; *Cataglyphis* (*Monocombus*) *cursor* st. *hellenica*, Santschi, 1929a: 35; *Cataglyphis hellenicus*, Agosti and Collingwood, 1987a: 59.]

*Cataglyphis italicus* (Emery)

*Myrmecocystus cursor* ssp. *italica* Emery, 1906: 48. Syntypes workers, Italy (Foggia, Lecce), MHNG, MSNG [examined]. [Later changes: *Cataglyphis cursor* ssp. *italicus*, Emery, 1914: 2; *Cataglyphis* (*Cataglyphis*) *cursor* ssp. *italica*, Emery, 1925: 264; *Cataglyphis* (*Monocombus*) *cursor* st. *italica*, Santschi, 1929a: 54; *Cataglyphis italicus*, Agosti and Collingwood, 1987b: 285.] (Description of female and male: Emery, 1914: 3; male genitalia: Emery, 1914: fig. 1.)

*Cataglyphis piliscapus* (Forel)

*Myrmecocystus cursor* var. *piliscapa* Forel, 1901: 66. Syntypes workers, France (Nîmes, leg. Forel), MHNG, NHMB [examined]. [Later changes: *Cataglyphis* (*Monocombus*) *cursor* st. *piliscapa*, Santschi, 1929a: 36; *Cataglyphis piliscapa*, Agosti and Collingwood, 1987b: 285.] (Descriptions: male, Santschi, 1929a: 36; biology: Cagniant, 1976, 1979.)

*Cataglyphis tibialis* Bondroit, 1918: 39. Syntypes workers, France (East Pyrenees, Banyuls, Taurinya). [Later change: *Cataglyphis cursor* var. *tibialis*, Santschi, 1925: 355.] [Synonymy by Santschi, 1929a: 36.]

Note. *Cataglyphis cursor*, Collingwood (1978: 73) is a misidentification and is either *C. piliscapus* or a yet undescribed species (Espadaler, personal communication). Cagniant's studies (1976, 1979) of the biology of *C. cursor* are studies of *C. piliscapus* (see Cagniant, 1979: 52).

*Cataglyphis altisquamis* group*Cataglyphis altisquamis* (E. André)

*Myrmecocystus altisquamis* E. André, 1881: 56. Syntypes workers, Syria (Antiliban; M. Abeille de Perrin), MNHP [examined]. [Later changes: *Myrmecocystus altisquamis* ssp. *altisquamis*, Emery, 1906: 56; *Cataglyphis* (*Cataglyphis*) *altisquamis*, Emery, 1925: 264; *Cataglyphis* (*Monocombus*) *altisquamis*, Santschi, 1929a: 34.] (Description of female: Forel, 1890b: xvii, misidentification.)

*Cataglyphis altisquamis* var. *bucharicus* Emery

*Cataglyphis* (*Cataglyphis*) *altisquamis* var. *bucharica* Emery, 1925: 264. Syntype workers, USSR (Buchar),

MHNG [examined]. [Later changes: *Cataglyphis altisquamis* var. *bucharica* Santschi, 1929a: 60. *Cataglyphis altisquamis* ssp. *bucharica*, Pisarski, 1967: 418.] [*Myrmecocystus altisquamis* r. *foreli* var. *bucharica*, Forel, 1904: 383, name not available.]

*Cataglyphis asiriensis* Collingwood

*Cataglyphis asiriensis* Collingwood, 1985: 286. Holotype and paratypes workers, Saudi Arabia (Sawdah mountain, 3000 m, 9 April 1983, leg. Collingwood), NHMB, CCAC [examined].

*Cataglyphis foreli* (Ruzsky)

*Myrmecocystus foreli* Ruzsky, 1903b: 36. Syntypes females, USSR (Turkmeniya: Kazandzhik, July 1902, leg. Arnoldov; Kizyl-Arvat, 29 April 1902, leg. Semenov; Ashkhabad, 5 May 1889, leg. Semenov and July 1902, leg. Arnoldov; Giauars, 2 May 1889, leg. Semenov; Uzh-adzhi, 18 May 1889, leg. Semenov.), CDA, MHNG [examined]. [Later changes: *Myrmecocystus altisquamis* r. *foreli*, Forel, 1904: 382; *Myrmecocystus altisquamis* ssp. *foreli*, Ruzsky, 1905: 437; *Cataglyphis* (*Cataglyphis*) *foreli*, Emery, 1925: 266; *Cataglyphis* (*Monocombus*) *foreli*, Santschi, 1929a: 29; *Cataglyphis foreli* ssp. *foreli*, Arnoldi, 1964: 1812.] (Description of male genitalia: Arnoldi, 1964: 1812, fig. 11.)

*Cataglyphis foreli* ssp. *murgabicus* Arnoldi

*Cataglyphis foreli* ssp. *murgabicus* Arnoldi, 1964: 1814. Holotype worker USSR (Turkmeniya, Imambaba, April 1912, Koshanzhikov), ZIL [examined]. Paratypes workers, same series.

*Cataglyphis foreli* ssp. *oxianus* Arnoldi

*Cataglyphis foreli* ssp. *oxianus* Arnoldi, 1964: 1813, figs 13, 14. Holotype worker, USSR (Turkmeniya, deserts of east Turkmeniya, Karakumy, 7 May 1911, leg. Golbek) ZIL [examined].

*Cataglyphis foreli* ssp. *piligerus* Arnoldi

*Cataglyphis foreli* ssp. *piligerus* Arnoldi, 1964: 1813. Holotype worker, USSR (Uzbekistan, Bukhara river, Mubarek, 1963, leg. Dlussky), paratypes same series, ZIL [examined].

*Cataglyphis gaetulus* Santschi

*Cataglyphis* (*Monocombus*) *gaetula* Santschi, 1929a: 33, figs 20, 22, 29. Syntypes workers, females, males, Morocco (Bir Rechid, leg. Thiéry), NHMB [examined].

*Cataglyphis gaetulus* var. *pilisquamis* Santschi

*Cataglyphis* (*Monocombus*) *gaetulus* var. *pilisquamis* Santschi, 1929a: 34. Syntypes workers, Morocco (Oued Isli; leg. Dr A. Nadig) [no syntypes in NHMB].

*Cataglyphis gracilens* Santschi

*Cataglyphis gracilens* Santschi, 1929a: 65. Syntypes workers, USSR (Zacaspiskaya obl. Dort-Kuyo?, 19. May 1889, Semenov) [no syntypes in NHMB]. [*Myrmecocystus altisquamis* ssp. *foreli* var. *gracilens* Ruzsky, 1905: 439; *Cataglyphis* (*Cataglyphis*) *cursor* ssp. *jakobsoni* var. *gracilens*, Emery, 1925: 264; names not available.]

*Cataglyphis hispanicus* (Emery)

*Myrmecocystus viaticus* ssp. *hispanicus* Emery, 1906: 57. Syntypes workers, Spain (Bejar, leg. M. E. Saunders), MHNG [examined]. [Later changes: *Myrmecocystus viaticus* var. *hispanicus*, Stitz, 1917: 348; *Cataglyphis viaticus* ssp. *hispanicus*, Menozzi, 1922: 332; *Cataglyphis* (*Cataglyphis*) *viatica* ssp. *hispanicus*, Emery, 1925: 266; *Cataglyphis* (*Monocombus*) *hispanicus*, Santschi, 1929a: 29.] [*Myrmecocystus viaticus* ssp. *niger* var. *hispanica* Forel, 1903: 267, name not available.]

*Cataglyphis hispanicus* var. *nigroides* Santschi

*Cataglyphis* (*Monocombus*) *hispanica* var. *nigroides* Santschi, 1929a: 59 (diagnosis in key). Syntypes workers, Portugal (S. Fiel leg. Wasmann), NHMB [examined]. [*Cataglyphis viaticus* st. *hispanicus* var. *nigroides*, Santschi, 1925: 346, name not available and nomen nudum.]

*Cataglyphis kurdistanicus* Pisarski

*Cataglyphis kurdistanicus* Pisarski, 1965: 417, figs 1–10. Holotype workers, Iraq (Salahaddin, No. 2875, 21 April 1961, leg. A. Riedel), IZPAN; Paratypes 17 workers of the same series. (Biology: Pisarski, 1965.)

*Cataglyphis mauritanicus* (Emery) nov. stat.

*Myrmecocystus viaticus* ssp. *mauritanicus* Emery, 1906: 56, figs 23 and 24 (worker), 57, figs 25 and 36 (male). Syntypes workers, males, Algeria, Morocco, Tunisia, MHNG, CDA [examined] [see note 1 below]. [Later changes: *Cataglyphis* (*Cataglyphis*) *viatica* ssp. *mauritanicus*, Emery, 1925: 266; *Cataglyphis* (*Monocombus*) *mauritanica*, Santschi, 1929a: 29; *Cataglyphis* (*Monocombus*) *viaticus* st. *mauritanica*, Santschi, 1929a: 31.] (Description of female: Santschi, 1929a: 31, fig. 23.)

Note 1. *Cataglyphis mauritanicus* is the oldest available name in the *Cataglyphis mauritanicus* species-complex and is therefore raised to species level.

*Cataglyphis viaticus* var. *tonsilis* Santschi

*Cataglyphis (Monocombus) viaticus* var. *tonsilis* Santschi, 1936: 209. Syntypes workers, females, males, Morocco (Ksar-el-Kbir near Zarjouka, 1901, leg. Bucket) NHMB, MNHP [examined]. [*Cataglyphis (Monocombus) viaticus* st. *mauritanica* var. *tonsilis* Santschi, 1929a: 32, fig. 21, name not available.]

*Cataglyphis viaticus* var. *velox* Santschi

*Cataglyphis (Monocombus) viatica* var. *velox* Santschi, 1929a: 30, figs 6, 34. Syntypes workers, Spain (Sevilla; De la Fuente and Dusmet), NHMB [examined]. [*Myrmecocystus viaticus*, Emery, 1908: 216; *Cataglyphis viaticus*, Santschi, 1929a: 29, 54; misidentifications.]

***Cataglyphis pallidus* group**

*Cataglyphis emeryi* (Karavaiev)

*Myrmecocystus emeryi* Karavaiev, 1909a: 34. Syntypes workers, USSR (Turkmeniya, Ashkhabad, Borodin, 1907, leg. Karavaiev, No. 1714), males and females (same locality, 1908, 30 April 1908, leg. Karavaiev), CDA, MHNG, ZMK [examined]. [Later changes: *Cataglyphis (Cataglyphis) emeryi*, Emery, 1925: 264; *Cataglyphis (Monocombus) emeryi*, Santschi, 1929a: 30.] (Biology: Karavaiev, 1909a: 37.)

*Cataglyphis emeryi* var. *abdominalis* Santschi

*Cataglyphis (Monocombus) emeryi* var. *abdominalis* Santschi, 1929a: 37. Syntypes workers, USSR (Turkmeniya, Ashkhabad, leg. Karavaiev.). [No syntypes available in NHMB.]

*Cataglyphis emeryi* st. *karawaiewi* Santschi

*Cataglyphis karawaiewi* Santschi, 1925: 354. Syntypes workers, USSR (Turkmeniya, Ashkhabad, leg. Karavaiev). NHMB [examined]. [Later change: *Cataglyphis (Monocombus) emeryi* st. *karawaiewi*, Santschi, 1929a: 37.]

*Cataglyphis pallidus* Mayr

*Cataglyphis pallida* Mayr, 1877: 9. Syntypes workers, males, USSR (Turkestan, Kysylkum) [re-described in Mayr, 1880: 28, translation of Mayr, 1877], MHNG [examined]. [Later changes: *Myrmecocystus pallidus*, André, 1882: 170; *Cataglyphis (Monocombus) pallida*, Santschi, 1929a: 53.] [*Myrmecocystus pallidus*, Forel, 1886a: 3 [misidentification = *C. hellenicus*; Forel, 1886b: 204].] (Biology: Karavaiev, 1909a and Dlussky, 1981.)

*Cataglyphis pilosulus* Kusnetzov-Ugamskij

*Cataglyphis pilosulus* Kusnetzov-Ugamskij, 1926: 71, figs 1–5. Syntypes workers, USSR (Turkestan: Ashkhabad, 25 April 1923; Bagir near Ashkhabad, 27 April 1923). [Later change: *Cataglyphis (Monocombus) emeryi* st. *karawaiewi* var. *pilosulus*, Santschi, 1929a: 37, name not available.]

***Cataglyphis bombycinus* group**

*Cataglyphis bombycinus* (Roger)

*Formica bombycina* Roger, 1859: 232. Syntypes workers, females, males, Egypt, Lybia, Sudan (Red Sea, Nubia, legs. Schaum, Ehrenberg, Sichel). [Later changes: *Cataglyphis bombycina*, Mayr, 1862: 701; *Myrmecocystus bombycinus*, Emery, 1891: 17; *Cataglyphis bombycina*, Wheeler and Mann, 1916: 173; *Cataglyphis (Machaeromyrma) bombycina*, Forel, 1916: 441; *Cataglyphis bombycina*, Menozzi, 1927a: 381; *Cataglyphis (Machaeromyrma) bombycina*, Santschi, 1929a: 30; *Cataglyphis bombycina*, Menozzi, 1932: 95.] (Description of male genitalia: Karavaiev, 1912a: 18.)

*Camponotus phaenogaster* Walker, 1871: 10. Syntypes workers, Egypt [no types to be found in the Walker collection, BMNH]. Syn. nov.

*Cataglyphis bombycinus* var. *bruneipes* (Santschi)

*Myrmecocystus (Cataglyphis) bombycinus* var. *bruneipes* Santschi, 1911: 287. Syntypes workers, Tunisia (Tozeur, 1908), MHNG, NHMB [examined]. [Later change: *Cataglyphis (Machaeromyrma) bombycina* var. *brunneipes*, Emery, 1925: 267.]

*Cataglyphis bombycinus* var. *sinaiticus* Wheeler and Mann

*Cataglyphis bombycina* var. *sinaítica* Wheeler and Mann, 1916: 173. Syntypes workers, Egypt (Wady Gazelle, Sinai), MCZ [not seen]. [Later change: *Cataglyphis (Machaeromyrma) bombycina* var. *sinaítica*, Emery, 1925: 267.]

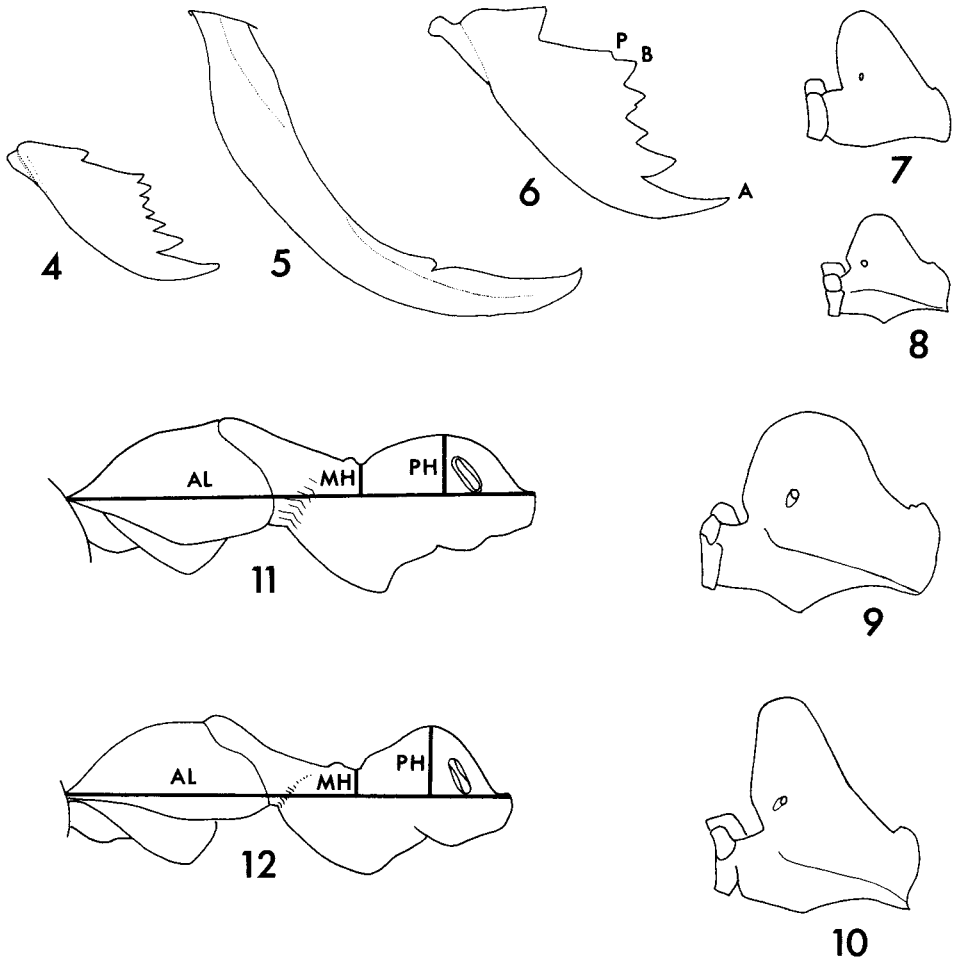


FIG. 4-12. 4: Mandible of a small worker of *C. bombycinus*; 5: falcate mandible of a large worker of *C. bombycinus*; 6: mandible of a worker of *C. nodus* A = apical tooth, B = basal tooth, P = postbasal tooth; 7: lateral view of the petiole of a worker of *C. aenescens*; 8: same of *C. ruber*; 9: same of *C. nodus*; 10: same of *C. altisquamis*; 11: lateral view of the alitrunk of *C. nodus*, AL = alitrunk length, MH = metanotum height; PH = propodeum height; 12: same of *C. urens*.

*Cataglyphis lucasi* (Emery)

*Myrmecocystus lucasi* Emery, 1898: 147. Holotype worker, Tunisia (el Asseli; leg. Hippolyte Lucas), MHNG [examined]. [Later changes: *Cataglyphis (Cataglyphis) lucasi*, Emery, 1925: 266; *Cataglyphis (Machaeromyrmex) lucasi*, Santschi, 1929a: 30.] (Descriptions: male, Emery, 1906: 60; biology: Bernard, 1948: 164.)

*Myrmecocystus lameerei* Forel, 1902a: 156. Syntypes workers, females, Algeria (Du Souf, entre Tougourt et El Oued, au bord de Maouiet-al-Caid, leg. Lameer). [Synonymy proposed by Emery in Forel, 1902b: 463.]

*Cataglyphis sabulosus* Kugler

*Cataglyphis sabulosa* Kugler, 1981: 84, figs 1-13. Holotype male, Israel (Ashdod, southern coastal plain, 26 May 1981, leg. J. Kugler); 1 allotype female and 38 paratypes workers, same series, TAU, BMNH [examined].

***Cataglyphis emmae* group***Cataglyphis emmae* (Forel)

*Formica* (*Proformica*) *emmae* Forel, 1909: 381. Syntypes worker, Algeria (dunes and hot springs of Biskra, leg. A. and E. Forel), MHNG [examined]. [Later changes: *Formica* (*Paraformica*) *emmae*, Forel, 1915: 95; *Cataglyphis* (*Paraformica*) *emmae*, Santschi, 1929a: 30; *Cataglyphis emmae*, Collingwood, 1985: 288.] (Descriptions: female and male, Delye, 1965: 52, figs 1–10; biology, Delye, 1965.)

*Cataglyphis emmae* var. *hoggarensis* Santschi

*Cataglyphis* (*Paraformica*) *emmae* var. *hoggarensis* Santschi, 1929a: 53 (footnote; description in Santschi, 1929b: 106; also described as new in Santschi, 1934b: 174). Syntypes 2 workers, Algeria (Hoggar, Tamanrasset, February 1928, leg. de Peyerimhoff), NHMB [examined].

***Cataglyphis nigripes* group***Cataglyphis nigripes* Arnoldi nov. stat.

*Cataglyphis setipes* ssp. *nigripes* Arnoldi, 1964: 1806. Syntypes workers, USSR (Georgia, Tiflis, leg. Mejunof), ZIL [examined]. [*Cataglyphis bicolor* st. *setipes* var. *nigripes*, Santschi, 1929a: 50, name not available.] (Description of male and male genitalia: Arnoldi, 1964: 1806, fig. 6.)

***Cataglyphis urens* group***Cataglyphis urens* Collingwood

*Cataglyphis urens* Collingwood, 1985: 290, fig. 15. Syntypes workers, males, Oman (Muscat, leg. Maindron) NHMB, MNHP [examined]. [*Cataglyphis* (*Cataglyphis*) *bicolor* st. *abyssinica* var. *urens*, Santschi, 1929a: 52, name not available.]

***Cataglyphis bicolor* group***Cataglyphis abyssinicus* (Forel)

*Myrmecocystus viaticus* r. *abyssinicus* Forel, 1904: 382. Syntypes workers, females, Ethiopia (Ingfal, leg. Kachovskii), MHNG [examined]. [Later changes: *Myrmecocystus bicolor* ssp. *bicolor* var. *abyssinicus*, Emery, 1908: 217, name not available; *Cataglyphis viaticus* ssp. *abyssinicus*, Wheeler, 1922: 944; *Cataglyphis* (*Cataglyphis*) *bicolor* var. *abyssinica*, Emery, 1925: 265; *Cataglyphis* (*Cataglyphis*) *bicolor* st. *abyssinica*, Santschi, 1929a: 51; *Cataglyphis bicolor* ssp. *abyssinica*, Menozzi, 1931: 155; *Cataglyphis abyssinica*, Collingwood, 1985: 284.]

*Cataglyphis adenensis* (Forel)

*Myrmecocystus viaticus* r. *adenensis* Forel, 1904: 382 (footnote). Syntypes workers, South Yemen (Aden, leg. Ris), MHNG [examined]. [Later changes: *Myrmecocystus bicolor* ssp. *adenensis*, Emery, 1906: 58; *Myrmecocystus viaticus* ssp. *adenensis*, Forel, 1907: 15; *Cataglyphis viaticus* ssp. *adenensis*, Wheeler, 1922: 944; *Cataglyphis* (*Cataglyphis*) *bicolor* ssp. *adenensis*, Emery, 1925: 265; *Cataglyphis* (*Cataglyphis*) *adenensis*, Santschi, 1929a: 41. *Cataglyphis adenensis*, Collingwood, 1985: 284.]

*Cataglyphis adenensis* var. *bugnioni* Santschi

*Cataglyphis adenensis* var. *bugnioni* Santschi, 1929a: 41. Holotype worker, Egypt (Suez, leg. Buginion), MHNG, MHMB [examined]. [*Cataglyphis viaticus* r. *adenensis* var. *bugnioni*, Forel, 1908a: 16; *Cataglyphis* (*Cataglyphis*) *bicolor* ssp. *adenensis* var. *bugnioni*, Emery, 1925: 265; *Cataglyphis adenensis* st. *livida* var. *bugnioni*, Santschi, 1929a: 55; names not available.]

*Cataglyphis bicolor* (Fabricius)

*Formica bicolor* Fabricius, 1793: 356. Syntypes males, North Africa (Barbary, leg. Desfontaines (Wheeler, 1922: 944)) [no types known to exist] [see note 1 below]. [Later changes: Synonymized with *Formica viatica*, F. Smith, 1861: 32; *Cataglyphis viatica*, Mayr, 1863: 402; re-erected as *Myrmecocystus bicolor*, Emery and Forel, 1879: 449; *Myrmecocystus bicolor* ssp. *bicolor*, Emery, 1906: 58; *Myrmecocystus viaticus* ssp. *bicolor*, Forel, 1907: 15; *Myrmecocystus bicolor*, Karavaiev, 1912b: 590; *Cataglyphis bicolor*, Emery, 1915: 22; *Cataglyphis viatica* ssp. *bicolor*, Wheeler and Mann, 1916: 173; *Myrmecocystus viaticus* r. *bicolor*, Stitz, 1917: 348; *Cataglyphis viaticus* ssp. *bicolor*, Wheeler, 1922: 944; *Myrmecocystus* (*Cataglyphis*) *bicolor*, Karavaiev, 1924: 306, *Cataglyphis* (*Cataglyphis*) *bicolor*, Emery, 1925: 264; *Cataglyphis bicolor*, Menozzi, 1927a: 380; *Cataglyphis* (*Cataglyphis*) *bicolor*, Santschi, 1929a: 41.]

*Formica megalocola* Foerster, 1850: 490. Syntype worker, Algeria [no types known to exist]. [Later changes:

Synonymy by Mayr, 1855: 382; re-erected as *Myrmecocystus viaticus* var. *megalocola*, Emery and Forel, 1879: 449; *Myrmecocystus viaticus* r. *megalocola*, Forel, 1890a: 7; *Myrmecocystus viaticus* var. *megalocola*, Forel, 1892: 306; *Myrmecocystus megalocola*, Dalla Torre, 1893: 217; *Myrmecocystus bicolor* ssp. *megalocola*, Emery, 1906: 58; *Myrmecocystus viaticus* ssp. *megalocola*, Forel, 1907: 15; *Cataglyphis (Cataglyphis) bicolor* ssp. *megalocola*, Emery, 1925: 265; Synonymy confirmed by Santschi, 1929a: 41.] (Descriptions of female and male: Emery, 1891: 16.) [See note 2 below.]

*Cataglyphis fairmairei* Foerster, 1850: 494. Syntypes males, Algeria [no types known to exist] [see note 3 below]. [Later change: As synonym of *Cataglyphis viaticus*, Smith, 1861: 32.] [Synonymy by Santschi, 1929a: 55.]

*Myrmecocystus albicans* ssp. *rotundinodis* Karavaiev, 1912a: 16. Syntype worker, Algeria (Oran). [Later change: *Cataglyphis (Cataglyphis) albicans* ssp. *rotundinodis*, Emery, 1925: 262.] [Synonymy by Santschi, 1929a: 41.]

Note 1. Zimsen (1964) could not find specimens labelled *Formica bicolor* in the Fabricius collection, and he supposed that the types should be in the collection of René Louriche Desfontaine, in the MNHP in Paris, but no such types could be found there.

Note 2. The types of *megalocolus* could not be found in the Foerster collection ZMHB (Koch, personal communication). Forel (1890a: 4, 9; also 1890b: 67) describes this race as a rather constant, scarlet form with a distribution on the Tell (eastern part of the Atlas mountains) being smaller than the reddish-black *viaticus* s. str. with a further southern distribution, to the oasis where he could not record *megalocolus*. Whereas *viaticus* builds nests at the edge of the palm forests in rocky soil, *megalocolus* excavates its nest in the grassland. This observation is confirmed by Wehner *et al.* (1983: map 2) where they mention a light and a dark form of *bicolor* in Tunisia. Emery (1891: 16) also described the male of *megalocolus* smaller than the male of *viaticus*, but doubted whether this male was correctly identified as *megalocolus*.

Note 3. The types of *fairmairei* could not be found in the Foerster Collection ZMHB (Koch, personal communication).

*Cataglyphis bicolor* var. *adustus* Santschi

*Cataglyphis bicolor* var. *adusta* Santschi, 1929a: 43. Syntypes workers, female, male, Tunisia (Djebel Trozza, 1000 m, leg. Kutter and Santschi), NHMB [examined].

*Cataglyphis bicolor* var. *basalis* Santschi

*Cataglyphis bicolor* var. *basalis* Santschi, 1929a: 42. Syntypes workers, females, males, Algeria (Duvivier, leg. Alluaud), Tunisia (Le Kef, leg. Normand), NHMB [examined].

*Cataglyphis bicolor* ssp. *bellicosus* (Karavaiev)

*Myrmecocystus (Cataglyphis) bicolor* ssp. *bellicosus* Karavaiev, 1924: 307. Syntypes workers, Iran (4 km south of Teheran, 23 September 1916, leg. Bocquillon, in quarry). [*Cataglyphis (Cataglyphis) bicolor* st. *setipes* var. *bellicosa*, Santschi, 1929a: 49, name not available.] (Biology: Karavaiev, 1924: 308.)

*Cataglyphis bicolor* var. *congolensis* Stütz

*Cataglyphis bicolor* var. *congolensis* Stütz, 1916: 396, fig. 10. Syntypes workers, Chad (Fort Archambault, 10 February 1911, leg. Schubotz). [Later changes: *Cataglyphis viaticus* ssp. *bicolor* var. *congolensis*, Wheeler, 1922: 945; *Cataglyphis (Cataglyphis) bicolor* st. *abyssinica* var. *congolensis*, Santschi, 1929a: 52; names not available.]

*Cataglyphis bicolor* var. *oasium* Menozzi

*Cataglyphis bicolor* var. *oasium* Menozzi, 1931: 95. Syntypes workers, females, males, Tunisia (Tozzeur, May 1909, leg. Santschi and Dumont). [Later change: *Cataglyphis (Cataglyphis) bicolor* st. *nodus* var. *oasium*, Menozzi, 1932: 95, name not available.] [*Cataglyphis bicolor* st. *nodus* var. *oasium*, Santschi, 1929a: 46, name not available.]

*Cataglyphis bicolor* st. *protuberatus* Crawley

*Cataglyphis bicolor* var. *protuberata* Crawley, 1920: 177. Syntypes workers, Iraq (Al Amarah = Amara?, 1918, leg. Buxton) [see note below]. [Later changes: *Cataglyphis bicolor* ssp. *protuberata*, Emery, 1925: 266; *Cataglyphis (Cataglyphis) bicolor* st. *protuberata*, Santschi, 1929a: 53.]

Note. In the Forel collection (MHNG) is one worker from 'NO-Perse' labelled as cotype; it is a worker of *isis* with the two small lateral processes of the mesonotum, which also occasionally occur in other species of the *bicolor* species-group.

*Cataglyphis bicolor* var. *pubens* Santschi

*Cataglyphis (Cataglyphis) bicolor* var. *pubens* Santschi, 1929a: 43. Syntypes workers, males, Morocco (Tangier, leg. Vaucher), NHMB [examined].

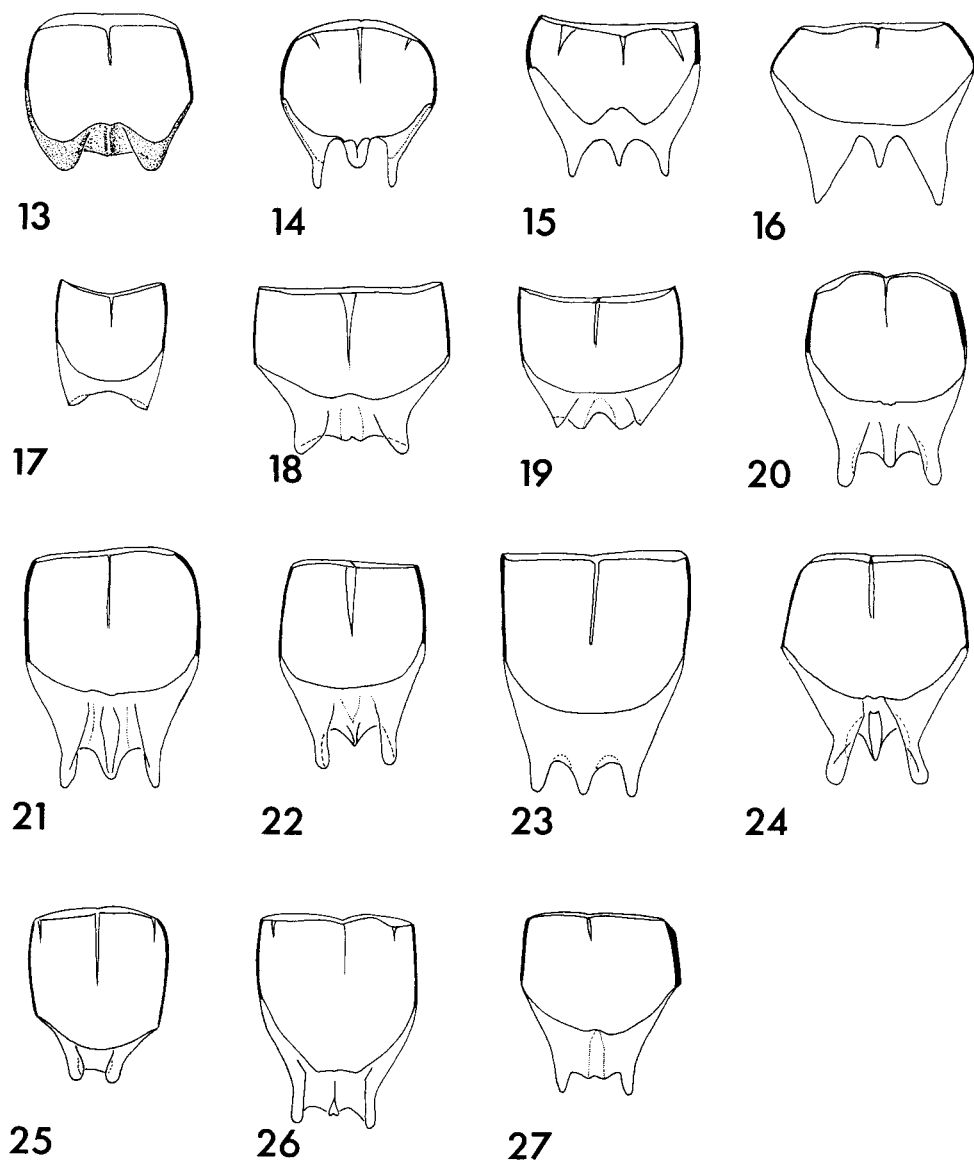


FIG. 13–27. Dorsal view of the subgenital plate. The apical or caudal part is sclerotized (shaded in fig. 13). 13: *C. cursor*; 14: *C. emeryi*; 15: *C. altisquamis*; 16: *C. bombycinus*; 17: *C. emmae*; 18: *C. urens*; 19: *C. nigripes*; 20: *C. diehlii*; 21: *C. bicolor* group sp. (dark from from Touggourt, Tunisia); 22: *C. niger*; 23: *C. nodus*; 24: *C. setipes*; 25: *C. viaticoides*; 26: *C. fortis*; 27: *C. ibericus*.

*Cataglyphis bicolor* var. *rufiventris* Emery

*Cataglyphis* (*Cataglyphis*) *bicolor* var. *rufiventris* Emery, 1925: 265. Syntypes workers, females, Greece (Corfu, leg. Dr Vejas), Bulgaria (Bazardjik and Stanimaka), MHNG [examined]. [*Myrmecocystus* (*Cataglyphis*) *viaticus* ssp. *orientalis* var. *rufiventris*, Forel, 1911b: 353; *Cataglyphis bicolor* st. *orientalis* var. *rufiventris*, Santschi, 1921b: 116; *Cataglyphis bicolor* st. *nodus* var. *rufiventris*, Santschi, 1929a: 44; names not available.]



*Cataglyphis bicolor* st. *seticornis* (Emery)

*Myrmecocystus viaticus* ssp. *seticornis* Emery, 1898: 149 [footnote]. Syntypes workers, Cote d'Ivoire (leg. Staudinger and Bang-Haas). [Later changes: *Myrmecocystus bicolor* ssp. *seticornis*, Emery, 1906: 58; *Cataglyphis viaticus* ssp. *setipes* var. *congolensis*, Wheeler, 1922: 945, name not available; *Cataglyphis* (*Cataglyphis*) *bicolor* ssp. *seticornis*, Emery, 1925: 266; *Cataglyphis* (*Cataglyphis*) *bicolor* st. *seticornis*, Santschi, 1929a: 47.]

*Cataglyphis bicolor* var. *sudanicus* (Karavaiev)

*Myrmecocystus bicolor* var. *sudanica* Karavaiev, 1912b: 590. Syntypes workers, males, Sudan (Khartum, Port Sudan). [Later change: *Cataglyphis* (*Cataglyphis*) *bicolor* var. *sudanica*, Emery, 1925: 265.] [*Cataglyphis bicolor* st. *abyssinica* var. *sudanica*, Santschi, 1929a: 56, name not available.] (Description of male genitalia: Karavaiev, 1912b: 591, fig. 2.)

*Cataglyphis diehlii* (Forel)

*Myrmecocystus viaticus* var. *diehlii* Forel, 1902a: 462. Syntypes workers, Algeria (Biskra, leg. Escherich) [Often misspelled as *diehli*.], MHNG, NHMB [examined]. [Later changes: *Myrmecocystus viaticus* r. *diehlii*, Forel, 1902b: 462; *Myrmecocystus bicolor* ssp. *diehli*, Emery, 1906: 58; *Myrmecocystus viaticus* ssp. *diehlii*, Forel, 1907: 15; *Myrmecocystus bicolor* ssp. *diehlii*, Karavaiev, 1912a: 17; *Cataglyphis* (*Cataglyphis*) *bicolor* ssp. *diehli*, Emery, 1925: 265; *Cataglyphis* (*Cataglyphis*) *bicolor* st. *diehli*, Santschi, 1929a: 51; *Cataglyphis diehlii*, Collingwood, 1985: 287.] [*Myrmecocystus viaticus* r. *desertorum* var. *diehlii*, Forel, 1902a: 156, name not available.] (Descriptions: female and male, Forel, 1902b: 462, 1909: 385; male genitalia, Wehner, 1986: 110, fig. 2B; biology, Forel, 1902b: 462, 1909: 385.)

*Cataglyphis indicus* Pisarski

*Cataglyphis indicus* Pisarski, 1961: 515, figs 1–3. Holotype worker, India (Matheran, 800 m, 1902, leg. L. Biro) IZPAN; 10 paratypes from the same series MNB; 5 paratypes of the same series IZPAN.

*Cataglyphis isis* (Forel)

*Myrmecocystus* (*Cataglyphis*) *diehlii* var. *isis* Forel, 1913: 434. Syntypes workers, Egypt (Suez, leg. Bugnion), MHNG [examined]. [Later changes: *Cataglyphis diehli* ssp. *isis*, Pisarski, 1967: 421. *Cataglyphis isis*, Collingwood, 1985: 288.] [*Myrmecocystus viaticus* ssp. *diehlii* var. *isis*, Forel, 1909: 385; *Cataglyphis* (*Cataglyphis*) *bicolor* ssp. *diehli* var. *isis*, Emery, 1925: 265; *Cataglyphis* (*Cataglyphis*) *bicolor* st. *nigra* var. *isis*, Santschi, 1929a: 50; names not available.]

*Cataglyphis laevior* Emery

*Cataglyphis* (*Cataglyphis*) *bicolor* var. *laevior* Emery, 1925: 265. Syntypes 5 workers, Algeria (SE-Algeria, 21 February 1913, leg. v. Geyr). [Later changes: *Cataglyphis* (*Cataglyphis*) *bicolor* st. *laevior*, Santschi, 1929a: 47; *Cataglyphis laevior*, Collingwood, 1985: 288.] [*Myrmecocystus viaticus* r. *bicolor* var. *laevior*, Stitz, 1917: 348, name not available.]

*Cataglyphis lunaticus* Urbani

*Cataglyphis lunatica* Urbani, 1969: 213. Holotype worker, Turkey (Egridir, vil. Isparta, 1100 m, 11 July 1967, P. Brignoli leg.) INER; Paratype 1 worker, same series, INER.

*Cataglyphis niger* (E. André)

*Myrmecocystus viaticus* var. *niger* E. André, 1881: 56. Syntypes workers, Israel (Jaffa), MNHP [examined]. [Later changes: *Myrmecocystus niger*, Forel, 1894: 402; *Myrmecocystus viaticus* ssp. *niger*, Emery, 1898: 126; *Myrmecocystus viaticus* ssp. *niger*, Forel, 1907: 15; *Myrmecocystus* (*Cataglyphis*) *viaticus* r. *niger*, Forel, 1913: 434; *Cataglyphis* (*Cataglyphis*) *bicolor* var. *nigra*, Emery, 1925: 265; *Cataglyphis bicolor* var. *nigra*, Menozzi, 1927a: 380; *Cataglyphis* (*Cataglyphis*) *bicolor* st. *nigra*, Santschi, 1929a: 50; *Cataglyphis* (*Cataglyphis*) *bicolor* var. *nigra*, Menozzi, 1933: 86; *Cataglyphis niger*, Collingwood, 1985: 290.] (Description of female: Forel, 1913: 434.)

*Cataglyphis nodus* (Brullé)

*Formica nodus* Brullé, 1832: 326. Syntype males, Greece (Peloponnese (Morée)). [Later changes: as synonym of *viaticus*, Mayr, 1861: 44; *Cataglyphis* (*Cataglyphis*) *bicolor* var. *nodus*, Emery, 1925: 265; *Cataglyphis bicolor* var. *nodus*, Menozzi, 1927b: 119; *Cataglyphis* (*Cataglyphis*) *bicolor* st. *nodus*, Santschi, 1929a: 43; *Cataglyphis* (*Cataglyphis*) *bicolor* var. *nodus*, Menozzi, 1933: 86; as synonym of *bicolor*, Wehner *et al.*, 1983: 7; *Cataglyphis nodus*, Arnoldi, 1964: 1802.] [= *Cataglyphis viaticus*, Zalesky, 1939: 239; *Cataglyphis viaticus*, Petrov, 1986: 11; misidentification.]

*Myrmecocystus viaticus* var. *orientalis* Forel, 1895: 228. Syntype worker, East Europe, MHNG [examined]. [Later changes: *Myrmecocystus viaticus* ssp. *orientalis*, Forel, 1907: 15; *Cataglyphis bicolor* st. *orientalis*, Santschi, 1921b: 116.] [Synonymy by Santschi, 1929a: 43.]

*Cataglyphis nodus* ssp. *caucasicolus* Arnoldi

*Cataglyphis nodus* ssp. *caucasicola* Arnoldi, 1964: 1803, figs 1a, 2. Holotype worker, USSR (Georgia, Tiflis, leg. Arnoldi); Androtype same locality; ZIL [examined].

*Cataglyphis nodus* ssp. *mesasiasticus* Arnoldi

*Cataglyphis nodus* ssp. *mesasiatica* Arnoldi, 1964: 1803, figs 1b, 3. Holotype worker, USSR (Turkmeniya, Kopet-Dag, Zhuly, 1935, leg. Arnoldi); Androtype same locality; ZIL [examined].

*Cataglyphis saharae* Santschi

*Cataglyphis (Cataglyphis) bicolor* st. *saharae* Santschi, 1929a: 48, fig. 3. Syntypes workers, Algeria (El Golea; Surcouf), NHMB [examined]. [Later change: *Cataglyphis saharae*, Collingwood, 1985: 291.]

*Cataglyphis savignyi* (Dufour)

*Formica savignyi* Dufour, 1862: 141. Lectotype male, Egypt (leg. Dufour) [here designated.] [Fig. 1. pl. 20 (male), fig. 2, pl. 20 in Savigny, 1826.] [see note below.], MNHP [examined]. [Later changes: = *Cataglyphis viaticus*, Synonymy by Emery and Forel, 1879: 449; *Cataglyphis (Cataglyphis) bicolor* st. *nodus* var. *savignyi*, Santschi, 1929a: 45, name unavailable; *Cataglyphis savignyi*, Billen, 1989: 301.]

Note. In the Dufour collection (MHNP) are two groups of specimens with *savignyi* labels, one with two damaged workers from Gizeh and a second with one damaged male (with dissected genitalia in an attached vial on the same pin) and one worker from North Africa. The workers belong to the *mauritanicus* complex of the *altisquamis* species-group and the male to the *niger* complex of the *bicolor* species-group. Since the male genitalia seem to show the characters of the greatest phylogenetic significance the male is chosen as lectotype.

Billen (1989) used *savignyi* as a specific name in a publication on morphology of the cloacal gland without further explanation. A final placement of the voucher specimen is difficult as the range of variation of all the species of the *bicolor* species-group is not known yet. The analysis of the chemical compounds of the Dufour's gland shows a different pattern from those of *niger* and an as yet unidentified species of the *nodus* complex (Morgan *et al.*, personal communication).

*Cataglyphis setipes* (Forel)

*Myrmecocystus viaticus* r. *setipes* Forel, 1894: 401. Syntypes workers, India (Nusseerabad, Rajpootana, leg. Glardon; Rai Bareli, leg. Simpson; Pachmarhi (Jubulpore), 1200 m, leg. Schurr), MHNG, CDA [examined]. [Later changes: *Myrmecocystus setipes*, Bingham, 1903: 312; *Myrmecocystus bicolor* ssp. *setipes*, Ruzsky, 1905: 430; *Myrmecocystus viaticus* ssp. *setipes*, Forel, 1907: 15; *Cataglyphis bicolor* ssp. *setipes*, Wheeler, 1922: 945; *Cataglyphis (Cataglyphis) bicolor* ssp. *seticornis*, Emery, 1925: 266; *Cataglyphis (Cataglyphis) bicolor* st. *setipes*, Santschi, 1929a: 49; *Cataglyphis setipes*, Collingwood, 1960: 65.]

*Cataglyphis setipes* ssp. *bergianus* Arnoldi

*Cataglyphis setipes* ssp. *bergiana* Arnoldi, 1964: 1805. Holotype workers, USSR (Kazakhstan, Kara Tau, Stanziya Mashat, leg. Berg.), ZIL [examined].

*Cataglyphis setipes* ssp. *dschambulicus* Tarbinskii

*Cataglyphis setipes* ssp. *dschambulica* Tarbinskii, 1976: 200. Holotype worker, USSR (Kirgizia, kolkhos 'Dzhambul', river Chu, 18 April 1961, leg. Protsenko); Paratypes 9 workers, same locality).

*Cataglyphis setipes* ssp. *karakalensis* Arnoldi

*Cataglyphis setipes* ssp. *karakalensis* Arnoldi, 1964: 1805, fig. 5. Holotype worker, USSR (Turkmeniya, Kara-Kala, leg. Arnoldi); androtype (same locality, 1952, leg. Kryshanovsky); ZIL [examined].

*Cataglyphis turcomanicus* (Emery)

*Myrmecocystus viaticus* var. *turcomanica* Emery, 1898: 126. Syntypes workers, USSR (Samarkand, Merw, leg. Shalberg), MHNG [examined]. [Later changes: *Cataglyphis bicolor* var. *turcomanica*, Crawley, 1920: 177. *Cataglyphis* ssp. *turcomanica*, Arnoldi, 1964: 1804.) [ *Cataglyphis (Cataglyphis) bicolor* ssp. *setipes* var. *turcomanica*, Emery, 1925: 266; *Cataglyphis (Cataglyphis) bicolor* st. *setipes* var. *turcomanica*, Santschi, 1929a: 49; names not available.] (Description of male: Karavaiev, 1912b: 591, Arnoldi, 1964: 1805.)

*Formica longipedum* Eichwald, 1841: 224. Syntypes workers USSR ('In arenosis Krasnowodskiensibus'). [Synonymy by Kolossov, 1932: 118.]

*Cataglyphis viaticus* (Fabricius)

*Formica viatica* Fabricius, 1787: 308. Lectotype worker (here designated), Spain (M. Vohl) ZMUC [examined; see note below]. [Later changes: *Monocombus viaticus*, Mayr, 1855: 382; *Cataglyphis viatica*, Mayr, 1861: 45; *Myrmecocystus viatica*, Emery and Forel, 1879: 449; *Myrmecocystus viaticus*, André, 1882: 167; *Cataglyphis viaticus*, Santschi, 1919: 246; *Cataglyphis (Cataglyphis) viatica*,

Emery, 1925: 266; *Cataglyphis (Monocombus) viatica*, Santschi, 1929: 29.] (Descriptions of female and male: Mayr, 1861: 45.) [*Cataglyphis viaticus*, Zalesky, 1939: 239 = *Cataglyphis nodus*? [misidentification].]

*Formica cephalotes* ssp. *europaea* Christ, 1791: 511. [Synonymy by Emery, 1892: 161.]

*Myrmecocystus viaticus* var. *desertorum* Forel, 1894: 402. Syntypes workers, Tunisia (Gabès) [no types in MHNG]. [Later changes: *Myrmecocystus viaticus* ssp. *desertorum*, Emery, 1898: 126; *Myrmecocystus viaticus* r. *desertorum*, Forel, 1902: 156; *Myrmecocystus viaticus* var. *desertorum*, Forel, 1904: 381; as synonym of *Myrmecocystus viaticus* ssp. *bicolor*, Forel, 1907: 15; re-erected as var.: *Myrmecocystus bicolor* var. *desertorum*, Karavaiev, 1912a: 17; *Myrmecocystus (Cataglyphis) bicolor* ssp. *desertorum*, Karavaiev, 1924: 306; *Cataglyphis (Cataglyphis) bicolor* st. *nodus* var. *desertorum*, Santschi, 1929a: 45, name unavailable; *Cataglyphis desertorum*, Collingwood, 1985: 286.] (Descriptions: female, Karavaiev, 1924: 306; male, Karavaiev, 1912a: 17; Santschi, 1929a: 46.) Synonymy reconfirmed.

Note. In the original description 'inmaculato petiolo nodo unico' (Fabricius, 1787: 308) indicates that this species probably belongs to the *bicolor* group.

In the Fabricius collection (ZMUC), three specimens are conserved under the name *viatica*. Two are badly damaged, but can be diagnosed as *viatica* by their maxillary palps and the nodiform petiole respectively. A third specimen is labelled *viatica*, Mus: S: & L: T, L [corresponding to Sehestedt and Tonder Lund Museum (Zimsen, 1964; Petersen, personal communication)] and Vohl, and represents the holotype. Martin Vohl was a Danish botanist, who gave Fabricius insects from North Africa and Spain. Unfortunately, the material was often not labelled appropriately and the localities have thus been confused (Zimsen, 1964; Petersen, personal communication). The choice of Spain as the type-locality (Forel, 1895: 228) was therefore arbitrary, and could as easily have been North Africa. The latter seems to be more reasonable because, as yet, no ants of the *bicolor* group have been recorded in Spain. Forel's decision has been disastrous, as ever since all records of *viaticus* and most of *bicolor* are misidentifications until Tinaut (1990) correctly pointed this out.

The examination of the holotype revealed that it does not belong to the *altisquamis* group as assumed by earlier authors (e.g. Emery, 1925; Santschi, 1929a; Arnoldi, 1968) but to the *bicolor* group. Characters to place this species are:

1. Maxillary palp-segments 3 and 4 elongated, MI > 90.
2. Petiole nodiform.

Apart from the placement within the *bicolor* group no synonymy with other species can be established yet.

#### *Cataglyphis albicans* group

##### *Cataglyphis alibabae* Pisarski

*Cataglyphis alibabae*, Pisarski, 1965: 419, figs 11–14. Holotype worker, Iraq (Khanaqin, No. 2865, 3 April 1961, leg. A. Riedel) IZPAN. Paratypes 8 workers of the same series, 1 worker Iraq (Al Fatha ad Djebel Hamrin (desert side), 15 April 1961, leg. A. Riedel) IZPAN. (Biology: Pisarski, 1965.)

##### *Cataglyphis albicans* (Roger)

*Formica albicans* Roger, 1859: 235. Syntype workers, North Africa [no types to be found]. [Later changes: *Cataglyphis albicans*, Mayr, 1862: 701; *Myrmecocystus viaticus* r. *albicans*, Emery and Forel, 1879: 449; *Myrmecocystus albicans*, Emery, 1891: 17; *Myrmecocystus albicans* ssp. *albicans*, Emery, 1906: 51; *Myrmecocystus albicans*, Karavaiev, 1911: 10; *Cataglyphis albicans*, Santschi, 1912: 149; *Cataglyphis albicans*, Santschi, 1919: 246; *Myrmecocystus (Cataglyphis) albicans*, Karavaiev, 1924: 305; *Cataglyphis (Cataglyphis) albicans*, Emery, 1925: 262; *Cataglyphis albicans*, Collingwood and Yarrow, 1969: 85.] [= *Myrmecocystus pallida*, Saunders, 1890: 202, misidentification.]

Forel (1890b: 67) mentioned two varieties, 'noire' and 'rougeatre' without giving further descriptions.

Male genital characters indicate that at least two species must be included under the current *albicans*: the type population from North Africa and the Iberian population, which differ in the sagitta and subgenital plate, the Iberian *albicans* sharing those characters with *fortis* of the same species-group (see drawings in Martinez, 1987: 128). Tinaut and Plaza (1989) propose, therefore, that *albicans* should be restricted to the North African species and that *ibericus* should be the name used for the Iberian species.

##### *Cataglyphis albicans* ssp. *armenus* Arnoldi

*Cataglyphis albicans* ssp. *armena* Arnoldi, 1964: 1808, figs 7, 8. Holotype worker, USSR (Armenia, Karabakh); androtype workers (same nest), ZIL [examined].

##### *Cataglyphis albicans* var. *auratus* Menozzi

*Cataglyphis albicans* var. *aurata* Menozzi, 1932: 95. Syntypes workers, Sudan (Omdurman near Khartum (#1916), Port Sudan (#1925, 1933, leg. Karavaiev), MHNG [examined]). [*Myrmecocystus albicans* ssp. *lividus* var. *auratus*, Karavaiev, 1911: 10, name not available: also senior synonym of

*Myrmecocystus albicans* ssp. *lividus* var. *arenaria*, Karavaiev, 1924: 306; *Cataglyphis* (*Cataglyphis*) *albicans* ssp. *livida* var. *aurata*, Emery, 1925: 262; *Cataglyphis albicans* ssp. *livida* var. *aurata*, Menozzi, 1927a: 380; *Cataglyphis* (*Cataglyphis*) *albicans* st. *livida* var. *aurata*, Santschi, 1929a: 55; names not available.] (Description of female: Menozzi, 1927a: 380.)

*Cataglyphis albicans* r. *cubicus* (Forel)

*Myrmecocystus albicans* r. *cubicus* Forel, 1903: 267. Syntypes workers, females, Morocco (Tangier, leg. A. Müller), MHNG [examined]. [Later change: *Cataglyphis* (*Cataglyphis*) *albicans* st. *cubica*, Santschi, 1929a: 55.] [*Myrmecocystus* (*Cataglyphis*) *albicans* ssp. *ruber* var. *cubica*, Karavaiev, 1924: 305; *Cataglyphis* (*Cataglyphis*) *albicans* ssp. *rubra* var. *cubica*, Emery, 1925: 263; *Cataglyphis* (*Cataglyphis*) *albicans* st. *rubra* var. *cubica*, Santschi, 1929a: 39; names not available.]

*Cataglyphis albicans* var. *fezzanensis* Bernard

*Cataglyphis albicans* var. *fezzanensis* Bernard, 1948: 163. Syntypes workers, females, males, Libya (Fezzân, El Abiod, leg. Bernard; Sebha and Oubâri, leg. Bernard), MNHP [examined].

*Cataglyphis albicans* ssp. *franchettii* Menozzi

*Cataglyphis albicans* ssp. *franchettii* Menozzi, 1931: 155, fig. in text. Holotype worker, Ethiopia (Dancalia, leg. Barone Franchetti).

*Cataglyphis albicans* var. *kairuanus* Santschi

*Cataglyphis albicans* var. *kairuana* Santschi, 1912: 149. Syntypes workers, Tunisia (central Tunisia), NHMB [examined]. [Later change: *Cataglyphis* (*Cataglyphis*) *albicans* var. *kairuana*, Emery, 1925: 262.]

*Cataglyphis albicans* var. *mixtus* (Forel) comb. nov.

*Myrmecocystus albicans* var. *mixtus* Forel, 1895: 229. Syntypes workers, Turkey (Edirne), MHNG [examined]. [Later changes: *Cataglyphis* (*Cataglyphis*) *albicans* ssp. *viaticoides* var. *mixta*, Emery, 1925: 263; *Cataglyphis* (*Cataglyphis*) *albicans* st. *livida* var. *mixta*, Santschi, 1929a: 55; names not available.]

*Cataglyphis albicans* var. *opacus* Santschi

*Cataglyphis albicans* var. *opaca* Santschi, 1912: 149. Syntypes workers, Tunisia and Algeria, MHNB [examined]. [Later changes: *Cataglyphis* (*Cataglyphis*) *albicans* var. *opaca*, Emery, 1925: 262; *Cataglyphis albicans* var. *opaca*, Menozzi, 1927a: 380; *Cataglyphis* (*Cataglyphis*) *albicans* var. *opaca*, Santschi, 1929a: 54.]

*Cataglyphis albicans* var. *targuius* Santschi

*Cataglyphis* (*Cataglyphis*) *albicans* var. *targuia* Santschi, 1929a: 55 (footnote; description in Santschi, 1929b: 106, fig. 8; also described as new in Santschi, 1934b: 175). Syntypes workers, Algeria (Hoggar, Tiguedaoui, 2700 m, February 1928, leg. de Peyerimhoff), MHNB [examined].

*Cataglyphis albicans* var. *vaucheri* (Emery)

*Myrmecocystus albicans* ssp. *vaucheri* Emery, 1906: 54. Syntypes workers, Morocco (Essaouira (= Mogador), leg. Vaucher), MHNG [examined]. [Later changes: *Cataglyphis* (*Cataglyphis*) *albicans* ssp. *vaucheri*, Emery, 1925: 263; *Cataglyphis* (*Cataglyphis*) *albicans* var. *vaucheri*, Santschi, 1929a: 38.]

*Cataglyphis argentatus* Radoszovski

*Cataglyphis argentata* Radoszovski, 1876: 140. Syntypes workers, Egypt or Ethiopia.

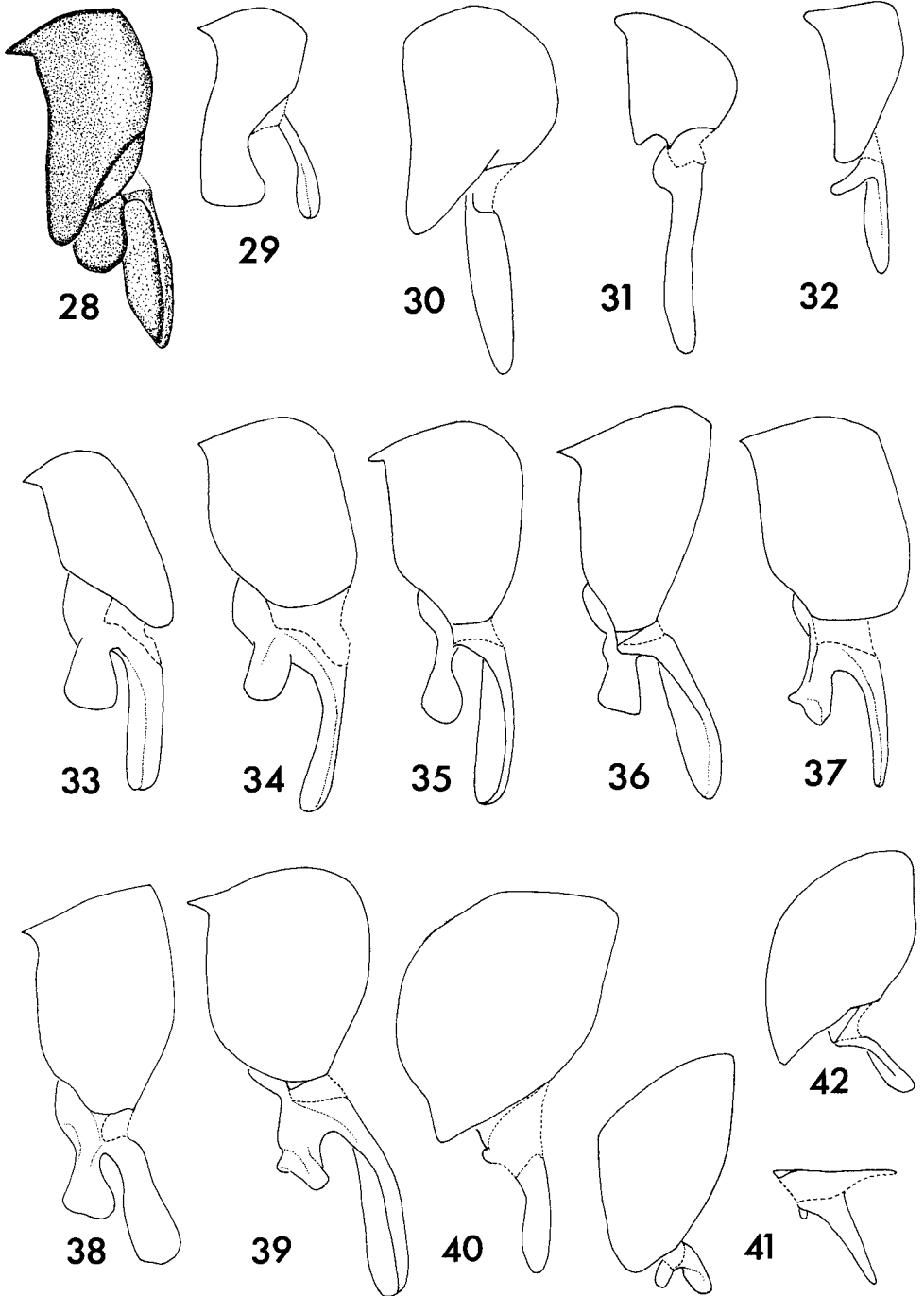
The placement of this species is tentative, as the type material is lacking and the description is ambiguous; all the morphological characters point to a relationship with *C. lividus* but the silvery hairs indicate a relationship with *bombycinus* or *laevior*.

*Cataglyphis canus* Santschi

*Cataglyphis albicans* var. *cana* Santschi, 1925: 356. Syntype worker, Morocco (Marrakech, leg. Vaucher), NHMB [examined]. [Later changes: *Cataglyphis* (*Cataglyphis*) *albicans* var. *cana*, Santschi, 1929a: 38; *Cataglyphis cana*, Collingwood, 1978: 73.] [*Myrmecocystus albicans* ssp. *vaucheri* var. *cana*, Emery, 1906: 54, name not available.]

*Cataglyphis cinnamomeus* (Karavaiev)

*Myrmecocystus albicans* ssp. *cinnamomea* Karavaiev, 1909b: 269. Syntypes worker, USSR (Turkestan), MHNG, NHMB [examined]. (Later changes: *Cataglyphis* (*Cataglyphis*) *albicans* st. *cinnamomea*, Santschi, 1929a: 55; *Cataglyphis cinnamomea*, Pisarski, 1967: 418; *Cataglyphis* (*Eomonocombus*) *cinnamomea*, Arnoldi, 1968: 1815.] [*Myrmecocystus albicans* ssp. *viaticoides* var. *cinnamomea*,



FIGS 28–42. Caudal view of the right stipes and squamula. 28: *C. cursor*; 29: *C. emeryi*; 30: *C. altisquamis*; 31: *C. bombycinus*; 32: *C. emmae*; 33: *C. urens*; 34: *C. nigripes*; 35: *C. diehlii*; 36: *C. bicolor* group sp. (dark form from Touggourt, Tunisia); 37: *C. niger*; 38: *C. nodus*; 39: *C. setipes*; 40: *C. viaticoides*; 41: *C. ibericus*; 42: *C. fortis*.

Karavaiev, 1909a: 37; *Cataglyphis albicans* ssp. *viaticoides* var. *cinnamomea*, Emery, 1925: 263; names not available.]

*Cataglyphis elegantissimus* Arnoldi

*Cataglyphis* (*Eomonocombus*) *elegantissima* [not *eiegantissima*, same page, misspelling] Arnoldi, 1968: 1815. Syntypes workers, USSR (Turkmenia, Kopet-Dag, 2500 m, 15/16 August 1935, No. 6549, leg. Golotin), ZIL [examined].

*Cataglyphis fortis* (Forel)

*Myrmecocystus albicans* var. *fortis* Forel, 1902a: 156. Syntypes worker, Algeria (Tougourt, sur le chemin de Temacin, leg. Diehl.), MHNG [examined]. [Later changes: *Cataglyphis* (*Cataglyphis*) *albicans* var. *fortis*, Emery, 1925: 262; *Cataglyphis* (*Cataglyphis*) *albicans* st. *fortis*, Santschi, 1929a: 55; *Cataglyphis fortis*, Wehner, 1983: 95.] (Descriptions of female and male: Wehner, 1983: 95; male genitalia: Wehner, 1983: 103, figs 9, 10; biology: Bernard, 1953, Wehner, 1983.)

*Cataglyphis halophila* Barnard, 1953: 48. Syntypes 5 workers, Tunisia (Chott Djerid, El Mensof, May 1951, leg. Bernard); Paratypes: 1 worker Algeria (Biskra, 1894, leg. Chobaut), MNHP [examined]. [Synonymy by Wehner, 1983: 95.]

*Cataglyphis ibericus* (Emery)

*Myrmecocystus albicans* ssp. *ibericus* Emery, 1906: 52. Syntypes workers, males, Spain and Portugal. [Later changes: *Cataglyphis albicans* st. *ibericus*, Santschi, 1919: 246; *Cataglyphis* (*Cataglyphis*) *albicans* ssp. *iberica*, Emery, 1925: 262; *Cataglyphis* (*Cataglyphis*) *albicans* st. *iberica*, Santschi, 1929a: 55; *Cataglyphis iberica*, Collingwood and Yarrow, 1969: 85.]

*Cataglyphis lividus* (E. André)

*Myrmecocystus albicans* var. *livida* E. André, 1881: 58. Syntypes workers, Israel (Jaffa) MNHP, MHNG [examined; see note 1 below *viaticoides*]. [Later changes: *Myrmecocystus albicans* r. *lividus*, Forel, 1902a: 156; *Myrmecocystus albicans* spp. *lividus*, Emery, 1906: 54; *Cataglyphis albicans* st. *lividus*, Wheeler and Mann, 1916: 173; *Myrmecocystus* (*Cataglyphis*) *albicans* ssp. *lividus*, Karavaiev, 1924: 305; *Cataglyphis* (*Cataglyphis*) *albicans* ssp. *lividus*, Emery, 1925: 262; *Cataglyphis* (*Cataglyphis*) *albicans* st. *lividus*, Santschi, 1929a: 55; *Cataglyphis albicans* ssp. *livida*, Menozzi, 1933: 84; *Cataglyphis livida*, Pisarski, 1967: 467.]

*Cataglyphis lividus* ssp. *bulgaricus* Atanassov

*Cataglyphis livida* ssp. *bulgarica* Atanassov, 1982: 213, fig. 4. Holotype worker, Bulgaria (Rhodope mountains, Ivailograd district, near Odrinzi, 22 May 1964, leg. N. Atanassov); Paratypes 20 workers and 5 females, same locality; NHMS.

*Cataglyphis lividus* ssp. *luteus* Pisarski

*Cataglyphis livida* ssp. *lutea* Pisarski, 1967: 418. Syntypes workers, Iran (leg. Doria). [*Myrmecocystus albicans* ssp. *viaticoides* var. *lutea*, Emery, 1906: 53; *Cataglyphis* (*Cataglyphis*) *albicans* ssp. *viaticoides* var. *lutea*, Emery, 1925: 263; names not available.] [= *Myrmecocystus pallidus*, Emery, 1877: 366, misidentification, Emery, 1906: 53.]

*Cataglyphis minimus* Collingwood

*Cataglyphis minima* Collingwood, 1985: 289, fig. 75. Holotype worker, Saudi Arabia (Bishah, 7 April 1983, leg. Collingwood), NHMB; paratypes workers, females, Saudi Arabia (Bishah, 7 April 1983 and desert west of Najran, 10 April 1983, leg. Collingwood), CCAC, CAD, NHMB [examined].

*Cataglyphis otini* Santschi

*Cataglyphis* (*Cataglyphis*) *albicans* st. *otini* Santschi, 1929a: 38 [misspelled as *odini* in Santschi, 1929a: 60]. Syntypes workers, Morocco (Rabat, August 1928, leg. Otin), NHMB [examined]. [Later change: *Cataglyphis otini*, Collingwood, 1978: 73.]

*Cataglyphis rosenhaueri* Santschi

*Cataglyphis albicans* st. *rosenhaueri* Santschi, 1925: 356. Syntypes workers, Spain (south Spain), NHMB [examined]. [Later change: *Cataglyphis rosenhauri* [misspelled], Collingwood and Yarrow, 1969: 85] [*Myrmecocystus albicans* ssp. *ruber* var. *rosenhaueri*, Emery, 1906: 53; *Cataglyphis* (*Cataglyphis*) *albicans* ssp. *rubra* var. *rosenhaueri*, Emery, 1925: 263; *Cataglyphis* (*Cataglyphis*) *albicans* st. *rubra* var. *rosenhaueri*, Santschi, 1929a: 55; names not available]

*Cataglyphis ruber* (Foral)

*Myrmecocystus albicans* r. *ruber* Forel, 1903: 268. Syntypes workers, Algeria (El Kreider, leg. A. Forel), MHNG [examined]. [Later changes: *Myrmecocystus albicans* ssp. *ruber*, Emery, 1906: 52; *Cataglyphis* (*Cataglyphis*) *albicans* ssp. *rubra*, Emery, 1925: 262; *Cataglyphis* (*Cataglyphis*) *albicans* st.

*rubra*, Santschi, 1929a: 39; *Cataglyphis rubra*, Collingwood, 1985: 291] [Descriptions of female and male: Santschi, 1929a: 39; male genitalia: Wehner, 1986: 109, fig. 2A.]

*Cataglyphis semitonsus* Santschi

*Cataglyphis (Cataglyphis) albicans* var. *semitonsa* Santschi, 1929a: 61. Syntypes workers, Algeria (Beni-Ounif, leg. Brouard), NHMB [examined]. [Later changes: *Cataglyphis albicans* var. *semitonsa*, Menozzi, 1932: 95; *Cataglyphis semitonsa*, Collingwood, 1985: 291.] [*Cataglyphis albicans* st. *vaucheri* var. *semitonsa*, Santschi, 1926: 236, name not available.]

*Cataglyphis theryi* Santschi

*Cataglyphis (Cataglyphis) theryi* Santschi, 1921a: 76. Holotype hermaphrodite or ergatandromorph, Morocco (between Meknès and Azou, leg. Théry), NHMB [examined]. [Later changes: *Cataglyphis (Cataglyphis) albicans* ssp. *theryi*, Emery, 1925: 263; *Cataglyphis (Cataglyphis) theryi*, Santschi, 1929a: 56.]

*Cataglyphis viaticoides* (E. André)

*Myrmecocystus albicans* var. *viaticoides* E. André, 1881: 57. Syntypes workers, Lebanon (Beyrouth, leg. Abeille), MNHP, MHNG [examined; see note below]. [Later changes: *Myrmecocystus albicans* r. *viaticoides*, Forel, 1902a: 156; *Myrmecocystus albicans* var. *viaticoides*, Forel, 1904: 383; *Myrmecocystus albicans* ssp. *viaticoides*, Emery, 1906: 53; *Cataglyphis (Cataglyphis) albicans* ssp. *viaticoides*, Emery, 1925: 263; *Cataglyphis (Cataglyphis) albicans* st. *viaticoides*, Santschi, 1929a: 55; *Cataglyphis (Cataglyphis) albicans* ssp. *viaticoides*, Menozzi, 1933: 85; *Cataglyphis viaticoides*, Arnoldi, 1964: 1809.] (Description of male genitalia: Arnoldi, 1964: 1809, fig. 9; distribution: Tinaut and Plaza, 1989: 197.)

Note. The syntypes do not correspond with the current conception (Kugler, 1988 and personal communication, Collingwood, personal communication) of *viaticoides*, since all the syntypes are uniform bright yellow and do not have a darker gaster.

Tinaut and Plaza (1989) point out that the bicoloured form in the Iberian peninsula might be *rosenhaueri* and not *viaticoides*, but do not give diagnostic characters to separate the taxa.

One worker syntype in MHNG is labelled 'Sevilla' and is possibly misidentified (= *rosenhaueri*!).

*Cataglyphis viaticoides* ssp. *cuneinodis* Arnoldi

*Cataglyphis (Cataglyphis) viaticoides* ssp. *cuneinodis* Arnoldi, 1964: 1810. Syntypes workers, USSR (Transcaucasica, Erivan-Gouv., Aras Thal bei Ordubad, 20 April 1914, leg. Woronov and Woltschanetzky, ZIL [examined]). [*Myrmecocystus (Cataglyphis) albicans* ssp. *ruber* var. *cuneinodis*, Karavaiev, 1924: 305; *Cataglyphis (Cataglyphis) albicans* st. *rubra* var. *cuneinodis*, Santschi, 1929a: 55; names not available.]

**Species incertae sedis**

*Cataglyphis bicoloripes* Walker

*Cataglyphis bicoloripes* Walker, 1871: 10. Syntypes females, Egypt (Cairo) [no types in BMNH]. [Later change: *Myrmecocystus bicoloripes*, Dalla Torre, 1893: 216.]

In Walker's collection at the BMNH no types could be found and the description is insufficient for the accurate placement of the species. If it is a *Cataglyphis* it must belong to the *bicolor* group.

**Names transferred to other genera**

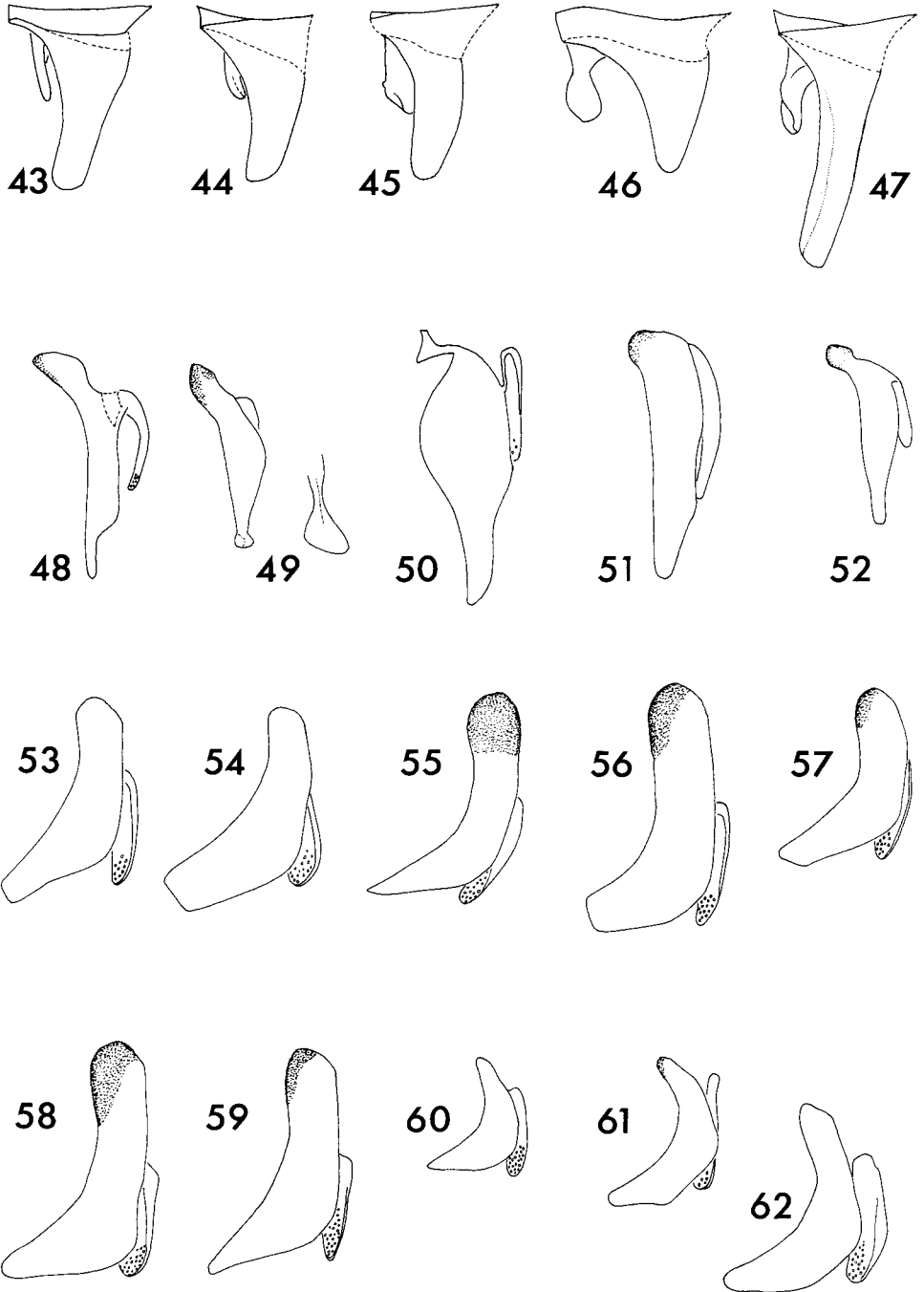
*Alloformica flavicornis* (Kusnetzov-Ugamskij) nov. comb.

*Cataglyphis cursor* ssp. *flavicornis* Kusnetzov-Ugamskij, 1926: 72. Syntypes workers, USSR (Turkestan, West Tian-Shan: Ak-Tash-mountains, 60 km northeast of Tashkent; Usun-Atshak; Peskem River; Ugam ridge north of Kisil valley; all between 2000 and 2600 m) MNHP [examined; see note below]. [Synonymy with *Cataglyphis cursor* ssp. *rockingeri* by Santschi, 1929a: 36.]

Note: In the MNHP, Paris, there is one cotype (worker) with five mandibular teeth, the apical not much longer than the subapical, a tubular first maxillary palp segment and a distinct reticulate sculpture on the head and alitrunk. This combination of characters diagnoses ants of the genus *Alloformica* (Agosti, in preparation). The emarginate occiput, which is unique within *Profomica*, *Alloformica* and *Cataglyphis*, separates *flavicornis* from the two other species within *Alloformica*.

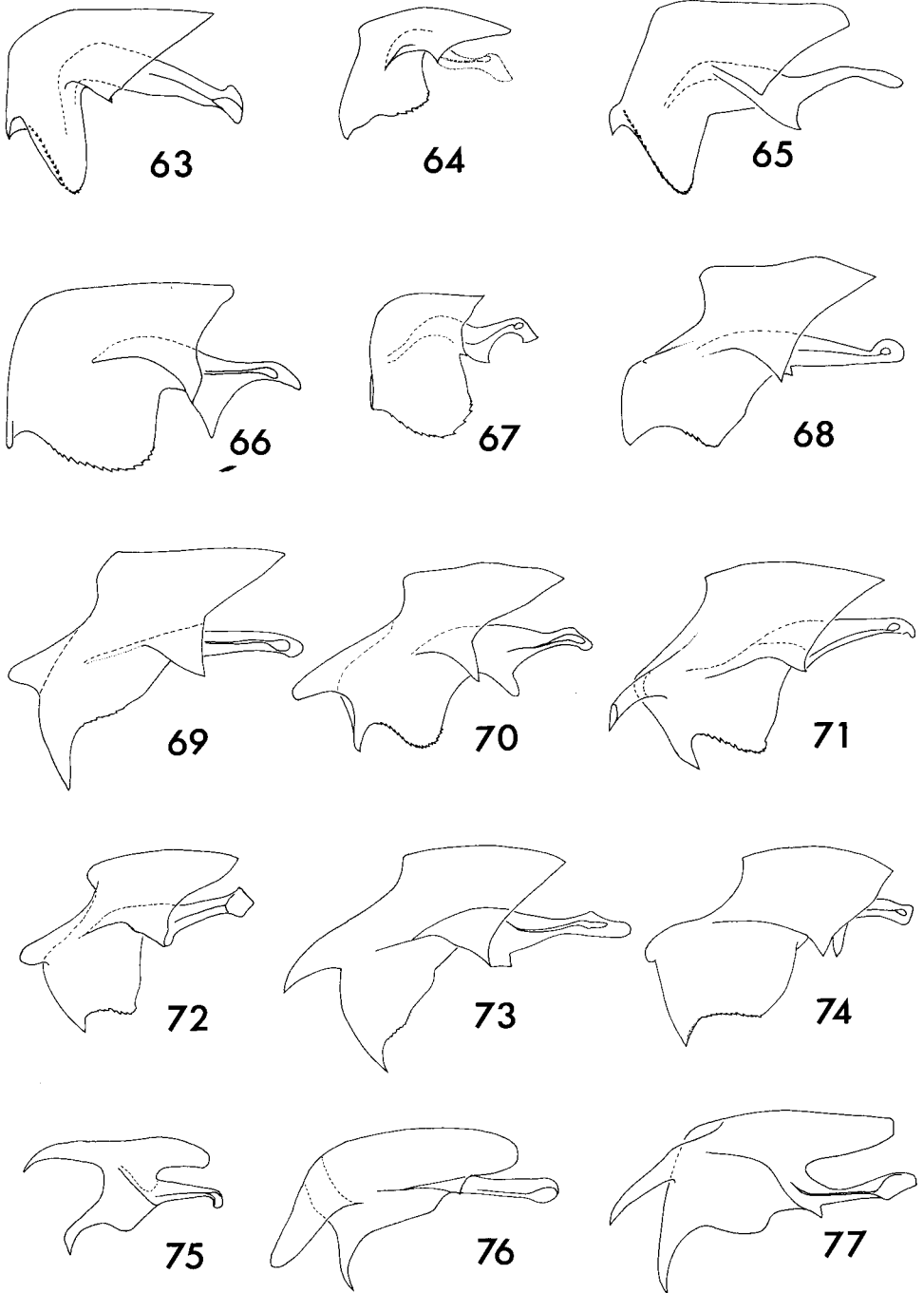
*Camponotus birmanus* (Collingwood)

*Cataglyphis birmana* Collingwood, 1962: 227, figs 8, 9. Holotype worker, Burma (Tenasserim, Malvedaung, 300 m, 25 November 1934, leg. R. Malaise) [Nov. comb. by Brown, 1967: 277.]



FIGS 43–62. 43–47: Lateral view of the stipes: 43: *C. diehlii*; 44: *C. bicolor* complex sp.; 45: *C. niger*; 46: *C. nodus*; 47: *C. setipes*. 48–62: median view of the right volsella: 48: *C. cursor*; 49: *C. emeryi*; 50: *C. altisquamis*; 51: *C. combycinus*; 52: *C. emmae*; 53: *C. urens*; 54: *C. nigripes*; 55: *C. diehlii*; 56: *C. bicolor* group sp. (dark form from Touggourt, Tunisia); 57: *C. niger*; 58: *C. nodus*; 59: *C. setipes*; 60: *C. viaticoides*; 61: *C. ibericus*; 62: *C. fortis*.





FIGS 63–77. Lateral view of the right sagitta: 63: *C. cursor*; 64: *C. emeryi*; 65: *C. altisquamis*; 66: *C. bombycinus*; 67: *C. emmae*; 68: *C. urens*; 69: *C. nigripes*; 70: *C. diehlii*; 71: *C. bicolor* group sp. (dark form from Touggourt, Tunisia); 72: *C. niger*; 73: *C. nodus*; 74: *C. setipes*; 75: *C. viaticoides*; 76: *C. ibericus*; 77: *C. fortis*.

*Proformica caucasea* (Santschi)

*Cataglyphis* (*Paraformica*) *caucasea* Santschi, 1925: 353. Syntype worker, USSR (Caucasus Tiflis, leg. Karavaiev), NHMB [examined]. [Later changes: *Paraformica caucasica* (*sic!*), Karavaiev, 1926: 199; *Proformica caucasea*, Arnoldi and Dlussky, 1978: 554.]

## Unavailable names

- Cataglyphis albicans* st. *rubra* var. *agilis* Santschi. Santschi, 1929a: 39. Syntypes workers, Tunisia (Tozzeur, 19 May 1927, leg. Santschi), Algeria (Biskra, leg. Surcouf; Ain Seffra, leg. Boitel) NHMB [examined].
- Cataglyphis albicans* st. *livida* var. *agnata* Santschi. Santschi, 1929a: 62 (diagnoses in key and in Santschi, 1929b: 107, fig. 10; also described as new in Santschi, 1934b: 176.). Syntypes 2 females, Algeria (Hoggar, Im Amdjel, 4 March 1928, leg. de Peyerimhoff). (Description of worker in Santschi, 1929b: 108), NHMB [examined].
- Cataglyphis albicans* st. *livida* var. *ambigua* Santschi. Santschi, 1929a: 40. Syntypes workers, Egypt (Cairo, leg. Forel), NHMB [examined].
- Myrmecocystus albicans* ssp. *livida* var. *arabica* Emery. Emery, 1906: 180. Syntype worker, Aden. [Later change: *Cataglyphis albicans* ssp. *livida* var. *arabica*, Emery, 1925: 262; *Cataglyphis albicans* st. *livida* var. *arabica*, Santschi, 1929a: 55.]
- Myrmecocystus albicans* ssp. *lividus* var. *arenaria* Forel. Forel, 1909: 384. Syntypes workers, Algeria (dunes by Biskra, Grande-Hamada, leg. Lameere), MHNG [examined]. [Later changes: *Cataglyphis albicans* st. *lividus* var. *arenaria*, Santschi, 1921a: 72; *Cataglyphis albicans* ssp. *livida* var. *arenaria*, Emery, 1925: 262; *Cataglyphis* (*Cataglyphis*) *albicans* st. *livida* var. *arenaria*, Santschi, 1929a: 40; names not available.] (Description of female: Santschi, 1929a: 40.)
- Cataglyphis bicolor* st. *nodus* var. *assyria* Santschi. Santschi, 1929a: 44. Syntypes workers, Iran (Susse, leg. Le Mout) [no types could be found in NHMB].
- Cataglyphis bicolor* st. *nodus* var. *drusa* Santschi. Santschi, 1929a: 44. Syntype worker, Syria (Ataib; leg. H. Gadeau de Kerville), NHMB [examined].
- Cataglyphis bicolor* st. *saharae* var. *bucculenta* Santschi. Santschi, 1929a: 48. Syntypes workers, Morocco (Bou Denib; leg. Théry), NHMB [examined].
- Cataglyphis bicolor* st. *nigra* var. *caerulescens* Santschi. Santschi, 1929a: 50. Syntypes workers, Syria (Antilibanon, Doumar; leg. Gadeau de Kerville), NHMB [examined].
- Cataglyphis bicolor* st. *nodus* var. *helladica* Santschi. Santschi, 1934a: 281. Syntypes workers, Greece (Athens, Akropolis, June 1933, leg. Santschi), NHMB [examined].
- Cataglyphis bicolor* st. *nigra* var. *pharao* Santschi. Santschi, 1929a: 51. Holotype worker, Egypt (Suez; leg. Reichensperger), NHMB [examined].
- Cataglyphis bicolor* st. *laevior* var. *rufidens* Santschi. Santschi, 1932: 95. Syntypes workers, females, Algeria (Tanzerouft desert, Reggan (Halebou), 26 January 1932, leg. Leclercq.) [no types could be found in NHMB].
- Cataglyphis* (*Monocombus*) *cursor* st. *hellenica* var. *dorica* Santschi. Santschi, 1929a: 35. Syntypes workers, Greece (Crete, La Cannée, leg. Sichebnin) [no types could be found in NHMB].
- Cataglyphis* (*Monocombus*) *cursor* ssp. *aenescens* var. *kuenlunensis* Stärke. Stärke, 1935: 269. Syntypes workers, USSR (Karakorum, Karakash valley, between Kawak pass and Sanju pass, 3700–3200 m, 16 September–5 October 1929; Khotan, 1350 m, 6–12 May 1930).
- Myrmecocystus cursor* ssp. *aenescens* var. *flavigastra* Karavaiev. Karavaiev, 1924: 303. Syntypes females, male, USSR (Turkestan, Samarkand, # 1828, # 1829 (Coll. Karavaiev, ZMK). [Later change: *Cataglyphis* (*Monocombus*) *cursor* st. *aenescens* var. *flavigastra* Santschi, 1929a: 53.] (Description of worker: Karavaiev, 1936: 266.)
- Cataglyphis* (*Monocombus*) *cursor* ssp. *aenescens* var. *maeotica* Karavaiev. Karavaiev, 1935: 110. Syntypes females, males, USSR (Ukraine, leg. Zhdanov).
- Cataglyphis hispidus* Menozzi. Menozzi in Eidmann, 1942: 255, fig. 2. Syntypes workers, Pakistan (Gor, north of Nanga Parbat, 19 May 1937, leg. Troll) [no description given]. nomen nudum.
- Cataglyphis* (*Monocombus*) *viatica* st. *mauritanica* var. *occidentalis* Santschi. Santschi, 1929a: 32, figs 19, 24. Syntypes worker, female, Morocco (Ain Leu–Azrou; leg. Théry), NHMB [examined].
- Cataglyphis* (*Monocombus*) *viatica* st. *mauritanica* var. *opaciventris* Santschi. Santschi, 1929a: 31, figs 24, 28. Syntypes worker, female, male, Tunisia (Le Kef, 900 m; leg. Dr Normand), NHMB [examined].

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