

# The phylogeny of the ant tribe Formicini (Hymenoptera: Formicidae) with the description of a new genus

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**Abstract.** The holarctic ant tribe Formicini is revised, the new genus *Bajcaridris* described, and possible phylogenetic relationships are discussed. The subgenus *Iberoformica* is synonymized with *Formica*. A synopsis, diagnosis and keys to the genera are provided.

## Introduction and History

Formicini ants are among the most dominant faunal elements within the holarctic region, and often display a decisive effect on the composition of the local fauna. Their dominance is due to their social and mainly predacious life style with often extensive colonies of nests which can include up to more than 1000 nests and several hundred million ants within one locality (Hölldobler & Wilson, 1990). This has not only resulted a wealth of publications on ecology and behaviour, but was the reason for the use of ants, especially of the *Formica rufa* group, in biological control. However, the systematics and taxonomy of this tribe remained utterly unresolved and has never been treated above the local fauna level.

The present study provides an historical review of the genus-level taxonomy of the Formicini, re-defines the tribe and the included genera, and provides a cladistic analysis of the tribe and a key to genera. A discussion of each genus includes synonymies, comments, distribution and biology. This study is the fourth step towards a generic revision and cladistic analysis of the formicine ants on a worldwide base (Agosti, 1990, 1991, 1992).

As conceived here, the tribe Formicini includes seven genera, all of which are limited to the northern temperate hemisphere, but only two of which have a holarctic distribution. Number of species included and ranges of the genera are given in the table below. The number of species represents described species only, and will certainly increase since species-level taxonomy remains utterly uninvestigated over the greater part of the ranges of these genera.

Genus	Distribution	No. of species
<i>Formica</i> L.	Holarctic	158
<i>Cataglyphis</i> Foerster	S.W. Palaearctic-Sahelian	61
<i>Proformica</i> Ruzsky	Palaearctic	25
<i>Polyergus</i> Latreille	Holarctic	5
<i>Bajcaridris</i> gen.n.	W. Palaearctic	3
<i>Rossomyrmex</i> Arnoldi	Central Asia/Spain	2
<i>Alloformica</i> Dlussky	Central Asia	3

The tribe Formicini was established by Emery (1916). He included *Formica*, *Cataglyphis* and *Polyergus*, and distinguished the tribe by the following characters: sepals of the proventriculus not reflected, short; antenna of females and workers with 12, those of males with 13 segments, articulated close to the clypeus; clypeal and antennal grooves confluent. Male genitalia large and robust. Emery (1916) separated *Lasius* and *Prenolepis* and placed those two genera, because of the small genitalia of their males and the shape of the proventriculus, into the tribe Plagiolepidini.

The earlier attempts at a classification of the formicine ants by Forel (1893, 1912, 1917), Emery (1895b) and Wheeler (1922) included in Formicini or later in Formicini the genera *Pseudolasius*, *Lasius*, *Formica*, *Polyergus*, *Myrmecocystus* and *Cataglyphis* (which had been a subgenus of *Myrmecocystus* for some time), and culminated in the classic system proposed by Emery (1925), separating those genera into the two tribes Formicini with *Formica*, *Cataglyphis*, *Paraformica* and *Polyergus* and Lasiini with *Pseudolasius*, *Paratrechina*, *Myrmecocystus*, *Prenolepis*, *Lasius* and *Andragnathus*. Ashmead's (1905) unexplained idiosyncratic system will not be treated here.

The situation remained unchanged until Wheeler & Wheeler (1970, 1985) reunited the Formicini and Lasiini into a single tribe, based on larval characters, and included the more recently described Australian genus *Teratomyrmex* (McAreavey, 1957). Dlussky & Fedoseeva (1988) added *Alloformica* and the fossil genera *Glaphyromyrmex*, *Leucotaphus* and *Protoformica* in his list. Hölldobler &

Wilson (1990) adopted this system for their synopsis of the ant genera of the world. Furthermore, they included *Bregmatomyrma* and indicated some doubt about this system by listing this taxon as 'Formicini and Lasiini'. Agosti (1991), by describing new characters, proposed a new system. From Hölldobler & Wilson's genera he included *Cataglyphis*, *Formica*, *Polyergus*, *Proformica*, *Rossomyrmex*, *Teratomyrmex* in the *Formica* genus group, *Acanthomyops*, *Lasius* and *Myrmecocystus* in the *Lasius* group, and *Bregmatomyrma* and *Pseudolasius* in the *Pseudolasius* genus group. *Andragathus* had already been synonymized with *Paratrechina* (Agosti & Bolton, 1990b). Thus, from Hölldobler & Wilson's Lasiini and Formicini taxon, only the genera belonging to Agosti's *Formica* genus group are included in the tribe Formicini as it is diagnosed here. *Teratomyrmex* is excluded because of its asepalous proventricule (Agosti, unpubl.). This makes a sister group relationship between Lasiini and Formicini highly unlikely (Agosti, 1991).

The following characters were used in the study of formicini ants, but refer mainly to the tribal or higher level (see diagnosis of the tribe; Agosti, 1991, and in prep.): the position of the antennal articulation (Forel, 1893); the structure of the clypeal and antennal groove (Emery, 1916), the propodeal spiracle, the male genitalia (Emery, 1916), and of the proventricule (Forel, 1912; Emery, 1916, Eisner, 1957); the structure of the frontal carina, the position of the propodeal spiracle, the articulation of the petiole into the alitrunk, the relative position of the hind coxal cavity, the structure of the ventral surface of the petiole and the first gastral segment, and the pilosity of the hind tibia (Agosti & Bolton, 1990a).

Larval characters seem to be of little use to discriminate between Formicini and Lasiini (Wheeler & Wheeler, 1970).

The karyology of Formicini is only partially investigated. All of the species of *Formica* ( $2n = 52, 54$ ; e.g. Hung, 1969; Hauschteck-Jungen & Jungen, 1976, 1983), *Polyergus* ( $2n = 52$ ; e.g. Hauschteck-Jungen, pers. comm.; Imai, 1966) and *Cataglyphis* ( $2n = 52$ ; e.g. Hauschteck-Jungen, pers. comm.; Imai *et al.*, 1984) so far investigated show a very consistent pattern with  $2n = 52$  or  $54$ . This is a higher number for each of the species analysed of *Lasius* and *Myrmecocystus* (see Crozier, 1975, for a compilation of karyotypes within the ants).

Behavioural characters are not included in this study. However, a comprehensive synthesis of behaviour and ecology, including Formicini ants, which might be the starting point for comparative ethological studies, is given by Hölldobler & Wilson (1990). The same publication also includes a synopsis of revisionary studies, regional faunas and distribution of all ant genera of the world, and thus does not need to be repeated here.

During this study it became evident that all the genera included are in need of a full-scale revision. Only *Cataglyphis* has recently been revised on a worldwide base (Agosti, 1990). The identity of almost all the subgenera and species can only be guessed from isolated descriptions, and monophyly has not been demonstrated for any of the

subgenera. For the purpose of this study, all the subgenera were sunken into synonymy, and should await future cladistic analyses to establish their validity. Species groups have the further advantage of not being formally recognized by the Code, and thus it is not as important whether the group is monophyletic or a mere operational taxon.

#### *Measurements and indices*

Morphological terminology in the text follows Hölldobler & Wilson (1990). All measurements are given as a minimum, maximum and, in parentheses, the median; the unit of measurement is mm; e.g. AL 1.23–1.45 (1.40).

*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.

*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 in front of the eye.

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

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

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

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

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

This study has mainly been based on specimens available at the following institutions: BMNH, CCAC, DAAC, ETHZ, and MHNG. Additional specimens were received from the institutions mentioned below.

#### *Depositories*

BMNH: Department of Entomology, The Natural History Museum, London, U.K.; CCAC: collection of C. A. Collingwood, Skipton, U.K.; CXE: Collection of X. Espadaler, Bellaterra, Spain; DAAC: collection of D. Agosti, Uster, Switzerland; DBAUG: Departamento de Biología Animal, Universidad de Granada, Spain; ETHZ: Entomologisches Institut, Eidgenössische Technische Hochschule, Zurich, Switzerland; IEE: Instituto Español de Entomología, Madrid, Spain; IZPAN: Instytut Zoologiczny, Polska Akademia Nauk, Warszawa, Poland; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Mass., U.S.A.; MHNG: Muséum d'Histoire Naturelle, Geneva, Switzerland; MNHP: Muséum Nationale d'Histoire Naturelle, Paris, France; MZL: Musée Zoologique, Lausanne, Switzerland; NHMB: Naturhistorisches Museum, Basel, Switzerland; ZMK: Zoologisk Museum, Copenhagen, Denmark; ZMMSU: Zoological Museum, Moscow State University, Moscow, U.S.S.R.

**Formicini Latreille**

Formicariae, Latreille, 1809: 124.

Formicini, Emery, 1925: 240 (with a list of tribal names published before 1925).

Formicini (part.), Wheeler & Wheeler, 1970: 101.

Formicini and Lasiini (part.), Hölldobler & Wilson, 1990: 18.

*Diagnosis.* Formicine ants with the following combination of characters (see discussion below):

**WORKER**

- 1 Mandible triangular and multidentate (except in *Polyergus* and large workers of some *Cataglyphis* spp. with falcate mandible) (Figs 2–9).
- 2 Tentorial pit widely separated from the antennal socket (Fig. 10).
- 3 Antennal articulation of the lateral side of the corner formed from clypeus and frontal carina (Fig. 10).
- 4 Frontal triangle at least indicated, mostly distinct and separated from the clypeus by a transverse suture (Fig. 10).
- 5 Frontal carina always present and beginning as a distinct crest in front of the antennal articulation and passing medially of the toruli, divergent. Frontal carina never laterally extended and forming frontal lobes, nor bordering an antennal scrobe, but often forming distinct ridges (Fig. 10).
- 6 Eye behind midlength of sides in full-face view.
- 7 Foramen magnum closely set to the occipital margin of the head.
- 8 Metanotum is a distinct part of the dorsal part of the alitrunk, on its sides two spiraculi which reach the dorsal outline viewed in lateral view (Figs 18–24).
- 9 Metapleural gland slit-shaped, extended laterally (Fig. 18).
- 10 Emargination of petiolar articulation in the alitrunk does not surpass cranially a line spanned between the two anteriormost points of the two hind coxal cavities (Fig. 32).
- 11 Propodeal spiracle slit-shaped or, if roundish, then the inner margin of the annular sclerite not parallel to the outer margin and the spiracle is minute (Fig. 18).
- 12 Propodeal spiracle placed close to the metanotum, distinctly set apart from the declivitous face of the propodeum (Fig. 18).
- 13 Shape of the alitrunk (Figs 18–24).
- 14 Hind tibiae with a double row of bristles on the ventral side (except in some species of the *Formica exsecta*-group, but then the underlying pubescence sparse (Fig. 33).
- 15 Claw with one or two long bristles spanning from its base to its apex (Fig. 34).
- 16 Formation of first gastral segment with the helcium enclosed by the tergite, and the ventral part separated from the sternite by a carina (Fig. 32).
- 17 Karyotype either  $2n = 52$  or  $2n = 54$ .
- 18 Proventriculus long sepalous, not reflected distally.

**FEMALE**

As workers, but with a complete set of flight-sclerites; occasionally some species of *Polyergus*, *Proformica*, *Bajcaridris* and *Cataglyphis* with ergatogynes.

- 19 Distinctly larger than the workers, except in some *Cataglyphis* species and some *Formica* species of the *microgyna*- and *exsecta*-group and occasionally within some species of the *fusca*-group.

**MALE**

- 20 Males distinctly larger than the workers, of the same size as the females (except in some *Cataglyphis* spp. with large workers and some *Formica* spp. and *Polyergus* spp. with micraner males, and *Bajcaridris* spp. with large males).
- 21 Genitalia large and robust, pointing ventrally (Fig. 25).
- 22 Pygostyli present (except in some *Cataglyphis* spp. of the *bicolor*-group (Fig. 40).

*Definition*

**WORKERS and FEMALES.** Formicine ants with PF 6,4 or less. PF 6,4 is predominant, reduced to 4,2 or 4,3 in *Polyergus* and to 5,4 in some species of the *Formica exsecta*-group. Mandible subtriangular with distinct teeth, 7–10 in *Formica*, 5 in *Allformica*, *Proformica* and most *Cataglyphis*, with the exception of the *C.bombycinus*-group with 6–7 teeth; in *Polyergus* and the large workers of *C.bombycinus* and *C.kurdistanicus* a falcate mandible without denticles. The apical tooth is always the largest. Clypeus extended laterally over the articulation of the mandible, separated posteriorly by a suture from the frontal triangle. Articulation of the antenna close to the posterior part of the clypeus and the lateral margin of the frontal triangle. Frontal carina with a crest, beginning in front of the toruli and extended posteriorly well behind the antennal insertions; if reduced, then a bulge with a fine carina still begins in front of the toruli. Antenna always 12 segmented and filiform, scape slightly thickening, distally, only in *Polyergus* and *Rossomyrmex* club-shaped with a thicker distal part. Eye medium sized in the anterior midlength of the head. Ocelli present, sometimes vestigial. Lateral sides of the triangle constituted by the three ocelli each with a long distinct bristle, except in species with a reduced pilosity such as some species of the *Formica exsecta*-group. The metanotum is a part of the dorsal outline of the alitrunk with the spiracles not meeting dorsally but reaching to the dorsal outline in lateral view. Propodeum rounded, declivitous face never meeting the basal face in an angle. Propodeal spiracle oval to slit-shaped, if oval then the annular sclerite never with parallel inner and outer margins; set close to the metanotum. Metanotal gland slit-shaped and extended laterally; in *Polyergus* reduced but indicated by some pilosity on a bulge. Hind tibiae with a double row of bristles on the ventral surface, except in some species of the *Formica exsecta*-group, but then no thick appressed pubescence

present. The emargination of the petiolar articulation never crossing a line spanning between the anteriormost points of the hind coxal cavities. Hind coxae closely set, meeting medially, in *Bajcaridris* slightly distant but never forming a U-shaped cavity as in *Lasius* (see Agosti, 1992). Petiole ventrally keeled, never rounded in cross-section; nodiform or squamiform, the scale or node never inclined cranially but always upright. The construction of the first gastral segment with the helcium in the tergite separated from the sternite by a basal transversal suture, the first tergite and sternite fused only on the anteriormost part; first gastral tergite high, except in *Polyergus* and *Rossomyrmex*.

Pubescence variable, pilosity variable in both density and shape. Individual hairs generally simple, thin and pointed to slightly keeled, in *Formica exsectoides*-group, *Polyergus* and *Rossomyrmex* truncated thick bristles at least on the dorsum of the pronotum, and in some species of the *Formica microgyna*-group and all species of *Bajcaridris* at least the hairs on the petiole and on the propodeum clavate.

Sculpture shining and smooth to dull and coarse, never either strongly rugose nor reticulate.

Wings usually present, often in the same species ergatogynes side by side with normal winged queens. Discoidal cell usually present, variable within some species of the *C. bicolor*-group.

Proventriculus always sepalous, the sepals never reflected distally.

**MALES.** As above but with the following modifications.

Mandible elongate triangular, falcate in *Polyergus*; masticatory margin of mandible with one apical tooth, rarely with a row of denticles as in *Formica sanguinea* and occasionally in some other species of the *Formica fusca*-group. Frontal carina reduced to a bulge. Eye enlarged, as long as one fourth of the lateral side of the head, as in *Cataglyphis*, to almost two thirds as in *Bajcaridris* and *Proformica oculatissima*. Ocelli present, small and in the same plane as the surface of the head in *Cataglyphis*, large and forming a distinct socket in *Bajcaridris* and *Proformica*. Petiole low and a transversal node, in *Cataglyphis* somewhat squamiform. Genitalia large and either uniform and simple with an outer valve which is distinctly separated into stipes and squamula, a clasper-like median valve or volsella with a cuspis and digitus and an inner valve or sagitta with a distinctly serrated ventral surface. *Bajcaridris*, *Cataglyphis* and *Proformica* with additional appendices. Subgenital plate present but variable.

Males of the same size as females, distinctly larger than the workers, except in *Bajcaridris*, some *Cataglyphis* of the *bicolor* and the *bombycinus*-groups with a large worker caste and some *Formica* of the *exsecta*-group.

Pilosity variable; a distinct dense long black pilosity in *Proformica* and otherwise generally a sparse pilosity with single, long acute hairs.

Usually uniform black or shining blackish brown in *Bajcaridris*, *Formica* and *Polyergus*. *Cataglyphis* variable, either the alitrunk yellow, yellow with three black longitudinal stripes or black and the gaster varying within the

species-groups from brownish black to a yellowish red. The latter is also the case within *Proformica*.

The diagnosis above is an attempt to separate all the seven genera of the Formicini from the rest of the Formicinae. Thus any formicine species not showing all the characters in combination and failing to conform to the definition is excluded from the tribe.

The phylogenetic significance of the characters can only partially be assessed, because of the lack of adequate cladistic analyses of the whole subfamily.

Nevertheless, *Melophorus* from the supposed paraphyletic tribe Melophorini from the *Formica* genus group (Agosti, 1991) might be the candidate sister group of the Formicini. They share as unique characters the arrangements of the bristles on the hind tibia, and the slit-shaped prododeal spiracle, but both might be symplesiomorphies for the Formicinae. The low number of teeth on the mandible might be a synapomorphy, assuming the high number of mandibular teeth as it is represented in *Nothomyrmecia* or in most of the dolichoderines, to be the plesiomorphic state for the Formicinae. The long, apically not reflexed, sepalous proventricule would in this case be an autapomorphy for the Formicini. The high chromosomal count ( $2n = 52$  or  $54$ ) and male genitalia characters can not be assessed, as no data from *Melophorus* is available. However, the following ground plan is assumed for the male genitalia. Subgenital plate with a cranio-median appendage; apically simple, spade-shaped; stipes without a median appendage; sagitta without a big gap between the ergot and the beginning of the serrated face.

Within the tribe, the phylogenetic relationships have been completely resolved (Fig. 1, Table 1 and Appendix). However, the paraphyletic genus *Formica* and the sister group relationship between *Polyergus* and *Rossomyrmex* need some explanation.

The paraphyly of *Formica* could have several reasons. This genus is easily recognized, and no-one has ever doubted its monophyly. However, it was always difficult to key this genus, because of the lack of autapomorphic characters. It thus seems that the paraphyly is an artefact, and further research will very likely reveal the missing characters. One particular characteristic of this genus is its highly diversified social behaviour which is not known from any of the other formicini genera. Characters involved in chemical communication, such as chemical compounds, might therefore be candidates. Further new characters might contribute to a resolution. Finally, the outcome of a molecular biological study of the subfamily (Agosti, in prep.) might yield some of the missing data. Therefore, although unsatisfactory at the moment, *Formica* is not fused with its sister group to resolve this unsatisfactory situation.

The sister group relationship of *Polyergus* and *Rossomyrmex* is supported by three synapomorphies, but doubts remain, despite the obvious confirmation of recent cladistic analyses of social parasites and their host relations within social Hymenoptera (e.g. Carpenter *et al.*, 1993; Agosti, 1994). The lack of the male caste in *Rossomyrmex* is certainly an obstacle in accepting this sister group. How-

**Table 1.** List of the apomorphies for the respective genera and nodes (Fig. 1). F, female; M, male; W, worker; the numbers refer to the respective characters in the data matrix and in the list of characters (Appendix). This list was compiled using NONA (Goloboff, 1993).

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*Alloformica* (W, 2) Worker caste: polymorphic → monomorphic  
 (W, 22) Body surface: smooth to chagrinated → roughly sculptured  
 (W, 28) Eyes: flat → domed  
 (W, 29) Scape: short SI <120 → long SI >120  
 (W, 30) Erect hairs on scape: absent → present

*Bajcaridris* (W, F, M, 1) Body size of sexuals relative to workers: same body size → taller  
 (W, 2) Worker caste: polymorphic → monomorphic  
 (W, 21) Size: AL >2 mm → AL <1.4 mm  
 (W, 31) First funicular segment: short → long  
 (M, 35) Subgenital plate apically: without → with two bristles  
 (M, 36) Volsella orientation: dorso-ventral → along body axis  
 (M, 37) Ventral-apex of sagitta: elongated → short  
 (M, 38) Sagitta: short → long  
 (M, 41) Front wing venation: developed → reduced  
 (M, 43) Ocelles: slightly enlarged → large  
 (M, 44) Ocelles: flat → raised  
 (M, 47) Eyes with: small ommatidia → large ommatidia  
 (M, 48) Eyes: almost hemispherical → flatter

*Cataglyphis* (W, 8) Shape of propodeal spiracle: small and ellipsoid → elongate and parallel-sided  
 (W, 26) Psammophore: absent → present

*Formica* (no autapomorphies)

*Polyergus* (W, 6) Number of mandibular denticles: six to nine denticles → no denticles at all  
 (M, F, 17) Hairs on hind margin of front wing: protruding over the margins → not present  
 (W, 23) Maxillary palp formula: 6,4 → lower  
 (W, 25) Mandible: triangular with masticatory face → falcate  
 (W, 27) Clypeus with apical face: convex → straight  
 (W, 33) Metapleural gland orifice: distinct → small

*Proformica* (M, 34) Ridge between stipes and volsella: present → absent  
 (M, 42) Erect hairs on head: few → dense pilosity

*Rossomyrmex* (W, 24) Maxillary palp segments: stout → long and slender  
 (W, 32) Occiput of head: emarginate → straight to convex

Node 8 (W, 3) First maxillary palp segment: round → flattened  
 (W, 7) J-shaped hairs on maxillary stipes: absent → present  
 (M, 15) Median appendage of sagitta: not present → present

Node 9 (W, 5) Fourth mandibular denticle, from apex to base: larger than third → smaller than third  
 (M, 11) Subgenital plate cranially: extended → not extended

Node 10 (M, 14) Sagitta with ergot and dorsal end of serrate face: confluent → widely separated  
 (M, 20) Shape of head in full frontal view: depressed → compressed

Node 11 (W, 2) Worker caste: polymorphic → monomorphic  
 (W, 4) Frontal carina: distinct and crest-shaped → bulge-like  
 (W, 9) First gastral segment: high → low

Node 12 (W, 6) Number of mandibular denticles: five → six to nine denticles

Node 13 (W, 8) Shape of propodeal spiracle: elongate and parallel-sided → small and ellipsoid  
 (M, F, 17) Hairs on hind margin of front wing: not present → protruding over the margins  
 (M, F, W, 50) Proventricule asepalous → scapalous

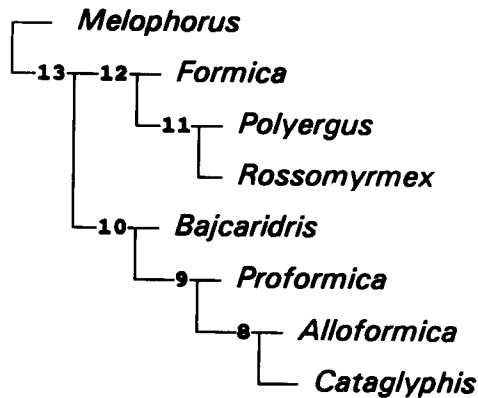
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ever, based on the data available, the position of the two genera as sister group of *Formica* is the most parsimonious placement.

The autapomorphies of the genera are given in Table 1.

A catalogue of the Formicini species is only available for the nearctic region (Smith, 1979).

The Formicini are among the dominant ants in the holarctic region, with the few exceptions in marginal



**Fig. 1.** Cladogram resulting from exhaustive search of the character matrix in Appendix 1 using Hennig86 (Farris, 1988) and NONA (Goloboff, 1993). This cladogram is stable to successive weighting. The consistency index is 0.97 and the retention index is 0.97. Node numbers correspond with the variables in Table 1.

- Genus *Bajcaridris* gen.n.
- Genus *Cataglyphis* Foerster
  - = *Monocombus* Mayr
  - = *Paraformica* Forel
  - = *Machaeromyrma* Forel
  - = *Eomonocombus* Arnoldi
- Genus *Formica* L.
  - = *Hypochira* Buckley
  - = *Formicina* Swainson and Shuckard
  - = *Serviformica* Forel
  - = *Raptiformica* Forel
  - = *Neoformica* Wheeler
  - = *Coptoformica* Müller
  - = *Adformica* Lomnicki
  - = *Iberoformica* Tinaut **syn.n.**
- Genus *Polyergus* Latreille
- Genus *Proformica* Ruzsky
- Genus *Rossomyrmex* Arnoldi

habitats such as regions with permafrost or permanent ice. However, the genera seem to follow general patterns. On the one hand, the large genera seem to replace each other ecologically; on the other hand, the smaller genera are specialized, and are distributed alongside the species of the large genera. *Formica* and *Cataglyphis* have only a narrow zone of overlap, with *Formica* being abundant in the temperate vegetation zone with deciduous or coniferous forests, and *Cataglyphis* with their northern boundary either congruent with the evergreen, laurophyllous and sclerophyllous mediterranean vegetation zone or the steppe zone and open vegetation within the southernmost coniferous or deciduous forests. *Formica* find their southern boundary in the Northern Oases of the Old World desert zone.

The smaller genera are either specialized as social parasites (*Polyergus* and *Rossomyrmex*), or seem to be confined to very restricted ecological niches (*Alloformica*, *Bajcaridris* and *Proformica*) and thus have a very local distribution, which does, however, not exclude a very large overall range of *Proformica*.

Behavioural and morphological variation is very uneven within the genera. Whereas *Formica* with well over 100 species has a tremendous variation in social behaviour, with almost all kinds of social parasitism to the very simple life style, with claustral nest foundation and small colonies to large homeostatic nest and colonies including several million specimens, the species show hardly any morphological variation. *Cataglyphis* is exactly the opposite, with an extreme variation especially in male genitalia but hardly any variation in social behaviour. The small genera show neither a great variation in morphological nor in behavioural characters.

**Synonymic synopsis of genera**

Tribe Formicini

Genus *Alloformica* Dlussky

**Key to genera**

*Worker, female*

- 1 Mandible falcate, without a preapical cleft (Fig. 7); clypeus compressed (Fig. 13); frontal carina reduced to a bulge (Fig. 13); maxillary and labial palps short and slender, PF 4,3 or 4,2 ..... *Polyergus*
- Mandible triangular with a dentate masticatory margin (Figs 2-4, 6, 8-9); even if extensively elongated with at least a distinct subapical cleft (Fig. 5). Clypeus trapezoidal, posteriorly distinctly separated from the frontal triangle (Fig. 10); frontal carinae present, beginning in front of the antennal articulation and about 3 times the length of the torulus diameter (Fig. 10), if reduced then still a crest present; maxillary and labial palps reaching at least up to the middle between the foramen magnum and the oral fossa, PF 6,4 or in some species of the *Formica exacta* group 5,4 ..... 2
- 2 Masticatory border of mandible with a row of 7-9 teeth or denticles, with a large apical tooth, a smaller subapical followed by a denticle and a row of 4-6 basal denticles (Fig. 6) ..... *Formica*
- Masticatory border of the mandible with a row of 5-6 denticles or teeth (Figs 2-4, 8) ..... 3
- 3 First maxillary palp segment flattened (Fig. 29); hairs at the base of the maxillary stipes longer than half the length of the stipes (Fig. 29) ..... *Cataglyphis*
- First maxillary palp segment round in diameter; hairs at the base of the stipes shorter than half the length of the stipes .... 4
- 4 Petiole without a lateral and dorsal crest (Figs 20, 24) ..... 5
- Petiole squamiform with a lateral and dorsal crest (Figs 22, 23) ..... 6
- 5 Mandible elongate with a row of denticles (Fig. 9); scape apically wider than twice the basal diameter, clavate, SI <100; frontal carina reduced to a minute ridge (Fig. 16); occiput of head emarginate (Fig. 16); body surface smooth and shining; petiole with a fringe of distinct bristles (Fig. 24). . *Rossomyrmex*
- Mandible triangular with a row of five teeth (Fig. 2); scape apically not wider than twice the basal diameter, SI >100;

- frontal carina distinct (Fig. 10); occiput of head convex; body surface sculptured and matted; petiole with erect hairs (Fig. 20) ..... *Alloformica*
- 6 Masticatory border of mandible with a row of five teeth, with apically the largest and basally the smallest tooth (Fig. 8); dimorphic worker cast (Figs 15, 17) ..... *Proformica*
- Masticatory border of mandible with five teeth or denticles, the three apical-most decreasing in size, the fourth distinctly larger than the third and the fifth (Fig. 3); monomorphic worker caste ..... *Bajcaridris*

### Males

(The males of *Alloformica* and *Rossomyrmex* are unknown)

- 1 Subgenital plate with a cranio-median appendage (Fig. 38). Genitalia simple, without appendages of the stipes of the sagitta (Fig. 50) or a prolongation of the part between the ergot and the serrated ventral part of the sagitta (Fig. 52) ..... 2
- Subgenital plate cranially either straight (Figs 35, 36) or with a broad, truncated extension (Figs 37, 39). Genitalia with a median appendage of the stipes (Fig. 56), a posterior projecting squamula (Fig. 45), and a prolongation of the part between the ergot and the serrated ventral part of the sagitta (Figs 43, 46, 49, 58) ..... 3
- 2 Mandible short, parallel sided, not meeting medially (Fig. 27); scapus shorter and not reaching the occiput (Fig. 27); without short hairs on the dorsal surface of the wings ..... *Polyergus*
- Mandible diverging distally, widest in the distal third, meeting medially (Fig. 26); scapus reaching at least the occiput (Fig. 26); dense short pilosity on the dorsal surface of the wings ..... *Formica*
- 3 Head wider than the alitrunk, similar to the head of the females; ocelli not on a socket; eye shorter than half the head length (Fig. 30); without short hairs on the dorsal surface of the wings ..... *Cataglyphis*
- Head narrower than the width of the alitrunk, distinctly dimorphic to the head of the females; ocelli forming a socket; eye longer than half the head length (Figs 28, 31); with dense short pilosity on the dorsum of the wings ..... 4
- 4 Head, alitrunk and petiole covered with a thick, long erect pilosity (Fig. 28); head and alitrunk surface with coarse and matt sculpture; subgenital plate with an apical, median laterally widened lobe as in Fig. 39; with lobe between stipes and volsella (Fig. 57); ventral part of the sagitta rounded (Fig. 58); body size larger than the workers ..... *Proformica*
- Head, alitrunk and petiole without thick pilosity (Fig. 31); smooth and shining surface of head and alitrunk; subgenital plate with a median, distally truncated processus (Fig. 37); no lobe between stipes and volsella; volsella 90° rotated, pointing caudally (Fig. 48); ventral part of the sagitta acute (Fig. 49); body size the same as workers. .... *Bajcaridris*

### *Alloformica* Dlussky (Figs 2, 10, 20)

*Alloformica* Dlussky, 1969: 219 [as subgenus of *Proformica*].  
Type-species: *Proformica (Alloformica) aberrans* Mayr, 1877: 7, by original designation.

*Alloformica* Dlussky; Brown, 1973: 178 [as synonym of *Proformica*].

*Alloformica* Dlussky; Dlussky & Fedoseva, 1988: 77.  
[Revived from synonymy, and raised to genus.]

*Comment.* *Alloformica* includes three species, *aberrans* Mayr, *flavicornis* Kuznetsov-Ugamsky and *nitidior* Forel, all only known by their worker caste. In the ZMMSU are a few males collected by Dlussky but yet undescribed. My notes made on a visit concern only the genitalia and not the overall morphology, such as head shape or pilosity. Nevertheless, the few notes support Dlussky & Fedoseva (1988) to separate *Alloformica* as a good genus from *Proformica*.

WORKER. Formicini ant with the following combination of characters:

- 1 Monomorphic worker caste.
- 2 Mandible with a row of declining teeth (Fig. 2).
- 3 Scape with distinct long erect hairs (Fig. 10).
- 4 SI > 100
- 5 Small, domed eye (Fig. 10).
- 6 Body surface roughly sculptured (Figs 10, 20)

FEMALE. Unknown

MALE (A few underscribed males are in the collection of the ZMMSU).

- 7 Subgenital plate with three apical appendages.
- 8 Stipes with a median appendix.

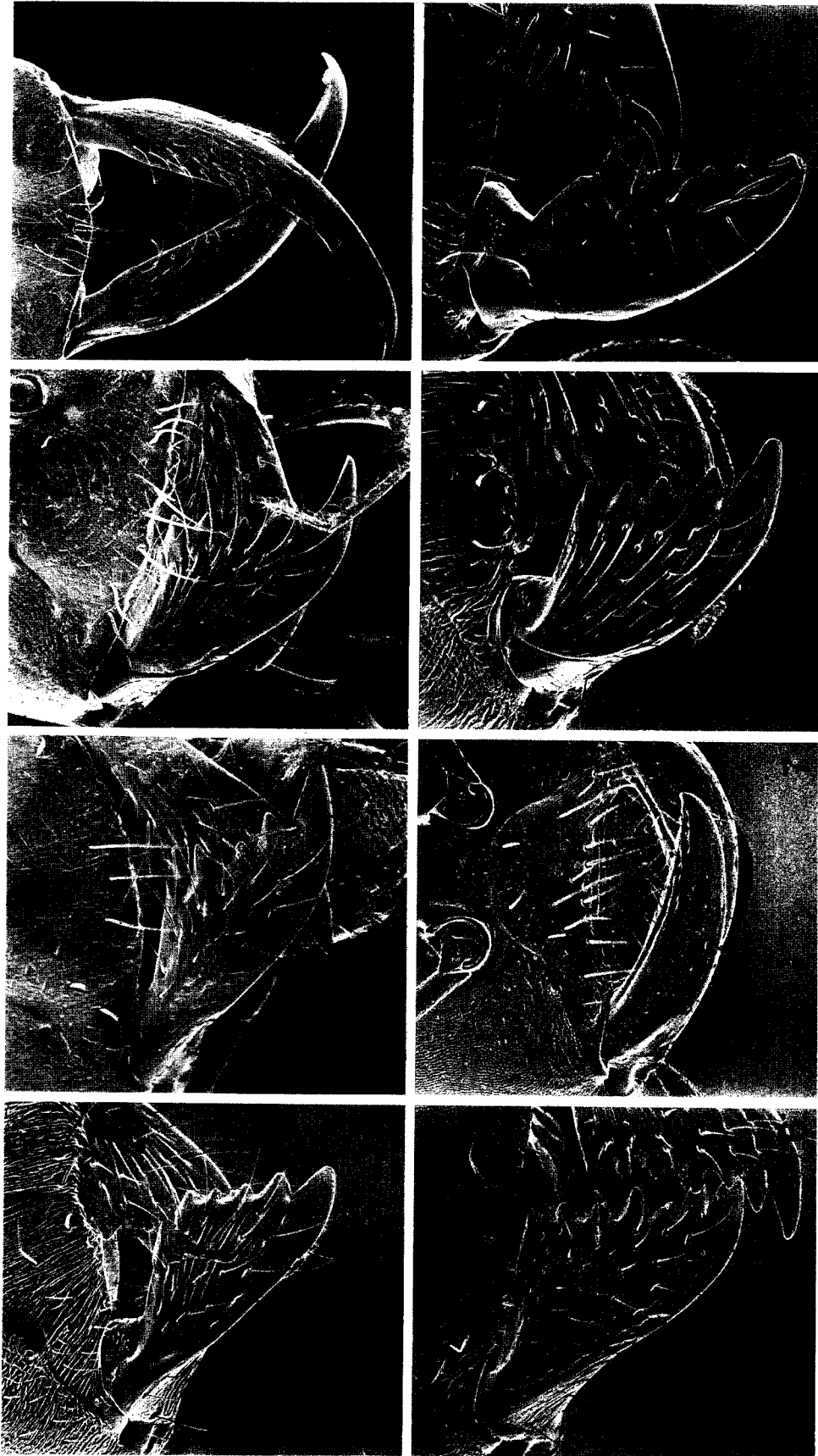
*Comparisons.* This genus is unique in its domed eye in combination with long erect pilosity on the scape, the rough sculpture and the erect petiole. The domed eye and the rough sculpture are autapomorphies.

*Distribution and biology.* The three species are only known from their type localities and a few additional localities. However, *aberrans* and *flavicornis* are the dominant ants in the herbaceous steppe on the foothills of the Zeravshanskiy mountains in Tadzhikistan, being important pollinators by visiting the flowers for nectar (Dlussky, 1981).

### *Bajcaridris* gen.n. (Figs 3, 14, 23, 31, 37, 47–49)

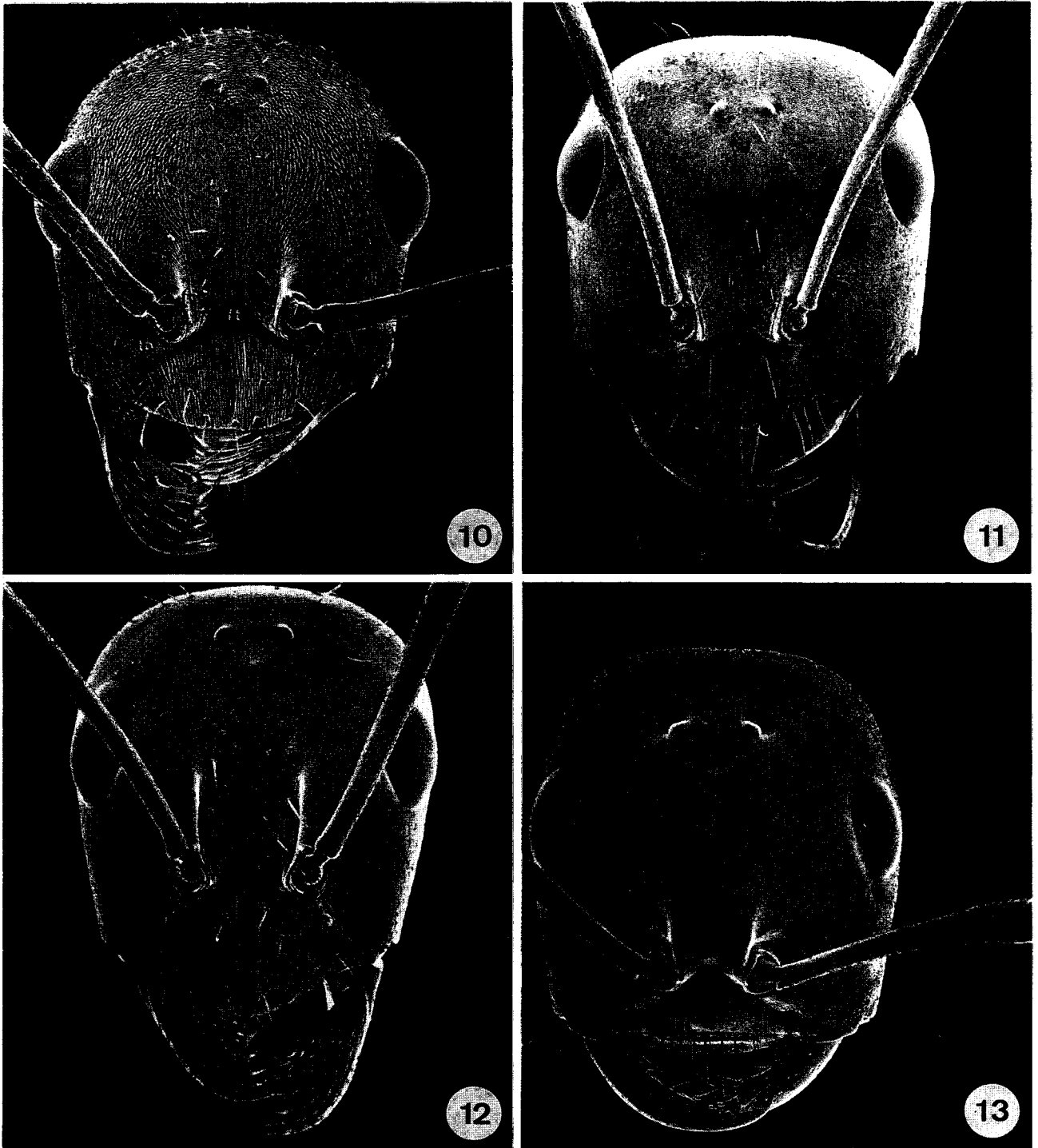
Type-species: *Proformica theryi* Santschi, 1936: 209.

*Comment.* *Bajcaridris* includes the three species *kraussi* Forel, *menoizzi* Santschi and *theryi* Santschi; the position of *oculatissima* Forel, described from a single male, is uncertain, as the gaster of the type is lacking. It seems reasonable that it might be a male of an east mediterranean *Proformica* (see discussion under *Proformica*). The males described by Espadaler & Cagniant (1987) are the only males out of a complete series with workers. The male of *kraussii* has been related by both Emery (1899) and Forel (1902) to this species, obviously because no others had been described by then. Nevertheless it is easily distinguishable by its



**Figs 2–9.** Mandibles of workers: (2) *Alloformica aberrans*; (3) *Bajacardiis theryi*; (4) *Cataglyphis bicolor*, standard dentition; (5) *Cataglyphis bombycinus*, major worker; (6) *Formica schaufussi*; (7) *Polyergus rufescens*; (8) *Proformica* sp.; (9) *Rossomyrmex minuchae*.



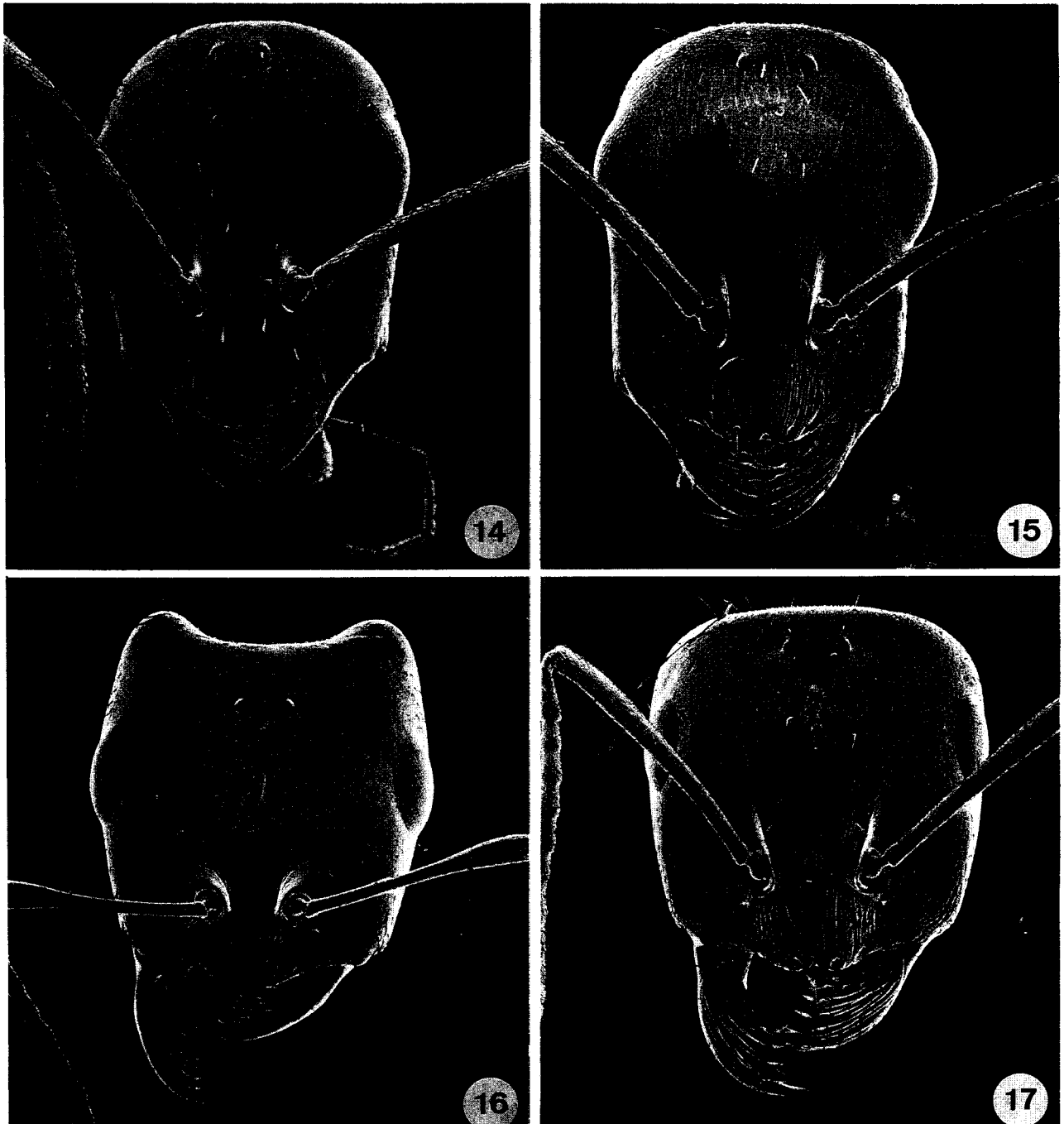


**Figs 10–13.** Frontal view of the head of workers. fc = frontal carina; ft = frontal triangle; tp = tentorial pit. (10) *Alloformica aberrans*; (11) *Cataglyphis bicolor*; (12) *Formica schaufussi*; (13) *Polyergus rufescens*.

genitalia, in which the outer valve is not fused as in *theryi* but separated in a squamula which overhangs the stipes and by the stipes being caudally blade-shaped. *B.menozzii* is only known from one single worker.

**WORKER.** Formicini ants with the following combination of characters:

- 1 Small (TL <1.4 mm), shining ants.
- 2 Mandible with 5 teeth, declining in size from apical to basal with the exception of the third tooth, which is



**Figs 14–17.** Frontal view of the head of workers: (14) *Bajcaridris theryi*; (15) *Proformica* sp., minor worker; (16) *Rossomyrmex minuchae*; (17) *Proformica* sp., major worker.

distinctly smaller than the subsequent and the precedent (Fig. 3).

3 First funiculus segment longer than the two subsequent together.

4 Frontal carina reduced to a bulge (Fig. 14).

5 Propodeal spiracle minute, ellipsoid (Fig. 23).

**FEMALE.** Inferred ergatogyne, because X. Espadaler

and H. Cagniant did not find a queen in nests they dug out (Espadaler & Cagniant, 1987).

**MALE.** Formicini ants with the following modifications:  
6 Small males, of the same size as workers (TL < 1.4 mm), shining.

7 Head compressed with a turban-like ocellar socket (Fig. 31).

- 8 Mandible short, subparallel (Fig. 31).
- 9 Terminal branches of the wing venation reduced.
- 10 Subgenital plate with a median apical, truncated appendix with two apical claws (Fig. 37).
- 11 Stipes without median appendices (Figs 47, 48).
- 12 Volsella rotated about 90° caudally; digitus horizontal, the tip of the cuspis *in situ* as long as the stipes, dorsoventrally oriented (Fig. 48).
- 13 Sagitta with a ventrally elongated apex, *in situ* as long as stipes; ventral side with few distinct teeth, the lateral plate of the two-folded sagitta protruding almost as far as the median plate with the teeth (Fig. 49).
- 14 Few scattered long, erect hairs all over the body.
- 15 Dense pilosity on the dorsal surface of the wings.

*Comparisons.* The workers differ by the combination of the following three characters from all the other ants of the tribe: dentition of the mandible with a small third tooth, clavate hairs and the first funicular segment which is longer than the two subsequent. The males are unique in the following combination of characters: the same size as the workers, a compressed head with distinct, large ocelli forming a socket, a unique subgenital plate with an unpaired median, caudal process, and a long pointed sagitta.

*Distribution and biology.* With the exception of *Bajcaridris theryi*, which has recently been rediscovered (Espadaler & Cagniant, 1987), all the three species have rarely been collected since they were described (*kraussi*: Forel, 1895, 1902, Emery, 1899; *menozzii*: (Santschi, 1923; *theryi*: Santschi, 1936). Their habitats are either in the oueds of the northern Sahara in Algeria (*kraussii* and *menozzii*) or in the meadows of the mountains of the Atlas in Morocco, where they are among the dominant ant species, building nests in the earth either below stones or with a distinct crater-shaped nest entrance (Espadaler & Cagniant, 1987).

**Cataglyphis Foerster** (Figs 4, 5, 11, 21, 29, 30, 32–36, 41–46)

*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; revived from synonymy as subgenus *Cataglyphis (Monocombus)* by Santschi, 1929: 30; synonymy reconfirmed by Agosti, 1990: 1462.]

*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, 1929: 30; synonymy by Hölldobler & Wilson, 1990: 18.]

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

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

*Comments.* This genus has recently been revised by Agosti (1990). Nine species groups have been recognized. A complete synonymy, full diagnoses and a key to the species groups are provided. An overview of the chemical compounds of the Dufour's and the mandibular glands of species of the major clades within *Cataglyphis* is given by Keegans *et al.* (1992).

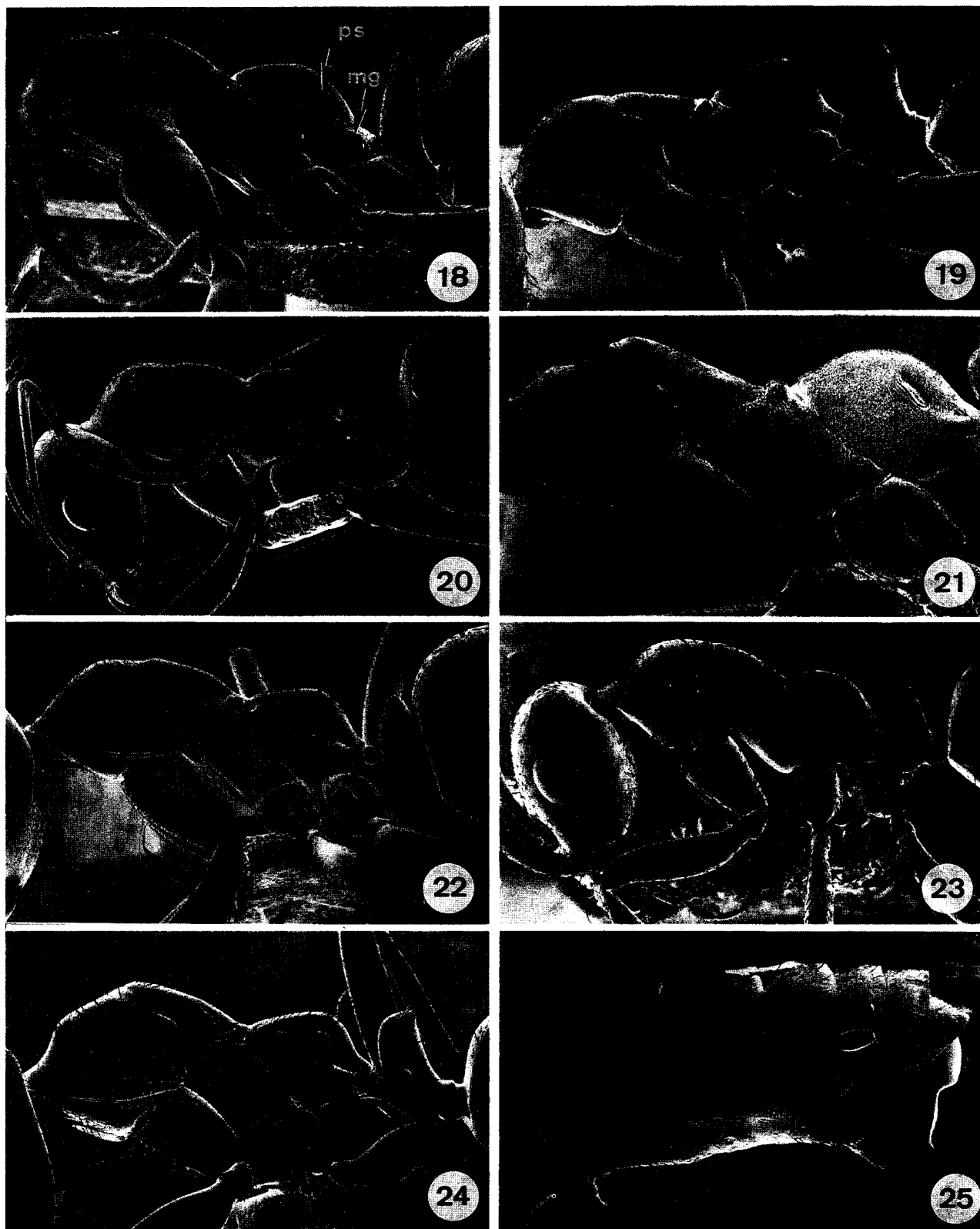
**WORKER and FEMALE.** Formicine ants with the following combination of characters:

- 1 Mandible large triangulate, a row of 5 teeth getting smaller from apical to basal. (In the *bombycinus*-group sometimes up to 7 teeth and larger workers with an elongate, falcate mandible.) (Figs 4, 5).
- 2 Macrochaetae (long J-shaped erect hairs) on the stipes of the maxillae which are as long as the stipes (Fig. 29).
- 3 Often a distinct psammophore formed by the macrochaetae on the stipes of the maxillae, the inner apical margin of the mandible and some long curved hairs on the third to fifth segment of the maxillary palps.
- 4 First maxillary palp segment compressed (Fig. 29).
- 5 Eye located distinctly behind the midlength of the head (Fig. 11).
- 6 Propodeal spiracles long and slit-shaped (Fig. 21).
- 7 Wings (female caste) with a straight frontal side and very few, short pubescence (length of the hairs << space between the hairs), hairs short and cone-shaped. Hind margin of front wings without a fringe of erect hairs.

**MALES.** As females, but with the following additions:

- 8 Body of the same size as the females.
- 9 Ocelli and eye only slightly enlarged in comparison to those in the female caste (Fig. 30).
- 10 Dorsal part of the ninth and tenth abdominal tergite sclerotized.
- 11 Subgenital plate three-lobed (Fig. 35), if seemingly truncated (Fig. 36), than the subgenital plate longitudinally stretched and thus forming a transversal opening between the subgenital plate and the genital capsule.
- 12 Stipes with a median appendage (Figs 41, 44).
- 13 The zone between the ergot and the beginning of the sagitta stretched (Fig. 43).
- 14 Front wing in comparison to the alitrunk short (WI >50).
- 15 Wings without dense pilosity on the dorsal surface.

Dimorphic worker castes are only present in *C. bombycinus*, *lucasi* and *kurdistanicus*; although there is an extensive size variation of the workers in some of the species, allometric growth is not preminent. No workers are known for *C. hanna*, a supposed inquiline of *bicolor* (Agosti, 1994).



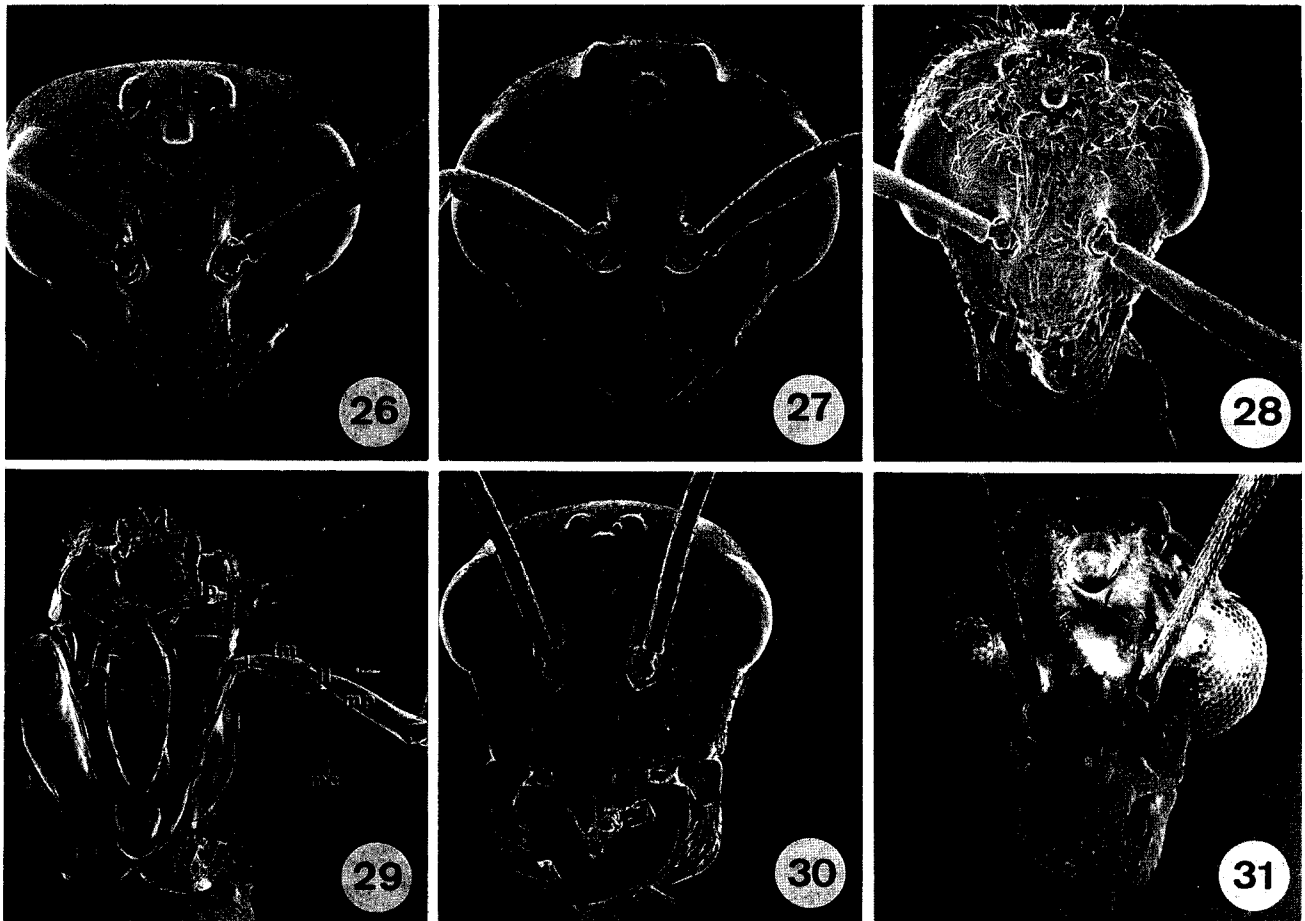
**Figs 18–25.** Lateral view of the alitrunk and petiole of workers. mg = metapleural gland orifice; ps = propodeal spiracle. (18) *Formica exsecta*; (19) *Polyergus rufescens*; (20) *Alloformica aberrans*; (21) *Cataglyphis bicolor*; (22) *Proformica* sp.; (23) *Bajcaridris theryi*; (24) *Rossomyrmex minuchae*. (25) Lateral view of the gaster of the male genitalia of *Formica sanguinea*.

**Comparisons.** The workers and females of this genus differ from all the other formicini ants by the combination of a flat first maxillary palpal segment, the long and slit-shaped propodeal spiracle, and the short wings with a very reduced pubescence; the males differ by the presence of a median appendix of the stipes, the 3-lobed subgenital plate (if it seems to be truncated then it is long and forming a distinct transversal opening between the subgenital plate and the genital capsule).

**Distribution and biology.** This genus is an inhabitant of the drier parts of the Palaearctic, such as the steppe, the savannah, the Mediterranean type ecosystem, and the deserts. Hardly any species are proper desert ants (such as *bombycinus*) but they live at the edge of the deserts in the wadis and the oases. Their habitats are from sea-level up to 2200 m. The species of the *bicolor*-group have a range of distribution from the beaches of Ghana to Vienna and Central Asia, from Morocco to the plains of the Ghanges (Wehner *et al.*, 1983), but not in Spain, and with a centre of diversity in the southeastern Mediterranean; the range of the *bombycinus*-group seems to be restricted to sandy deserts of North Africa and Middle East; the species of

the *emmae* group have been found in Morocco, Algeria and Tunisia on the southern side of the Atlas mountains (Delye, 1965), in Baluchistan (Agosti, 1990), and recently in the desert-like southeastern part of Spain (Tinaut, 1993); the *pallidus*-group is restricted to the deserts of central Asia. The *altisquamis*-group has a range from the Iberian Atlantic coast to central Asia and from north of the Sahara and the Asir mountains to central Asia via the southern side of the Mediterranean sea. Finally, the *cursor*-group is distributed from Portugal to eastern Mongolia along the north side of the Mediterranean sea, with the southernmost extensions on the Antiliban and the Brahui-Range in Pakistan. The species of the *cursor*-group are living in the most mesic habitats of all the *Cataglyphis* species, the species of the *pallidus* and the *bombycinus* group in the hottest areas (Agosti, 1990).

The biology of all the *Cataglyphis* species is rather uniform and hardly known. The information points generally towards a mongynous, mono- or oligocalic lifestyle, with independent nest founding and rather small colonies. The nests are always in the soil, often with only one entrance and a distinct crater made out of dug-out soil.



**Figs 26–31.** Head of males in frontal view. (26) *Formica sanguinea*. (27) *Polyergus rufescens*; (28) *Proformica* sp. (29) Maxillo-labial complex of *Cataglyphis bicolor*. lp = labial palpus; mc = macrochaetae; mp = maxillary palpus: I, II = first, second segments. (30) *Bajcaridris theryi*; (31) *Cataglyphis bicolor*.

Thelytoky has been demonstrated in *piliscapus* (Cagniant, 1979). *C. hanna*e, the only inquiline and social parasitic ant within *Cataglyphis*, was found in a nest of *bicolor*, which does not appear to be its sister species (Agosti, 1994). Foraging is mostly organized on an individual basis without recruitment (Wehner *et al.*, 1983; Wehner, 1987). A summary of the biology of many of the *Cataglyphis* species is to be found in Dlussky (1981).

**Formica Linnaeus** (Figs 6, 12, 18, 25, 26, 38, 50–52)

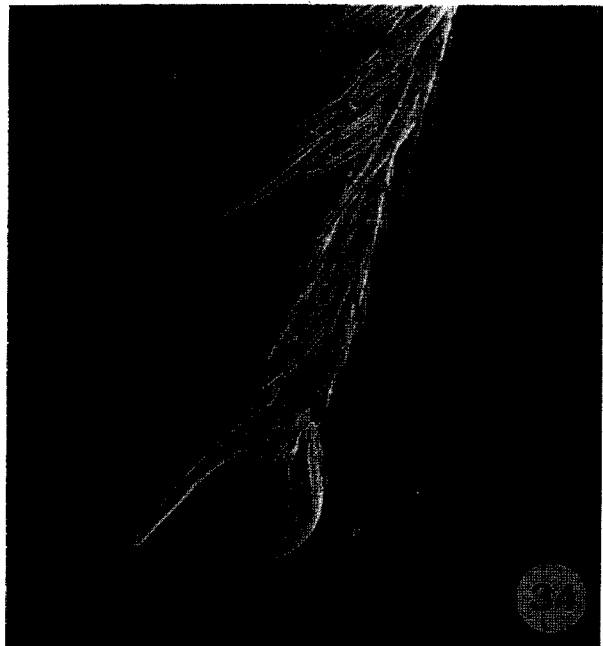
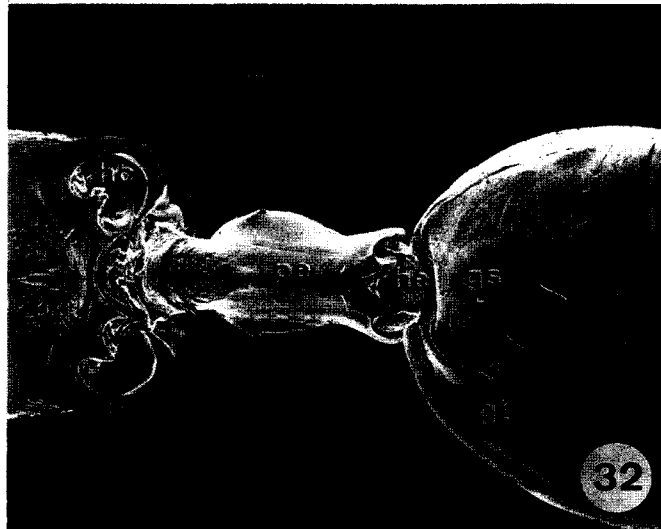
*Formica* Linnaeus, 1758: 579. Type-species: *Formica rufa*

Linnaeus, 1758: 580; by subsequent designation of Curtis, 1829: 752. [Replacement type by Yarrow, 1954b.].

*Hypochira* Buckley, 1866: 169 [as subgenus of *Formica*]. Type-species: *Formica (Hypochira) subspinosa* Buckley, 1866: 169; by monotypy. [Synonymy by Dalla Torre, 1893: 192.].

*Formicina* Swainson & Shuckard, 1840: 172. Type-species: *Formica rufa* L., 1758: 580; by subsequent designation of Wheeler, 1911: 164. [Synonymy by Wheeler, 1911: 164.].

*Serviformica* Forel, 1913: 361 [as subgenus of *Formica*]. Type-species: *Formica fusca* L., 1758: 580; by original designation. [Synonymy by Wheeler, 1922: 699.].



**Figs 32–34.** (32) Ventral view of the alitrunk, petiole, and first gastral segment of the worker of *Cataglyphis bicolor*. gs = first gastral sternite; gt = first gastral tergite; he = helcium; hx = hind coxae; pe = petiole. (33) Hind tibiae of the worker of *Cataglyphis*. (34) Claw of a worker of *Cataglyphis bicolor*.

*Raptiformica* Forel, 1913: 361 [as subgenus of *Formica*].

Type-species: *Formica sanguinea* Latreille, 1798: 37; by original designation. [Provisional synonymy by Wilson & Brown, 1955: 114; Synonymy re-confirmed here.]

*Neofornica* Wheeler, 1913a: 82 [as subgenus of *Formica*].

Type-species: *Formica pallidefulva* Latreille, 1802: 174; by original designation. [Also as new in Wheeler, 1913b: 548.]. [Synonymy by Buren, 1968: 39.].

*Coptoformica* Müller, 1923: 133 [diagnosis in key] [as subgenus of *Formica*]. Type-species: *Formica exsecta* Nylander, 1846: 909; by subsequent designation of Donisthorpe, 1941: 37. [Synonymy by Hölldobler & Wilson, 1990: 18.].

*Adformica* Lomnicki, 1925: 164 [as subgenus of *Formica*]. Type-species: *Formica exsecta* Nylander, 1846: 909; by subsequent designation of Donisthorpe, 1927: 316. (Junior synonym of *Coptoformica*) [Synonymy by Donisthorpe 1941: 37.].

*Iberoformica* Tinaut, 1990: 282. [as subgenus of *Formica*]. Type-species: *Formica subrufa* Roger, 1859: 251, by original designation. **Syn.n.**

*Comment.* The last full-scale revision of *Formica* (Wheeler, 1913b) included keys to all the species. A critical review of the systematics (only palaeartic species included), distribution and use in biological control of *Formica* has been compiled by Dlussky (1967). Gösswald's idiosyncratic view of the *Formica rufa* group includes an extensive list with many references from the very productive time in the 1970s and 1980s when a lot of attention was paid to the use of wood ants for biological control of pests and their conservation (Gösswald, 1989; see also the extensive bibliography in Cotti, 1963). Revisions of species groups were prepared by Yarrow (1954a, British *fuscus* group; 1955, British *rufa* group), Francoeur (1973, nearctic *fuscus* group). Keys to the nearctic species are provided by Creighton (1950), and by Francoeur (1973) for the *fuscus* group, and for the palaeartic region, or parts of it, by Dlussky (1967), Kutter (1977), Collingwood (1978a, b), Agosti & Collingwood (1987b).

Creighton (1950), Wilson & Brown (1954), Buren (1968) and more recently Tinaut (1990) discussed extensively the status of the subgenera within *Formica*. Their elevation of the palaeartic species of *Proformica* to generic level is here confirmed. The reconsideration of the status of species groups such as the *sanguinea* group must be subject of a revisionary study of the genus, including material from the whole holarctic region. As no sister groups of any of the subgenera are known, all the subgenera are suppressed and replaced by informal species groups (see above).

Generally, species groups can be defined by shared characters, such as the emarginate occiput or the toothless basal margin of mandible (*exsecta* group), the notch in the anterior margin of the clypeus (*sanguinea* group), or the life style such as the construction of large ant mounds (e.g. *rufa* or *exsectoides* group). But there are always some species whose placement remains doubtful. For example, should *uralensis* be included within the *rufa* group because of its lifestyle or within the *fuscus* group because of its

karyotype? Thus, speaking of species groups is more cautious and reflects the preliminary understanding of this genus more accurately.

Emery (1895a) transferred *Formica subspinosa* into *Dolichoderus*. No type material is available and the description is inaccurate. Therefore it is reasonable to keep *subspinosa* within *Formica* bearing in mind its uncertain status.

**WORKER.** Formicini ant with the following combination of characters:

- 1 Mandible with a row of 7–10 teeth or denticles on the masticatory border. The apical tooth is the largest followed by 2 of decreasing size. The fourth is larger than the third, and the subsequent teeth. Basal face and masticatory border meet in a right-angle (Fig. 6).
- 2 Maxillary palps reaching behind the midlength of the buccal cavity and the foramen magnum (except in some species of the *Formica exsecta*-group).
- 3 Eye with more than 250 ommatidia, placed laterally, slightly behind the midlength of the head (Fig. 12).

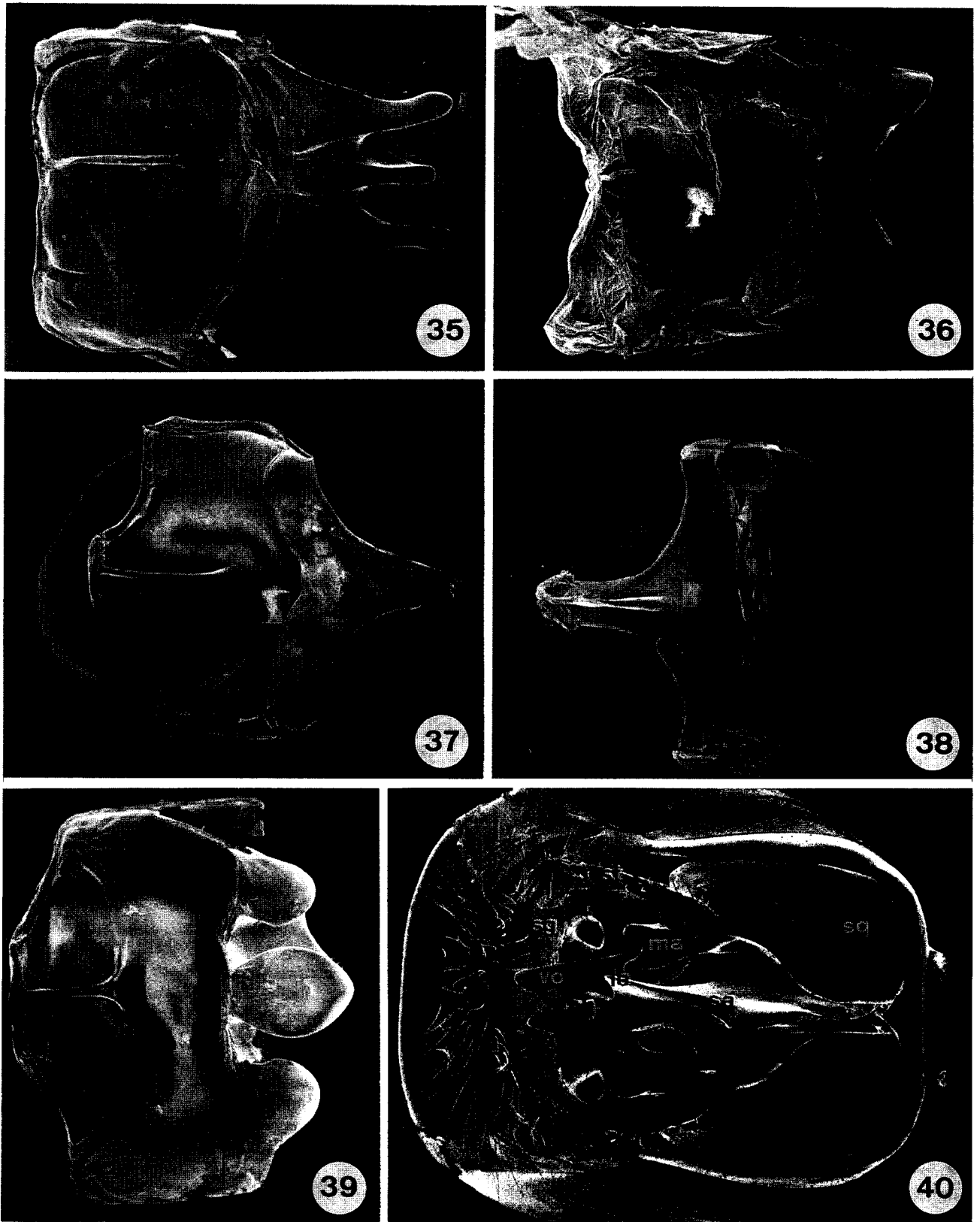
**FEMALE.** As worker but with the following modifications:

- 4 All flight sclerites developed (except for some rare ergatogynes occurring some times in *Formica sanguinea*).
- 5 Distinct dimorphism between worker and female caste with distinctly larger females than the workers (except for some species in the *exsecta*- and the *microgyna*-group, where microgynes occur).
- 6 Wings with dense, short pilosity on the dorsal surface.

**MALE.** Formicini ant but with the following modifications:

- 7 Of the same size as the female.
- 8 Head approximately the same width as the alitrunk.
- 9 Mandible with a large apical tooth, sometimes followed by a row of denticles (Fig. 26).
- 10 Frontal carinae reduced and not reaching far behind the posterior side of the toruli (Fig. 26).
- 11 Eye approximately one third of the head length.
- 12 Ocelli slightly biased, forming a somewhat raised triangle on the frons (Fig. 26).
- 13 Subgenital plate with a median cranial and two lateral processes and a sclerite on each side, spade-shaped (Fig. 38).
- 14 Pygostyli developed.
- 15 Stipes and squamula fused, limits of the two segments medially indicated by a ridge; squamula never overhanging the blunt subparallel sided stipes caudally (Fig. 50).
- 16 Sagitta with a short interspace between the ergot and the dorsal beginning of the sagittate part which is shorter than the ergot (Fig. 52).
- 17 Wings with dense pilosity on the dorsal surface.

*Comparisons.* The presence of more than six denticles with the two apical being the largest, followed by a very small third and a row of at least four medium sized, but variable teeth on the mandible is unique among the Formicini. The male is different from all the other Formicini in the



**Figs 35–40.** Subgenital plate of males: (35) *Cataglyphis bicolor*; (36) *Cataglyphis emmae*; (37) *Bajcaridris theryi*; (38) *Formica rufa*; (39) *Proformica* sp. (40) Hind view of the male genitalia of *Cataglyphis savignyi*. la = lateral appendix of sagitta; ma = median appendix of stipes; ps = pygostyli; sa = sagitta; sg = subgenital plate; sq = squamula; st = stipes; vo = volsella.



presence of the basal appendix of the subgenital plate and the mandibles which meet medially and are never falcate.

*Distribution and biology.* *Formica* is a holarctic genus. It is rarely found in zones with less than 250 mm rainfall per year, and most of the species are found in the temperate zones in biotopes with deciduous or coniferous trees. In North America the distribution is extended further into subdesertic and desertic region than in the palaeartic region. In the latter, *Formica* spp. are often found in oases in the temperate zone, but not in subtropical deserts. The *exsecta*, *exsectoides* and *rufa* groups, with species building extensive and tall mounds in which they can maintain a homeostasis, are restricted even further North; the most southern parts are regions with winter rainfall, and only the timberline is than populated by *Formica* species.

Unlike all the other genera within the tribe, the species of *Formica* are quite variable in their behaviour. Behaviour patterns vary from simple life-style with claustral nest founding, small monogynous colonies, to very extensive polycalic, polygynous colonies with over 300 million workers in 45,000 interconnected nests (Higashi & Yamuchi, 1979), to slavemaking (e.g. species of the *sanguinea* group), social parasitic life-styles with or without workers, to an inquilinistic way of life (see Hölldobler & Wilson, 1990). Another remarkable feature is the ability to maintain for days a mean temperature within the nest during phases with higher or lower outside temperatures. A compilation of the biology is included and compared with that of other ant species in Hölldobler & Wilson (1991).

The wood ants are of economic and conservational importance, especially species of the palaeartic *rufa* group. Their economic impact is two-fold. On the one hand these species are important predators of forest insects; on the other hand they maintain extensive aphid colonies to yield honeydew. The presence of the latter is an important carbohydrate source for honey bees, and the presence of the wood ants can raise the yield of honey produced by bees by over 20%. An extensive bibliography on wood ants was prepared by Cotti (1963).

The palaeartic wood ants are on IUCN's red data lists, as well as protected by many of the European governments (Day, 1991).

### ***Polyergus* Latreille (Figs 7, 13, 19, 27, 53–55)**

*Polyergus* Latreille, 1804: 179. Type-species: *Formica rufescens* Latreille, 1798: 44; by monotypy.

*Comments.* Although probably the most prominent among the Amazon ants (dulotic ants; see Hölldobler & Wilson, 1990), the taxonomy of the species is not well understood. The main problem might be the resolution of species specific character and those induced through different hosts. An old but still useful overview of the North American species is given by Creighton (1950) and Wheeler (1968); the male genitalia are described by Clausen (1938), Forbes & Brassel (1962) and Wheeler (1968).

**WORKER.** Formicini ant with the following combination of characters:

- 1 Head subquadrangular, eye in the posterior part of the midlength of the head (Fig. 13).
- 2 Mandible falcate, the masticatory border regularly and densely incised (Fig. 7).
- 3 PF 4,2, or 4,3, but the maxillary palps not reaching behind the midlength between the buccal cavity and the foramen magnum.
- 4 Clypeus compressed (Fig. 13).
- 5 Frontal carina reduced, but still beginning in front of the antennal articulation and at least as long as the posterior part of the torulus (Fig. 13).
- 6 Metapleural gland indistinct with a slit-shaped surface encircled by erect hairs on a bulla-shaped basal part of the propodeum (Fig. 19).
- 7 First gastral tergite very low (Fig. 19).

**FEMALE.** As worker but with the following modifications:

- 8 Either all flight sclerites developed or ergatogyne.
- 9 Wings without pilosity on the dorsal surface.

**MALE.** Formicini ant with the following combination of characters:

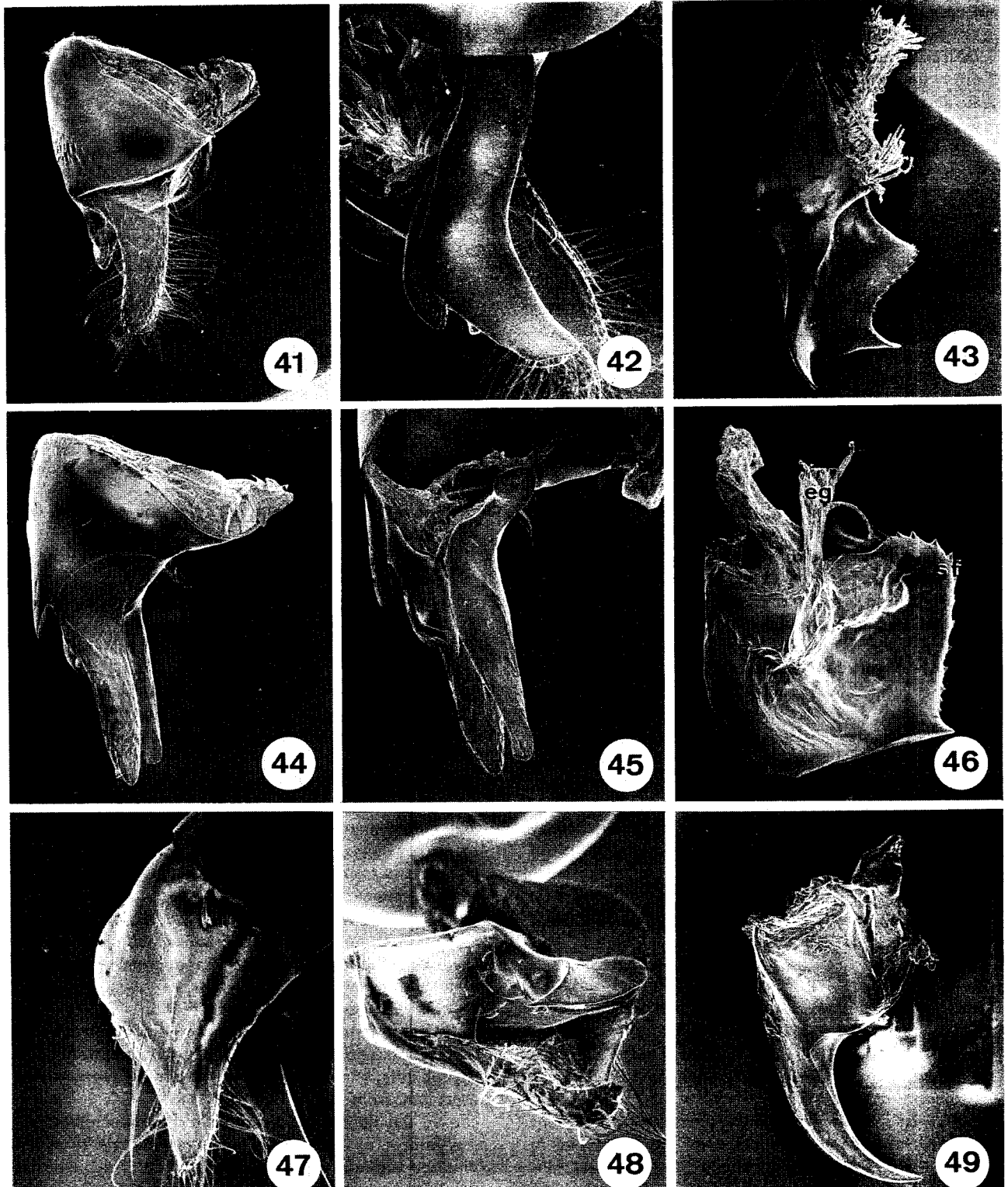
- 10 Mandible short (but meeting medially), falcate to pointed (Fig. 27).
- 11 Antennal scape short, not extended beyond the occiput.
- 12 Pygidial gland present.
- 13 Subgenital plate with a short apico-cranial appendage (Fig. 38).
- 14 Sagitta without an extended space between the ergot and the beginning of the serrated face (Fig. 55).
- 15 Wings without pilosity on the dorsal surface.

*Comparisons.* This is an easily recognizable genus within Formicini with all three castes having a falcate mandible. The falcate mandible has no preapical cleft as in the case of some *Cataglyphis* species. In addition, the males have a short antennal scape and they are always much smaller than the females.

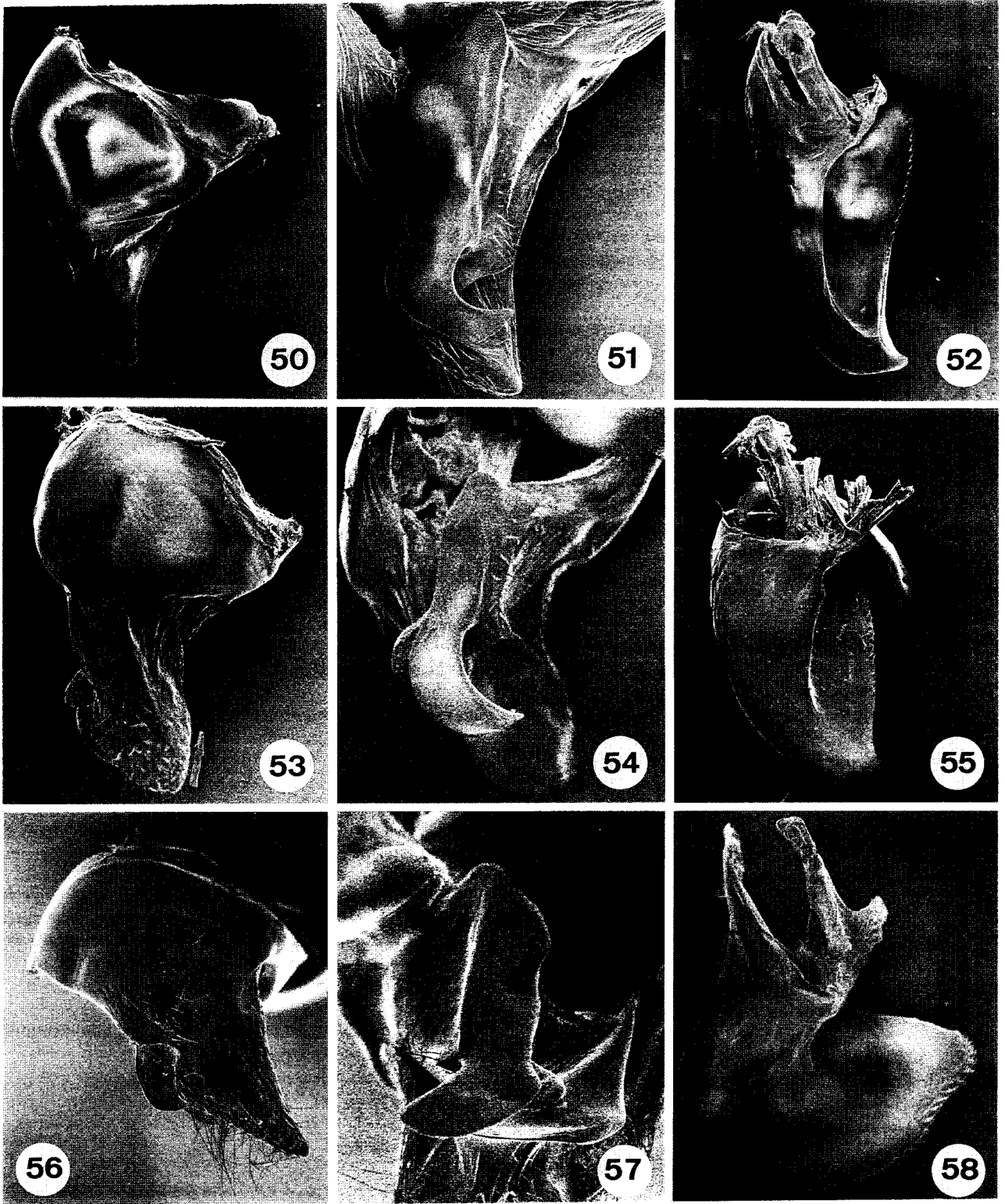
*Distribution and biology.* This is a holarctic genus with three species in the palaeartic region and two species in the nearctic. The preferred habitats are open sunny places in meadows and in steppe within the forest and steppe vegetation zones where its hosts co-occur.

*Polyergus* is a very uniform genus, concerning both morphology and behaviour. All the species are obligatory dulotic ants, and the slave ants are always *Formica* spp., especially from the *fusca* group. Slave raids are usually carried out during day-time and in groups without prior recruitment by scouts. The nests include up to several hundred workers, and usually one queen. The queens are sometimes ergatogynes. Mating flight is generally in June and July. The freshly mated female needs to start the new colony by getting adopted by a colony of a *Formica* species, and by subsequent killing of the host queen.

A description of the raids is given by Forel (1874), and a synthesis and list of species and hosts is provided by Hölldobler & Wilson (1990).



**Figs 41–49.** Male genitalia: squamula and stipes; volsella; sagitta. eg = ergot; sf = serrated face. (41–43) *Cataglyphis bicolor*; (44–46) *Cataglyphis emmae*; (47–49) *Bajcaridris theryi*.



**Figs 50–58.** Male genitalia: squamula and stipes; volsella; sagitta. (50–52) *Formica rufa*; (53–55) *Polyergus rufescens*; (56–58) *Proformica* sp.

**Proformica Ruzsky** (Figs 8, 15, 17, 22, 28, 39, 56–58)

*Proformica* Ruzsky, 1902: 13 [as subgenus of *Formica*].

Type-species: *Formica nasuta* Nylander, 1856: 66; by monotypy. [Raised to genus: Bondroit, 1918: 40.]

*Comments.* This genus is hardly known and no complete series including all castes have been described (Dlussky, 1969). Approximately fifteen species are included in *Proformica*, which is in need of a revisionary study at species level. The species of the former Soviet Union have been described and revised by Dlussky (1969). Collingwood (1978a) provided a key to fauna of the Iberian peninsula, and Agosti & Collingwood (1987a, b) a synonymic list and a key to the Balkan species.

The following diagnosis and descriptions are mainly based on loans of undescribed specimens or on recently collected material by C. A. Collingwood and D. Agosti.

**WORKER.** Formicini ant with the following combination of characters:

- 1 Dimorphic worker caste, with larger workers with a subquadrangular head and minor workers with an elongate head (Figs 15, 17).
- 2 Second and third funicular segments shorter than the first.
- 3 Mandible with a row of teeth declining from apex to the base (Fig. 8).

**FEMALE.** As worker but with the following modifications:

- 3 Larger or of the same size as the large workers.
- 4 Ergatogyne, sometimes with an enlarged alitrunk and some additional sclerites, never seen with a full set of flight sclerites.
- 5 Wings with dense pilosity on the dorsal surface.

**MALE.** Formicini ant with the following combination of characters:

- 6 Of the same size as the females.
- 7 Head narrower or of the same width as the alitrunk (Fig. 28).
- 8 Alate, a full set of flight sclerites developed.
- 9 Subgenital plate with a transversal hole distal to the median apical appendage (Fig. 39).
- 10 Stipes an acute, apically rounded triangle (Fig. 56).
- 11 Sagittae apically rounded, the dorsal beginning of the sagittate part distinctly set apart from the ergot (Fig. 58).
- 12 Head, alitrunk and petiole covered with a thick, erect pilosity (Fig. 28).
- 13 Wings with dense pilosity on the dorsal surface.

*Comparisons.* The females and workers are different from *Formica* in the teeth formula which is regularly declining in *Proformica* and with less than six teeth. The dimorphic worker caste and the short funicular segments separates *Proformica* species from the species of the *Cataglyphis* genus complex. The combination of the small head (in comparison to the alitrunk), the very long and dense pilosity, the shape of the subgenital plate and the

median lobe of the stipes is unique within the Formicini.

*Distribution and biology.* *Proformica* has a patchy distribution within the palaeartic region, from Mongolia through Central Asia, Caucasus, Balkans to Spain, but not in the Alps or the Apennines. The species are living in open habitats, such as grasslands above the timberline, the steppic zones or on the Mediterranean seashore.

So far, all nests which have been dug out indicate a strict monogyny and ergatogynous queens. Closer examination nevertheless revealed some flight sclerites are developed, which could also be due to an allometric growth of the alitrunk, as the same development can be observed in the large workers of *Cataglyphis bombycinus* or in those of the *bicolor* group, living in the same nest as proper females.

The nests are generally small and include a few hundred workers. The presence of honey-pot ants in some of the species (e.g. *epinotalis*) is unique among the Formicini. Mating flight takes place in June and July.

*P. epinotalis* and *longiseta* are slaves of *Rossomyrmex proformicarum* and *minuchae* respectively (Arnoldi, 1928; Marikovski, 1974; Tinaut, 1981).

**Rossomyrmex Arnoldi** (Figs 9, 16, 24)

*Rossomyrmex* Arnoldi, 1928: 299. Type-species: *Rossomyrmex proformicarum* Arnoldi, 1928: 300; by original designation.

**WORKER.** Formicini ant with the following combination of characters:

- 1 Shining and smooth surface.
- 2 Mandible subtriangular with a row of indistinct denticles on the masticatory border (Fig. 9).
- 3 Maxillary and labial palps filiform.
- 4 Scapus clavate (Fig. 16).
- 5 Frontal carina reduced but present as a ridge medial to the antennal sockets (Fig. 16).
- 6 Head with an emarginate occiput (Fig. 16).
- 7 Hind tibia with a dense pubescence; the double row of bristles on the ventral side present but hardly developed.
- 8 Petiole brick-like, with very distinct bristles on the dorsal anterior crest, pointing backwards (Fig. 24).
- 9 First gastral tergite low (Fig. 24).

**FEMALE.** As worker but with the following modifications:

- 10 All flight sclerites present.
- 11 Wings with dense pilosity on dorsal surface.
- 12 Wings long,  $WI > 150$ .

**MALE:** unknown.

*Comparisons.* The worker and female are diagnosed by the combination of the emarginate occiput, the slender, long maxillary palps, the shining surface of alitrunk and head, and the teeth formula of the mandible.

*Distribution and biology.* The distribution areas of the two species as well as the one of their hosts (*Proformica* species) are widely separated. *R. proformicarum* (with

*P. epinotalis* as slave) is distributed in south-east Kazakhstan (Arnoldi, 1928; Marikovskiy, 1974), and *minuchae* (*P. longiseta*) in the Sierra Nevada, Spain (Tinaut, 1981). *R. proformicarum* is living in the transitional zone from the steppe to the desert, and *minuchae* is living in subalpine and alpine meadows.

Both the species are slave makers with small colonies with 20–200 ants and are monogynous. The slave raids differ from those of *Polyergus*. The recruited workers are carried to the nest to be raided, and not only pupae but larvae and eggs are taken. The description of a raid by Marikovskiy (1974) indicates the use of polarized light in orientation. A detailed description and discussion of the biology, nest size and structure, foraging, diurnal and annual activity are given by Arnoldi (1932), Marikovskiy (1974) and Tinaut (1981), and a comparison with other species is provided by Hölldobler & Wilson (1990).

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**Appendix**

Data set including fifty characters used to infer the phylogeny of the Formicini. Potential synapomorphic characters are followed by autapomorphies for the genera. The character states given in the data matrix correspond with the assumed ground plan for the genera. *Melophorus* is included as outgroup.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45				
<i>Melophorus</i>	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	5				
<i>Alloformica</i>	0	0	0	0	0	0	1	1	1	2	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1	0	0	0	1	0	0	1	1	0	1	1	1	1	0	0	0	1	0	1	1	0	1	0	1
<i>Bajcaridris</i>	0	0	1	0	1	0	1	2	0	1	0	0	1	0	0	1	0	0	1	1	0	1	1	1	0	1	1	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	
<i>Cataglyphis</i>	1	1	0	0	0	0	1	1	1	2	1	0	0	1	1	0	0	0	1	1	0	1	1	1	1	0	0	1	1	0	0	1	1	0	1	1	1	1	0	0	1	1	0	1	1	1	1	1	
<i>Formica</i>	1	1	1	0	1	1	1	0	1	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0	0	1	1	0	1	1	1	1	0	0	1	1	0	1	1	1	1	0	0	1	1	1	
<i>Polyergus</i>	1	0	1	1	2	2	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	0	1	1	0	1	1	0	1	0	0	1	1	0	0	1	
<i>Proformica</i>	1	1	1	0	0	1	0	1	1	1	2	1	0	1	0	0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	0	0	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	
<i>Rossomyrmex</i>	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

*Shared characters (potential synapomorphies)***WORKER and FEMALE**

- 1 Size polymorphic worker and reproductive castes (0); monomorphic (1).
- 2 Worker caste monomorphic (0); polymorphic (1).
- 3 First maxillary palp segment in cross-section flattened (Fig. 29) (0); round (1).
- 4 Frontal carina distinct and crest-shaped (Fig. 11) (0); bulge-like (Fig. 13) (1).
- 5 Fourth mandibular denticle, from apex to base, smaller than third (Fig. 8) (0); larger than third (Fig. 3) (1); no denticles at all (Fig. 7) (2).
- 6 Mandible with five denticles (Fig. 8) (0); six to nine denticles (Fig. 6) (1); no denticles at all (Fig. 7) (2).
- 7 Maxillar stipes with long J-shaped hairs of the same length as the stipes (Fig. 29) (0); short hairs (1).
- 8 Propodeal spiracle small and ellipsoid (Fig. 18) (0); elongate and parallel-sided (Fig. 21) (1).
- 9 First gastral segment, in lateral view and relative to the propodeum, low (0); high (1).

**MALE**

- 10 Subgenital plate apically spade-shaped (Fig. 38) (0); trilobed (Fig. 35) (1); pointed (Fig. 37) (2).
- 11 Subgenital plate cranially extended (Fig. 38) (0); not extended (Fig. 35) (1).
- 12 Subgenital plate with cranial extension pointed (Fig. 38) (0); truncated (Fig. 37) (1); not present (Fig. 35) (2).
- 13 Squamula and stipes laterally fused (0); at least cranially separated by a membranous area (1).
- 14 Sagitta with ergot and dorsal end of serrate face widely separated (Fig. 46) (0); confluent (Fig. 52) (1).
- 15 Stipes with median appendage (Fig. 40) (0); without (1).
- 16 Wings with pubescence on the dorsal and ventral face (0); not present or at most very short and cone-shaped (1).
- 17 Front wings with hind margin with erect hairs protruding over the margins (0); no fringe of hairs present (1).
- 18 Wings relative to alitrunk short, WI <150 (0); long, WI >180 (1).
- 19 Front wing with the frontal margin up to the pterostigma straight (0); curved (1).
- 20 Head in full frontal view compressed (Fig. 31) (0); depressed (Fig. 26) (1).

*Autapomorphies***WORKER and FEMALE**

- 21 Small ants, AL <1.4 mm (0); larger AL >2 mm (1).
- 22 Body surface roughly sculptured (Fig. 10) (0); smooth (Fig. 16) to finely chagrinated (Fig. 11) (1).
- 23 Maxillary palp formula 6,4 (0); lower (1).
- 24 Maxillary palp segments long and filiform (0); stout (1) (Fig. 14).
- 25 Mandible falcate (Fig. 7) (0); with a distinct basal, masticatory and outer face (Fig. 6) (1).
- 26 Psammophore formed by long J-shaped hairs on the mandible, the stipes of maxilla and the gula present (0); absent (1).
- 27 Clypeus with apical face convex (Fig. 12) (0); straight (Fig. 13) (1).
- 28 Eyes domed (Fig. 10) (0); flat (Fig. 13) (1).
- 29 Long scape, SI >120 (0); shorter scape, SI <120 (1).
- 30 Scape with erect pilosity (Fig. 10) (0); without (1).
- 31 First funicular segment longer than the two subsequent (0); shorter (1).
- 32 Head in full frontal view with occiput emarginate (Fig. 16) (0); straight (13) to convex (Fig. 10) (1).
- 33 Metapleural gland orifice distinct (Fig. 18) (0); small (Fig. 19) (1).



## MALE

- 34 At base of stipes, i.e. between stipes and volsella, crest (Fig. 57) (0); no crest present (1).
- 35 Subgenital plate apically with two bristles (0); without (1).
- 36 Volsella oriented along body axis (0); dorso-ventrally (1).
- 37 Sagitta with the ventral apex elongated (Fig. 49) (0); short (Fig. 41) (1).
- 38 Sagitta reaching in situ as far ventrally as stipes, viewed in lateral view (0); sagitta shorter (1).
- 39 Dorsal part of the ninth and tenth abdominal tergite sclerotized (0); membranous (1).
- 40 Pygidial gland present (0); absent (1).
- 41 Terminal branches of front wing venation reduced (0); extended to almost the margins of the wing (1).
- 42 Head with few scattered erect hairs (Fig. 31) (0); dense pilosity (Fig. 28) (1).
- 43 Ocelles, in comparison to those in the worker caste, slightly enlarged (Fig. 26) (0); distinctly larger (Fig. 31) (1).
- 44 Ocelles raised and forming a triangular socket (Fig. 31) (0); not forming a socket (Fig. 26) (1).
- 45 Mandible basally divergent (Fig. 28) (0); convergent (Fig. 27) (1).
- 46 Mandible with apical cleft (Fig. 28) (0); without (Fig. 27) (1).
- 47 Eyes with large ommatidia (Fig. 31) (0); small ommatidia (Fig. 28) (1).
- 48 Eyes almost hemispherical (Fig. 31) (0); flatter (Fig. 28) (1).
- 49 Scape short, not extended beyond the occiput (Fig. 27) (0); extended beyond the occiput (Fig. 30) (1).
- 50 Proventricule short, asepalous (0); long, sepalous (1).