MONOMORIUM Mayr

(Figs 18–100)

Monomorium Mayr, 1855: 452. Type-species: *Monomorium monomorium* **nom. n.** (replacement name for *Monomorium minutum* Mayr, 1855: 453, junior secondary homonym of *Atta minuta* Jerdon, 1851: 105 [= *M. pharaonis* (L.), 1758: 580]); by monotypy. [See note 1, below.]

Trichomyrmex Mayr, 1865: 19. Type-species: *Trichomyrmex rogeri* Mayr, 1865: 19; by monotypy. [Synonymy by Ettershank, 1966: 82.]

Lampromyrmex Mayr, 1868: 93. Type-species: *Monomorium mayrianum* Wheeler, 1915: 45 (replacement name for *Lampromyrmex gracillimus* Mayr, 1868: 95 (ex Baltic amber), junior secondary homonym of *Monomorium gracillimum* (Smith), 1861*a*: 34); by monotypy. [Synonymy by Wheeler, 1915: 45; Ettershank, 1966: 82.]

Holcomyrmex Mayr, 1878: 671. Type-species: *Holcomyrmex scabriceps* Mayr, 1878: 672; by subsequent designation of Bingham, 1903: 280. [Synonymy by Ettershank, 1966: 82.]

Epoecus Emery, 1893*a*: cclxxvi. Type-species: *Epoecus pergandei* Emery, 1893*a*: cclxxvi; by monotypy. [Synonymy by Ettershank, 1966: 82.]

Wheeleria Forel, 1905: 171. Type-species: *Wheeleria santschii* Forel, 1905: 171; by monotypy. [Junior homonym of *Wheeleria* Tutt, 1905: 37 (Lepidoptera).]

Wheeleriella Forel, 1907*c*: 145 (replacement name for *Wheeleria* Forel, 1905: 171). [Synonymy by Ettershank, 1966: 82.]

Epixenus Emery, 1908*a*: 556. Type-species: *Monomorium advena* Brown & Wilson, 1957: 244 (replacement name for *Epixenus andrei* Emery, 1908*a*: 557, junior secondary homonym of *Monomorium andrei* Saunders, 1890: 204); by subsequent designation of Wheeler, 1911: 163. [Synonymy by Brown & Wilson, 1957: 244.]

Mitara Emery, 1913: 261 [as subgenus of *Monomorium*]. Type-species: *Monomorium laeve* Mayr, 1876: 101; by original designation. [Synonymized with *Monomorium (Lampromyrmex)* by Emery, 1922: 183 and Wheeler, 1922: 162.]

Chelaner Emery, 1914: 410 [as subgenus of *Monomorium*]. Type-species: *Monomorium (Chelaner) forcipatum* Emery, 1914: 410; by subsequent designation of Emery, 1922: 168. [Raised to genus by Ettershank, 1966: 93.] **Syn. n.**.

Notomyrmex Emery, 1915: 190 [as subgenus of *Monomorium*]. Type-species: *Atta antarctica* Smith, 1858: 167; by original designation. [Synonymized with *Chelaner* by Ettershank, 1966: 93.] [See note 2, below.]

Xeromyrmex Emery, 1915: 190 [as subgenus of *Monomorium*]. Type-species: *Formica salomonis* L., 1758: 580; by original designation. [Synonymy by Ettershank, 1966: 82.]

Parholcomyrmex Emery, 1915: 190 [as subgenus of *Monomorium*]. Type-species: *Myrmica gracillima* Smith, 1861*a*: 34 [= *Monomorium destructor* (Jerdon), 1851: 105]; by original designation. [Synonymy by Ettershank, 1966: 82.]

Syllophopsis Santschi, 1915: 259 [as subgenus of *Monomorium*]. Type-species: *Monomorium modestum* Santschi, 1914*b*: 17; by monotypy. [Raised to genus by Santschi, 1921*b*: 119.] **Syn. n.**

Corynomyrmex Viehmeyer, 1916: 134 [as subgenus of *Monomorium*]. Type-species: *Monomorium (Corynomyrmex) hospitum* Viehmeyer, 1916: 133; by monotypy. [Provisional synonymy by Ettershank, 1966: 82, here confirmed.]

Isolcomyrmex Santschi, 1917: 296 [as subgenus of *Monomorium*]. Type-species: *Monomorium santschianum* Ettershank, 1966: 92 (replacement name for *Holcomyrmex santschii* Forel, 1907*d*: 203, junior secondary homonym of *Monomorium santschii* (Forel), 1905: 171); by original designation. [Synonymy by Ettershank, 1966: 82.]

Paraphacota Santschi, 1919*a*: 90. Type-species: *Paraphacota surcoufi* Santschi, *1919a*: 90 [= *Monomorium subopacum* (Smith), 1858: 127]; by monotypy. [Synonymy by Santschi, 1927: 243.]

Equestrimessor Santschi,1919*a*: 92 [as subgenus of *Monomorium*]. Type-species: *Holcomyrmex chobauti* Emery, 1897*a*: 418; by subsequent designation of Donisthorpe, 1943*b*: 644. [Synonymy by Ettershank, 1966: 82.]

Xenhyboma Santschi, 1919*c*: 405. Type-species: *Xenhyboma mystes* Santschi, 1919*c*: 405 [= *Monomorium medinae* Forel, 1892*b*: 454]; by monotypy. [Provisional synonymy by Ettershank, 1966: 82, confirmed by Espadaler, 1982: 112.]

Protholcomyrmex Wheeler, 1922: 162 [as subgenus of *Monomorium*]. Type-species: *Monomorium rothsteini* Forel, 1902*b*: 444; by original designation. [Synonymized with *Chelaner* by Ettershank, 1966: 93.]

Ireneidris Donisthorpe, 1943*a*: 81. Type-species: *Ireneidris myops* Donisthorpe, 1943*a*: 81 [= *Monomorium talpa* Emery, 1911: 252]; by original designation. [Synonymy by Ettershank, 1966: 82.]

Schizopelta McAreavey, 1949: 14. Type-species: *Schizopelta falcata* McAreavey, 1949: 15; by original designation. [Synonymized with *Chelaner* by Ettershank, 1966: 93.]

Pharaophanes Bernard, 1952: 238 (attributed to Santschi; without description and without designation of type-species). [Nomen nudum.]

Note 1, the type-species of *Monomorium*.

Since its inception as a genus the type-species of *Monomorium* has been stated as *M. minutum* Mayr (1855), but for some unknown reason all later authors appear to have overlooked the fact that *minutum* Mayr is a junior secondary homonym of *Atta minuta* Jerdon (1851), which is itself a junior synonym of *M. pharaonis* (L.).

Jerdon's short diagnosis of *Atta minuta* and his description of its habits leaves no doubt that its true identity is *pharaonis*. He says that 'this minute species makes a temporary nest in various situations, in an empty box, between the back of a book and its leaves, even among the loose pages of a book, in an empty shell, &c. &c. Nothing is used in its construction, a shelter from the light merely being sought for.' He also says that it is 'very common in the Carnatic and most of India', and that it 'appears to prefer dead animal matter to saccharine or vegetable products.'

As far as I can ascertain *minuta* Jerdon appeared as a synonym of *pharaonis* for the first time in Emery (1892) and the synonymy is repeated in Dalla Torre (1893). Earlier Mayr (1878) had suggested that *minuta* Jerdon and *vastator* Smith were conspecific. Examination of the *vastator* type-material confirms that its synonymy with *pharaonis* by Donisthorpe (1932) was correct. Bingham (1903) included *minuta* Jerdon as a synonym of *pharaonis* and it is most likely that he had access to, and examined, Jerdon's now vanished material.

All this serves to confirm that *Atta minuta* Jerdon truly belongs in *Monomorium* and is a valid junior synonym of *pharaonis*. This leaves *M. minutum* Mayr as a junior homonym in need of a replacement name.

In the past some 17 infraspecific taxa of *minutum* Mayr have been described. None of these infraspecific names applied to southern European forms (the type-locality of *minutum* Mayr is in Italy) and only one, *chinense* Santschi, was described from the Palaearctic region. Other supposed infraspecific forms of *minutum* Mayr originated in the Afrotropical region, Madagascar, Sri Lanka, Java, Hawaii, Samoa, North America and Brasil. Examination of the available type-material of these forms and comparison of that material with the type-series of *minutum* (in NMV) leads me to conclude that only *chinense*, *javanum* Forel, and *liliuokalanii* Forel (= *samoanum* Santschi) belong in the same species-complex as *minutum* Mayr. The last two names were given as junior synonyms of *minutum* by Wilson & Taylor (1967) but I do not consider them conspecific and suspect that they may in fact be synonymous with *chinense*, which appears to be valid and distinct from *minutum* Mayr. Finally I suspect that the southern European populations currently referred to as *minutum* Mayr may in truth consist of two separate species.

Hence none of the current infraspecific names is taxonomically available as a replacement for the junior homonym *minutum* Mayr, and I have designated the name *Monomorium monomorium* as a replacement for *M. minutum* Mayr.

Note 2, authorship and date of *M. antarcticum*, type-species of *Notomyrmex*.

Earlier catalogues such as Mayr (1863), Dalla Torre (1893), and Emery (1922) all regarded Smith (1858) as the author of the species-level name *antarctica*, but Brown (1958) and Ettershank (1966) refer the name to White and date it 1848. Brown gives Hutton (1881) as the authority for this date but the entry under *antarctica* in this last publication refers back only to Smith (1858).

Smith's (1858: 167) notation of this name gives '*Atta antarctica*' and is sub-headed '*Formica antarctica*, White, Zool. Erebus & Terror, pt. 2.' The section of the 'Zoology of the Voyage of H.M.S. Erebus & Terror' which deals with insects has Adam White and Arthur Gardiner Butler as joint authors, and the date on this part is given as 1846–1874! However, the 'contents' of volume 2 indicate that the insects were dealt with in two sections, the first of which, pp. 1–24, was by White and is dated 1846. The second part, pp. 25–51, was by Butler and is dated 1874. This same information is repeated in the massive review of early entomological literature by Horn & Schenkling (1929), who added that plates 1–6 accompanied pp. 1–24, which appeared in 1846 with White as author.

Unfortunately the name *antarctica* in the 'Voyage of H.M.S. Erebus & Terror' publication is on page 27 and plate 7, as *Aphaenogaster antarctica*, and appeared in 1874 with Butler as author. Secondary notations below this name include '*Formica antarctica*, White Ms, tab. 7, f. 13,' and '*Atta antarctica*, Smith, Cat. Hymenopt. Ins. 6 p. 167,' indicating that Butler was aware that the name was already extant in the literature and available by dint of Smith's (1858) publication.

All this internal evidence seems to show that Smith had access to the then unpublished notes of White referring to insects of the Erebus & Terror voyage which had not been included in White's (1846)

publication (which finally appeared in Butler, 1874). Thus by using the name *Atta antarctica*, and producing a description of the species from White's unpublished manuscript, Smith (1858) became the valid author of the name.

WORKER. Minute (TL < 1·5) to moderate (TL *ca* 8.0) sized monomorphic to polymorphic myrmicine ants. Palp formula predominantly 2,2 but counts of 5,3; 3,3; 2,3; 1,2; and 1,1 are known in some individuals or discrete species-groups. Mandibles with 3–5 teeth (4 is the vastly predominant count) which decrease in size from apex to base. Basalmost tooth sometimes reduced to a minute offset denticle. Median clypeal seta conspicuous. Median portion of clypeus raised, the raised section longitudinally bicarinate; the carinae usually distinct but sometimes reduced or blunt and rounded. Frontal carinae absent behind frontal lobes. Antennal scrobes absent. Antennae 10–12 segmented (most frequently 12), usually with a conspicuous 3-segmented club but in some the club 4-segmented or not clearly defined; club never of 2 segments. Eyes present, usually conspicuous but reduced in some; reduced to a single ommatidium in the *fossulatum*-group (Fig. 94). Eyes situated at or in front of the midlength of the head side. Metapleural glands of moderate size, never enormously hypertrophied. Metapleural lobes usually small and rounded. Metanotal groove present, commonly impressed. Propodeal dorsum usually unarmed and rounding into the declivity, some individuals or whole species-groups with the propodeum angulate, denticulate, or with short angular lamelliform projections; developed propodeal spines extremely rare. Propodeal spiracle usually circular and located at about the midlength of the sclerite, rarely slightly behind the midlength; the spiracle oval to slit-shaped in the *scabriceps*-group (Fig. 33). Fore coxae larger than middle and hind coxae but not grossly enlarged. Petiole pedunculate anteriorly, the petiolar spiracle usually close to or at the node, only rarely close to the midlength of the peduncle (*scabriceps*-group, Fig. 33, and some Australian species). Petiole node generally subconical to cuneate in profile, and narrowly rounded above. Petiolar peduncle with a small anteroventral process, only rarely the process vestigial or lacking. Sting strong to very feebly developed, in many linear-subspatulate apically but lacking lamelliform appendages at an angle to the long axis of the sting.

FEMALE. Larger than conspecific worker, sometimes very much larger. Head not disproportionately small in comparison to alitrunk, the HW usually equal to or greater than the maximum width of the mesoscutum, only rarely slightly narrower. Usually alate and with a full complement of flight sclerites but numerous species with apterous to extremely ergatoid females, these wingless forms showing a finely stepped morphoclinal reduction in size and number of alitrunk sclerites (Figs 27–30). A few species with worker-female intergrades. Characters as worker but eyes larger and sometimes slightly behind the midlength of the sides. Ocelli present except in some extreme ergatoids. Short flattened propodeal spines occur in a few ergatoids. On the forewings of alates the radial cell is always open and cross-vein *r-m* absent. Cross-vein *m-cu* is conspicuous in a few groups (Figs 18, 19) but is usually absent. Species of the *scabriceps*-group show its disappearance (Figs 19–21) and sometimes an individual may have *m-cu* present on one forewing but absent from the other. In small or minute species of all groups cross-vein *cu-a* tends to vanish (Figs 23, 24). Primitively all veins are tubular and strongly sclerotized (Figs 18–21) but in most groups the veins are predominantly depigmented and flattened, or reduced to vestigial lines (Figs 22, 23). In the last case *R* + *Rs* and *2r* plus the distal portion of *Rs* usually remain broader and more strongly sclerotized than the remaining veins (Figs 22, 23). Axillae frequently large and almost meeting at the midline, in some groups the axillae partially or wholly fused and stretching as a band across the entire dorsum. Mesoscutum and scutellum never abutting, always separated by the axillae or, where the axillae are separated mid-dorsally, by a broad impression.

MALE. Usually the same size as or a little smaller than the conspecific female, generally much larger than the worker but in the *scabriceps*- and *destructor*-groups the males are very small indeed. Head width at maximum about equal to the width of the mesoscutum except in the two groups just mentioned, where the head is disproportionately small and much narrower than the mesoscutum. PF as in workers. Mandibles with 1–4 (usually 3–4) teeth, the basalmost sometimes reduced to a minute denticle. Median clypeal seta conspicuous, median portion of clypeus not bicarinate. Antennae with 11–13 segments, not clavate apically. Scape cylindrical to globular, first funicular segment cylindrical to globular (Figs 25, 26). Eyes large, usually situated near the midlength (Fig. 25) but in the *scabriceps*- and *destructor*-groups situated anteriorly, abutting the clypeus (Fig. 26). Ocelli conspicuous, turreted in some groups. Parapsidal furrows distinct to vestigial. Notauli usually absent, only rarely present. Mesoscutum frequently with a V-shaped unsculptured or more weakly sculptured area anteromedially. Venation as alate female. Axillae small and separated by a transverse impression, sometimes fused to scutellum and more rarely also fused to scutum. Axillae extend as a band across the dorsum in *scabriceps*- and *destructor*-groups. Male frequently more strongly sculptured than conspecific female or worker.

Monomorium is a large and extremely diverse genus which contains at present some 300 valid species, of which about half occur in the Afrotropical zoogeographical region. The estimate of the world fauna is very much a guess as the species of most zoogeographical regions have never been revised or subjected to any synthesizing taxonomic treatment. As the genus is defined here the vast majority of *Monomorium* species inhabit the Old World, particularly the tropics. Very few endemic species occur in North America (DuBois, 1986), and even fewer in the neotropical region where *Monomorium* is mostly replaced by an extensive *Solenopsis* fauna (Kempf, 1972). The main centres of speciation of *Monomorium* include Africa and Australia, with secondary centres in the Oriental region (Bingham, 1903) and Madagascar. The Malagasy fauna is particularly interesting as it contains some small endemic species-groups, one of which (with two indeterminate species) shows the highest and hence most primitive PF count (5,3) yet encountered in the genus. In general the species-groups of *Monomorium* are not restricted to a single zoogeographical region but tend to be widely distributed. However, some small specialized groups have a much more restricted range. Most species-groups remain to be defined on a world-wide basis. The groups occurring in the Afrotropical region, revised below, are so defined, but the large and fascinatingly diverse Australasian fauna contains a good number of endemic species-groups which await accurate delineation. After Africa Australia contains the most diverse and widely radiated fauna of the genus and a taxonomic study of it is long overdue, especially in the light of the fact that the Neotropical genera *Nothidris* and *Antichthonidris* appear to be nothing more than isolated fractions of this fauna.

Workers of *Monomorium* show a striking morphological diversity from group to group but within species-groups tend to be relatively uniform in structure. The most strongly modified forms include the large granivores of the *scabriceps*-group, but these constitute only a small fraction of the fauna, most species of which are scavengers or active predators. Females for the most part share the characters exhibited by the workers. In some groups, particularly the *salomonis*- and *monomorium*-groups, there is a marked tendency for the females to become apterous and ergatoid. It has been postulated (Bolton, 1986*b*) that this phenomenon is associated with a shift in dispersal strategy from mating flight followed by claustral nest founding to autoparasitism followed by colony fission. Males remain poorly known in the genus but for the most part present a fairly uniform habitus except in the *scabriceps*- and *destructor*-groups where they have convergently come to resemble the males of *Solenopsis*.

Monomorium contains some of the world's most widely distributed and successful tramp-species, including the cosmopolitan *pharaonis* (L.) and *floricola* (Jerdon), the pantropical *destructor* (Jerdon), and the Old World tropical *latinode* Mayr, *subopacum* (Smith), and *talpa* Emery.

Apart from the references given above, recent taxonomic works on *Monomorium* at species-level are very sparse. Mention may be made of Wilson & Taylor (1967) for the Polynesian fauna, Baroni Urbani (1964*a*, 1964*b*, 1968*b*) for the Italian fauna, Bernard (1968) for the west European fauna, Brown (1958) for the fauna of New Zealand, Collingwood (1978) for the fauna of the Iberian Peninsula. Older synoptic studies, now rather outdated but still retaining some value include Arnold (1916), Bingham (1903), Emery (1908*a*, 1908*b*), and Santschi (1936).

The genus-level synonyms of *Monomorium*

The current genus-level synonymy of *Monomorium* is extensive, including some 22 names at the present time. Discounting nomina nuda these names consist of a number of supposed oddities which were originally described as separate small genera, and a welter of moderately to extremely poorly defined subgenera which were described in the first quarter of this century. In terms of the species-group concept employed in this paper the various genus-level synonyms are dispersed as follows among the groups.

Species-group in this paper.	Genus-level synonyms of *Monomorium* applicable to that group.
M. salomonis-group	*Epixenus, Paraphacota, Wheeleriella, Xenhyboma, Xeromyrmex.*
M. scabriceps-group	*Holcomyrmex, Trichomyrmex.*
M. destructor-group	*Equestrimessor, Isolcomyrmex, Parholcomyrmex.*
M. fossulatum-group	*Ireneidris, Syllophopsis.*
M. monomorium-group	*Corynomyrmex, Epoecus, Lampromyrmex, Mitara.*
M. forcipatum-group	*Chelaner, Notomyrmex.*
M. falcatum-group	*Schizopelta.*
M. rothsteini-group	*Protholcomyrmex.*

Phacota, included by Ettershank (1966) as a synonym of *Monomorium*, is here returned to its previous status as a separate genus, for reasons given under its discussion, p. 281.

Baroni Urbani (1964*a*: 50) described a genus *Xenoaphaenogaster* based on a single worker discovered in a nest of *Aphaenogaster pallida* (Nylander). The holotype and only known specimen of the type-species, *X. inquilina* Baroni Urbani, has since been lost. In the original description Baroni Urbani placed

Xenoaphaenogaster in the tribe Solenopsidini as it was then understood, close to *Monomorium*. Later Brown (1973) treated the name as a provisional synonym of *Monomorium*, a position reiterated by Krombein *et al.* (1979). This placement is certainly incorrect and *X. inquilina* is not to be associated with *Monomorium* or its close relatives. In my opinion, based on the original description and figures, the now-vanished holotype of *X. inquilina* may well have been a minor worker of *Pheidole pallidula* (Nylander). I hereby provisionally synonymize *X. inquilina* under *P. pallidula*, so that the genus-level name *Xenoaphaenogaster* falls into the synonymy of *Pheidole*.

Genus-level names applicable to the *Monomorium salomonis*-group.

Wheeleriella Forel (1907*c*).

Forel (1905) erected the name *Wheeleria santschii* for a monomoriine inquiline female found with *M. salomonis* in Tunisia. He observed that it was 'probably a parasitic derivative of the genus *Monomorium*.' Later Forel (1907*c*) noted that the genus-level name *Wheeleria* was preoccupied, and proposed *Wheeleriella* as a replacement.

In the following two decades the names of four more inquilines were added to *Wheeleriella*. These included *wroughtoni* Forel (1910*a*) from India (which is incidentally a junior homonym of *M. wroughtoni* Forel (1902), a replacement name is proposed below), and *adulatrix* Santschi (1913*b*), *rufescens* Santschi (1926*b*), and *insidiosa* Santschi (1926*b*), all from Tunisia. The last three names were all treated as infraspecific forms of *santschii* by Santschi (1926*b*) and the present survey regards them all as very minor variations within the species-limits of *santschii*, and hence junior synonyms of that name.

All samples known to the present have been found at the entrances to nests or within nests of *salomonis*-group members. According to Forel (1906) and Santschi (1913*b*) females of *santschii* approach the host nest and wait for a while at the entrance. They are soon accepted by the host workers and gain entry to the nest. Shortly thereafter the host workers kill their own reproductive female and adopt the inquiline, which goes on to lay numerous eggs. These produce only females and males; the worker caste has been lost.

The name *Wheeleriella* was summarily synonymized with *Monomorium* by Ettershank (1966), without further comment. Whilst agreeing totally with Ettershank's conclusion it must be pointed out that the former members of *Wheeleriella* are, morphologically, only very slightly modified from other members of the *salomonis*-group, and that the five names formerly included in *Wheeleriella* represent at most two, and possibly even only one, valid species.

The females are very obviously specialized members of the *salomonis*-group in which the eighth funicular segment is enlarged to form a 4-segmented club and the occipital margin of the head has become strongly concave. The same modification of the head occurs weakly in the males, but their funiculi are normal for the *salomonis*-group. In both sexes the mesoscutum is flattened and bulges forward anteriorly so that it overhangs the pronotum, and in females the petiole and postpetiole nodes are anteroposteriorly compressed. These last two characters occur, though not as strongly developed, elsewhere in the *salomonis*-group. For example, the female of *afrum* André shows modifications in structure that are surprisingly like those of *santschii*. Unlike *santschii*, however, *afrum* retains a worker caste. I suspect that the female of *afrum* may be a temporary social parasite. The two species presently recognized, which formerly constituted *Wheeleriella*, are as follows.