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The *Monomorium carbonarium* species group in the Nearctic and Europe (Hymenoptera: Formicidae)

Bernhard Seifert

Department of Entomology, Senckenberg Museum of Natural History Görlitz, Am Museum 1, 02826 Görlitz, Germany
E-mail: bernhard.seifert@senckenberg.de

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Abstract

A taxonomic revision of the independently living species of the *Monomorium carbonarium* species group, considering 14 described and two newly described taxa, is provided. Taxonomic decisions were based on Numeric Morphology-Based Alpha-Taxonomy considering 22 morphometric characters in 129 samples with 411 workers and 78 gynes. A diagnosis of the group and a key for the workers of the ten recognized independent species is given. Discrete gyne dimorphism – that is, development of volant winged gynes and wingless gynes – is more widely distributed in the group than previously known. This lead in the past, in connection with insufficiency for species separation in workers, to erroneous description of intraspecific gyne morphs as different species by DuBois (1986). *Monomorium minimum* (Buckley 1867), *M. minimum emersoni* Gregg 1945 and *M. trageri* DuBois 1986 are recognized as junior synonyms of *M. carbonarium* (Smith 1858) whereas *M. wheelerorum* DuBois 1986 and *M. minimum* subsp. *cyaneum* Wheeler 1914 fall under junior synonymy of *M. ergatogyna* Wheeler 1904. *Monomorium peninsulatum* Gregg 1945 is confirmed as junior synonym of *M. viridum* Brown 1943. *Monomorium gallicum* n.sp. from W Europe and *M. lorenzoi* n.sp. from S California are described as new. All species can be clustered in the worker caste by multivariate analyses. Species delimitation of gynes is insufficiently solved due to small sample size, polymorphism and unavailable gynes in two species. Within the eight species confirmed for the New World and having their origin there, only *Monomorium carbonarium* was introduced to Europe. Three species are found in Europe of which two, *M. gallicum* n.sp. and *M. monomorium*, are absent from the Nearctic. Supercoloniality, known from Europe in *M. carbonarium* and *M. gallicum* n.sp. and not reported so far from the Nearctic, is supposed to be a new development that took place within the last three decades. Supercolonies of the latter two species were observed in nine local populations introduced to urban environments in France, Germany and the Netherlands.

Keywords: cryptic species, supercoloniality, invasive species, numeric morphology-based alpha-taxonomy

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1. Introduction

After the turn of the millennium two supercolonial species of tiny blackish *Monomorium* ants appeared in urban habitats of France, Germany and the Netherlands. They are frost resistant, may establish permanent outdoor colonies and cause a lot of problems. Their supercolonies may grow to enormous size and they invade households. They penetrate here tiny crevices and may cause short circuits in electric installations such as rooters, laptops or relays. Due to their vast numbers that flood living rooms and kitchens they are a big nuisance for humans. They are polyphagous and take up each usable food source such as, for instance, fat deposits in cooker hoods. Housewives are not amused when hundreds of these tiny beasts suddenly topple down into their meals some minutes after they began with cooking.

The two species are related to *Monomorium carbonarium* (Smith 1858) and attempts to give them a valid name (e.g. Seifert 2018) remained speculative as long as no revision of the 17 taxa described so far in the *M. carbonarium* group from the Nearctic and Europe has been done. Referring to the oldest available name among the species in consideration, I collect these taxa under the name *Monomorium carbonarium* group. Including the species described here as new, this group contains 10 taxa of independently living species and 3 taxa confirmed or supposed to be workerless inquilines. The latter three – *Monomorium pergandei* (Emery 1892), *M. talbotae* DuBois 1986 and *M. inquilinum* DuBois 1986 – are exempt from treatment here as this revision is focusing on independent species.

There is no chance to get some reasonable order into the taxonomic chaos within the *Monomorium carbonarium* group without numerically recording morphological characters in a reproducible way and evaluating these data in exploratory and hypothesis-driven data analyses. In his revision, incorporating 15 Nearctic taxa of this group, DuBois (1986) did not provide reproducible data of how to separate workers and gynes. His measuring at magnifications of 80x and rounding the data to 0.01 mm was an approach inadequate to the tiny objects investigated. Except for few species with extreme character expression, DuBois' measuring data are virtually useless both by their inaccuracy and by the mode he presented them. To give an example which accuracy is required here: The dorsomedian length of the third funiculus segment contributes significantly to separate the workers of *M. carbonarium* and *M. gallicum* n. sp. and is 22.6 ± 1.6 µm in the former and 25.8 ± 1.5 µm in the latter – expressed in millimeters, the difference is 0.0032.

The second disadvantage of DuBois' revision was basing his taxonomy on morphological differences between gynes – mainly using subjective assessment of sculpture, pilosity and mesosoma shape assisted by very coarse line drawings. Firstly, for many of the supposed species only single samples with gynes are available while there is plenty of workers. Small sample size means uncertain decisions. Secondly, fueled by decisions based on single gyne samples and inability to separate the workers, there is a high risk in species groups with gyne polymorphism to misinterpret intraspecific morphs as different species. Winged gynes and wingless gynes represent different dispersal and colony-founding strategies. When both morphs are developed in a species they may have a regionally differing frequency – for example, *Monomorium carbonarium* develops both morphs in the Nearctic whereas in Europe only the wingless gyne seems to occur. Furthermore, it is rare that both morphs occur within the same nest. In fact, Dubois underestimated the frequency of intraspecific gyne polymorphism in the *M. carbonarium* group and reported this only for *Monomorium trageri* DuBois 1986 and *M. viridum* Brown 1943. The opinion of Stefan Cover (formerly MCZ Cambridge) expressed in an e-mail to the author 17 November 2015 tells a very different story and is probably close to the truth: "So far, all free-living species in the group have both alate and wingless queen morphs, with the exception of *M. emarginatum* from the northeastern US which appears to have only alate queens, and *M. ebeninum* from the Caribbean, which has only wingless queens. *M. trageri* may be the wingless morph of *M. minimum*. All of the species are polygynous, but none of the species develop unicolonial populations, or are more than occasional pests in buildings here."

This paper would have been unthinkable without the loans from five big natural history museums in the USA containing altogether some 1750 pinned specimens. This number appears sufficient for a sound revisionary work. However, to my great disappointment, only about 15% of the specimens could be evaluated for the full set of 20 morphological characters. Mounting these tiny ants adequately is a big challenge for manual skill which the majority of collectors did not meet. Most of specimens were partially drowned in glue that was often not soluble in water or any apolar solvent. If soluble, the time-consuming re-mounting was only occasionally done because of the high risk to damage the fragile specimens. Furthermore, the transverse placement of the ants on the tipped paper sheets frequently prevented bilateral measurement of characters (important for reducing the noise of data) because the pin or sheet blocked the view from one side. Problematic was also that many collectors did not care to have clean nest samples on a pin or in a series. This causes difficulties when cryptic species are under study – for example the type series of *Monomorium cyaneum* Wheeler 1906 labelled by DuBois (1986) contained two species. To complete the account of troubles with the provided material – some specimens were mounted on paper sheets so thin that they swung up and down under the gentle convection currents of air usually occurring in the laboratory. This could be nerve-racking or causing surrender when structures had to be measured with accuracies of 1 µm.

Which improvement of our knowledge on the *Monomorium carbonarium* group this revisionary paper will provide ? A success is that the taxonomic situation for the three species occurring in Europe was clearly solved. As for the New World, this revision should be considered as the first attempt to bring a reasonable structure into a horribly difficult ant group based on testable arguments. I express the hope that my conception of the nine independently living species recognized there may provoke future American myrmecologists to have a closer look on the ants living at their doorsteps. My classification concept for this region has to be checked by ambitious approaches that combine high-quality morphometry with analysis of nuclear DNA.

2. Material

NUMOBAT data were recorded in a total of 129 samples with 411 worker individuals and 78 gynes. This included five single-gyne samples without associated workers. With the exception of type specimens and other samples of special relevance, data of this material are not presented in detail in the main text of this paper but listed up in the electronic supplementary information SI1, SI2 and SI3. The abbreviations of type depositories are as follows:

AMNH New York – American Museum of Natural History New York, USA

CAS San Francisco – California Academy of Sciences San Francisco, USA

MCZ Cambridge – Museum of Comparative Zoology of the Harvard University, Cambridge, USA

MHN Genève – Muséum d'histoire naturelle de Genève, Genève, Switzerland

NHM London (formerly BMNH) – Natural History Museum London , England

NHM Los Angeles – Natural History Museum of Los Angeles County, Los Angeles, USA

NHM Wien – Naturhistorisches Museum Wien, Wien, Austria

NMNH Washington – National Museum of Natural History Washington, DC. , USA

SMN Görlitz – Senckenberg Museum für Naturkunde, Görlitz, Germany

3. Methods

Equipment and measurement procedures

A pin-holding stage, permitting full rotations around X, Y, and Z axes and a Leica M165C high-performance stereomicroscope equipped with a 2.0x planapochromatic objective (resolution 1050 lines/mm) was used for spatial adjustment of specimens at magnifications of 120-360x. A Schott KL 1500 cold–light source equipped with two flexible, focally mounted light–cables, providing 30°–inclined light from variable directions, allowed sufficient illumination over the full magnification range and a clear visualization of silhouette lines. A Schott KL 2500 LCD cold–light source in combination with a Leica coaxial polarized–light illuminator provided optimal resolution of tiny structures and microsculpture at highest magnifications. Simultaneous or alternative use of the cold-light sources depending upon the required illumination regime was quickly provided by regulating voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 52 % of the visual field was used. To avoid the parallax error (see section 2.2.1 in Seifert 2002), its measuring line was constantly kept vertical within the visual field. Z-stack images of mounted specimens were produced with a KEYENCE VHX-7000 digital microscope using magnifications between 100 and 1000x. Depending on the object properties, illumination was varied between sectorial or full ring lighting, sectorial or complete coaxial lighting and multi-lighting as combination of ring and coaxial lighting.

The morphometric characters and terminology

Twenty-two phenotypic characters, 19 in workers and 19 in gynes, were investigated and numerically recorded. In bilaterally developed characters, arithmetic means of both body sides were calculated. All measurements were made on mounted and fully dried specimens.

CL: maximum cephalic length in median line; the head must be carefully tilted to the position yielding the true maximum; excavations of hind vertex and/or clypeus reduce CL.

ClSpD: distance of the tips of the large paramedian clypeal dents

CW: maximum cephalic width; this is either across and including the eyes or posterior of the eyes.

CS: cephalic size; the arithmetic mean of CL and CW, used as a less variable indicator of body size.

EL: eye length, maximum diameter of compound eye over all structurally visible ommatidia.

ExCly: maximum depth of excavation between the tips of paramedian clypeal dents; this is usually given in frontodorsal view.

FL: maximum distance of frontal carinae; if no maximum is defined by a constriction, set FL equal to FRS.

FL/FR: index of anterior divergence of frontal carinae. It is 1.0 when the frontal carinae are parallel and set to 1.0 when these diverge caudad on their whole length.

FR: minimum distance of the frontal carinae posterior of the FL level; if no maximum is defined by a constriction, set FR equal to FRS.

FRS: distance of the frontal carinae immediately caudal of the posterior intersection points between frontal carinae and the lamellae dorsal of the torulus. If these dorsal lamellae do not laterally surpass the frontal carinae, the deepest point of scape corner pits may be taken as reference line. These pits take up the inner corner of scape base when the scape is fully switched caudad and produce a dark triangular shadow in the lateral frontal lobes immediately posterior of the dorsal lamellae of scape joint capsule (Fig. 1).

Fu2: median length of second funiculus segment in dorsal view. Dorsal view is given when the swiveling plane of 1st funiculus segment is positioned in the visual plane. Take

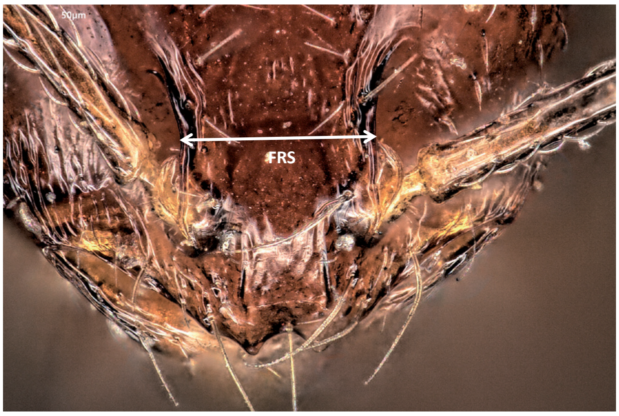


Figure 1. measuring FRS

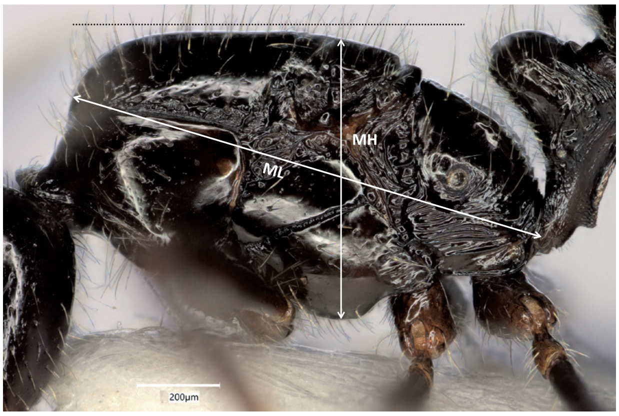


Figure 2. measuring mesosoma length (ML) and mesosoma height (MH) in gynes

Figure 3. measuring petiole length (PeL), petiole height (PeH) and postpetiole height (PpH)

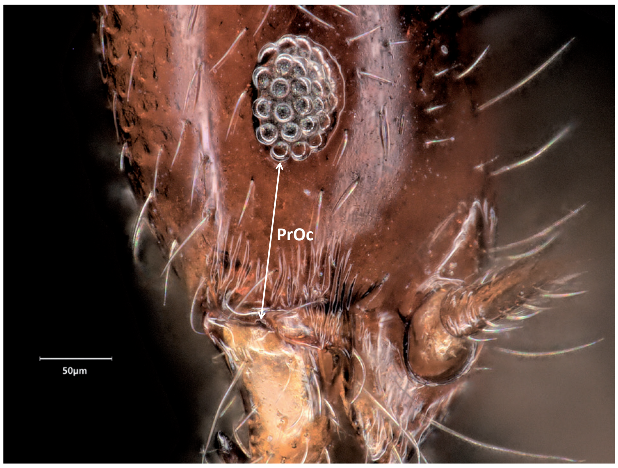


Figure 4. measuring preocular distance (PrOc)

care to really measure median length as the segment‘s sides have unequal length and to recognize the real distal margin of the segment. The latter has a very thin cuticle, frequently producing a narrow, shining ribbon that seems to be, by optical impression, demarcated from the rest of the segment. The median line of the segment is visualized by center of the patch reflecting the coaxial light.

Fu3: median length of third funiculus segment measured under the conditions given for Fu2.

Full face view: Dorsal aspect of head with both maximum head width and maximum median head length in visual plane

MH (only gynes, Fig. 2.): with mesosoma in lateral view and measured orthogonal to the dorsal profile formed by mesonotum and scutellum, MH is the longest measurable ***section*** line of mesosoma at mesopleural level (not height above all).

ML: mesosoma length; anterior measuring point in workers: transition point of the anterior pronotal slope to the anterior pronotal shield; anterior measuring point in gynes: frontalmost point of the pronotal slope; posterior measuring point in both workers and gynes: caudalmost margin of the propodeal lobe (Fig. 2).

MGr: Depth of metanotal groove or depression, measured from the tangent connecting the dorsalmost points of promesonotum and propodeum.

MW: mesosoma width; this is in workers maximum pronotal width, in gynes the maximum mesosoma width frontal of the tegulae.

OceD (only gynes): minimum distance between the inner margins of posterior ocellae.

OD (only gynes): Maximum transverse diameter of midocellus.

PeH: petiole height (Fig. 3). A straight imagination of ventral petiolar profile at node level is the reference line perpendicular to which the maximum height of petiole node is measured at node level. This is the height of a section line but not height above all.

PeL: petiole length (Fig. 3).

PeW: maximum width of petiole.

PpH: postpetiole height (Fig. 3); the straight section of the margin line between dorsal and ventral sclerites is the reference line perpendicular to which the maximum height of postpetiole is measured.

PpW: maximum width of postpetiole.

PrOc: preocular distance (Fig. 4); the shortest distance between the anterior eye margin and the sharp frontal margin of the gena. Caution: do not confuse this with the beaded rim of the mandible that is often very closely appressed to the genal margin.

SL: maximum straight-line scape-length excluding the articular condyle.

NUMOBAT: Explorative and supervised data analyses, classification and statistical testing

Formation of species hypotheses was done by running five different forms of exploratory data analyses (EDA) considering the morphological standard characters specified above. Four EDA methods using nest centroids as input data, named NC clustering, were applied. These were hierarchical NC-Ward clustering, the hierarchical method NC-part.hclust and the iterative vector-quantization method NC-part.kmeans – both implemented in partitioning algorithms based on recursive thresholding (for details see Csősz & Fisher 2015). As a fourth method, NC-NMDS. kmeans, a nonmetric multidimensional scaling combined with iterative vector-quantization (Seifert & al. 2013) was applied. All four methods of NC-clustering are excellent in formation of initial hypotheses but they tend to obscure intermediate morphologies possible generated by interspecific hybridization and introgression. Revealing such cases requires further analytical steps: checking the data sample by sample and analyzing them in the simple two-dimensional vectorial space. This was preferentially done by principle component analysis (PCA) with a maximum of three considered entities and often with character reduction. Alternatively, the position of suspicious samples was checked by wild-card runs in a linear discriminant analysis (LDA). Checking samples with controversial classifications was done by an interaction of NC clustering and a controlling LDA in which these samples were run as wild-cards, following the rationale described in Seifert & al. (2013). The final classification ("final species hypothesis") was established by the LDA in an iterative procedure and there remained no undecided cases even if their posterior probabilities were close to 0.5. PCA, LDA, ANOVA and X^2 tests were run with the SPSS 15.0 software package.

4. Results

4.1 Diagnosis of the *Monomorium carbonarium* species group

Workers of the *Monomorium carbonarium* species group can be identified by the following character combination. Distribution Nearctic and West Palaearctic, with the majority of species in the Nearctic. Median portion of clypeus raised and with two paramedian carinae which end in two paramedian clypeal spines. These spines occasionally can be reduced to short, blunt dents (as in *Monomorium monomorium*). Minimum distance between frontal carinae much larger than distance of clypeal dents: ratio FR/ClSpD over all species 2.482 ± 0.270 [1.791, 3.292], n=403. Maxillary and labial palps both 2-segmented. Antennae with 12 segments and a distinct 3-segmented club. Central area of vertex smooth and shiny without any microsculpture, longitudinal rugulae often present on frontal lobes and genae. Mandibles usually with 4 teeth, their dorsal plane smooth and shiny, unsculptured except for hair-pits. Metanotal groove markedly impressed with well-developed cross-ribs. Propodeal dorsum smooth and shiny and with 1-3 pairs of standing setae. Lateral surface of metapleuron always longitudinally carinulate. Comment: Polynesian-Australasian *Monomorium* species related to or conspecific with *M. liliuokalanii* Forel 1899 show in many characters similarities to *M. monomorium* but the ratio FR/ClSpD is here 1.326 ± 0.030 in five specimens based on image evaluation in www.antbase.org.

4.2 On intraspecific gyne polymorphism and gyne-based classification

High frequency of intraspecific gyne polymorphism, the small number of only 78 gynes available for study and the rarity of samples containing both gynes and workers did not allow to develop reliable numeric systems for species delimitation in gynes. Checking the placement of type specimens by wild-card runs in a LDA, which was successful in worker material, was also not reliable here due to low sample size. Yet, some conclusions can be drawn from principal component analyses. The first result is the existence of a clear gap between the morphologies of winged and wingless gynes. Winged gynes are characterized by full development of all mesosoma sclerites without fusion of the sclerites that are necessary for wing movement whereas wingless gynes have these sclerites fused. This definition is important when no remains of shed wings are detectable or when wingless gynes are large and have an overall mesosomal shape similar to that of winged gynes. The best characters to separate winged and wingless gynes are mesoma shape and the size of compound eye and midocellus.

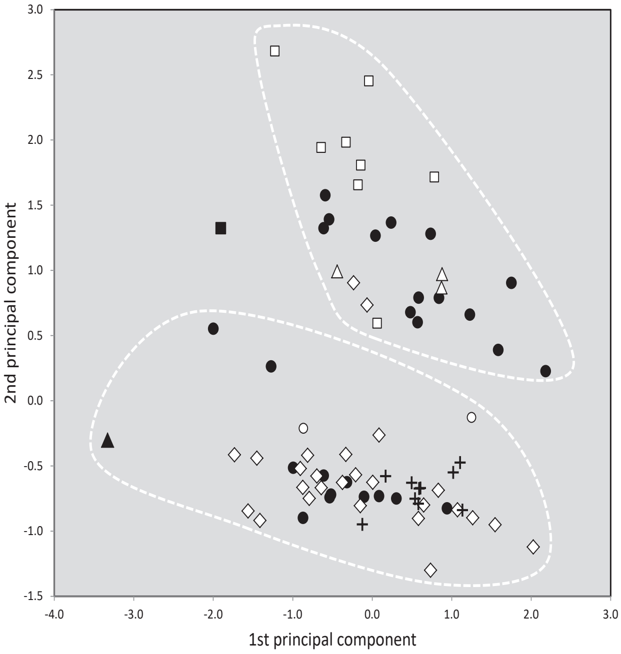


Figure 5. Principal component analysis separating winged gynes (upper cluster) and wingless gynes (lower cluster) of *Monomorium carbonarium* (black dots), *M. ergatogyna* (white rhombs), *M. viridum* (white squares), *M. emarginatum* (white triangles), *M. gallicum* n.sp. (black crosses), *M. monomorium* (white dots), *M. ebeninum* (black triangle) and *M. compressum* (black square). The gyne of *M. compressum* is dislodged because of extreme morphology.

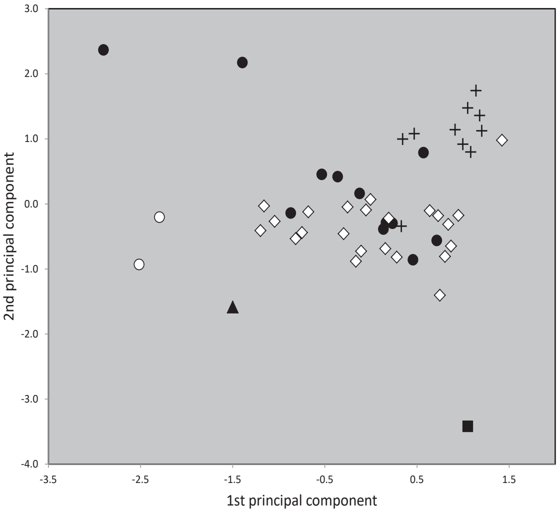


Figure 6. Principal component analysis of wingless gynes of *Monomorium carbonarium* (black dots), *M. ergatogyna* (white rhombs), *M. gallicum* n.sp. (black crosses), *M. monomorium* (white dots), *M. ebeninum* (black tiangle, type specimen) and *M. compressum* (black square, type specimen).

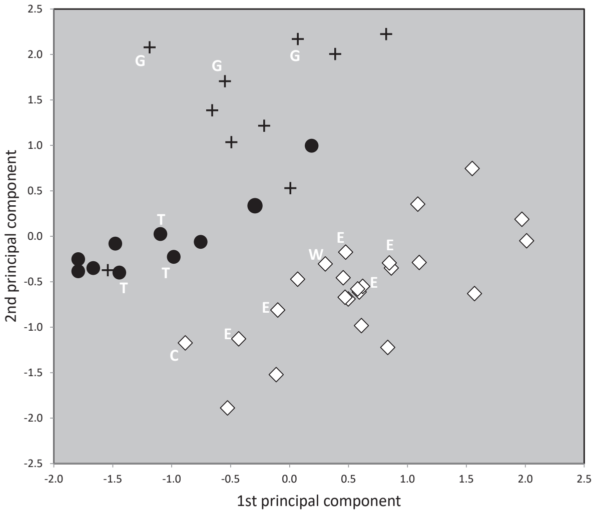


Figure 7. Principal component analysis of wingless gynes of *Monomorium carbonarium* (black dots), *M. ergatogyna* (white rhombs) and *M. gallicum* n.sp. (black crosses). Acronyms indicate the placement of type specimens: W – holotype of *M. wheelerorum*, C – paratype of *M. cyaneum*, T – types from holotype nest of *M. trageri*, G – types from holotype nest of *M. gallicum* n.sp., E – types from holotype nest of *M. ergatogyna.*

A discriminant 14.5*ML/CS+12.53*MW CS+23.905*EL/CS-7.732*MH/CS-18.224*OD/CS-32.84 offers a perfect separation with winged gynes having values < 0.5 and winged gynes those > 1.0. A PCA using these characters (Fig. 5) shows the presence of both winged wingless gynes in *Monomorium carbonarium* and *M. ergatogyna*. Two wingless gynes in *M. carbonarium* (SaNo 141, upper black dots in the lower cluster of Fig. 5) were as large as winged gynes and in overall mesosoma morphology similar to the winged gynes. Here a very close inspection revealed a fusion of the wing-movement sclerites and a wild-card run in the LDA given above resulted in posterior probabilities of 0.9999 and 0.8942 (for mating behaviour of these gynes see under Biology in the section of *Monomorium carbonarium*). *Monomorium viridum* was available only in winged gynes but DuBois (1986) reported that wingless gynes are occasionally present in this species.

Accordingly we have evidence for occurrence of both winged and wingless gynes in at least three species. In this context the opinion of Stefan Cover, who has seen a lot of living and dead nest samples from the Nearctic, is repeated: “So far, all free-living species in the group have both alate and wingless queen morphs, with the exception of *M. emarginatum* from the northeastern US which appears to have only alate queens, and *M. ebeninum* from the Caribbean, which has only wingless queens. *M. trageri* may be the wingless morph of *M. minimum*” (S. Cover pers. comm. 14 November 2015).

A separate analysis of winged and wingless gynes allowed further conclusions. A PCA was run considering 50 wingless gynes of 6 species and all characters shown in Tab. 5. Fig. 6 shows the clearly separate position of *Monomorium compressum*, *M. ebeninum*, *M. monomorium* and of the two large wingless gynes of *M. carbonarium*. After removing these extreme specimens from analysis, the PCA considering the characters FL/CS, PpW/CS, SL/CS, Fu3/CS and MH/CS provides a rather good separation of *Monomorium gallicum* n.sp., *M. ergatogyna* and *M. carbonaria* with only one outlier in *M. carbonarium* and *M. gallicum* n.sp. (Fig. 7). The three type gynes of *Monomorium trageri* DuBois 1986 are placed within the *M. carbonarium* (Smith 1858) cluster which confirms the junior synonymy concluded from worker types (see below). The paratype gyne of *M. cyaneum* DuBois 1986 and the holotype gyne of *M. wheelerorum* DuBois 1986 are placed within the cluster of *M. ergatogyna* Wheeler 1906 which confirms their junior synonymy concluded from the worker types (see below).

4.3 Key to the workers

Species delimitation is not very difficult until couplet 5 but determinations in couplets 6–8 require a complex system of measurements to get a sufficiently reliable result. Note: the discriminant functions in species with very small sample size (*Monomorium* *compressum*, *M. lorenzoi* n.sp. , *M. ebeninum*, *M. marjoriae*) are overfitted – i.e. they violate the rule that the number of specimens in the smallest class must be at least three times larger than the number of considered characters. Yet, there is much hope in the latter three taxa that a clear species separation will be confirmed when a larger sample size will be available because these species differ very strongly.

1a Clypeal spines reduced to short, blunt, often two-cusped dents; as result median clypeal excision very shallow, ExCly 7.0 ± 1.8 µm. Smallest species of the group and very short-scaped, SL < 320 µm. With all measurements in mm, discriminant 104.9*ExCly +21.70*SL-18.98 < 0 [error 0% in 29 individuals]. Mediterranean parts of the W Palaearctic (Figs. 8–10). ....***monomorium***

1b Clypeal spines or dents longer; if short, then not blunt (Fig. 15); ExCly 45.4 ± 7.9 µm. Scape longer, SL >315 µm. Discriminant > 0 [error 0% in 374 individuals]..................**2**

2a Frons very narrow, scape long, petiole very short and low, eye rather large. With all measurements in mm, discriminant 53.02*SL+142.62*EL-137.74*FL-63.08*PEL-6.326 > 0 [error 0% in 3 individuals]. Southern California (Figs. 29, 30). ....***lorenzoi n.sp.***

2b Frons wider, scape shorter, petiole longer, eye smaller. Discriminant < 0 [error 0% in 379 individuals]........3

3a Head much elongated, CL/CW 1.263 ± 0.007. Frontal carinae approached and notably diverging frontad, FL/CS 0.244 ± 0.006, FL/FR 1.099 ± 0.021. Metanotal groove very deep, MGr/CS 7.20 ± 0.68%. Propodeum edged, its dorsal profile and posterior slope forming a blunt angle of ± 128° (Fig. 12). All body surfaces with exception of few rugulae on frontal lobes, ventrolateral area of metapleuron and genae glabrous and shiny. With all measurements in mm, discriminant 188.18*MGr-24.58*CW+55.07*FL-180.91*FR+75.58*PpW+7.22 > 0 [error 0% in 9 individuals]. Entire Caribbean? (Figs. 11, 12)................***ebeninum***

3b Character combination different. Discriminant < 0 [error 0% in 362 individuals]. **4**

4a Eye very small and mesosoma very slender; ML/EL > 6.50, ML/ MW >2.27. With all measurements in mm, discriminant 58.74*ML-90.994*MW-70.39*EL-4.487 > 0 [error 0% in 8 individuals]. Posterior slope and dorsal profile of propodeum forming a distinct angle of 130° with a clear corner (Fig. 14). Clypeal dents short (Fig. 15), ExCly / CS 2.53 ± 0.40 %. Scape very long, SL/CS 0.887 ± 0.006. Mexico (Figs. 13-15)............................***marjoriae***

4b Eye larger and mesosoma less slender; ML/EL < 6.50, ML/ MW <2.27. Discriminant < 0 [error 0% in 354 individuals]. Posterior slope and dorsal profile of propodeum not forming a distinct corner. Clypeal excision often deeper...**5**

5a Clypeal spines usually thin and very acute (Fig. 18). Lateral area of mesopleuron dorsad to metanotal groove strongly longitudinally rugulose. Scape long, SL/CL 0.806 ± 0.013 [0.781,0.829]. With all measurements in mm, discriminant 69.54*SL-119.67*CL+144.6*PrOc+155.3*EL-124.4*FR+80.04*PpH+6.71 >0 [error 0% in 15 individuals]. Eastern USA from New Jersey south to Florida (Figs. 16-18)...***viridum***

5b Clypeal spines thicker and not very acute. Lateral area of mesopleuron dorsad to metanotal groove less strongly longitudinally rugulose or smooth. Scape shorter, ratio SL/CL 0.741 ± 0.022 [0.680, 0.800]. Discriminant < 0 [error 0.3% in 339 individuals]. **6**

6a Scape very short, SL/CW 0.826 ± 0.018. With all measurements in mm, discriminant 40.60*SL-107.65*EL+70.89*PeH+46.53*PpH-44.89*ML+203.84*Fu3-1.271 < 0 [error 0% in 30 individuals]. USA: New York, Pennsylvania, Massachusetts, Maryland, Minnesota, Virginia, Utah, New Mexico (Figs. 19, 20). ....***emarginatum***

6b Scape longer, SL/CW 0.899 ± 0.028. Discriminant > 0 [error 0.6% in 309 individuals]. **7**

7a With all measurements in mm, discriminant 53.48*CL-102.883*CW+35.66*ClSpD-33.88*PeL+95.6*PpH+560.03*Fu3-4.835 > 1 [error 0% in 23 nest samples of at least two individuals]. Only Europe: autochthonous in SW France, introduced to Germany, here supercolonial (Figs. 21, 22). ....***gallicum n.sp.***

7b Discriminant < 1 [error 0% in 73 nest samples of at least two individuals]...**8**

8a With all measurements in mm, discriminant 119.56*FR-41.27*CL-48.54*SL+71.56*ClSpD+76.86*PeH-112.12*PpW+45.7*PeW+85.16*MGr+54.94*PpH-35.54*CW+666.86*EL+78.32*FL +27.54*MW+0.0586 > 0 [error 0% in 42 nest samples of at least two individuals]. Widely distributed in the USA and Mexico; introduced to Madeira, France, Germany and the Netherlands; in the latter two countries supercolonial [Figs. 23, 24]. ....***carbonarium***

8b Discriminant > 0 [error 0% in 32 nest samples of at least two workers]. Only Nearctic.......................................**9**

9a With all measurements in mm, discriminant 75.34*CW-40.31*CL+200.9*ExCly-27.28*EL+23.46*PeW-26.81*ML+0.008 > 0 [error 7.4% in 95 individuals and 0% in 30 nest samples of at least two individuals). Mainly California, Nevada, Texas, New Mexico and Mexico but also Idaho, Mississippi,Tennessee and Virginia (Figs. 25, 26)..***ergatogyna***

9b Discriminant < 0 [error 0% in 8 individuals and 0% in 2 nest samples]. Only confirmed for Mexico (images of type gyne Figs. 27, 28)....................................***compressum***

Figure 8. Head of *Monomorium monomorium* in full face view; Spain: Cordoba, 2013

Figure 9. Lateral aspect of *Monomorium monomorium*; Spain: Cordoba, 2013

Figure 10. Clypeus of *Monomorium monomorium* in frontodorsal view; Spain: Cordoba, 2013

Figure 11. Head of *Monomorium ebeninum* in full face view; Grenadines: Beguia Island 2015; from www.antweb.org, photo Michele Esposito

Figure 12. Lateral aspect of *Monomorium ebeninum*; Grenadines: Beguia Island 2015; from www.antweb.org, photo Michele Esposito

Figure 13. Head of *Monomorium marjoriae* in full face view; Mexico: Santiago Ixcuintla, coll. T. Pergande

Figure 14. Lateral aspect of *Monomorium marjoriae*; Mexico: Santiago Ixcuintla, coll. T. Pergande

Figure 15. Clypeus of *Monomorium marjoriae* in frontodorsal view; Mexico: Santiago Ixcuintla, coll. T. Pergande

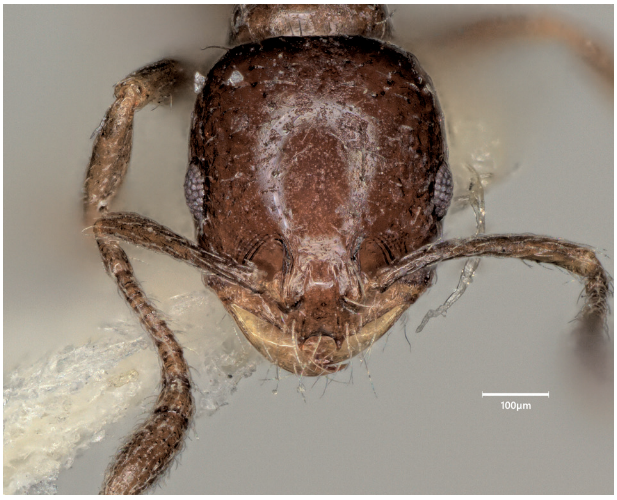


Figure 16. Head of *Monomorium viridum* in full face view; Florida: Sarasota, 1950

Figure 17. Lateral aspect of *Monomorium viridum*; Florida: Sarasota, 1950

Figure 18. Clypeus of *Monomorium viridum* in frontodorsal view; Florida: Sarasota, 1950

Figure 19. Head of *Monomorium emarginatum* in full face view, holotype; Utah: Green Canyon, 1976

Figure 20. Lateral aspect of *Monomorium emarginatum*; Utah: Green Canyon, 1976

Figure 21. Head of *Monomorium gallicum* n.sp. in full face view, holotype; France: Chapelle de St. Radegonde, 2021

Figure 22 Lateral aspect of *Monomorium gallicum* n.sp., holotype; France: Chapelle de St. Radegonde, 2021

Figure 23. Head of *Monomorium carbonarium* in full face view; Netherlands: Zwartevaal, 2022

Figure 24. Lateral aspect of *Monomorium carbonarium*; Netherlands: Zwartevaal, 2022

Figure 25. Head of *Monomorium ergatogyna* in full face view; USA: San Bruno Mountain State Park, 2024

Figure 26. Lateral aspect of of *Monomorium ergatogyna*; USA: San Bruno Mountain State Park, 2024

Figure 27. Head of *Monomorium compressum*, paratype wingless gyne; Mexico: Hidalgo: San Miguel

Figure 28. Lateral aspect of *Monomorium compressum*, paratype wingless gyne; Mexico: Hidalgo: San Miguel.

Figure 29. Head of *Monomorium lorenzoi* n.sp. in full face view, holotype; USA: Mission Trail Park, 2024

Figure 30. Lateral aspect of of *Monomorium lorenzoi* n.sp., holotype; USA: Mission Trail Park, 2024

4.4 Treatment by species

Monomorium carbonarium (Smith 1858)

***Myrmica carbonaria* Smith 1858** [type investigation]
This species has been described from Madeira. Investigated were four worker syntypes labelled “Madeira”, “Smith coll. pres. by Mrs. Farren White 99-303.”, “SYNTYPE” and “ANTWEB CASENT0902279”; depository NHM London. The type series is centrally placed within the Nearctic-European *Monomorium carbonarium* cluster. For more details see below under Taxonomic Comments.

***Monomorium minimum* (Buckley 1867)**
[syn. nov., type investigation].
This taxon has been described as *Myrmica (Monomarium)*[sic!] *minima* Buckley 1867 from Texas. Buckley (1867) gave only the terra typica: “Common in Central Texas”. According to Creighton (1950) and DuBois (1986) no type material could be identified in any collection in the USA including that of the Academy of Sciences Philadelphia. Accordingly, DuBois (1986) fixed a neotype for *Monomorium minimum* (Buckley) in a winged gyne from Texas labelled “Bastrop St. Pk., Tex. June 9, 1954 W. Clayd, T-119”, “*Monomorium minimum* (Buckley) Neotype M. DuBois 1983” and “M.C.Z. NEOTYPE 32921”, depository MCZ Cambridge. Unfortunately there is no worker material associated to the neotype to have a more reliable classification. *Monomorium carbonarium* develops large and small winged gynes (see Tab. 5). The latter are most similar to winged gynes of *M. ergatogyna* and the neotype with CS=0.736 mm may belong to both species (Tab. 5). Twelve worker-associated small winged gynes of *M. carbonarium* but only two worker-associated winged gynes of *M. ergatogyna* were available for comparison. Running the neotype of *M. minimum* as wild-card in a stepwise LDA considering all characters shown in Tab. 5 it is allocated to *M. carbonarium* with p>0.98. Yet, this is a weak suggestion because of strong character overfitting and the high variance and small sample size in the comparison samples. A better argument in favor of a synonymization with *M. carbonarium* is its higher abundance in Texas: 11 evaluable worker samples of *Monomorium*, all collected before 1947, were available from Texas of which 91% belonged to *M. carbonarium* and only 9% to *M. ergatogyna*. The situation today may differ. The third supporting argument is the higher frequency of winged gynes in the studied Nearctic material of *M. carbonarium*: the ratio of winged gynes vs. wingless gynes was 14 : 5 in *M. carbonarium* but 2 : 24 in *M. ergatogyna*. These arguments multiply to a fair probability that *M. minimum* from Texas should be a junior synonym of *M. carbonarium*. A really convincing argumentation is not possible at the current stage.

***Monomorium minimum emersoni* (Gregg 1945)**
[syn. nov., type investigation]
This taxon has been described from Globe /Arizona (holotype series) and Austin / Texas (paratypes) and San Marcos / Texas (paratypes). In NMNH Washington are 1 paratype winged gyne plus 51 worker paratypes on 17 pins all labelled “Austin Tex. IV-6-1937 A Emerson” [printed] and “Monomorium minimum emersoni subsp. nov. R. Gregg det R Gregg” [handwritten by Gregg himself]. As it is not clear if this large material represents a nest sample, two worker series with remote placement in the box and the gyne were morphometrically investigated. The gyne data allow no decision – is either a small winged gyne of *M. carbonarium* or a winged gyne of *M. ergatogyna*. However, the two worker series were allocated to *M. carbonarium* with p=0.9999 and 0.9982. Nevertheless, the synonymization with *M. carbonarium* stated here is risky as the holotype series from Globe was not studied. Based on abundance of species in the region the holotype series could also belong to *M. ergatogyna* or *M. emarginatum*. If belonging to the latter, *M. emersoni* would become a senior synonym. The holotype series from Globe was not available.

***Monomorium trageri* DuBois 1986**
[syn. nov., type investigation]
This taxon has been described from Gainesville in Alachua County, Florida based on a nest population collected from beneath a board in a cow pasture. The specimens investigated from the holotype nest are as follows. Holotype wingless gyne labelled “Florida: Alachua C., Gainesville April 5, 1980 J.C.Trager” and “*Monomorium trageri* Holotype M. Dubois 1983”; 1 paratype wingles gyne, 1 paratype worker with same locality label, depository NMNH Washington. 1 worker and 1 wingless gyne from holotype nest labelled “Florida: Alachua C., Gainesville April 5, 1980 J.C.Trager” and “*Monomorium trageri* Paratype M. DuBois 1983.” [blue, bleached label, year not clearly visible], depository AMNH New York. 1 worker and 1 wingles gyne from the holotype nest labelled “Florida: Alachua C., Gainesville April 5, 1980 J.C.Trager” and “*Monomorium trageri* Paratype M. DuBois 1983.” [blue, bleached label, year not clearly visible], depository CAS San Francisco. The wingless gyne from CAS has a malformed propodeum and waist segments and is not included in the analysis. *Monomorium trageri* is synonymized here with *M. carbonarium* because the worker sample is allocated to the *M. carbonarium* cluster with p = 0.9989 if run as wild-card in a LDA

and because the three evaluable type wingless gynes are placed in a PCA close to wingless gynes of *M. carbonarium* (Fig. 7). For more details see below under Taxonomic Comments.

All material examined. Numeric phenotypical data were taken in 45 samples with 141 workers and 27 gynes. The material came from France (12 samples), Germany (1), Mexico (1), Netherlands (3), Portugal (3) and USA (25). For details see supplementary information SI1, SI2 and SI3.

Geographic range. Widely distributed over the USA south to Mexico. Introduced to West and Central Europe. Altitudinal records range from sea level up to 2900 m (at 20°N in Mexico).

Description: --Worker (Tab. 3; Figs. 23, 24; key). Very small, CS 470 ±22 µm. Head moderately long, CL/CW 1.191 ± 0.027. Dents on clypeal margin moderately long (ExCly/CS 4.80 ± 0.58%), not very acute and moderately distant (ClSpD/CS 11.42 ±0.97%). Frontal carinae moderately distant and slightly diverging frontad (FL/CS 0.285 ± 0.008, FR/CS 0.276 ± 0.008, FL/FR 1.031 ± 0.021). Eye and preocular distance moderately large (EL/CS 0.205 ± 0.007, PrOc/CS 0.224 ±0.010). Scape and funiculus segments moderately long (SL/CS 0.807 ± 0.021, Fu2/CS 6.38 ± 0.21 %, Fu3/CS 4.82 ± 0.25%). Mesosoma rather short but relatively wide (ML/CS 1.179 ± 0.028, MW/CS 0.581 ± 0.014). Metanotal groove moderately deep, MGr/CS 5.24 ± 0.66%. Dorsum and slope of propodeum in profile forming a convex curve. Petiole rather wide and high (PeW/CS 0.289 ± 0.018, PeH/CS 0.378 ± 0.013). Postpetiole moderately wide and rather high (PpW/CS 0.316 ± 0.017, PpH/CS 0.294 ± 0.011). All body surfaces with exception of few rugulae on frontal lobes, ventral mesopleuron, ventrolateral area of metapleuron and genae glabrous and shiny. All body parts homogenously dark brown to jet black; mandibles, lateral clypeus and antennal funiculus lighter brown.

--Gyne (Tabs. 4, 5): The Nearctic population is extremely polymorphic in gynes, developing winged and wingless gynes with strong size variation in each morph. The sparse material available does not allow to propose diagnostic determination characters. The large winged gynes are probably better to identify as a combination of short scape and long petiole (Tab. 5).

Taxonomic comments. The description above does not present a single diagnostic character which results in the uncomfortable situation that species delimitation from *M. ergatogyna* and *M. gallicum* n.sp. is only possible by multivariate analyses. A species hypothesis was formed by NC-part.hclust considering the 12 characters CS, CL/CW, SL/CS, EL/CS, ClSpD/CS, MW/CS, PpW/CS, PeH/CS, PeL/CS, PpH/CS, MGr/CS, Fu3/CS. Within a total of 96 samples, it proposed three clusters and five outliers. In the controlling LDA, these clusters were accepted as species hypothesis and the outliers were run as wild-cards. The final species hypothesis of these runs is given in Fig. 33. It indicated that NC-part.hclust misclassified only one sample of *M. gallicum* n.sp. whereas the clusters later identified as *M. ergatogyna* and *M. carbonarium* were incompletely separated (Fig. 31). This result was repeated by a PCA in which *M. gallicum* n.sp. formed a well separated and constricted cluster (Fig. 32). One sample of *M. carbonarium* that approached *M. gallicum* n.sp. cluster was run as wild-card in the LDA and confirmed as the former species. In order to improve the separation of *M. carbonarium* and *M. ergatogyna*, *M. gallicum* n.sp. was excluded from analysis and NC-part.hclust was run using the 11 characters FR/CS, PeH/CS, SL/CS, ClSpD/CS, PpW/CS, MGr/CS, PeW/CS, EL/CS, PpH/CS, FL/CS, MW/CS. The analysis proposed two clusters and seven outliers within a total of 73 samples (Fig. 34). The final species hypothesis indicated that NC-part.hclust misclassified two samples. A PCA and NC-NMDS.kmeans run with the same data misclassified three and five samples respectively. Note: The cluster named above *M. carbonarium* was divided by NC-part.hclust into three subclusters. I decided to give these sublusters no taxonomic rank because NC-part.hclust tends to oversplit and because the resulting sample size of these subclusters became too small to reasonably check the data by the controlling LDA. Anyway, these data show the need for further research and that some of the synonymizations proposed in this paper under *M. carbonarium* might possibly be reversed.

Biology. The unresolved species delimitation in the past does not allow to use literature sources on life history and habitat selection referring to the situation in the New World. Some 200 samples in American museum collections labelled by DuBois as "*Monomorium minimum*" are a random mixture of *M. carbonarium, M. ergatogyna* and *M. emarginatum*. These three species are abundant and widely distributed in the USA which prevents any probabilistic interpretation of published biological data based on zoogeography. The more advanced species delimitation presented here and published information on particular classified samples allows to extract some fragments of life history: *M. carbonarium* is extremely gyne polymorphic in America with the winged gyne most certainly representing an ability for long-range flight-dispersal and independent colony foundation. Most colonies seem to be polygynous. Winged gynes are present in polygynous colonies but the wingless gynes are the dominant gyne morph in very polygynous (in Europe supercolonial) colonies. In a polygynous colony from Gainesville / Florida (type location of *M. trageri*), 10% of the queens were winged gynes and 90% wingless gynes and the latter were mated intranidally (DuBois 1986). All over the USA, young winged gynes with wings and males were found in the nests from 6 June to 24 July with the bulk in July. Wingless gynes were observed to perform female calling, dispersed on the whole plant of a waist-high *Ailanthus* bush and were accompanied by a retinue of workers. One to multiple alate males engaged on a single female but the mating count was uncertain (SaNo 141, 24 June 2023, Washington D.C., Brendon Boudinot pers. comm. 2024). Only wingless gynes are known so far from Madeira and West Europe which seems to contrast the very polymorphic situation in the Nearctic. This reduction to wingless gynes and the very recent occurrence as invasive pest ant in urban areas of West Europe support the assumption that the European population was founded by introduction from America. Supercoloniality has not been reported so far from the USA but in five of the 16 European locations. One supercolony in a greenhouse in the Netherlands caused a lot of problems there and another supercolony in a school yard in southern France expanded its territory by 18 m within a year. The distribution over main habitat types in Europe was 14 findings in urban, semi-urban or rural habitats and 2 findings in "natural" habitats (i. e., habitats with lowest anthropogenic influence such as coastal grey dunes or pastures). This distribution seems to differ from the situation in the sympatric and biologically very similar *Monomorium gallicum* n.sp. where 16 findings were made in the first habitat group but 7 in the latter. The soil of the urban habitats can be fully sealed with almost no vegetation being present.

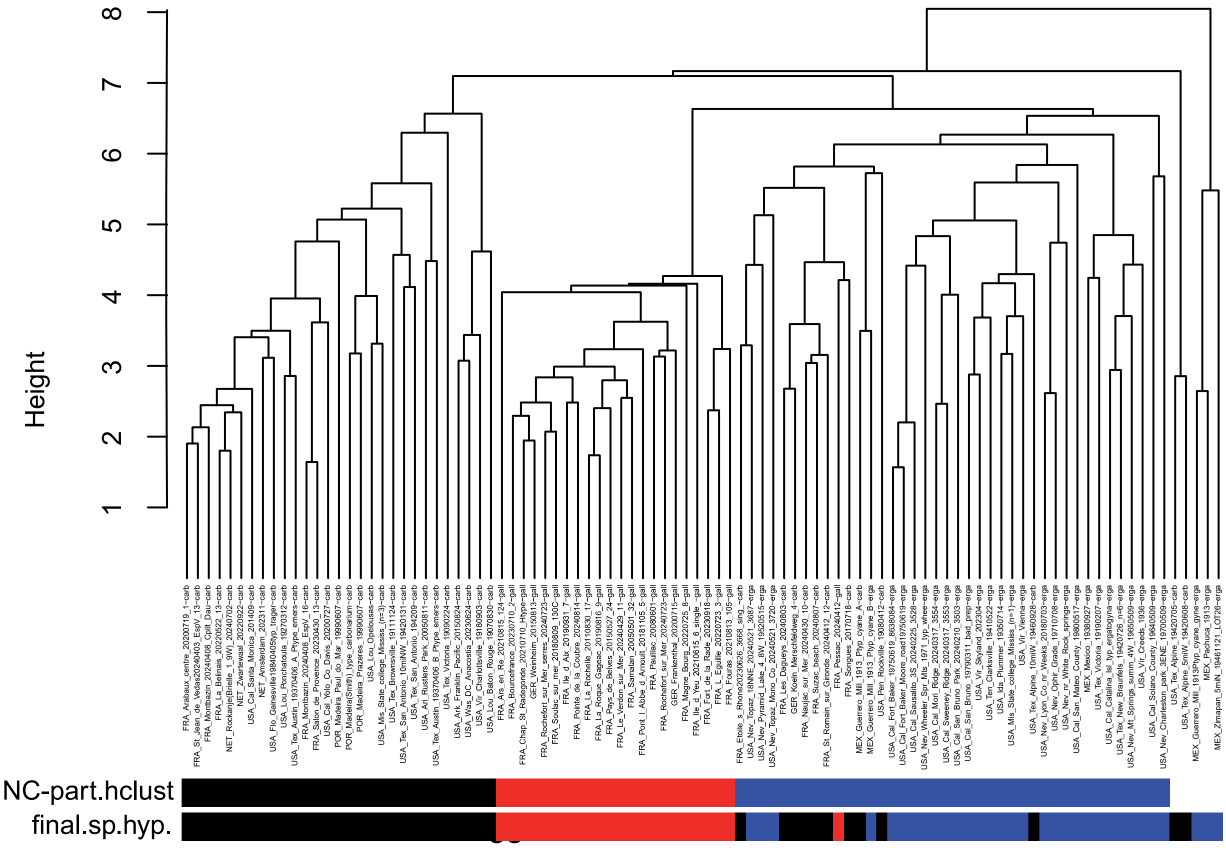
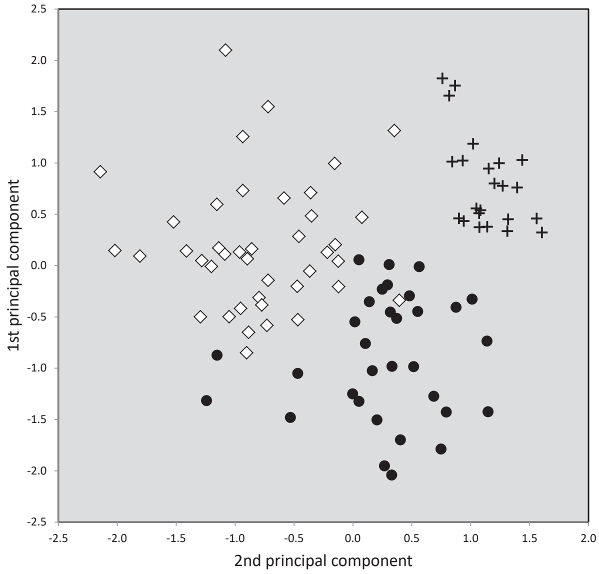


Figure 31. NC-part.hclust analysis of workers of *Monomorium carbonarium* (black bars), *M. ergatogyna* (blue bars), and *M. gallicum* n.sp. (red bars). The empty bar refers to outliers.



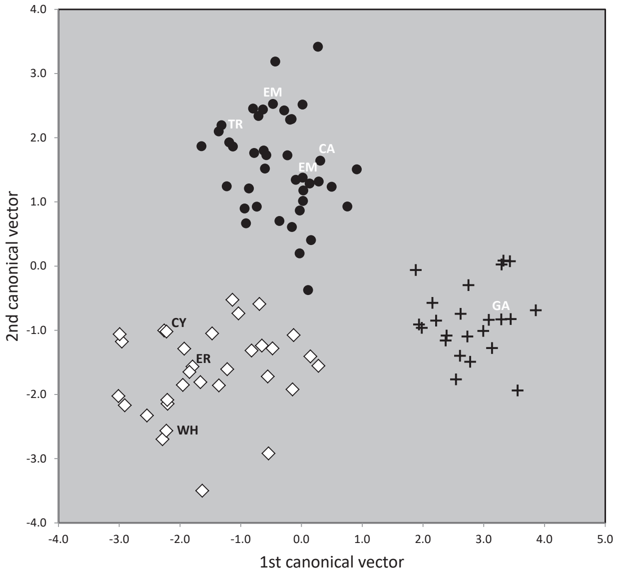


Figure 32 (left). Sample means of principal component analysis considering 12 characters measured in workers of of *Monomorium carbonarium* (black dots), *M. ergatogyna* (white rhombs), and *M. gallicum* n.sp. (black crosses).

Figure 33 (right). Sample means of a linear discriminant analysis considering 12 characters measured in workers of of *Monomorium carbonarium* (black dots), *M. ergatogyna* (white rhombs), and *M. gallicum* n.sp. (black crosses). Acronyms indicate the placement of type specimens: CA – type sample of *M. carbonarium*, CY – paratype sample of *M. cyaneum*, EM – paratype sample of *M. emersoni*, ER – type sample of *M. ergatogyna*, GA – type sample of *M. gallicum* n.sp., TR – type sample of *M. trageri*, WH – type specimen of *M. wheelerorum.*

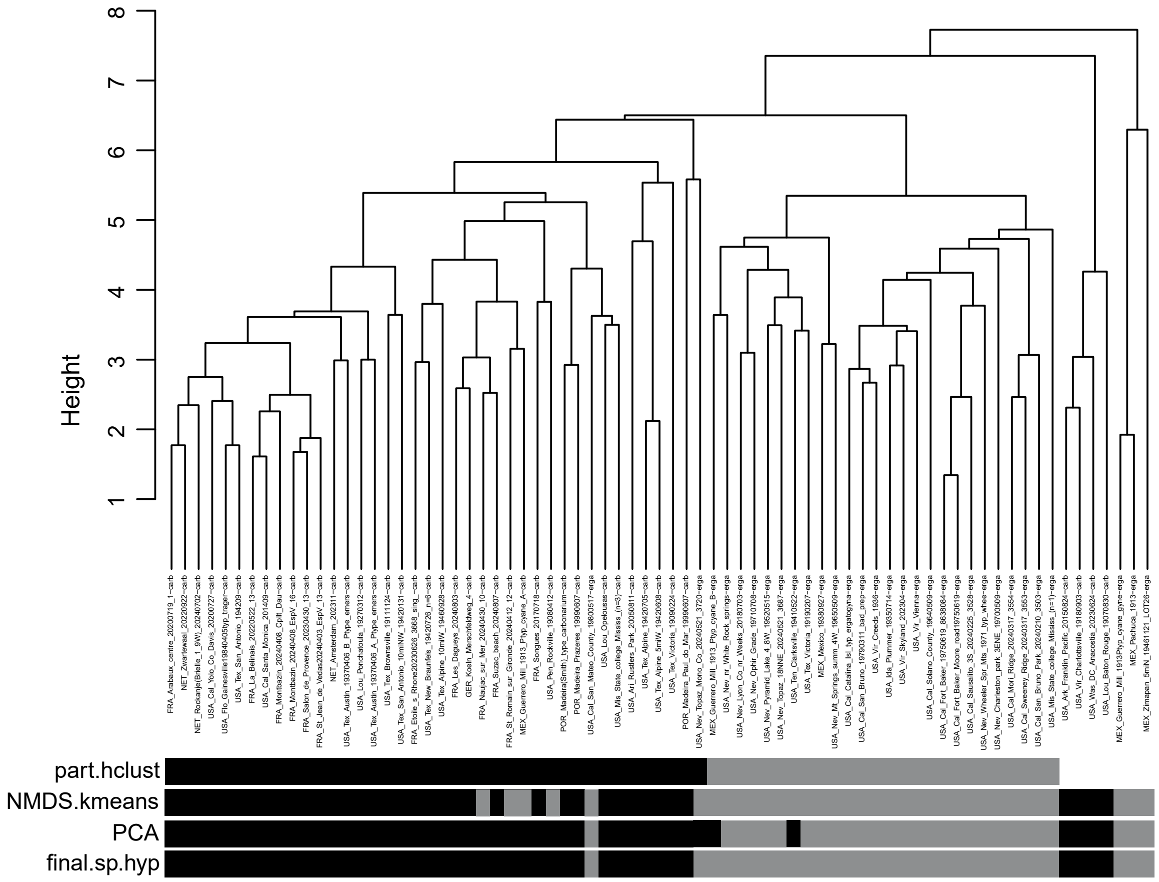


Figure 34. Results of three exploratory data analyses (EDAs) of worker samples of *Monomorium carbonarium* (black bars) and *M. ergatogyna* (grey bars). Shown is the NC-part.hclust dendrogram and results of NC-NMDS.kmeans and Principal Component Analysis. The empty space in the NC-part.hclust bar refers to outliers. The mean error of the three EDAs relative to the final species hypothesis is 5.0%.

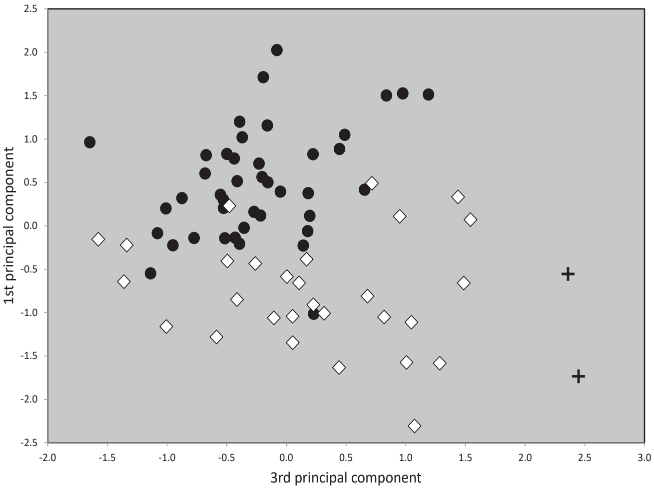


Figure 35. Sample means of principal component analysis considering 19 characters measured in workers. *Monomorium carbonarium* – black dots, *M. ergatogyna* – white rhombs, *M. compressum* – black crosses.

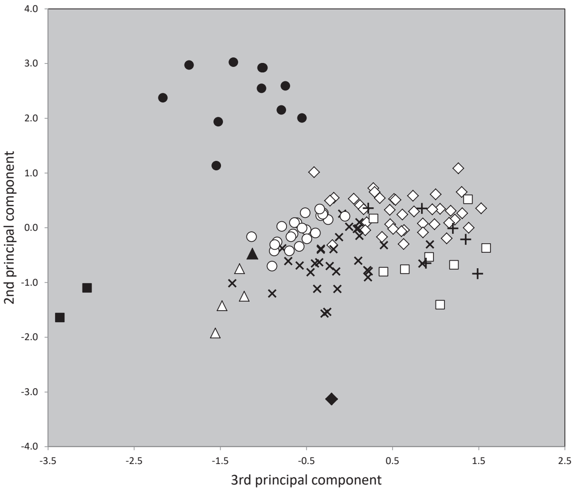


Figure 36. Sample means of principal component analysis considering 19 characters measured in workers. *Monomorium monomorium* – black dots, *M. marjoriae* – black squares, *M. lorenzoi* – black rhomb, *M. ebeninum* – white triangles, *M. ergatogyna* – black X, *M. compressum* – black triangle, *M. gallicum* n.sp. – white dots, *M. carbonarium* – white rhombs, *M. viridum* – black crosses, *M. emarginatum* – white squares.

Table 1. Sample means of posterior probabilities in wild-card runs in a 3-class LDA in workers of the species *Monomorium carbonarium* (n=141), *M. ergatogyna* (n=99)and *M. gallicum* n.sp. (n=73). The sample mean of posterior probabilities is the geometric mean of posterior probabilities of n workers for a given class dived by the sum of the geometric means of all classes considered.

sample (n = number of workers)	***carbo-narium***	***ergato-gyna***	***gallicum* n.sp.**
syntypes *carbonarium*, Madeira (n=4)	**0.9968**	0.0008	0.0024
paratypes *emersoni*, Austin, series A (n=3)	**0.9999**	0.0001	0.0000
paratypes *emersoni*, Austin, series B (n=3)	**0.9953**	0.0032	0.0015
syntypes *trageri*, Gainesville (n=3)	**0.9987**	0.0013	0.0000
syntypes *ergatogyna*, Catalina Island (n=7)	0.0063	**0.9936**	0.0001
type *wheelerorum*, Wheeler Spring Mountains (n=1)	0.0001	**0.9999**	0.0000
series from Wheeler Springs summit, near type locality (n=4)	0.0030	**0.9969**	0.0000
paratypes *cyaneum*, Guerrero Mill, series with gyne (n=4)	0.0973	**0.9027**	0.0000
paratypes *cyaneum*, Guerrero Mill, series A without gyne (n=5)	**0.9827**	0.0171	0.0002
paratypes *cyaneum*, Guerrero Mill, series B without gyne (n=3)	0.0031	**0.9965**	0.0005
holotype series *compressum*, San Miguel (n=4)	0.0001	**0.9184**	0.0815
holotype series *gallicum* n.sp., Chapelle-St.-Radegonde (n=3)	0.0001	0.0000	**0.9999**

Monomorium ergatogyna Wheeler 1904

***Monomorium minutum* subsp. *ergatogyna* Wheeler 1904** [type investigation]
This species has been described from Catalina Island near Los Angeles based on "numerous workers and eight females taken from three different nests" (Wheeler 1904). Morphometrically investigated were 5 syntype wingless gynes and 6 syntype workers from AMNH New York labelled: "Catalina I Cala. C.F. Baker", "TYPE nO A.M.N.H." "*Monomorium ergatogyna* Wheeler Paralectotype M. DuBois 1981".

The workers from the type sample are allocated to the *Monomorium ergatogyna* cluster with p = 0.9936 in a wild-card run of a 3-class LDA considering the species *Monomorium carbonarium, M. ergatogyna* and *M. gallicum* n.sp. and all 19 numeric characters of workers (Tab. 1). The five wingless type gynes are well separated in a PCA from the two next similar species (Fig. 7).

***Monomorium wheelerorum* DuBois 1986**
[syn. nov., type investigation]
This taxon has been described from Wheeler Spring in the Spring Mountains, Clark County in Nevada, 2012 m based on material collected by G.C & J. Wheeler. Investigated was the holotype wingless gyne labelled "NEVADA: Clark Co. WHEELER SPRING SPRING Mts., 6600', APRIL 1 1971 G. + J. Wheeler 1561", "LACM ENT 164441" and "Monomorium wheelerorum Holotype M. DuBois 1983"; 1 paratype worker from holotype nest on another pin with same collecting data and "LACM ENT 275330", and "Monomorium wheelerorum Paratype M. DuBois 1983"; depository Los Angeles Country Natural History Museum. 1 paratype wingless gyne and 2 paratype workers labelled "NEVADA: STOREY Co. OPHIR GRADE, 2 mi WSW VIRGINIA CITY, 8 JULY 1971 6500', G. + S. WHEELER 2280", "Monomorium wheelerorum Paratype M.DuBois 1983", depository NMNH Washington.

The worker of the holotype sample is allocated to the *Monomorium ergatogyna* cluster with p = 0.9999 in a wild-card run of a 3-class LDA considering the species *Monomorium carbonarium*, *M. ergatogyna* and *M. gallicum* n.sp. (Tab. 1). A similarly clear allocation with p = 0.9969 is also given for a sample of four workers from Wheeler Springs summit (close to the holotype locality) and the two paratype workers from Ophir Grade (p = 1.0000). The wingless holotype gyne was placed in a PCA within the cluster of wingless *M. ergatogyna* gynes considering all numeric characters (Fig. 7).

***Monomorium minimum* subsp. *cyaneum* Wheeler 1914**
[syn. nov., type investigation]
This taxon has been described from the state of Hidalgo, Mexico based on "numerous workers and females taken at Guerrero Mill under stones in rather damp places on the sides of the canyons" (Wheeler 1914). Morphometrically investigated was a paratype wingless gyne plus three paratype workers labelled "Guerrero Mill. Hidalgo. Mexico W.M. Mann", "PARATYPE", "WM Mann 1954 Collection"; depository NMNH Washington. The three paratype workers were allocated to the *Monomorium ergatogyna* cluster with p = 0.9965 in a wild-card run of a 3-class LDA considering the species *Monomorium carbonarium, M. ergatogyna* and *M. gallicum* n.sp. (Tab. 1). The paratype wingless gyne was placed within the *M. ergatogyna* cluster in a PCA (Fig. 7). Note: There are some 180 workers in NMNH Washington labelled by DuBois as paratypes of *Monomorium cyaneum*. These belong to two species (see Tab. 1) and cluster either with *M. ergatogyna* or *M. carbonarium*. Since the lectotype gyne (designated by DuBois 1986) and workers associated to this gyne were not investigated, it cannot be excluded that *M. cyaneum* is instead a junior synonym of *M. carbonarium*. However, because the ratio of *M. ergatogyna* vs. *M. carbonarium* in morphometrically investigated worker samples from Mexico as a whole was 5 : 1, the synonymization stated above appears more probable.

All material examined. Numeric phenotypical data were taken in 30 samples with 95 workers and 26 gynes. The material came from Mexico (4 samples) and the USA (26 samples). For details see supplementary information SI1, SI2 and SI3..

Geographic range. Widely distributed over the USA south to Mexico. Introduced to West and Central Europe. Altitudinal records range from sea level up to 2900 m (at 20°N in Mexico).

Description: --Worker (Tab. 3; Figs. 23, 24; key). Very small, CS 464 ±21 µm. Head moderately long, CL/CW 1.204 ± 0.024. Dents on clypeal margin moderately long (ExCly/CS 4.58 ± 0.68%), not very acute and moderately distant (ClSpD/CS 10.38 ± 0.96%). Frontal carinae moderately distant and slightly diverging frontad (FL/CS 0.274 ± 0.008, FR/CS 0.263 ± 0.008, FL/FR 1.041 ± 0.026). Eye and preocular distance moderately large (EL/CS 0.199 ± 0.009, PrOc/CS 0.224 ±0.009). Scape and funiculus segments moderately long (SL/CS 0.817 ± 0.022, Fu2/CS 6.36 ± 0.36%, Fu3/CS 4.83 ± 0.28%). Mesosoma short and rather narrow (ML/CS 1.161 ± 0.032, MW/CS 0.567 ± 0.015). Metanotal groove moderately deep, MGr/CS 4.63 ± 0.70%. Dorsum and slope of propodeum in profile forming a convex curve. Petiole rather wide but moderately high and long (PeW/CS 0.282 ± 0.017, PeH/CS 0.361 ± 0.010, PeL/CS 0.425 ± 0.013). Postpetiole moderately wide and high (PpW/CS 0.317 ± 0.013, PpH/CS 0.284 ±0.011). All body surfaces with exception of few rugulae on frontal lobes, ventral mesopleuron, ventrolateral area of metapleuron and genae glabrous and shiny. All body parts homogenously dark brown to jet black; mandibles, lateral clypeus and antennal funiculus lighter brown.

--Gyne (Tabs. 5 and 6): Both winged and wingless gynes are developed but the latter are much more frequent. The sparse material available, in particular of winged gynes, does not allow to propose diagnostic determination characters but at least the wingless gynes are separated from those of *M. carbonarium* and *gallicum* n.sp. by a PCA considering all 19 characters (Fig. 7).

Taxonomic comments. The worker is very similar to *M. carbonarium* and does not show any diagnostic character. As result, the separation from *M. ergatogyna* and *M. gallicum* n.sp. is only possible by stepwise multivariate analyses (Figs. 31-34, for details see above).

Biology. The unresolved species delimitation in the past does not allow to use literature sources and I can only refer here to the sparse information connected with material determined in this revision. Wheeler (1914) reported his subspecies cyaneum to occur in rather damp and moist places within a xerothermous environment. Four nest samples collected in California by Lorenzo Fraysse (SaNo 115-118) were found in chaparral – twice under stones and once each under grass and in a wet mossy path embankment. Two nest samples collected in Nevada were found in semideserts. Winged gynes are much rarer than wingless gynes and young winged gynes were observed in the investigated material 2 July 1919, 26 July 1942.

Monomorium compressum Wheeler 1914

***Monomorium minimum* subsp. *compressum* Wheeler 1904** [type investigation]

This taxon has been described from the state of Hidalgo, Mexico based on "four females and several workers taken at San Miguel beneath a stone" (Wheeler 1914). Investigated were a paratype wingless gyne and four paratype workers from the holotype nest labelled "San Miguel. Hidalgo, Mexico W. M. Mann" and "WM Mann 1954 Collection"; depository NMNH Washington. The status of a different species was maintained here due to the very different gyne (Tab. 5, Figs. 6, 27, 28). The workers are in nearly all characters fully within the range of *Monomorium ergatogyna* or *M. carbonarium* (Tab. 3) but are possibly separable by multivariate analyses (see below). It is puzzling how DuBois could determine in the NMNH Washington collection worker samples from four other localities in Mexico as *M. compressum* since the differential characters stated in his key are useless

All material examined. Only the holotype nest sample and another one with four workers were available for investigation.

Geographic range. Only the holotype sample from locality San Miguel in the Mexican state of Hidalgo and the sample of four investigated workers from Mexico (city?) was available.

Description: --Worker (Tab. 3, key). Most similar to *M. carbonarium* and *M. ergatogyna* with almost no morphometric character being outside the range of variation of that species. The differential characters supposed below have to be checked in a larger sample. Very small, CS 453 ±19 µm. Head more elongated than in *M. carbonarium* and *M. ergatogyna*, CL/CW 1.247±0.008. Dents on clypeal margin shorter than in *M. carbonarium* and *M. ergatogyna* (ExCly/CS 3.04 ± 0.47%), not very acute and moderately distant (ClSpD/CS 10.12 ± 0.90%). Frontal carinae moderately distant and very slightly diverging frontad (FL/CS 0.270 ± 0.007, FR/CS 0.266 ± 0.003, FL/FR 1.017 ± 0.012). Eye and preocular distance moderately large (EL/CS 0.206 ± 0.004, PrOc/CS 0.227 ±0.005). Scape and funiculus segments moderately long (SL/CS 0.812 ± 0.009, Fu2/CS 6.13 ± 0.39%, Fu3/CS 4.96 ± 0.32%). Mesosoma longer than in *M. carbonarium* and *M. ergatogyna* and moderately wide (ML/CS 1.207 ± 0.018, MW/CS 0.561 ± 0.016). Metanotal groove rather shallow, MGr/CS 4.29 ± 0.55%. Dorsum and slope of propodeum in profile forming a convex curve or a suggested very blunt angle. Petiole moderately wide, high and long (PeW/CS 0.260 ± 0.017, PeH/CS 0.358 ± 0.008, PeL/CS 0.428 ±0.011). Postpetiole rather wide and moderately high (PpW/CS 0.316 ± 0.021, PpH/CS 0.276 ±0.012). All body surfaces with exception of suggested rugulae on lateral frontal lobes, genae and ventrolateral area of metapleuron glabrous and shiny. Head, mesosoma, waist and appendages brown, gaster blackish brown.

--Gyne (Tab. 5, Figs. 27, 28): The morphometric data and images reveal a unique gyne morphology.

Taxonomic comments. The unique gyne morphology should justify the status as a good species but worker identification is most difficult. In an attempt to separate the Nearctic triple *Monomorium carbonarium*, *M. ergatogyna* and *M. compressum*, it was possible to isolate the two samples of *M. compressum* by a PCA using the 13 characters FR/CS, PeH/CS, ExCly/CS, SL/CS, ML/CS, ClSpD/CS, MGr/CS, CL/CW, PpW/CS, PpH/CS, FL/FR, PeW/CS, EL/CS (Fig. 35). I consider this result as provisional.

Biology. Nothing is known except for polygynous colony demography.

Monomorium gallicum n.sp.

Etymology: belonging to Gallia, a province of the Roman Empire largely coincident with modern France and the area where most findings of the new species were made.

Type material. Holotype worker labelled " FRA: 47.16846, 0.25379, 75 m, Chapelle Sainte Radegonde, swarming, Gouraud 2021.07.10-4", "Holotype *Monomorium gallicum* Seifert"; 5 worker paratypes and 2 wingless gyne paratypes on two separate pins from the holotype nest with same collecting data but "Paratypes *Monomorium gallicum* Seifert"; all this material deposited in SMN Görlitz.

All material examined. Morphometrically investigated were 23 nest samples with 73 workers and 10 gynes. They came from France (21 samples) and Germany (2 samples). For details see supplementary information SI1, SI2, SI3.

Geographic range and supposed origin. The vouchers from France concentrate to a zone of some 70000 km² in SW France influenced by Atlantic climate from sea level to 168 m, with border points Ile-d'Yeu in the northwest (46.69°N, 2.28°W), Chapelle Sainte Radegonde in the northeast (47.17°N, 0.25°E), La Roque-Gageac in the east (44.83°N, 1.19°E] and Samatan in the south (43.49°N, 0.93°E). The two introduced supercolonial populations in urban regions around Mannheim in SW Germany are 42 km apart. The species was not found in the investigated Nearctic material and should be of European or at least Old World origin. Assuming an autochthonous European origin appears somewhat problematic. Bernard (1968) described the presence of an ant that he called *Monomorium minutum* Mayr 1855 for West Europe and the whole Mediterranean. Unable to separate *Monomorium monomorium, M. carbonarium* and *M. gallicum* n.sp., it appears likely that he collected two or three species under this name. However, it is strange that he did not report any observation suggesting supercoloniality. Supercolonies should also not have escaped the attention of other 20th century myrmecologists such as C. Collingwood but there are no reports for this. *Monomorium gallicum* n.sp. was either not present in Europe in that time or its colonies remained unobtrusive for most of their evolutionary history and developed a supercolonial demography only recently. The latter idea is not far-fetched as very recent occurrence of supercolonies in urban environments is documented for example in *Plagiolepis pygmaea* (Latreille 1798) from France (Charrier et al. 2020) as well as Switzerland and Germany in 2019 and 2021 (my own unpublished data).

Diagnosis: --Worker (Tab. 3; Figs. 23, 24; key). Rather small, CS 480 ±18 µm. Head longer than in *M. carbonarium*, CL/CW 1.242 ± 0.023. Dents on clypeal margin moderately long (ExCly/CS 4.42 ± 0.54%), not very acute and moderately distant (ClSpD/CS 11.48 ±0.79%). Frontal carinae moderately distant and slightly diverging frontad (FL/CS 0.286 ± 0.007, FR/CS 0.276 ± 0.007, FL/FR 1.036 ± 0.020). Eye rather small and preocular distance moderately large (EL/CS 0.199 ± 0.005, PrOc/CS 0.229 ±0.007). Scape and funiculus segments rather long, 3rd funiculus segment significantly longer than in *M. carbonarium* (SL/CS 0.824 ± 0.012, Fu2/CS 6.74 ± 0.30%, Fu3/CS 5.35 ± 0.22%). Mesosoma slightly longer than in *M. carbonarium* and rather narrow (ML/CS 1.204 ± 0.027, MW/CS 0.571 ± 0.010). Metanotal groove moderately deep, MGr/CS 4.94 ± 0.62%. Dorsum and slope of propodeum in profile forming a convex, suggestedly angulate curve. Petiole rather wide and high but moderately long (PeW/CS 0.293 ± 0.012, PeH/CS 0.380 ± 0.010, PeL/CS 0.438 ±0.014). Postpetiole rather wide and higher than in *M. carbonarium* (PpW/CS 0.328 ± 0.012, PpH/CS 0.306 ±0.008). All body surfaces with exception of few rugulae on frontal lobes, ventral mesopleuron, ventrolateral area of metapleuron and genae glabrous and shiny. All body parts homogenously dark brown to jet black; mandibles, lateral clypeus and antennal funiculus lighter brown.

--Gyne (Tab. 5): Only wingless gynes are known so far. Most individuals are morphometrically separable from wingless gynes of *M. carbonarium* in a PCA (Fig. 7). Perhaps it is also possible to separate them from the latter species by the steeper slope of frontal petiole profile.

Taxonomic comments. The very clear separation of worker samples from *M. carbonarium* and *M. ergatogyna* has been demonstrated above (Figs. 31, 33; Tab. 1).

Biology. (synthesis of information from C. Gouraud, B. Kaufmann, C. Galkowski, G. Heller pers. comm.). Coastal habitats in France include white and grey dunes, edge of dune groves with maritime pines and holm oaks, cliffs, dry grasslands and road sides. In rural and urban habitats it is found in gardens and parks and once in a greenhouse with *Begonia*. Occurrence in fully sealed urban habitats such as parking grounds or streets was repeatedly reported and is possible if there is some greenery (trees, flower beds etc.) nearby. Nests are under stones, in dead wood, fence posts and old stone walls. The species is frost resistant: the colony in Weinheim survived the cold winters 2009/2010 and 2011/12. It is very polygynous and may dominate a site where it coexists with *Lasius psammophilus*, *Formica cf. selysi* in dune environment and is also able to establish in dune sites colonized by species of the *Tapinoma nigerrimum* group. Competing ant species are very effectively repelled by gaster-flagging during which an irritating poison gland secretion is released from the extruded sting. Very populous supercolonies were observed in four localities in urban environments. The supercolony in Weinheim became a nuisance in houses and caused damage to electronic installations. On smooth ground the foraging radius may extend more than ten meters. Trophobiotic organisms on bushes and trees such as aphids and scale insects may be visited by huge files of workers. It is extremely polyphagous using nectar and pollen, dead invertebrates, diverse foodstuffs in households and was seen to retrieve small seeds with elaiosomes. Large arthropods are disintegrated by numerous workers at the site after having repelled competitors. There is one observation of swarming 10 July 2021 from France when the wingless gynes climbed on grasses, branches or other elevated points at the periphery of the nest (SaNo 50). Such behavior makes only sense in order to better attract flying males of other colonies by sex pheromones. This observation corresponds to the case reported above for wingless gynes of *Monomorium carbonarium*. It remains to be investigated if winged gynes are really absent in this species.

Monomorium ebeninum Forel 1891

***Monomorium minutum* r. *ebeninum* Forel 1891**
[types investigated]

The species has been described from the Caribbean islands St. Vincent and St. Thomas. Investigated were the lectotype gyne labelled “Typus”, “Monomorium minutum Mayr r. ebeninum Forel St. Vincent”, “Monomorium ebeninum Forel Lectotype M. DuBois 1983”, “ANTWEB CASENT0908695”; 9 paratype workers labelled “Typus”, “ebeninum Forel”, “Monomorium St.Thomas (Antille) 14 X 78”, “ANTWEB CASENT0908696”; all material deposited in MHN Genève.

All material examined. Numeric phenotypical data were taken in the lectotype gyne from St. Vincent and 4 worker samples with 9 individuals from St. Thomas and Barbados. For details see supplementary information SI1, SI2, SI3.

Geographic range. Probably entire Caribbean and, so far, not reliably confirmed from outside this region. Images in www.antweb.org (CASENT0729633, CASENT0318457) showing worker specimens from the Grenadines can be referred to this species. DuBois (1986) reported the species from over 40 localities in the Caribbean and Middle America but it is unclear how he could determine these samples based on the useless characters given in his key and species description.

Diagnosis: --Worker (Tab. 2, Figs. 1, 12, key). Very small, CS 445 µm. Head longer than in most species of the group, CL/CW 1.263 ± 0.025. Dents on clypeal margin rather short (ExCly/CS 3.11 ± 0.49%), not very acute and moderately distant (ClSpD/CS 10.36 ±1.26%). Frontal carinae more approached (FR/CS 0.244 ± 0.006) and more diverging frontad than in related species (FL/CS 0.268 ± 0.006, FL/FR 1.099 ± 0.021). Eye and preocular distance moderately large (EL/CS 0.206 ± 0.009, PrOc/CS 0.231 ±0.003). Scape and funiculus segments moderately long (SL/CS 0.834 ± 0.011, Fu2/CS 6.47 ± 0.37 %, Fu3/CS 5.07 ± 0.11%). Mesosoma moderately long and wide (ML/CS 1.230 ± 0.028, MW/CS 0.566 ± 0.007). Metanotal groove very deep, MGr/CS 7.20 ± 0.68%. Propodeum edged, its dorsal profile and posterior slope rather straight and forming a blunt angle of ± 130° (Fig. 12). Petiole rather wide and high (PeW/CS 0.289 ± 0.015, PeH/CS 0.377 ± 0.008). Postpetiole wide and rather high (PpW/CS 0.356 ± 0.009, PpH/CS 0.289 ±0.017). All body surfaces with exception of few rugulae on frontal lobes, ventrolateral area of metapleuron and genae glabrous and shiny. All body parts homogenously dark brown to jet black.

--Gyne (Tab. 5; Figs. 27, 28): According to the morphometric data of the lectotype gyne given in Tab. 5, there is hope that this species could be well separable in this caste as a combination of small FR/CS, MW/CS, MH/CS and large EL/CS as well as by the overall shape.

Taxonomic comments. The lectotype is in a PCA well separated from all other wingless gynes (Figs. 5, 6). Based on the characters underlined in the description above, the worker is comparably easy to determine. With all measurements in mm, a discriminant 152.22*FR-206.87*MGr-113.08*ExCly-69.2*PpW/CS-3.0 < 0 separates the nine available *Monomorium ebeninum* specimens fully from the 390 workers of all other species of the *M. carbonarium* group.

Biology. Wheeler (1905) reported nesting under stones, in cavities of *Tillandsia* species and dry twigs of buttonwood bushes with up to 12 queens per nest. According to Smith (1936) its colonies are populous and polygynous with the nests found in both soil and wood, back of the leaf sheaths of corn and bananas, in cabbage heads, *Tillandsia* plants and in *Hibiscus sabdariffa* fruits. The same author reported exceeding trophobiosis with scale insects and aphids and strong predatory activity. According to Wolcott & Martorell (1937) it predates on eggs of the sugarcane moth borer *Diatraea saccharalis* Fabricius. Males were observed in Jamaica 14 March 1911 and in the Bahama Islands 31 May 1904 (DuBois 1986). The species is assumed to have only wingless gynes (S. Cover pers. comm.).

Monomorium marjoriae DuBois 1986

Monomorium marjoriae **DuBois 1986**
[description, zoogeography]
The species has been described by a single nest sample from Mexico: Nayarit: Puga (DuBois wrote "Punga" – obviously a misspelling). These types were not available but this taxon shows exceptionally clear characters to allow an identification even by the rough description of DuBois (1986).

All material examined. Numeric phenotypical data were taken in two samples with 8 workers from Tepic and Santiago Ixcuintla in Mexico. For details see supplementary information SI1, SI2.

Geographic range. The three known sites in Mexico – Puga (21.58°N, 104.82°W, 700 m), Tepic (21.50°N, 104.89°W, 937 m) and Santiago Ixcuintla (21.81°N, 105.21°W, 17 m) – are situated in the Province Nayarit.

Diagnosis: --Worker (Tab. 2, Figs. 13-15, key). Comparatively large, CS 504 ± 11 µm. Head moderately long, CL/CW 1.226 ± 0.024. Dents on clypeal margin short (ExCly/CS 2.53 ± 0.40%), not very acute and moderately distant (ClSpD/CS 9.31 ± 0.46%). Frontal carinae moderately approached (FR/CS 0.266 ± 0.009) and only weakly diverging frontad (FL/CS 0.274 ±0.010, FL/FR 1.033 ±0.024). Eye smaller and preocular distance larger than in other species (EL/CS 0.187 ± 0.004, PrOc/CS 0.252 ±0.004). Scape and funiculus segments much longer than in most other species (SL/CS 0.887 ± 0.006, Fu2/CS 6.67 ± 0.28%, Fu3/CS 5.53 ± 0.09%). Mesosoma more slender than in all other species (ML/CS 1.270 ± 0.013, MW/CS 0.536 ± 0.006). Metanotal groove rather deep, MGr/CS 5.41 ± 0.64%. Dorsal profile and posterior slope of propodeum straight and forming a distinct angle of 130° with a clear corner (Fig. 14). Waist segments moderately high and wide (PeW/CS 0.280 ± 0.016, PeH/CS 0.372 ± 0.007, PpW/CS 0.329 ± 0.013, PpH/CS 0.290 ± 0.005). All body surfaces rather smooth, with exception of few rugulae on frontal lobes, ventrolateral area of meso- and metapleuron and genae. Lighter colored than other species: Head brown to dark brown, mesosoma yellowish-brown to brown, gaster brown to dark brown, mandibles yellowish-brown.
--Gyne: unknown

Taxonomic comments. Based on the characters underlined in the above description, the worker is comparably easy to determine and clearly separated as distinct cluster by explorative data analyses. The second and third component of a principal component analysis considering all 19 characters placed the *M. marjoriae* as well as those of M. *monomorium* and M. *lorenzoi* n.sp. widely separate from the samples of the seven remaining species of the M. *carbonarium* species complex (Fig. 36).

Biology. Unknown.

Monomorium viridum Brown 1943

Monomorium viridis **Brown 1943**
[type investigation]
This species has been described on males, gynes and workers from Lakehurst in New Jersey. Investigated were a paratype winged gyne labelled:"Paratype Monomorium viridum Brown" [hand-written by Brown], "Lakehurst VIII-25-40 N.J. W.L. Brown" and "USNM paratype No 58070" and series of five workers labelled "Paratype Monomorium viridum Brown" [hand-written by Brown], "Lakehurst VI-14-42 N.J. W.L. Brown", "USNM paratype No 58070" and "CASENT 0105770 ANTWEB"; both series deposited in NMNH Washington.

Monomorium peninsulatum **Gregg 1945**
[syn., type investigation]
This taxon has been described from Florida: Dade Co., South Miami based on gynes and workers. Investigated were three paratype winged gynes and nine workers on four pins from NMNH Washington all labelled "So. Miami Fla VII-8-41 EV Gregg" "Crater in sandy soil pine palmetto", "Paratype No. 57281 U.S.N.M."

I confirm the synonymy stated by DuBois (1986). The type workers of *M. penisulatum* as well as another worker sample from Florida do not show any differences to the material of *M. viridum* from more northern latitudes. The smaller head size and larger ClSpD of the southern population are within the normal range of intraspecific variation known for the *M. carbonarium* species group.

All material examined. Numeric phenotypical data were taken in 5 samples with 15 workers and 8 winged gynes. For details see supplementary information SI1, SI2, SI3. All this material originated from the eastern states of the USA

Geographic range. Only known from lowland areas of the eastern states of USA: New York (40.79°N,74.31°W), New Jersey, North Carolina and Florida (25.76°N, 80.19°W) from sea level up to 23 m.

Diagnosis: --Worker (Tab. 2, Figs. 16-18, key). Very small, CS 460 ± 22 µm. Head much shorter than in most species of the group, CL/CW 1.147 ± 0.015. Dents on clypeal margin rather long (ExCly/CS 5.67 ±0.99%), very acute and widely distant (Fig. 18, ClSpD/CS 12.68 ± 0.97%). Frontal carinae more diverging frontad than in most other species (FL/FR 1.077 ± 0.46, FL/CS 0.286 ± 0.007, FR/CS 0.266 ± 0.012). Eye and preocular distance moderately large (EL/CS 0.210 ± 0.007, PrOc/CS 0.240 ±0.009). Scape and funiculus segments very long (SL/CS 0.861 ± 0.014, Fu2/CS 6.86 ± 0.43%, Fu3/CS

5.27 ± 0.24%). Mesosoma moderately long and wide (ML/CS 1.218 ± 0.019, MW/CS 0.582 ± 0.013). Metanotal groove deep, MGr/CS 6.07 ± 0.93%. Dorsal and caudal profile of propodeum not meeting in an angle, as a whole more or less convex. Petiole moderately wide but higher than in most other species (PeW/CS 0.285 ± 0.012, PeH/CS 0.394 ± 0.011). Postpetiole moderately wide but higher than in other species (PpW/CS 0.356 ± 0.009, PpH/CS 0.315 ± 0.009). Lateral area of mesopleuron dorsad to metanotal groove strongly longitudinally rugulose. Head, mesosoma and gaster dark brown to brown; mandibles antennae and lateral margin of clypeus yellow brown. According to DuBois (1986) the occipital region of head and the dorsum of mesosoma show a green tint in living or freshly dead individuals.

--Gyne (Tab. 4): The winged gyne should be easily recognized by its low head length index (CL/CW 0.941 ± 0.022) and very large diameter of midocellus (OD/CS 0.133 ± 0.012). A wingless gyne was not available but the data of DuBois (1986) suggest that these have a lower head length index than wingless gynes of other species.

Taxonomic comments. The species is comparably easy to recognize as a combination of the characters underlined above.

Biology. It seems that DuBois (1986) could reliably identify this species and I follow here his statements on live history: The main habitat are open areas with sandy soil. Nest entrances may be marked by craters of ejected sand having a diameter of 12-20 cm. Nest populations are polygynous usually having up to five (rarely up to 60) reproductive gynes. Alates have been observed in July. The morphology of winged gynes indicates a potency for flight-dispersal and independent colony foundation. Wingless gynes were observed in two localities.

Monomorium emarginatum DuBois 1986

***Monomorium emarginatum* DuBois 1986**

[type investigation]

This species has been described on males, gynes and workers from near Amissville in Virginia. Investigated were the holotype winged gyne labelled "2mi w Amissville Rappahannock Co.", VIGINIA June 21, 1957 W.L.Brown E.O. Wilson", "M.C.Z. Holotype 32922", "Monomorium emarginatum Holotype M. DuBois 1983"; One paratype winged gyne and 3 paratype workers on the same pin labelled "Brewster C.Cod P.rig. and oak on sand", "Mass. VIII.4. 1955 W.L.Brown", "M.C.Z. Paratype 32922", "Monomorium emarginatum Paratype M. DuBois 1983"; depository MCZ Cambridge.

All material examined. Numeric phenotypical data were taken in 9 samples with 30 workers and three winged gynes. For details see supplementary information SI1, SI2, SI3. All this material originated from the USA.

Geographic range. Apparently widely distributed in the USA. Vouchers are from the states New York, Pennsylvania, Maine, Massachusetts, Maryland, Virginia, North Dakota, Utah and New Mexico from sea level up to 2044 m in New Mexico.

Diagnosis: --Worker (Tab. 2, Figs. 19-20, key). Very small, CS 460 ± 25 µm. Head rather short, CL/CW 1.180 ± 0.026. Dents on clypeal margin moderately long (ExCly/CS 4.20 ± 0.75%), not very acute and rather widely distant (ClSpD/CS 9.99 ± 0.93%). Frons moderately wide and frontal carinae only very slightly diverging frontad (FL/FR 1.039 ± 0.24, FL/CS 0.269 ± 0.008, FR/CS 0.259 ± 0.009). Eye large and preocular distance moderately large (EL/CS 0.217 ± 0.008, PrOc/CS 0.223 ±0.009). Scape and 3rd funiculus segment very short (SL/CS 0.757 ± 0.014, Fu2/CS 5.67 ± 0.27%, Fu3/CS 4.22 ± 0.29%). Mesosoma relatively short and relatively wide (ML/CS 1.181 ± 0.035, MW/CS 0.583 ± 0.015). Metanotal groove moderately deep, MGr/CS 4.49 ± 0.74%. Dorsal and caudal profile of propodeum not meeting in an angle, as a whole more or less convex. Petiole narrow, short and low (PeW/CS 0.267 ± 0.014, PeL/CS 0.406 ±0.015, PeH/CS 0.344 ± 0.011). Postpetiole moderately wide but very low (PpW/CS 0.296 ± 0.013, PpH/CS 0.260 ± 0.010). Lateral area of mesopleuron smooth. Head, mesosoma and gaster dark brown to brown; mandibles and lateral clypeus yellow brown.

--Gyne (Tab. 4): Only winged gynes are known. Rather large (CS 807 ± 15 µm). Very short head, scape and petiole (CL/CW 0.978 ±0.021, SL/CS 0.704 ± 0.021, PEL/CS 0.613 ± 0.015). The short median furrow on posterior mesonotum, called diagnostic by DuBois (1986), is occasionally also found in other species.

Taxonomic comments. The worker is comparatively easy to recognize as a combination of the characters underlined above. With all measurements given in mm, the three gynes are separable from the 24 winged gynes of other species by the discriminant 48.34*SL+34.27*PpW-35.905*CW-4.336PeL-12.723 < 0.

Biology. Largely unknown. Alate winged gynes were observed in the nests 21 June 1957 (Amissville), 3 August 2000 (Androscoggin), 4 August 1955 (Cape Cod). The colony from Androscoggin / Maine was found as a "crater nest in fine sand on an open spot with sparse vegetation within a Bracken Wintergreen stand" (S. Cover). The workers from Green Canyon / Utah were found "on blossoming *Cirsium lanceolatum*" (G.F.Knowlton).

Monomorium lorenzoi n.sp.

Etymology: dedicated to the collector Lorenzo Fraysse.
Type material. Holotype plus two paratype workers on the same pin labelled “USA: 32.83908, -117.04528, 85 m Mission Trail Park, sandy river bank, riparian vegetation, L. Fraysse 2024.03.22-3569”
All material examined. Only the type sample was available. For details see supplementary information SI1, SI2.
Geographic range. Only the type locality is known.
Description: --Worker (Tab. 2, Figs. 27, 28, key). Very small, CS 454 ± 5 µm. Head elongated, CL/CW 1.248 ± 0.014. Dents on clypeal margin moderately long (ExCly/CS 4.08 ± 0.17%), not very acute and widely distant (ClSpD/CS 11.03 ± 0.66%). Frons very narrow and frontal carinae only very slightly diverging frontad (FL/FR 1.028 ± 0.25, FL/CS 0.247 ± 0.009, FR/CS 0.240 ± 0.008). Eye larger than in other species and preocular distance moderately large (EL/CS 0.225 ± 0.005, PrOc/CS 0.214 ±0.003). Scape and 3rd funiculus segment long (SL/CS 0.843 ± 0.012, Fu2/CS 6.35 ± 0.37%, Fu3/CS 5.27 ± 0.21%). Mesosoma moderately long but very narrow (ML/CS 1.186 ± 0.009, MW/CS 0.537 ± 0.002). Metanotal groove moderately deep, MGr/CS 4.80 ± 0.35%. Dorsal and caudal profile of propodeum forming an angle of 140°. Petiole narrow, extremely short and very low (PeW/CS 0.265 ± 0.012, PeL/CS 0.386 ±0.003, PeH/CS 0.334 ± 0.008). Postpetiole moderately wide and low (PpW/CS 0.306 ± 0.011, PpH/CS 0.272 ± 0.015). All surfaces of head, mesosoma and gaster glabrous with exception few longitudinal carinulae on lateral parts of frontal lobes, lateral parts of clypeus, ventrolateral metapleuron and caudolateral mesopleuron (continuing dorsad into the metanotal groove). Head, mesosoma and gaster black; mandibles and lateral clypeus yellow brown.
--Gyne: unknown.
Taxonomic comments. The combination of the characters underlined above is diagnostic. The description of a new species based on a single nest sample appears justified because of all three specimens represent a combination of extreme character expressions. A simple index of three shape variables FL/CS * PeL/CS / (EL/CS) is 0.425 ± 0.004 [0.422, 0.430] in the types of *M. lorenzoi* n.sp. but 0.604 ± 0.052 [0.449,0.765] in 400 specimens of all other species. The hypothesis that the type sample of *M. lorenzoi* n.sp. could represent nothing but a simple monogenous mutant of the abundant species *M. ergatogyna* appears unlikely because the three shape variables, representing different body parts, are not correlated in 83 workers of the latter species. The mean Pearson’s correlation coefficient between the three variables is in *M. ergatogyna* 0.089 ± 0.033 – for comparison this coefficient is in the same sample 0.752 between PeW/CS and PpW/CS, 0.696 between FL/CS and FR/CS or 0.601 between Fu2/CS and Fu3/CS.
Biology. The few specimens were collected foraging on very low vegetation immediately around the nest entrance. The latter was a very small hole in the ground (<1mm of diameter) without any soil ejections around, in thin but very compacted ferruginous sand (on a well-trodden path). The micro-habitat was the path delimiting a low riparian vegetation from a drier grassland.

Monomorium monomorium Bolton 1987

***Monomorium monomorium* Bolton 1987**
[type investigation]
Replacement name for *Monomorium minutum* Mayr 1855 [junior secondary homonym of *Atta minuta* Jerdon 1851].

This species has been described under the name *Monomorium minutum* from Italy. Mayr (1855: 453) gave three type localities “Lombardie (Villa)...Insel Lido bei Venedig (Strobel)...im Kirchenstaate bei Imola (Pirazzoli)”. Investigated were 1 syntype worker labelled “Venedig Lido Coll. G. Mayr”, “ zu Zool. bot. Gesell Wien Bd. V. p. 273“, „Monomor. minutum det. G. Mayr“, “Type“; 1 syntype worker labelled “Lido, Strobl“, “minutum G. Mayr Type”, “TYPUS”, “ANTWEB CASENT 091600”; depository of both samples NHM Wien.
Comment. The text of the description of *Atta minuta* Jerdon 1851 is as follows: “Worker barely 1/12th of an inch long (= 2 mm B.S.), head oblong, eyes minute, advanced; thorax narrow; abdominal pedicles long, narrow, the first much more raised than the second; antennae gradually thickening, of a rufous color with the abdomen somewhat darker of fuscous. Female about 1/3 of an inch long (=8 mm !, B.S.), similar in form to the worker, abdomen larger proportionally, and head smaller...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...Nothing is used in its construction...” This original description does not give any drawing of the ants and makes genus or species identification questionable. The conclusion of Bolton (1987) that *Atta minuta* Jerdon belongs to the genus *Monomorium* and that it is a junior synonym of *Monomorium pharaonis* (Linnaeus 1758) is speculative. The reported total length of the gyne of 8 mm speaks against this. Dry mounted gynes of *M. pharaonis* have a total length of 4 to 5 mm and even living, physogastric gynes will never be longer than 6 mm. Anyway, I do not perform here a name reversal by depositing *Atta minuta* under Incertae Sedis and maintain the current use.

All material examined. Numeric phenotypical data were taken in 11 samples with 29 workers. The material originated from France (4 samples), Greece (1), Italy (1), Netherlands (1) and Spain (4).For details see supplementary information SI1, SI2.

Geographic range. The unclear species separation of the tiny blackish *Monomorium* in the past led to controversial interpretations if this species is of European origin or introduced here (see Gómez et al. 2024). I have strong doubts that *M. monomorium* can be considered as a true tramp species with cosmopolitan distribution since the separation from similar Orientalic or Polynesian-Australasian species was so far not clear. This refers in particular to species or populations related to or conspecific with *Monomorium liliuokalanii* Forel 1899 (see statements in the diagnosis of the *M. carbonarium* group above). As long as no counter-evidence is presented, I consider *Monomorium monomorium* as truly West Palaearctic-Mediterranean and as a strongly under-recorded species. All available samples are from elevations below 150 m a.s.l. in Spain, S France, Italy and Greece. The finding in the Netherlands is an introduction with plant material.

Diagnosis: --Worker (Tab. 2, Figs. 8–10, key). Smallest species of the *M. carbonarium* group, CS 407 ± 17 µm. Head rather short, CL/CW 1.179 ± 0.028. Clypeal spines reduced to short, blunt, often two-cusped dents (Fig. 10); as result median clypeal excision extremely shallow, ExCly/CS 1.71 ± 0.44%, ExCly 7.0 ± 1.8 µm. Frons wide and frontal carinae only very slightly diverging frontad (FL/FR 1.043 ± 0.21, FL/CS 0.294 ± 0.008, FR/CS 0.282 ± 0.006). Eye small and preocular distance moderately large (EL/CS 0.183 ± 0.006, PrOc/CS 0.221 ±0.010). Scape and 2nd funiculus segment very short (SL/CS 0.742 ± 0.012, Fu2/CS 4.82 ± 0.39%, Fu3/CS 3.70 ± 0.29%). Mesosoma relatively short and moderately wide (ML/CS 1.188 ± 0.026, MW/CS 0.577 ± 0.011). Metanotal groove rather shallow, MGr/CS 3.72 ± 0.87%. Dorsal and caudal profile of propodeum forming a continuous convexity (Fig. 9). Petiole moderately wide, long and high (PeW/CS 0.276 ± 0.017, PeL/CS 0.428 ±0.010, PeH/CS 0.362 ± 0.012). Postpetiole moderately wide and high (PpW/CS 0.313 ± 0.016, PpH/CS 0.282 ± 0.010). Dorsal surface of head glabrous with exception of longitudinal carinulae or rugulae on lateral clypeus. Contact area of mesopleuron and mesonotum with metapleuron and propodeum from ventral margin up to metanotal groove longitudinally carinulate or microrugulose. Head, mesosoma and gaster medium to dark brown.

--Gyne (Tab. 5): The two available wingless gynes are similar to winged gynes by their high and rather long mesosoma. However, the mesosomal sclerites necessary for wing movements are fused and there are no remains of shed wings detectable. Hence these gynes are classified as wingless gynes which is also confirmed by a PCA (Fig. 5). They are separable from other wingless gynes of the species group alone by the ratio SL/MH that is 0.658 and 0.706 in *M. monomorium* whereas it is > 0.760 in all known wingless gynes of the other species.

Taxonomic comments. If there is no unknown cryptic diversity, *M. monomorium* should be safely determinable considering the characters underlined above or given in the key.

Biology. (according to Emery 1916, Wagner et al. 2018, Gomez et al. 2024, M. Mei pers. comm., F. Rigato pers. comm., J. Reyez-Lopez pers. comm., A. Scupola pers. comm.): Nest populations are rather small and weakly polygynous. Supercolonies or occurrence as pest species have never been observed. The nests are easily overlooked due to small forager populations, minute size, rather slow movements and a tiny entrance hole of less than 1 mm width without any soil ejections surrounding it. It was observed to tend honeydew-producing insects on citrus trees. Among 11 sampling spots with habitat data, 6 were on alluvial, sandy soils close to sea and 3 on sandy lagoon soils at the Mediterranean Sea. The habitats are open or light stands of trees and shrub, often natural or semi-natural, but also a camping place, an urban park, an archeological site and a garden center in the Netherlands.

4.5 Morphometric tables

Table 2. Morphometric data of worker individuals of more easily separable *Monomorium carbonarium* group species given as arithmetic mean ± standard deviation [lower extreme, upper extreme].

	monomorium (n=29)	***emarginatum*** (n=30)	***marjoriae*** (n=8)	***viridum*** (n=15)	***lorenzoi n.sp.*** (n=3)	***ebeninum*** (n=9)
CS [µm]	407 ± 17 [369,433]	460 ± 25 [418,524]	504 ± 11 [490,522]	460 ± 22 [434,500]	454 ± 5 [449,460]	445 ± 17 [410,469]
CL/CW	1.179 ± 0.028 [1.135,1.246]	1.180 ± 0.026 [1.134,1.242]	1.226 ± 0.024 [1.178,1.255]	1.147 ± 0.015 [1.119,1.170]	1.248 ± 0.014 [1.234,1.262]	1.263 ± 0.025 [1.227,1.305]
SL/CS	0.742 ± 0.012 [0.716,0.769]	0.757 ± 0.014 [0.737,0.789]	0.887 ± 0.006 [0.879,0.897]	0.861 ± 0.014 [0.834,0.882]	0.843 ± 0.012 [0.830,0.855]	0.834 ± 0.011 [0.815,0.849]
Fu2/CS [%]	4.82 ± 0.39 [4.07,5.60]	5.67 ± 0.27 [5.14,6.31]	6.67 ± 0.28 [6.11,7.06]	6.86 ± 0.43 [6.16,7.57]	6.35 ± 0.37 [6.13,6.77]	6.47 ± 0.37 [5.98,7.10]
Fu3/CS [%]	3.70 ± 0.29 [2.84,4.24]	4.22 ± 0.29 [3.65,4.64]	5.53 ± 0.09 [5.40,5.65]	5.27 ± 0.24 [4.73,5.68]	5.27 ± 0.21 [5.07,5.48]	5.07 ± 0.11 [4.93,5.21]
FL/CS	0.294 ± 0.008 [0.276,0.312]	0.269 ± 0.008 [0.251,0.287]	0.274 ± 0.010 [0.260,0.287]	0.286 ± 0.007 [0.276,0.305]	0.247 ± 0.009 [0.240,0.257]	0.268 ± 0.006 [0.258,0.276]
FR/CS	0.282 ± 0.006 [0.268,0.291]	0.259 ± 0.009 [0.238,0.276]	0.266 ± 0.009 [0.250,0.279]	0.266 ± 0.012 [0.247,0.283]	0.240 ± 0.008 [0.233,0.248]	0.244 ± 0.006 [0.233,0.252]
ML/CS	1.188 ± 0.026 [1.127,1.230]	1.181 ± 0.035 [1.124,1.258]	1.270 ± 0.013 [1.252,1.293]	1.218 ± 0.019 [1.192,1.263]	1.186 ± 0.009 [1.179,1.196]	1.230 ± 0.028 [1.202,1.300]
MW/CS	0.577 ± 0.011 [0.549,0.597]	0.583 ± 0.015 [0.563,0.613]	0.536 ± 0.006 [0.526,0.545]	0.582 ± 0.013 [0.555,0.602]	0.537 ± 0.002 [0.535,0.539]	0.566 ± 0.007 [0.553,0.573]
PeW/CS	0.276 ± 0.017 [0.250,0.312]	0.267 ± 0.014 [0.239,0.293]	0.280 ± 0.016 [0.262,0.302]	0.285 ± 0.012 [0.272,0.307]	0.253 ± 0.013 [0.242,0.267]	0.289 ± 0.015 [0.272,0.308]
PpW/CS	0.313 ± 0.016 [0.277,0.340]	0.296 ± 0.013 [0.270,0.316]	0.329 ± 0.013 [0.312,0.347]	0.307 ± 0.011 [0.291,0.323]	0.306 ± 0.011 [0.298,0.319]	0.335 ± 0.021 [0.310,0.362]
PeL/CS	0.428 ± 0.010 [0.404,0.448]	0.406 ± 0.015 [0.385,0.436]	0.456 ± 0.008 [0.440,0.465]	0.456 ± 0.020 [0.431,0.498]	0.386 ± 0.003 [0.385,0.389]	0.449 ± 0.017 [0.428,0.472]
PeH/CS	0.362 ± 0.012 [0.344,0.395]	0.344 ± 0.011 [0.321,0.368]	0.372 ± 0.007 [0.364,0.382]	0.394 ± 0.011 [0.373,0.405]	0.334 ± 0.008 [0.327,0.343]	0.377 ± 0.008 [0.364,0.392]
PpH/CS	0.282 ± 0.010 [0.267,0.305]	0.260 ± 0.010 [0.240,0.287]	0.290 ± 0.005 [0.285,0.298]	0.315 ± 0.009 [0.305,0.342]	0.272 ± 0.015 [0.260,0.288]	0.289 ± 0.017 [0.256,0.313]
MGr/CS [%]	3.72 ± 0.87 [2.42,5.58]	4.49 ± 0.74 [2.68,5.58]	5.41 ± 0.64 [4.34,6.48]	6.07 ± 0.93 [4.41,7.28]	4.80 ± 0.35 [4.44,5.13]	7.20 ± 0.68 [6.46,8.66]
EL/CS	0.183 ± 0.006 [0.168,0.194]	0.217 ± 0.008 [0.200,0.236]	0.187 ± 0.004 [0.182,0.194]	0.210 ± 0.007 [0.195,0.222]	0.225 ± 0.005 [0.221,0.231]	0.206 ± 0.009 [0.193,0.215]
PrOc/CS	0.221 ± 0.010 [0.197,0.239]	0.223 ± 0.009 [0.206,0.241]	0.252 ± 0.004 [0.245,0.257]	0.240 ± 0.009 [0.225,0.259]	0.214 ± 0.003 [0.211,0.217]	0.231 ± 0.003 [0.227,0.237]
ExCly/CS [%]	1.71 ± 0.44 [0.69,2.68]	4.20 ± 0.75 [2.15,6.07]	2.53 ± 0.40 [2.10,3.26]	5.67 ± 0.99 [3.67,6.86]	4.08 ± 0.17 [3.97,4.27]	3.11 ± 0.49 [2.28,3.92]
ClSpD/CS [%]	11.15 ± 2.24 [8.57,15.55]	9.99 ± 0.93 [8.04,12.10]	9.31 ± 0.46 [8.44, 9.78]	12.68 ± 0.97 [11.18,14.66]	11.03 ± 0.66 10.53,11.78]	10.36 ± 1.26 [8.65,10.83]

Table 3. Morphometric data of worker individuals of *Monomorium carbonarium* group species of difficult separation given as arithmetic mean ± standard deviation [lower extreme, upper extreme]. Data of the easily separable species *M. emarginatum* and *M. lorenzoi* are repeated for comparison.

	gallicum n.sp. (n=73)	***carbonarium*** (n=141)	***ergatogyna*** (n=95)	***viridum*** (n=8)	***lorenzoi n.sp.*** (n=30)	***ebeninum*** (n=3)
CS [µm]	480 ± 18 [437,521]	468 ± 22 [417,539]	464± 21 [401,503]	453 ± 19 [426,482]	460 ± 25 [418,524]	454 ± 5 [449,460]
CL/CW	1.242 ± 0.023 [1.175,1.290]	1.191 ± 0.025 [1.144,1.269]	1.204 ± 0.022 [1.154,1.257]	1.247 ± 0.008 [1.234,1.260]	1.180 ± 0.026 [1.134,1.242]	1.248 ± 0.014 [1.234,1.262]
SL/CS	0.824 ± 0.012 [0.790,0.847]	0.806 ± 0.021 [0.752,0.855]	0.817 ± 0.022 [0.758,0.862]	0.812 ± 0.009 [0.796,0.827]	0.757 ± 0.014 [0.737,0.789]	0.843 ± 0.012 [0.830,0.855]
Fu2/CS [%]	6.74 ± 0.30 [6.05,7.65]	6.38 ± 0.32 [5.49,7.22]	6.36 ± 0.36 [5.60,7.19]	6.13 ± 0.39 [5.65,6.62]	5.67 ± 0.27 [5.14,6.31]	6.35 ± 0.37 [6.13,6.77]
Fu3/CS [%]	5.35 ± 0.22 [4.88,6.03]	4.82 ± 0.25 [3.88,5.38]	4.83 ± 0.28 [4.07,5.50]	4.96 ± 0.32 [4.31,5.39]	4.22 ± 0.29 [3.65,4.64]	5.27 ± 0.21 [5.07,5.48]
FL/CS	0.286 ± 0.007 [0.268,0.305]	0.285 ± 0.008 [0.267,0.307]	0.274 ± 0.008 [0.256,0.295]	0.270 ± 0.007 [0.261,0.280]	0.269 ± 0.008 [0.251,0.287]	0.247 ± 0.009 [0.240,0.257]
FR/CS	0.276 ± 0.007 [0.262,0.294]	0.276 ± 0.008 [0.255,0.299]	0.263 ± 0.008 [0.244,0.283]	0.266 ± 0.006 [0.257,0.275]	0.259 ± 0.009 [0.238,0.276]	0.240 ± 0.008 [0.233,0.248]
ML/CS	1.204 ± 0.027 [1.134,1.277]	1.180 ± 0.028 [1.119,1.261]	1.161 ± 0.032 [1.091,1.259]	1.207 ± 0.018 [1.171,1.223]	1.181 ± 0.035 [1.124,1.258]	1.186 ± 0.009 [1.179,1.196]
MW/CS	0.571 ± 0.010 [0.549,0.596]	0.582 ± 0.014 [0.556,0.649]	0.567 ± 0.015 [0.534,0.606]	0.561 ± 0.014 [0.540,0.576]	0.583 ± 0.015 [0.563,0.613]	0.537 ± 0.002 [0.535,0.539]
PeW/CS	0.293 ± 0.012 [0.260,0.325]	0.290 ± 0.018 [0.245,0.337]	0.282 ± 0.017 [0.247,0.335]	0.260 ± 0.017 [0.240,0.294]	0.267 ± 0.014 [0.239,0.293]	0.253 ± 0.013 [0.242,0.267]
PpW/CS	0.328 ± 0.012 [0.302,0.364]	0.316 ± 0.016 [0.287,0.378]	0.317 ± 0.013 [0.285,0.352]	0.316 ± 0.021 [0.292,0.348]	0.296 ± 0.013 [0.270,0.316]	0.306 ± 0.011 [0.298,0.319]
PeL/CS	0.438 ± 0.014 [0.404,0.479]	0.439 ± 0.015 [0.408,0.471]	0.425 ± 0.013 [0.390,0.459]	0.428 ± 0.011 [0.404,0.437]	0.406 ± 0.015 [0.385,0.436]	0.386 ± 0.003 [0.385,0.389]
PeH/CS	0.380 ± 0.010 [0.361,0.405]	0.378 ± 0.013 [0.324,0.424]	0.361 ± 0.010 [0.336,0.386]	0.358 ± 0.008 [0.347,0.369]	0.344 ± 0.011 [0.321,0.368]	0.334 ± 0.008 [0.327,0.343]
PpH/CS	0.306 ± 0.008 [0.290,0.327]	0.294 ± 0.011 [0.271,0.325]	0.284 ± 0.011 [0.253,0.306]	0.276 ± 0.012 [0.263,0.293]	0.260 ± 0.010 [0.240,0.287]	0.272 ± 0.015 [0.260,0.288]
MGr/CS [%]	4.94 ± 0.62 [2.6,6.0]	5.24 ± 0.66 [3.0,7.3]	4.63 ± 0.70 [2.8,6.2]	4.29 ± 0.55 [3.6,5.1]	4.49 ± 0.74 [2.68,5.58]	4.80 ± 0.35 [4.44,5.13]
EL/CS	0.199 ± 0.005 [0.190,0.214]	0.205 ± 0.007 [0.186,0.227]	0.199 ± 0.009 [0.180,0.228]	0.206 ± 0.003 [0.201,0.210]	0.217 ± 0.008 [0.200,0.236]	0.225 ± 0.005 [0.221,0.231]
PrOc/CS	0.229 ± 0.007 [0.210,0.242]	0.224 ± 0.010 [0.203,0.247]	0.224 ± 0.009 [0.206,0.250]	0.227 ± 0.005 [0.221,0.236]	0.223 ± 0.009 [0.206,0.241]	0.214 ± 0.003 [0.211,0.217]
ExCly/CS [%]	4.42 ± 0.54 [2.97,5.49]	4.82 ± 0.58 [3.01,6.78]	4.58 ± 0.68 [2.97,6.46]	3.04 ± 0.47 [2.37,3.57]	4.20 ± 0.75 [2.15,6.07]	4.08 ± 0.17 [3.97,4.27]
ClSpD/CS [%]	11.48 ± 0.79 [9.91,13.68]	11.42 ± 0.99 [9.03,13.87]	10.38 ± 0.96 [8.35,14.89]	10.12 ± 0.90 [8.33,11.31]	9.99 ± 0.93 [8.04,12.10]	11.03 ± 0.66 10.53,11.78]

Table 4. Morphometric data of winged gynes of *Monomorium carbonarium* group species given as arithmetic mean ± standard deviation [lower extreme, upper extreme].

	viridum (n=8)	***carbonarium* large** (n=4)	***carbonarium* small** (n=10)	***ergatandria*** (n=2)	***emarginatum*** (n=3)
CS [µm]	846 ± 41 [803,915]	844 ± 11 [832,859]	727 ± 37 [675,776]	721 ± 6 [717,725]	807 ± 15 [790,817]
CL/CW	0.941 ± 0.022 [0.908,0.974]	1.054 ± 0.018 [1.038,1.077]	1.069 ± 0.038 [0.973,1.114]	1.103 ± 0.011 [1.095,1.111]	0.978 ± 0.021 [0.966,1.002]
SL/CS	0.771 ± 0.009 [0.757,0.786]	0.731 ± 0.016 [0.716,0.752]	0.787 ± 0.012 [0.768,0.804]	0.787 ± 0.006 [0.782,0.791]	0.704 ± 0.021 [0.690,0.729]
Fu2/CS [%]	6.19 ± 0.37 [5.64,6.77]	5.92 ± 0.13 [5.78,6.10]	6.70± 0.27 [6.34,7.01]	6.98 ± 0.29 [6.78,7.19]	5.86 ± 0.20 [5.64,6.01]
Fu3/CS [%]	5.32± 0.26 [4.78,5.48]	4.67 ± 0.20 [4.49,4.95]	5.28 ± 0.39 [4.66,5.75]	5.29 ± 0.31 [5.07,5.51]	4.45 ± 0.28 [4.29,4.77]
FL/CS	0.322 ± 0.008 [0.314,0.338]	0.307 ± 0.012 [0.293,0.320]	0.301 ± 0.011 [0.284,0.323]	0.304 ± 0.008 [0.298,0.309]	0.304 ± 0.028 [0.291,0.321]
FR/CS	0.314 ± 0.011 [0.293,0.327]	0.295 ± 0.011 [0.283,0.306]	0.292 ± 0.016 [0.262,0.320]	0.298 ± 0.016 [0.286,0.309]	0.301 ± 0.015 [0.288,0.317]
ML/CS	2.094 ± 0.070 [1.943,2.178]	1.952 ± 0.069 [1.910,2.055]	2.002 ± 0.031 [1.955,2.057]	2.014 ± 0.031 [1.992,2.036]	2.008 ± 0.021 [1.986,2.027]
MW/CS	0.965 ± 0.057 [0.853,1.045]	1.012 ± 0.065 [0.914,1.052]	0.885 ± 0.076 [0.816,1.060]	0.843 ± 0.013 [0.834,0.852]	0.916 ± 0.044 [0.868,0.954]
MH/CS	1.309 ± 0.079 [1.157,1.422]	1.194 ± 0.041 [1.165,1.252]	1.137 ± 0.027 [1.103,1.180]	1.122 ± 0.031 [1.100,1.145]	1.189 ± 0.011 [1.177,1.196]
PeW/CS	0.485 ± 0.013 [0.465,0.502]	0.490 ± 0.030 [0.463,0.532]	0.490 ± 0.033 [0.448,0.522]	0.464 ± 0.025 [0.448,0.482]	0.419 ± 0.023 [0.395,0.440]
PpW/CS	0.582 ± 0.029 [0.535,0.637]	0.593 ± 0.027 [0.566,0.629]	0.599 ± 0.037 [0.530,0.646]	0.585 ± 0.029 [0.564,0.606]	0.487 ± 0.041 [0.462,0.534]
PeL/CS	0.674 ± 0.033 [0.639,0.724]	0.729 ± 0.013 [0.718,0.747]	0.687 ± 0.024 [0.657,0.724]	0.658 ± 0.010 [0.650,0.665]	0.613 ± 0.015 [0.599,0.629]
PeH/CS	0.552 ± 0.019 [0.524,0.580]	0.558 ± 0.012 [0.550,0.575]	0.552 ± 0.020 [0.516,0.580]	0.535 ± 0.032 [0.512,0.558]	0.493 ± 0.031 [0.469,0.527]
PpH/CS	0.511 ± 0.039 [0.449,0.568]	0.453 ± 0.018 [0.433,0.473]	0.466 ± 0.036 [0.410,0.511]	0.450 ± 0.010 [0.443,0.457]	0.424 ± 0.020 [0.411,0.447]
EL/CS	0.300 ± 0.019 [0.261,0.324]	0.286 ± 0.009 [0.277,0.297]	0.276 ± 0.011 [0.263,0.295]	0.277 ± 0.023 [0.261,0.293]	0.268 ± 0.012 [0.254,0.279]
PrOc/CS	0.207 ± 0.015 [0.191,0.240]	0.211 ± 0.005 [0.207,0.218]	0.209 ± 0.004 [0.203,0.217]	0.192 ± 0.011 [0.184,0.200]	0.220 ± 0.003 [0.216,0.222]
ExCly/CS [%]	3.41 ± 0.79 [2.07,4.15]	4.43 ± 0.39 [4.16,4.99]	4.34 ± 0.76 [3.54,5.92]	3.63 ± 0.27 [3.44,3.82]	3.45 ± 1.35 [1.91,4.43]
ClSpD/CS [%]	13.94 ± 1.87 [10.08,15.63]	10.96 ± 1.61 [9.68,13.11]	11.62 ± 1.01 [10.22,13.03]	10.53 ± 0.41 [10.24,10.82]	10.25 ± 2.97 [7.49,13.39]
OD/CS	0.133 ± 0.012 [0.117,0.148]	0.090 ± 0.006 [0.082,0.096]	0.087 ± 0.005 [0.077,0.097]	0.087 ± 0.013 [0.078,0.097]	0.079 ± 0.002 [0.076,0.081]
OceD/CS	0.221 ± 0.013 [0.196,0.239]	0.227 ± 0.013 [0.218,0.244]	0.251 ± 0.017 [0.221,0.280]	0.232 ± 0.014 [0.231,0.233]	0.235 ± 0.014 [0.225,0.245]

Table 5. Morphometric data of wingless gynes of *Monomorium carbonarium* group species given as arithmetic mean ± standard deviation [lower extreme, upper extreme].

	monomorium (n=2)	***carbonarium*** **large** (n=2)	***carbonarium*** **small** (n=9)	***ergatandria*** (n=24)	***gallicum n.sp.*** (n=10)	***compressum*** type	***ebeninum*** type
CS [µm]	634 ± 8 [628,640]	842 ± 14 [832,851]	666 ± 13 [646,693]	697 ± 43 [626,778]	685 ± 10 [660,694]	622	660
CL/CW	1.084 ± 0.039 [1.057,1.112]	1.086 ± 0.002 [1.085,1.088]	1.086 ± 0.028 [1.031,1.126]	1.090 ± 0.034 [1.037,1.140]	1.101 ± 0.011 [1.083,1.112]	1.168	1.107
SL/CS	0.719 ± 0.015 [0.709,0.730]	0.713 ± 0.008 [0.707,0.718]	0.758 ± 0.018 [0.731,0.791]	0.784 ± 0.020 [0.744,0.819]	0.774 ± 0.012 [0.751,0.798]	0.797	0.762
Fu2/CS [%]	5.80± 0.05 [5.76,5.83]	6.71 ± 0.85 [6.11,7.31]	6.58± 0.33 [6.23,7.23]	6.65 ± 0.35 [6.06,7.33]	6.80 ± 0.35 [6.29,7.44]	5.99	5.73
Fu3/CS [%]	4.62 ± 0.09 [4.55,4.68]	5.14 ± 0.43 [4.84,5.45]	5.28 ± 0.21 [4.97,5.67]	5.19 ± 0.21 [4.90,5.73]	5.78 ± 0.41 [5.25,6.42]	4.87	4.93
FL/CS	0.315 ± 0.007 [0.310,0.320]	0.331 ± 0.004 [0.328,0.333]	0.322 ± 0.006 [0.313,0.329]	0.308 ± 0.011 [0.285,0.326]	0.329 ± 0.009 [0.319,0.346]	0.298	0.302
FR/CS	0.290 ± 0.009 [0.272,0.308]	0.320 ± 0.012 [0.311,0.328]	0.317 ± 0.009 [0.298,0.329]	0.304 ± 0.011 [0.278,0.321]	0.319 ± 0.009 [0.305,0.334]	0.294	0.269
ML/CS	1.886 ± 0.027 [1.867,1.905]	1.846 ± 0.021 [1.831,1.860]	1.659 ± 0.028 [1.612,1.702]	1.701 ± 0.056 [1.606,1.806]	1.681 ± 0.041 [1.623,1.738]	1.468	1.691
MW/CS	0.759 ± 0.016 [0.747,0.770]	0.786 ± 0.038 [0.759,0.813]	0.719 ± 0.022 [0.668,0.742]	0.712 ± 0.023 [0.677,0.778]	0.732 ± 0.011 [0.713,0.749]	0.633	0.656
MH/CS	1.056 ± 0.030 [1.034,1.077]	1.092 ± 0.000 [1.092,1.093]	0.902 ± 0.024 [0.870,0.942]	0.934 ± 0.047 [0.807,1.022]	0.936 ± 0.040 [0.845,0.995]	0.671	0.806
PeW/CS	0.431 ± 0.008 [0.426,0.437]	0.511 ± 0.011 [0.504,0.519]	0.460 ± 0.027 [0.421,0.507]	0.469 ± 0.031 [0.420,0.533]	0.508 ± 0.021 [0.462,0.534]	0.374	0.443
PpW/CS	0.456 ± 0.023 [0.440,0.472]	0.656 ± 0.015 [0.645,0.667]	0.550 ± 0.042 [0.508,0.636]	0.560 ± 0.025 [0.505,0.602]	0.623 ± 0.030 [0.547,0.652]	0.487	0.516
PeL/CS	0.615 ± 0.011 [0.607,0.621]	0.740 ± 0.005 [0.737,0.743]	0.650 ± 0.041 [0.597,0.711]	0.628 ± 0.031 [0.579,0.722]	0.649 ± 0.042 [0.577,0.697]	0.554	0.597
PeH/CS	0.498 ± 0.006 [0.494,0.502]	0.581 ± 0.001 [0.580,0.581]	0.535 ± 0.013 [0.521,0.567]	0.539 ± 0.020 [0.499,0.585]	0.569 ± 0.021 [0.523,0.606]	0.480	0.530
PpH/CS	0.439 ± 0.004 [0.436,0.442]	0.474 ± 0.013 [0.464,0.483]	0.478 ± 0.018 [0.452,0.505]	0.464 ± 0.026 [0.410,0.521]	0.508 ± 0.022 [0.468,0.535]	0.415	0.466
EL/CS	0.240 ± 0.010 [0.232,0.247]	0.264 ± 0.001 [0.264,0.265]	0.253 ± 0.006 [0.245,0.262]	0.245 ± 0.008 [0.233,0.260]	0.254 ± 0.006 [0.245,0.264]	0.232	0.280
PrOc/CS	0.223 ± 0.015 [0.213,0.234]	0.212 ± 0.015 [0.202,0.223]	0.216 ± 0.006 [0.204,0.222]	0.229 ± 0.010 [0.210,0.246]	0.218 ± 0.004 [0.212,0.225]	0.247	0.209
ExCly/CS [%]	2.29 ± 0.07 [2.24,2.34]	3.66 ± 0.47 [3.32,3.99]	3.31 ± 0.40 [2.61,3.93]	4.10 ± 0.71 [2.52,5.26]	3.07 ± 0.48 [2.09,3.67]	1.60	3.85
ClSpD/CS [%]	12.18 ± 4.21 [9.20,15.15]	12.07 ± 0.05 [12.03,12.11]	11.26 ± 0.47 [10.36,11.87]	10.36 ± 1.20 [7.98,12.39]	11.31 ± 1.12 [10.36,13.46]	8.55	10.13
OD/CS	0.098 ± 0.002 [0.096,0.100]	0.099 ± 0.004 [0.096,0.102]	0.086 ± 0.013 [0.069,0.110]	0.085 ± 0.010 [0.070,0.106]	0.094 ± 0.005 [0.085,0.101]	0.060	0.049
OceD/CS	0.244 ± 0.028 [0.224,0.264]	0.209 ± 0.012 [0.200,0.217]	0.247 ± 0.011 [0.234,0.272]	0.248 ± 0.020 [0.217,0.292]	0.263 ± 0.007 [0.253,0.273]	0.228	0.193

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