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AN APPRAISAL OF *MYRMICA BERGI* RUZSKY, 1902 AND RELATED SPECIES (HYMENOPTERA: FORMICIDAE)

ALEXANDER RADCHENKO[1], GRAHAM W. ELMES[2] and MICHAŁ WOYCIECHOWSKI[3]

[1]*Laboratory of Social and Myrmecophilous Insects, Museum and Institute of Zoology, Polish Academy of Sciences, 64, Wilcza St., 00-679, Warszawa, Poland; e-mail: rad@usenc.kiev.ua*
[2]*Centre for Ecology and Hydrology, Winfrith Technology Centre, Winfrith Newburg, Dorchester, Dorset DT2 8ZD, United Kingdom; e-mail: gwe@ceh.ac.uk*
[3]*Jagiellonian University, Institute of Environmental Sciences, Gronostajowa St. 3, 30-387 Kraków, Poland; e-mail: rowoycie@cyf-kr.edu.pl*

Abstract.— An ecological survey of North Mongolian *Myrmica* yielded a species similar to, but quite distinct from *M. bergi* and its close relative *M. gallienii*. The Mongolian species conformed to the type specimen of *M. bergi* subsp. *divergens*. Therefore it is raised to species status and a redescription of the workers and first descriptions of the queens and males are provided. *M. bergi* was known to be unusually variable for *Myrmica* species, at times different regional populations have been described as separate species, subspecies or varieties. A morphometric analysis of *M. bergi* shows that there is both a valid morphological and geographical basis to the "old" forms. This is discussed in terms of the formation of the steppe zone and the isolation of the Mongolian and Siberian steppes, which left *M. divergens* as the only representative of the *scabrinodis*-group of *Myrmica* species east of Lake Baikal. It is hypothesised that periodic interruptions of the western steppes by transgressions of the Caspian Sea, sufficiently isolated bordering populations of *M. bergi* to produce the geographical patterns in morphological variation seen today.

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Key words.— Ants, taxonomy, *Myrmica bergi*, *M. divergens*, *M. gallienii*, steppe–zone, biogeography.

INTRODUCTION

Myrmica bergi Ruzsky, 1902 is considered to be a member of the *scabrinodis*-group of *Myrmica* species (Radchenko 1994a, c) and is probably most closely related to *M. gallienii* Bondroit. *M. bergi* was first described in Russian (Ruzsky 1902a) and again in German (Ruzsky 1902b) based on workers, collected by L. Berg in the vicinity of the Aral Sea (from Tas-Bulak on the west coast of Aral Sea, 5.VII.1900; the mouth of river Syr-Daria, Raim, 7/8.V.1901; Ak-Dzhulpas on the north-east coast of Aral Sea, 26.V.1901; Kazalinsk, bank of river Syr-Daria, 13.IV.1901).

The following year, *M. bergi* was recorded from a sandy area near Khanskaya Stavka, in the Astrakhan' region of Russia (Ruzsky 1903). In the same paper Ruzsky also described a new variety – *M. rugosa* var. *kirgisica*, based on workers taken in the same region (the vicinity of Astrakhan' and a sandy area near Khanskaya Stavka). Ruzsky (1905) added a new record for *M. bergi*: queens and males taken by L. Berg in 1903, on the lower part of the Ili river, near Lake Balkhash in the Semirechensky Region (modern Kazakhstan), and described another new variety (*M. bergi* var. *barchanica*) from workers, collected by Ruzsky and Gordiagin in June 1902, from a sandy area near Khanskaya Stavka. It is almost certain that ants recorded in 1903 as *M. bergi*, were from the same populations as those described as var. *barchanica* in 1905. Furthermore, careful reading of Ruzsky's papers indicates that var. *barchanica* was described from material collected at the same time and from the same locality as var. *kirgisica*. We, therefore, suggest, that vars. *kirgisica* and *barchanica* were probably just local variants within a single regional population of *M. bergi*.

Crawley (1920) described *M. bergi* var. *fortior* (name praeocc.) from workers was taken from NW Persia (Iran); it was given the replacement name *M. bergi persiana* (Weber 1947). Another variety, *M. bergi* var. *divergens* (Karavaiev 1931) was described from a single worker taken in 1925 from southern Yakutia (East Siberia). Finally, *Myrmica kamyschiensis* (Arnol'di 1934) was described from workers and queens taken in 1923 on the coast of lagoon Sivash and in Kamysh-Burun, near Kerch, in the Crimea (southern Ukraine). In the same paper Arnol'di (1934) noted that *M. bergi* had been found near Astrakhan', Sarepta (now vicinity of Volgograd) and the river Terek (eastern Caucasus). Other notes on the ecology and/or distribution of *M. bergi* were published by Kuznetsov-Ugamsky (1927), Marikovsky (1962), Arnol'di (1976) and Tarbinsky (1976).

In his monographic review of *Myrmica*, Weber (1947) considered *M. kamyschiensis* to be a subspecies of *M. bergi* and simply listed the other infraspecific names of *M. bergi*. On the other hand, Arnol'di (1970) synonymised var. *barchanica* with *M. bergi*, and considered var. *kirgisica* as a northern, and *kamyschiensis* – as a western subspecies of *M. bergi*. More recently, Seifert (1988) formally synonymised var. *kirgisica* and subsp. *kamyschiensis* with *M. bergi*, and Radchenko (1994c) synonymised subsp. *divergens* and subsp. *persiana* with *M. bergi*. Therefore, all previously described infraspecific forms of *M. bergi* are currently considered as synonyms of the nominative species.

We re-examined this situation when we obtained excellent samples of *Myrmica* ants from West Khentii, North Mongolia that were collected as part of a survey of Mongolian biodiversity (Muehlenberg et al. 2000; and see acknowledgements). The samples included a species with female castes similar to *M. bergi* but with quite distinct males. After careful study of the existing types of *M. bergi* and its infraspecific forms, and a large proportion of the specimens available in collections we identified the Mongolian species as *M. bergi* subsp. *divergens*. In this paper we elevate *M. divergens* to species level, redescribe workers (using a more modern approach) and describe queens and males. We confirm that although the other "old" infraspecific forms are correctly synonymised with *M. bergi*, they illustrate a high degree of geographically patterned variation between *M. bergi* populations that is unusual for *Myrmica* species.

MATERIALS AND METHODS

Collections and type specimens examined

We compared specimens of *M. divergens* from Mongolia (collected by Woyciechowski) with specimens of *M. bergi*, *M. gallienii* and *M. rugulosa* Nylander (collected by Elmes and Radchenko at many sites throughout Europe, Caucasus and Asia Minor) and with specimens held by the following institutions: Zoological Institute of Russian Academy of Sciences, St.-Petersburg (ZIN); Zoological Museum of Moscow State University (ZMMU); Institute of Zoology of Ukrainian National Academy of Sciences, Kiev (including Karavaiev's collection) (IZK); Museum and Institute of Zoology of Polish Academy of Sciences, Warsaw (MIZ); Institute royal des Sciences naturelles de Belgique, Bruxelles (ISNB), Zoological Museum of the University of Helsinki (including Nylander's collection) (ZMUH), University Museum, Oxford (UMO); the Elmes collection, UK (ELMES).

Full details, location and notes on the examined type specimens of *M. bergi* and its infraspecific forms are given under Taxonomy (below). Otherwise, we examined the type specimens of *M. gallienii* (ISNB), and its synonyms *M. limanica* Arnol'di (ZMMU, IZK), *M. limanica obensis* Arnol'di (ZMMU), *M. limanica* nat. *chersonensis* (ZMMU), *M. jacobsoni* Kutter (ZMMU), also >100 workers and >25 queens and males from West and East Europe, Turkey and West Siberia. We also examined the type specimens of *M. rugulosa* (ZMUH) and its synonym var. *sulcinodo-rugulosa* Nasonov (ZMMU), and >100 workers and >25 queens and males from West and East Europe.

Morphometric analysis

We measured the lectotype and 3 paralectotypes of *M. bergi*, the holotype of var. *divergens*, 4 syntypes of *M. bergi kamyschiensis*, the lectotype and 2 paralectotypes of var. *barchanica*, the lectotype and 5 paralectotypes of *M. bergi persiana* and the lectotype and 1 paralectotype of *M. gallienii*. *M. rugulosa* was not included in the morphometric analysis because it clearly differs from the other species. Measurements were also made on: a sample of 30 workers selected at random from the different colony series, and all available males and queens of *Myrmica divergens* from Mongolia; 19 workers (ZMMU) from Middle Asia (Uzbekistan, Kirgizstan and Tadzhikistan) and southern Kazakhstan, which we identified as *M. bergi* s. str.; 20 workers (ELMES) of *M. bergi kamyschiensis*, each from a different colony taken from the steppe habitat of southern Ukraine similar to that recorded for the syntypes; 14 workers (ZIN) recently collected from the South-Volga region of Russia where the types of var. *kirgisica* and var. *barchanica* were taken (we treat these as var. *kirgisica*); 20 workers (ELMES) of *M. gallienii*, a single worker from different colonies from Germany, Austria, Poland, Belarus, Ukraine and Turkey.

Full details of the measurements used (accurate 0.01 mm) can be found in our previous studies of *Myrmica* (Radchenko and Elmes 1998, 1999, 2001a, b; Radchenko et al. 2001; Elmes et al. 2002). Throughout this paper we abbreviate them as: HL – head-length; HW – head-width (behind the eyes); FW – minimum frons-width; FLW – maximum width between the frontal lobes; SL – scape-length; AL – alitrunk-length; HTL – hind tibia-length; PNW – pronotum-width (workers); PL – petiole-length; PPL – postpetiole-length; PW – petiole-width; PPW – postpetiole-width; PH – petiole-height; PPH – postpetiole-height; ESL – propodeal spine-length; ESD – distance between tips of propodeal spines; AH – alitrunk-height; SCW – scutum-width and SCL – length of scutum

+ scutellum were measured for males and queens (no distinction is made in this paper between dealate, fertilised queens and young, alate gynes). The indices used were: CI = HL/HW; FI = FW/HW; FLI = FLW/FW; SI_1 = SL/HL; SI_2 = SL/HW; PI_1 = PL/PH; PI_2 = PL/HW; PPI_1 = PPL/PPH; PPI_2 = PPH/PPW; PPI_3 = PPW/PW; PPI_4 = PPW/HW; ESLI = ESL/HW; ESDI = ESD/ESL; HTI = HTL/HW; AI = AL/AH; HTI = HTL/HW; SCI = SCL/SCW.

Canonical variate analysis

Besides calculating indices, the morphometrics of workers were used to make a Canonical Variate Analysis (CNVA) of the three species: *M. divergens*, *M. bergi* and *M. gallienii*. For a detailed explanation of the methods see Blackith and Rayment (1971) and for its application to *Myrmica* ants see Elmes (1978), Elmes and Thomas (1985), Elmes et al. (2002), Radchenko et al. (2001). In simple terms this method attempts to maximise the between-group to within-group variance ratio by searching for a linear combination of the original morphometrics (discriminant functions or Canonical Variates, CVs) that emphasise differences which exist between the groups while at the same time minimising differences between individuals within the groups. The number of CVs possible are one less than the number of groups, e.g. 3 groups result in 2 CVs. The method cannot discriminate between groups unless real differences exist in the original morphometrics, but the advantage of using CNVA over simple ratios is that differences between many of the original variables are combined in a few CVs which usually have greater overall discriminatory power. Very occasionally, with some combination of groups, the numerical algorithm used cannot resolve between two "competing" CVs (this was the case in one of our analyses reported below). For convenience the CV scores are standardised to have unit average within-group variance and an overall mean of zero. The method assumes that the original measurements are normally distributed and that the within-group variances are homogenous, in which case the within-group CV scores should all have the same spread with confidence limits equal to $\chi^2_{(df = 1)}$.

TAXONOMY

Myrmica divergens Karavaiev

Myrmica bergi var. *divergens* Karavaiev 1931: 105, w; Weber 1947: 473.
Myrmica bergi subsp. *divergens*: Pisarski 1969: 227; Dlussky, Pisarski 1970: 85; Pisarski, Krzysztofiak 1981: 155; Bolton 1995: 278; synonymy by Radchenko 1994c: 76. Revived from synonymy, raised to species and description queens and males, present paper.

Material examined. Holotype, worker: "Isl. Khar'yalakh, 50 km lower Olekminsk, 11.vi.1925, L. Bianki" (label in Russian) (IZK). Also > 200 workers, 17 queens and 9 males from different places in Mongolia (MIZ, ZMMU, IZK, ELMES) (distribution see on Fig. 29).

Redescription of workers (Figs 1–7; Table 1).

Head longer than broad, with weakly convex sides and occipital margin, and rounded occipital corners. Anterior clypeal margin broadly rounded, not prominent, usually without notch medially, but in some workers can be very shallowly notched. Frontal carinae feebly curved, frons wide. Antennal scape relatively short, sharply curved at its base, usually not angular and with no trace of a carina or lobe; in some workers the curvature can be bluntly but distinctly angled (compare Figs 4 and 7). Mandibles with 7–9 teeth.

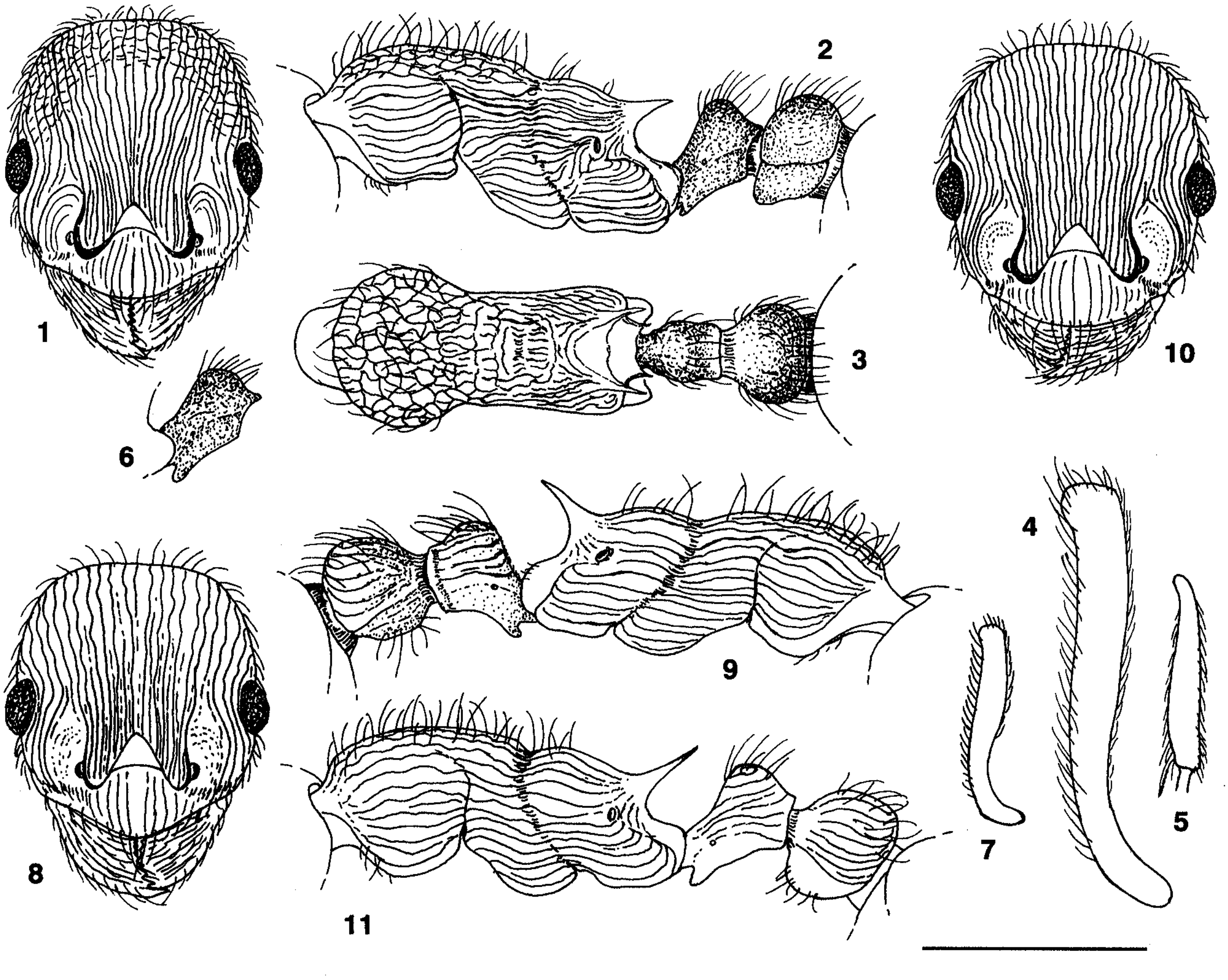
Alitrunk with slightly convex promesonotal dorsum; promesonotal suture indistinct (seen from above); metanotal groove distinct but not very deep. Propodeal spines relatively short to very short, acute and straight, seen in profile they are wide at base, projecting backwards at an angle less than 45°, not curving downwards; seen from above they range from slightly divergent to slightly convergent. Petiole with distinct peduncle, its anterior surface concave, meeting dorsal surface at a blunt rounded angle; dorsal surface usually broadly rounded but can be feebly convex, short plate, slightly inclined posteriorly (compare Figs 2 and 6). Postpetiole shorter than high, with convex dorsum. Spurs on middle and hind tibiae well developed and pectinate.

Usually only frons with longitudinal, slightly sinuous rugae, remainder part of head dorsum with reticulation, but reticulation sometimes developed only on occiput and lateral parts of head dorsum. Antennal sockets surrounded by rugae. Clypeus with longitudinal rugae. Sides of alitrunk with longitudinal, partly sinuous rugae, promesonotal dorsum with coarse reticulation. Usually petiole only punctured laterally, sometimes with very fine reticulation and a few specimens can have a more developed, but never coarse reticulation (compare Figs 2 and 6); petiolar node dorsally with fine short sinuous rugulae and/or fine reticulation. Postpetiole with fine longitudinally-concentric rugulosity or even striation. Surfaces between rugae on the head and alitrunk smooth and shiny.

Hairs on head margins and alitrunk dorsum abundant, erect to suberect, quite long and slightly curved; antennal scape with suberect and tibiae with subdecumbent hairs. Whole body more or less bicoloured: alitrunk and waist light reddish or dark red to reddish-brown, appendages somewhat lighter; head and gaster darker, brownish-black to black.

Queens (first description) (Figs 12–16; Table 1).

Generally like workers in shape of head and character of sculpture, colour and pilosity of the body, apart from having a relatively wider head with more convex lateral and occipital margins (compare indices in Table 1), slightly coarser sculpture on head and alitrunk,



Figures 1–11. Details of structure of *M. divergens* (1–7; 1–5, holotype), *M. bergi* (8, 9, paralectotype) and *M. gallienii* (10, 11, lectotype) (workers). (1, 8, 10) Head, frontal view, (2, 9, 11) alitrunk and waist in profile, (3) alitrunk and waist from above, (4, 7) antennal scape in profile, (5) hind tibia, (6) petiole in profile. Scale bar = 1 mm (for Fig. 4 = 0.5 mm).

alitrunk dorsum without reticulation, only with coarse longitudinal rugae (compare Figs 1–3 and 12–14).

Males (***first description***) (Figs 19–23; Table 1).

Head slightly longer than broad, with convex occipital margin and sides, and broadly rounded occipital corners; anterior clypeal margin widely rounded, in some specimens very shallowly notched medially. Frontal carinae gently curved. Antennal scape short, antennae 13-jointed, antennal club 4-jointed; 2nd funicular joint more than 1.5 times longer (never less) than 3rd joint. Masticatory margin of mandibles distinct, with 6–7 acute teeth.

Alitrunk relatively long, scutum slightly convex, and scutellum does not project dorsally above scutum when seen in profile. Propodeum with blunt rounded denticles. In profile, petiole relatively high, with narrowly rounded dorsum of node, its anterior surface straight; postpetiole higher than long, with convex dorsum.

Frons with distinct longitudinally-concentric rugulae, lateral parts of head dorsum at most with very fine striation; whole surface of head also finely but densely punctured; clypeus with longitudinal striation or fine rugulae, much finer punctured, appears more or less shiny. Scutum in front of Mayr's furrows usually with fine longitudinal striation, but can be more or less smooth; remainder usually with fine longitudinal rugae or striation and fine punctations; dorsally, propodeum with dense but not coarse rugulosity or striation. Propleurae densely but not coarsely punctured, appearing dull; mesopleurae with fine longitudinal rugulosity or striation, sides of propodeum with more coarse longitudinal rugosity; surface between rugae smooth and shiny. Petiole and postpetiole smooth and shiny, at most with very fine superficial punctations on petiolar node.

Head and alitrunk with very abundant, long, curved erect hairs. Antennal scape and legs with short, straight

Morphometrics								Indices							
	Workers (31)			Queens (5)		Males (13)			Workers (31)			Queens (5)		Males (13)	
	Holotype	mean	range	mean	range	mean	range		Holotype	mean	range	mean	range	mean	range
HL	1.18	1.13	0.96–1.20	1.21	1.20–1.25	0.92	0.86–0.97	CI	1.16	1.15	1.12–1.18	1.10	1.08–1.12	1.06	1.05–1.09
HW	1.02	0.98	0.86–1.06	1.11	1.09–1.14	0.87	0.79–0.92	FI	0.44	0.44	0.41–0.48	0.44	0.42–0.45		
FW	0.45	0.43	0.38–0.50	0.49	0.48–0.50			FLI	1.18	1.13	1.07–1.19	1.09	1.08–1.13		
FLW	0.53	0.49	0.42–0.54	0.53	0.52–0.54			SI1	0.75	0.76	0.73–0.79	0.75	0.73–0.77	0.37	0.35–0.39
SL	0.88	0.85	0.76–0.91	0.90	0.89–0.92	0.34	0.31–0.36	SI2	0.86	0.87	0.82–0.91	0.82	0.80–0.83	0.40	0.38–0.42
AL	1.66	1.59	1.37–1.75	2.01	2.00–2.01	2.00	1.86–2.08	PI1	1.15	1.27	1.15–1.36	1.23	1.17–1.29	1.18	1.11–1.20
HTL	0.86	0.85	0.71–0.92	0.93	0.91–0.96	1.13	1.06–1.16	PI2	0.44	0.49	0.44–0.54	0.51	0.50–0.53	0.58	0.56–0.61
PNW	0.72	0.71	0.61–0.79					PPI1	0.75	0.77	0.71–0.83	0.72	0.69–0.74	0.79	0.75–0.83
PL	0.45	0.48	0.43–0.51	0.56	0.54–0.58	0.51	0.48–0.53	PPI2	0.98	1.00	0.92–1.05	0.99	0.97–1.00	1.01	0.96–1.06
PW	0.29	0.29	0.26–0.34	0.38	0.36–0.40	0.34	0.31–0.38	PPI3	1.55	1.55	1.46–1.67	1.54	1.48–1.61	1.49	1.34–1.61
PH	0.39	0.38	0.33–0.41	0.46	0.45–0.46	0.43	0.40–0.45	PPI4	0.44	0.46	0.42–0.49	0.53	0.52–0.54	0.58	0.56–0.63
PPL	0.33	0.35	0.31–0.38	0.42	0.40–0.43	0.41	0.40–0.41	ESLI	0.24	0.27	0.22–0.31	0.26	0.25–0.28		
PPW	0.45	0.46	0.40–0.51	0.58	0.58–0.59	0.51	0.50–0.53	ESDI	1.58	1.42	1.13–1.90	1.69	1.55–1.79		
PPH	0.44	0.46	0.40–0.51	0.58	0.56–0.58	0.51	0.48–0.54	HTI	0.84	0.86	0.81–0.90	0.84	0.83–0.86	1.30	1.24–1.34
ESL	0.24	0.26	0.21–0.31	0.29	0.28–0.31			AI				1.80	1.79–1.81	1.62	1.56–1.68
ESD	0.38	0.37	0.31–0.41	0.49	0.48–0.50			SCI				1.37	1.35–1.39	1.33	1.29–1.37
AH				1.11	1.11–1.12	1.23	1.16–1.29								
SCW				0.99	0.97–1.01	1.07	1.01–1.12								
SCL				1.35	1.34–1.39	1.42	1.35–1.49								

Table 1. The mean and range of morphometrics (mm) and indices of the holotype and a sample of workers, queens and males (number in parenthesis) of *Myrmica divergens*.

suberect to subdecumbent hairs; first 7 funicular joints of antennae with longer, and joints of antennal club with much shorter subdecumbent hairs. Colour of body blackish-brown to black, appendages somewhat lighter.

Myrmica bergi Ruzsky

Myrmica bergi Ruzsky 1902a: 12, w; 1902b: 473 (also described as a new species); 1903: 314; 1905: 675, w,q,m; Emery 1908: 166; 1921: 37; Arnol'di 1934: 160; Weber 1947: 472; Arnol'di 1970: 1839; 1976: 556 (in Key); Tarbinsky 1976: 45; Seifert 1988: 11; Radchenko 1994a: 42; 1994b: 143 (in Key); 1994c: 76; Bolton 1995: 277, not Sadil 1952: 244 (misidentification; referred material belongs to *M. gallienii*; see Arnol'di 1970).

Myrmica rubra L. r. *bergi*: Forel 1904a: 374.

Myrmica rugosa var. *kirgisica* Ruzsky 1903: 314, w; 1905: 659; Emery 1908: 168; 1921: 40; Weber 1947: 464; synonymy by Seifert 1988: 11; Radchenko 1994c: 76; confirmed in present paper.

Myrmica rubra var. *kirgisica*: Forel 1907: 18.

Myrmica bergi subsp. *kirgisica*: Arnol'di 1970: 1839.

Myrmica bergi var. *barchanica* Ruzsky 1905, 678, w; Emery 1908: 173; 1921: 37; Weber 1947: 473; synonymy by Arnol'di 1970: 1839; Seifert 1988: 11; Radchenko 1994c: 76; confirmed in present paper.

Myrmica bergi var. *fortior* Crawley 1920: 163, w (nom. praeocc., junior primary homonym of *Myrmica smythiesi* var. *fortior* Forel 1904b; replacement name – *M. bergi* subsp. *persiana* Weber, 1947: 474); synonymy by Radchenko 1994c: 76; confirmed in present paper.

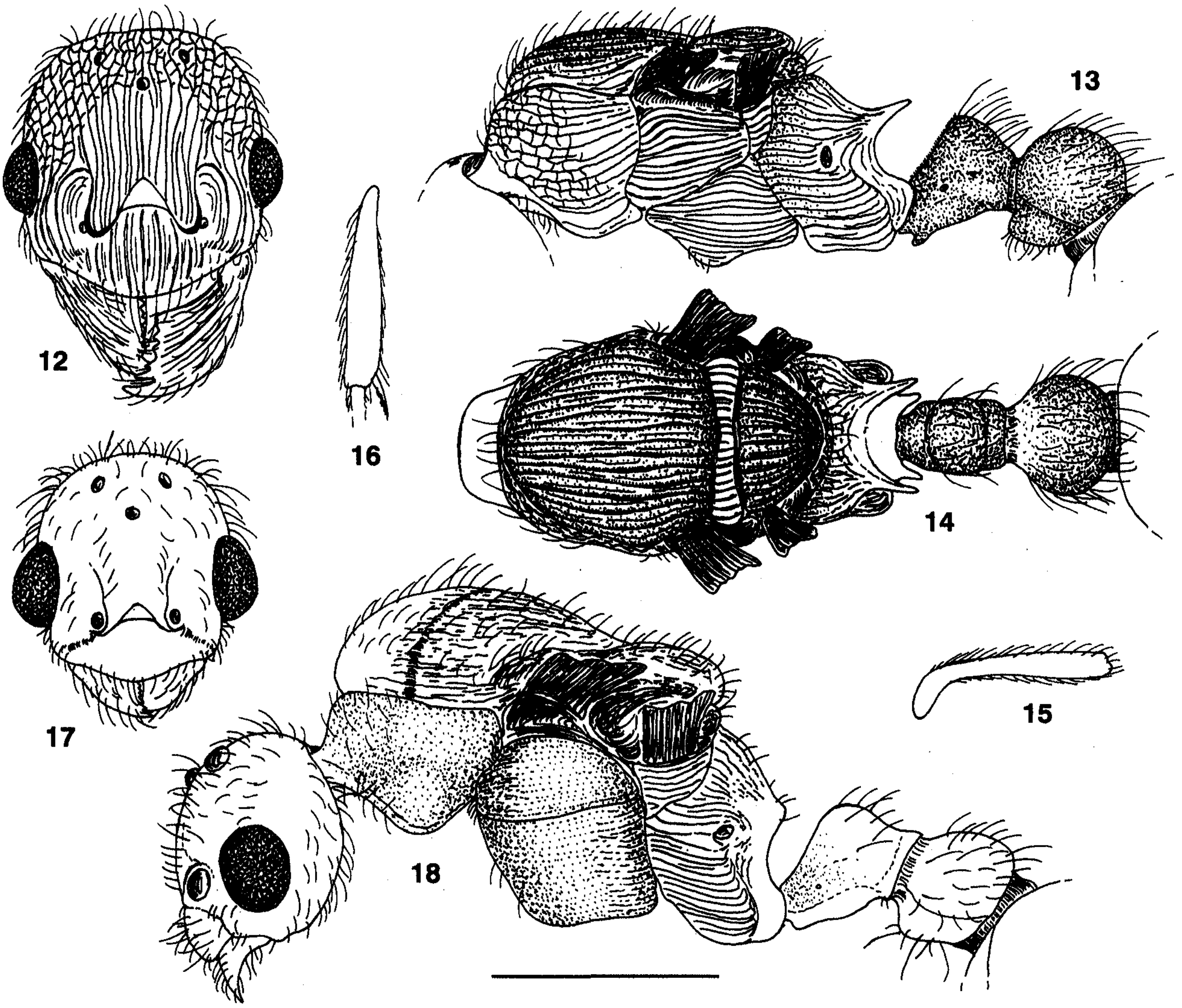
Myrmica bergi subsp. *persiana*: Bolton 1995: 281.

Myrmica kamyschiensis Arnol'di 1934: 159, w,q; Karavaiev 1936: 272, w,m; synonymy by Seifert 1988: 11; Radchenko 1994c: 76; confirmed in present paper.

Myrmica bergi subsp. *kamyschiensis*: Weber 1947: 474; Arnol'di 1970: 1838.

Material examined. Below we give the full details on the labels of the type material of *M. bergi* and its infraspecific forms; we do not list the collection details of the non-type material examined but we plot the locations on a map (Fig 29).

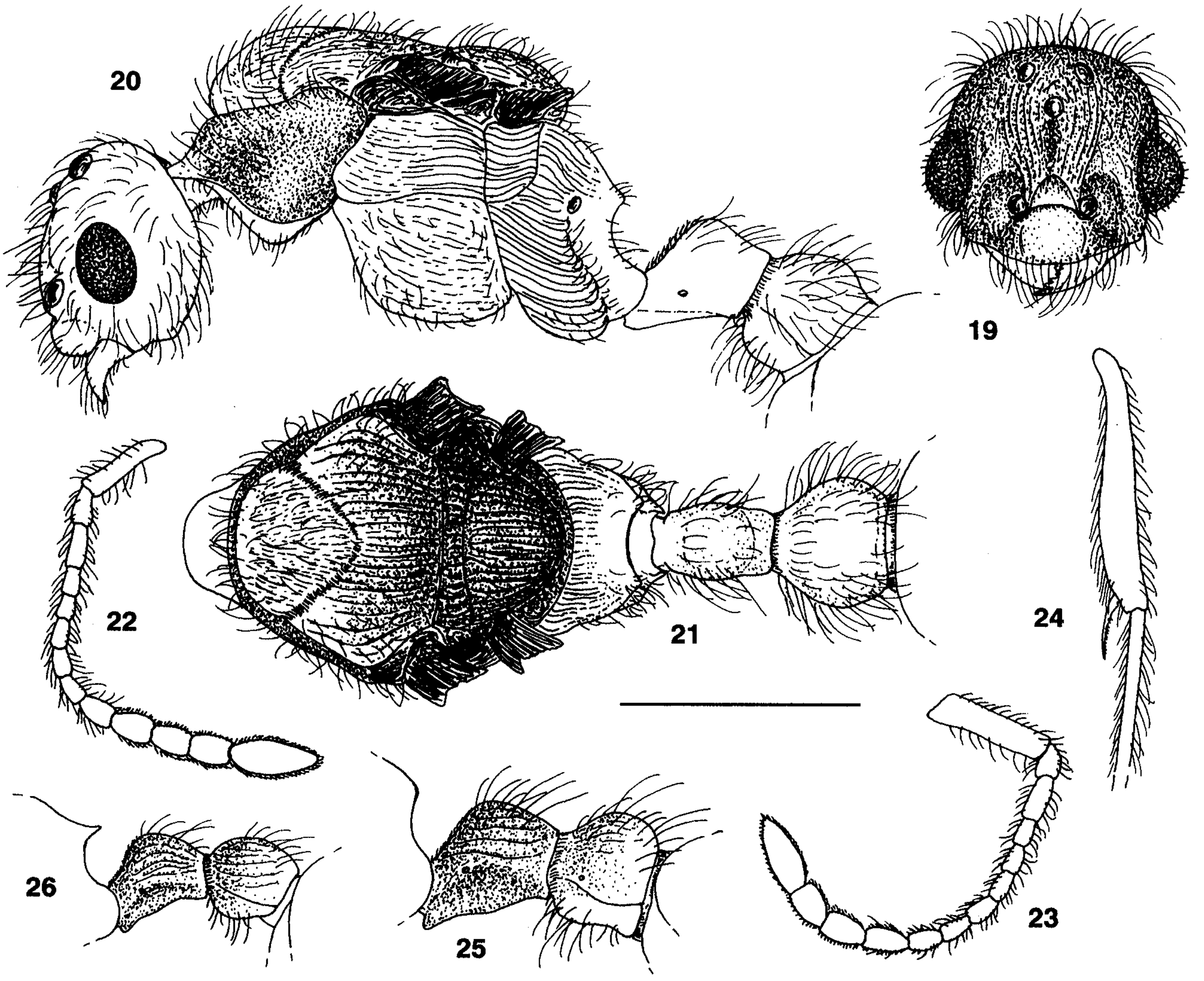
Myrmica bergi s. str. Lectotype worker (our designation): "Aral Sea, L. S. Berg, 1901" plus label "Lectotype" (written by Arnol'di's own hand)



Figures 12–18. Details of structure of *M. divergens* (12–16, queens) and *M. gallienii* (17–18, males). (12, 17) Head, frontal view, (13) alitrunk and waist in profile, (14) alitrunk and waist from above, (15) antennal scape in profile, (16) hind tibia , (18) head, alitrunk and waist in profile. Scale bar = 1 mm.

(ZMMU); paralectotypes (our designation): 2 workers on the same pin as lectotype (ZMMU); 1 worker, with same label as lectotype (IZK); 1 worker, "Kazalinsk, 1901, Berg" (ZMMU). Also >100 workers, 20 queens and 15 males from Kazakhstan, Uzbekistan, Kirgizstan and Tadzhikistan (ZMMU, ZIN). We chose as lectotype the middle of three workers from the Aral Sea, on a pin labelled by Arnol'di as "Lectotype" because we could not find in either ZMMU or ZIN specimens with the details published by Arnol'di (1970: 1839): "As lectotypes (Sic!) I designate worker – Tas-Bulak near Aral Sea (L. S. Berg), male – Frunze, Kirgizia (Arnol'di)". Concerning the male, Arnol'di was in error because he could not add to the type series a specimen collected by himself many years after the first description of the species.

Myrmica bergi var. *barchanica* and subsp. *kirgisica*. Lectotype worker (our designation) of *barchanica:* "Myrmica bergi var. barchanica Ruszs, Khanskaya Stavka, ryn'-peski, 6.vi.1902, M. Ruzsky" (label in Russian, written by Ruzsky's own hand) (ZMMU); paralectotype worker (our designation): "Myrmica bergi var. barchanica Ruszs, Khanskaya Stavka, peski, 5.vi.1902, M. Ruzsky" (label in Russian, written by Ruzsky's own hand) (ZIN). Also >50 workers, 8 queens and 5 males from Astrakhan' and Volgograd Regions (ZMMU, ZIN, IZK, ELMES). The types of var. *kirgisica* most probably are lost. There is in ZMMU a label "Lectotype, M. bergi kirgisica", written by Arnol'di's own hand, on a pin with workers from "Astrakhansky zapovednik [= Astrakhan' Natural Reserve], 10.vi.60, pody, Pisarev". However, Arnol'di was again in error considering as lectotype specimens collected 58 years after the first description, at best one could be a neotype. Despite these specimens Arnol'di (1970) neither designated a lectotype nor neo-



Figures 19–26. Details of structure of *M. divergens* (19–23) and *M. bergi* (24–26; 24, 25, "subsp." *kamyschiensis;* 26, "androlectotype" of *M. bergi* s. str. according to Arnol'di) (males). (19) Head, frontal view, (20) head, alitrunk and waist in profile, (21) alitrunk and waist from above, (22, 24) antenna, (23) hind tibia and tarsus, (25, 26) waist in profile. Scale bar = 1 mm.

type for var. *kirgisica*. Following recommendations of the International Code of Zoological Nomenclature for this kind of situation, we have not designated neotype for subsp. *kirgisica*.

Myrmica bergi subsp. *persiana* (replacement name for *M. bergi* var. *fortior* Crawley). Lectotype worker (our designation): "NW Persia, 1919, P. A. Buxton", "Myrmica bergi var. fortior Crawley" (UMO); paralectotypes (our designation): 6 workers with same labels (UMO and ZMMU). Also 6 workers, 1 queen, Talysh, Zuvant (ZMMU).

Myrmica bergi subsp. *kamyschiensis*. Syntype workers (our designation): 1 worker labelled "A 888", "M. bergi kamyschiensis", "Holotype" (all written in Arnol'di's own hand) (ZMMU); 2 workers labelled *"Paratype"* by Arnol'di otherwise with same labels (ZMMU); 1 worker "No. 888, Kerch', Kamysh-Burun, 21.iv.23, K. Arnol'di" (written in Arnol'di's own hand) (IZK). Also >100 workers, several tens queens and males from southern Ukraine, Rostov and Stavropol' Regions of Russia (ELMES, IZK). We consider Arnol'di's specimens as syntypes because he did not designate any type specimens in his original description (Arnol'di 1934). We are sure that Arnol'di added his "type" labels much later, probably when he revised *Myrmica* in the 1960s, because he followed his later opinion on the taxonomic status of this form, labelling the specimens "*M. bergi kamyschiensis*" rather than "*M. kamyschiensis*" as in his original description.

In the remaining, non taxonomic, part of this paper we use the following abbreviations of the various old infraspecific names to refer to the different populations of *M. bergi* studied: *bergi* s. str. = *M. bergi* from Middle Asia and southern Kazakhstan; *persiana* = *M. bergi* from Iran and

	M. gallienii (22)		*M. bergi* s. str. (23)		*kamyschiensis* (24)		*kirgisica* (17)		*persiana* (6)	
	mean	range	mean	range	mean	range	mean	range	mean	range
Morphometrics										
HL	1.17	1.06–1.26	1.19	1.06–1.39	1.28	1.16–1.44	1.22	1.12–1.30	1.32	1.24–1.38
HW	1.04	0.93–1.12	1.07	0.95–1.26	1.14	1.04–1.30	1.09	0.96–1.18	1.17	1.10–1.22
FW	0.44	0.36–0.50	0.47	0.41–0.55	0.49	0.45–0.55	0.47	0.44–0.49	0.51	0.47–0.54
FLW	0.49	0.40–0.54	0.52	0.47–0.59	0.55	0.50–0.62	0.52	0.48–0.55	0.56	0.54–0.57
SL	0.94	0.84–1.02	0.98	0.91–1.12	1.03	0.96–1.16	0.99	0.90–1.08	1.09	1.06–1.12
AL	1.62	1.44–1.78	1.74	1.53–2.11	1.87	1.66–2.09	1.72	1.62–1.80	1.85	1.76–1.94
HTL	0.87	0.76–0.94	0.92	0.81–1.11	0.95	0.86–1.08	0.90	0.80–1.02	0.99	0.92–1.04
PNW	0.73	0.66–0.82	0.75	0.64–0.87	0.79	0.72–0.90	0.75	0.66–0.82	0.80	0.78–0.82
PL	0.45	0.36–0.50	0.51	0.45–0.57	0.49	0.41–0.59	0.47	0.44–0.53	0.56	0.47–0.62
PW	0.31	0.27–0.38	0.31	0.25–0.36	0.31	0.27–0.35	0.30	0.27–0.32	0.33	0.32–0.35
PH	0.39	0.35–0.43	0.41	0.35–0.53	0.41	0.35–0.46	0.40	0.36–0.43	0.43	0.41–0.45
PPL	0.34	0.29–0.41	0.42	0.36–0.49	0.41	0.30–0.56	0.42	0.38–0.45	0.40	0.38–0.42
PPW	0.48	0.43–0.54	0.47	0.41–0.55	0.50	0.39–0.57	0.47	0.40–0.52	0.53	0.51–0.55
PPH	0.50	0.42–0.55	0.47	0.42–0.55	0.52	0.46–0.61	0.48	0.43–0.53	0.54	0.51–0.56
ESL	0.38	0.30–0.45	0.33	0.24–0.43	0.31	0.25–0.39	0.31	0.23–0.46	0.33	0.26–0.41
ESD	0.47	0.39–0.58	0.42	0.32–0.50	0.43	0.34–0.50	0.41	0.37–0.47	0.42	0.38–0.47
Indices										
CI	1.13	1.09–1.18	1.12	1.07–1.16	1.12	1.05–1.21	1.13	1.10–1.17	1.13	1.10–1.15
FI	0.43	0.39–0.45	0.44	0.42–0.45	0.43	0.40–0.46	0.43	0.40–0.46	0.44	0.43–0.44
FLI	1.09	1.04–1.14	1.10	1.04–1.15	1.12	1.06–1.19	1.11	1.08–1.15	1.10	1.06–1.15
SI1	0.80	0.72–0.83	0.82	0.76–0.86	0.81	0.70–0.87	0.81	0.75–0.85	0.82	0.80–0.85
SI2	0.91	0.82–0.95	0.92	0.84–0.96	0.90	0.84–0.95	0.91	0.83–0.96	0.94	0.91–0.96
PI1	1.14	0.86–1.29	1.26	0.94–1.37	1.19	1.05–1.39	1.18	1.09–1.35	1.30	1.12–1.41
PI2	0.43	0.36–0.47	0.48	0.43–0.51	0.43	0.38–0.50	0.44	0.40–0.47	0.48	0.43–0.52
PPI1	0.69	0.61–0.77	0.90	0.81–0.96	0.78	0.64–0.98	0.88	0.83–0.91	0.74	0.68–0.78
PPI2	1.04	0.98–1.09	0.99	0.93–1.05	1.05	0.96–1.23	1.02	0.94–1.08	1.02	0.98–1.06
PPI3	1.56	1.21–1.64	1.55	1.45–1.72	1.58	1.44–1.70	1.56	1.48–1.68	1.61	1.51–1.72
PPI4	0.46	0.43–0.48	0.44	0.41–0.49	0.44	0.36–0.49	0.43	0.39–0.46	0.46	0.43–0.49
ESLI	0.36	0.31–0.41	0.30	0.25–0.41	0.27	0.21–0.30	0.28	0.24–0.40	0.29	0.21–0.34
ESDI	1.24	1.08–1.45	1.31	1.02–1.78	1.40	1.13–1.68	1.34	0.93–1.61	1.28	1.10–1.58
HTI	0.84	0.79–0.88	0.86	0.81–0.89	0.84	0.78–0.91	0.83	0.79–0.88	0.85	0.84–0.87

Table 2. The mean and range of morphometrics (mm) and indices of a sample of workers (number in parenthesis) of *Myrmica gallienii* and *M. bergi* (*M. bergi* s. str. from NE Kazakhstan, *kamyschiensis* from S Ukraine, *kirgisica* from Astrakhan' region, Russia and *persiana* from NE Iran).

Talysh (Azerbaidzhan); *kamyschiensis* = *M. bergi* from southern Ukraine, and Rostov and Stavropol' Regions of Russia; *kirgisica* = *M. bergi* from north Caspian region, including the type specimens of var. *barchanica*.

DISCUSSION

Morphometric analysis

The measurements and indices are summarised as Tables 1 and 2. Although small differences can be found in some of the indices for workers of the different species, the main characters for separating *M. divergens* from *M. gallienii* and other forms of *M. bergi* were ones of shape and sculpture (see Discussion). We used CNVA to first investigate whether the clear separation of these three species based on non-metric characters would be reflected morphometrically. The results showed that *M. gallienii*, *M. bergi* and *M. divergens* could be discriminated solely on morphometrics with a confidence of 95% (Fig. 27a), the lectotypes and holotype respectively falling well within the 95% confidence limits for their groups. The sample for *M. bergi* included specimens of *bergi* s. str., *kamyschiensis*, *kirgisica* and *persiana*. The type specimens of *barchanica* (= *kirgisica*), *persiana* and *kamyschiensis* all fell within the cluster for *M. bergi* with the exception of one syntype of *kamyschiensis* (the specimen labelled as holotype by Arnol'di).

We next asked whether, based purely on morphometrics, any of the forms of *M. bergi* might also be discriminated. The analysis was run again separating *M. bergi*

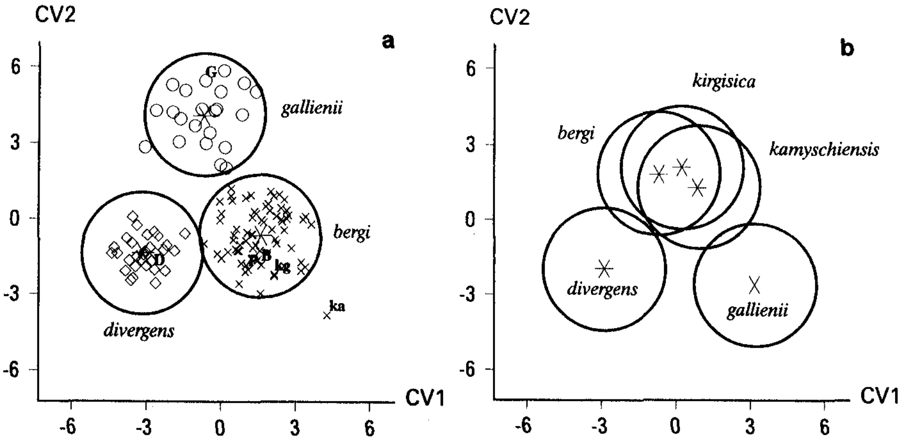


Figure 27. A canonical variate discrimination of workers of *M. divergens* (diamonds), *M. bergi* (crosses) and *M. gallienii* (circles) based on 16 morphometrics, the large circles represent the 95% confidence limit about the species' means (asterisk). Upper figure (a) shows the CV scores for all the workers with the position of the Holotype or Lectotype specimens: G = *M. gallienii*, B = *M. bergi* s. str., D = *M. divergens*, P = form *persiana*, ka = form *kamyschiensis* and kg = form *kirgisica* (note actually Lectotype *barchanica*, see text). Lower figure (b) as (a) but with forms *bergi* s. str., *kamyschiensis* and *kirgisica* treated as separate species.

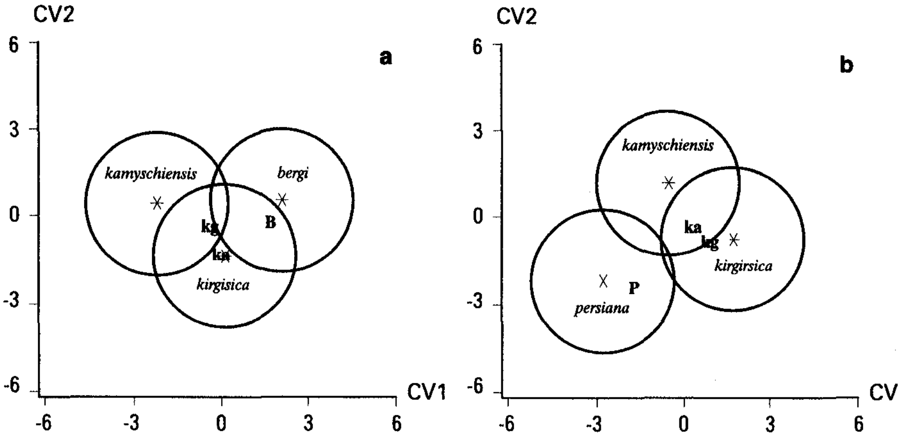


Figure 28. A canonical variate discrimination of the forms of *M. bergi*. The large circles represent the 95% confidence limit about the means (asterisk), position of type specimens indicated as in Fig. 27. Upper figure (a) compares form *bergi* s. str. with *kamyschiensis* and *kirgisica*. Lower figure (b) compares form *persiana* with *kamyschiensis* and *kirgisica*.

into *bergi* s. str., *kirgisica* and *kamyschiensis*, but omitting the small number of *persiana* (Fig. 27b). All three of the forms of *M. bergi* overlay one another when plotted on the two major CVs, which jointly account for 80% of the total variance in morphometrics. However, there was some evidence that *kamyschiensis* differed from *bergi* s. str. on the minor CV3 and CV4 axis (not illustrated). This confirmed that while *M. divergens* is morphologically sufficiently distinct to be considered a separate species there was not sufficient differences within *M. bergi* to elevate any other of its infraspecific forms to species level. Nevertheless, there was a suggestion of structured pattern in the variation in morphometry within the *M. bergi*.

When an analysis was run separately on just *bergi* s. str., *kamyschiensis* and *kirgisica* an interesting pattern emerged (Fig. 28a), we could separate *bergi* s. str. from *kamyschiensis* with a confidence > 92%, but the specimens *kirgisica* were intermediate to both. Interestingly, the same observation was also made by Arnol'di (1970), based on a less formal discrimination than our CNVA, who stated "by all main features [kirgisica] coincides partly with bergi, partly with kamyschiensis". We used the discriminant variates from this analysis to calculate CV values for the six type specimens of *persiana* and superimposed these onto Fig. 28a (not illustrated); this suggested that *persiana* was more similar to *kamyschiensis* and was unlikely to be classified with *bergi* s. str. Unfortunately, we could not included *persiana* directly in an analysis with the other three forms because the numerical algorithm could not resolve the discrimination (see Methods). Therefore we dropped *bergi* s. str. and substituted *persiana* (Fig. 28b). The analysis showed a discrimination (confidence. 95%) between *kirgisica* and *persiana* with *kamyschiensis* being discriminated (confidence > 92%) from *persiana*.

Taken together, the results illustrated in Figure 28 suggest a geographically structured pattern in morphometric variation between *M. bergi* populations. There would appear to be an east-west cline with the extreme eastern and western populations being quite distinct, represented by the forms *bergi* s. str. and *kamyschiensis* respectively. Similarly, there is possibly a more disjunct cline between north Caspian populations and Iranian populations represented by *kirgisica* and *persiana* respectively.

Taxonomic position of *M. divergens*

Myrmica species are generally grouped into to 10 or more species-groups using combinations of morphological features of both males and females (see Radchenko 1994a, Radchenko and Elmes 2001b). Based on the female castes, *M. divergens* could belong to either the *scabrinodis*-group or *lobicornis*-group of *Myrmica*. For example, the same series workers can have some individuals with an anterior clypeal margin that is only broadly rounded , as in the *scabrinodis*-group, while others have a shallowly notched clypeus, as in the *lobicornis*-group. Also some species from both groups have, like *M. divergens*, antennal scape that is sharply curved, or even slightly angulate, at the base with no trace of a carina or lobe. This last feature also distinguishes *M. divergens* from all *schencki*-group species which are typified by the presence of vertical lobe (or at least denticle) on the base of antennal scape. If males are available, their short antennal scape ($SI_1 < 0.40$, $SI_2 < 0.43$) make it is impossible to mistake *M. divergens* with any known species from the *lobicornis*-group ($SI_1 > 0.65$, $SI_2 > 0.68$). Therefore we place *M. divergens* in the *scabrinodis*-group on its combination of male and female features.

Within the *scabrinodis*-group, *M. divergens* workers closely resemble *M. bergi* and *M. gallienii* and are less like *M. rugulosa*. However *M. divergens* workers have a distinctly bicoloured body, whereas the whole body of *M. gallienii* and *M. rugulosa* is yellowish-red to reddish, and are generally smaller than *M. gallienii* and *M. bergi* (see Tables 1 and 2), although not as small as *M. rugulosa*. More importantly, *M. divergens* differs from the others: by much less developed reticulation on the head dorsum (except for *M. rugulosa*) (compare Figs 1, 8, 10 and 12); by a much less sculptured, rounded petiolar node (seen in profile) in contrast to the other species which have a petiole with distinct dorsal plate and longitudinal rugosity (compare Figs 2, 6, 9 and 11); by more strongly curved frontal carinae and more developed frontal lobes (FLI larger while FI subequal, see Tables 1 and 2); also from *M. gallienii* workers differ by distinctly shorter propodeal spines (compare ESLI in Tables 1 and 2).

Males of *M. divergens* well differ from those of *M. bergi* by shorter antennal scape ($SI_1 < 0.40$, $SI_2 < 0.43$ *versus* $SI_1 > 0.50$, $SI_2 > 0.53$; Figs 22 and 24) and by a shorter and higher petiole, which is smooth and shiny whereas that of *M. bergi* males is relatively longer and lower, with more distinct peduncle, and never smooth an shiny (usually it is punctured and with rugae, or at least coarse striation, compare Figs 20, 25 and 26). Although the general body-shape and relatively short antennal scape of *M. divergens* males is very similar to that of *M. gallienii*, they are clearly more hairy (compare Figs 17–18 and 19–20); furthermore, the eyes of *M. divergens* males have microscopic hairs. They differ from *M. rugulosa* males by a distinctly longer 2nd funicular joint (> 1.5 times longer than the 3rd joint compared to 1.3 – 1.4 times in *M. rugulosa*).

If only female castes are available, *M. divergens* might possibly be confused with two Siberian species from the *lobicornis*-group, the sympatric *Myrmica kaszhenkoi* Ruzsky or the Far Eastern species, *M. displicentia* Bolton (= *M. bicolor* Kupyanskaya), which also have distinctly bicoloured bodies. However, *M. displicentia* has a more narrowly rounded, subtriangular petiolar node (in profile) compared to *M. divergens*. Workers of *M. divergens* differ from *M. kaszhenkoi* by a slightly finer sculpture on the head dorsum (frons level with the eyes having >15 sinuous rugae *versus* <12), by its more pronounced metanotal groove, reticulated promesonotal dorsum and finer more sinuous longitudinal rugae on the sides of the alitrunk (compare description and Figs 2, 3 for *M. divergens*, with Radchenko 1994c, d).

Comparative ecology

Relatively little is published about the ecology of *M. bergi*. From our own observations we know that *kamyschiensis* is commonly associated with intrazonal, wet habitats around salted lakes and along sea coasts in the steppe zone of southern Ukraine. It can form large polygynous colonies which build soil mounds among *Phragmites* and has several behavioural adaptations that enable it to cope with periodic flooding (Bondar' et al., 1998). This agrees with Arnol'di's (1934) statement "Characteristic for salty bogs". However, we have also found small colonies nesting directly in the soil in short moist, grazed grassland near to the more characteristic salt-lake margins, and on the banks of the river Dnieper. *M. bergi* s. str. appears to have a similar ecology to *kamyschiensis*. Tarbinsky's (1976) writes that *M. bergi* living in Kirgizia "Lives up to altitude 1600 m, along river and stream banks, near Salix and Hippophaë shrubs, or near Phragmites, in semi-shaded places. It nests in sandy soil, sometimes with small mounds, but usually without them. In the morning and evening ants forage on open sand but during the day, in shade under shrubs or Phragmites". Tarbinsky also said colonies are "quite large compared to other Myrmica species", which agrees with our observations on *kamyschiensis*, and *"monogynous"* which is atypical for *kamyschiensis*. Ruzsky (1905) recorded that *barchanica* nested in sandy soils with a rich vegetation, mainly *Populus* and *Salix*.

Woyciechowski collected most colonies of *M. divergens* from "Riparian Woodland" at about 1000 m a.s.l. on the south-facing bank of the Jeröö river, and some from "Shrublands" about 1100 m a.s.l that border the steeper valley sides. Riparian Woodland was dominated by *Betula plathyphylla* with an understory of *Padus asiatica, Betula fruticosa, B. fusca, Crataegus sanguinea, Rosa acicularis, Dasiphora fruticosa, Ribes rubrum, Spirea salicifolia* and *Salix* spp., whereas Shrubland is dominated by a dense mixture of *Betula* *fruticosa, B. fusca, Crataegus sanguinea* and *Salix* spp. (see Muehlenberg et al. 2000). *M. divergens* were found living in the soil, under and in moss and frequently in grass tussocks by B. Pisarski who gave the habitat of *M. divergens* in Mongolia as "dry steppe, nests in the soil..." (Pisarski 1969). The type specimen of *M. divergens* were taken much further north on an island in the river Lena. It seems probable that *M. divergens* inhabits an intrazonal habitat between riparian meadows and steppe with rivers providing the main routes for connection between populations.

There appears to be a considerable commonality of ecology between *M. divergens, M. gallienii* and the infraspecific forms of *M. bergi*. Dispersal appears to be mainly via the margins of rivers. Although *M. bergi* is associated with the southern steppe or even desert zonez, it is less xerophilous than one might imagine being particularly adapted to the salty conditions created in the wetter areas. By general ecology *M. divergens* appears to be more similar to *M. gallienii*. Both are adapted to colder habitats and are associated with dampish meadows, that surround freshwater lakes and marshes, and river margins. This habitat requirement frequently brings *M. gallienii* into competition with *M. rubra* and *M. scabrinodis* (see Pętal 1981), which possibly limits its northern distribution. *M. gallienii* often forms very large polygynous colonies (see Elmes and Pętal 1990) like *kamyschiensis*, whereas the general absence of dealate queens in the Mongolian *M. divergens* nest samples, suggests that their colonies were probably smaller and less polygynous, like those of *M. bergi* s. str.

Biogeography

The canonical variate analysis of morphometrics showed that *M. divergens* clearly discrimates from *M. bergi* and *M. gallienii* with almost all the measurements contributing to the discrimination (Fig. 27). However, unusually for *Myrmica* species, *M. bergi* is quite variable morphologically, a fact also noted by Arnol'di (1970) who called it "a polymorphic species, forming several races". We interpreted the results of our CNVA on the infraspecific forms of *M. bergi* being produced by east-west and north-south clines. The reason for this is probably a disjunct distribution of *M. bergi* populations which becomes clearer when the known records are plotted on a distribution map (Fig. 29).

During the Miocene period there existed an uninterrupted steppe zone from North Caucasus till Mongolia. One can speculate that the *scabrinodis*-group evolved a "proto-bergi" to exploit the semi-arid and arid habitats throughout the steppe zone. This might have derived from a form more similar to *M. gallienii* which first colonised the cooler, more northern parts of the steppes. Later, in the middle or late Pliocene, the eastern steppes populations were isolated from those of Central-Asian by boreal taiga forests, coming from the north, and especially by desertification to the south creating habitat too dry for

Figure 29. Map of distribution of *M. divergens* and *M. bergi*.

any *Myrmica* species. Simultaneously, the steppe zone extended westward, into southeast Europe, and southward along the west Caspian Sea coast to Transcaucasia and into northern Iran. Thus the *gallienii*-like "protobergi", isolated in the Mongolian and south Siberian steppes, evolved into *M. divergens* and remains the only representative from the *scabrinodis*-group east of Lake Baikal (Fig. 29). Whereas the more central populations might then have given rise to *M. gallienii* which spread into the wetter north-western grasslands following the retreat of the ice. Certainly *M. divergens* seems morphologically closer to *M. gallienii* particularly in the male caste. This left the populations which evolved into the modern *M. bergi*, restricted to the hot southern steppes and mountain steppe zones of Central Asia, and using the intrazonal habitats near rivers and lakes to penetrate into the arid southern desert regions.

Why should the modern *M. bergi* populations show such high levels of infraspecific morphological variability, compared to many other wide spread *Myrmica* species [e.g. *M. rubra* (L.), *M. ruginodis* Nyl., *M. sulcinodis* Nyl.]? We suggest that the present range of *M. bergi* has been interrupted many times by transgressions of the Caspian Sea. Sometimes this sea has been smaller than at present but often much more extensive, in periods of maximal transgression it reached 50–55° North, sometimes connecting with the Azov and Black Seas. Consequently, the Central Asian populations (*M. bergi* s. str.) have been isolated many times from the more western populations which in turn, at times of maximal transgression of the Caspian, have been isolated from southern populations (such as *persiana*). However, the duration of periods of isolations were probably insufficient for the formation of separate species and during times of Caspian minimals, the populations migrated back into the new lands, probably via river and sea margins, and intermingled in numerous hybrid zones. This hypothesis might be testable by DNA analysis.

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