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Formica sentschuensis Ruzsky 1915 and *Formica tibetana* n.sp. – two unique and little known *Formica* species from Tibet (Hymenoptera: Formicidae)

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Abstract

This study presents the taxonomic description and ecological data of two unique ant species, *Formica sentschuensis* Ruzsky 1915 and *Formica tibetana* n.sp., found in the high-altitude grasslands of the Tibetan Plateau. Based on expeditions conducted in 2011 and 2012, *F. tibetana* n.sp. was identified as a distinct species. It develops locally an unusual nest architecture showing a flat, hardened, south-facing upper surface that optimizes solar heat absorption for early brood development. Morphological analyses revealed that *F. tibetana* n.sp. and *F. sentschuensis* form a common clade that may have split off near to the root of the genus *Formica*. Both species are characterized by a rare anteromedian clypeal excavation, a feature otherwise known for the Palaearctic only in *Formica sanguinea* Latreille, 1798 and several Nearctic species of the *Formica sanguinea* group. Morphology does not indicate a close relatedness of *F. tibetana* n.sp. and *F. sentschuensis* with members of the *Formica sanguinea* group which is supported by full absence of dulosis and independent single-queen colony foundation confirmed for *F. tibetana* n.sp. A stereomicroscopic analysis of morphological traits, including shape characters, seta characters and absolute body size proved that both species are clearly separable on worker individual level. This study provides insights into the biology of *F. tibetana* n.sp. and shows that the species plays a significant role in the Tibetan grassland ecosystems.

Keywords: *Formica* ants, Tibetan Plateau, high-altitude ecosystems, numeric morphology-based alpha-taxonomy, nest architecture adaptation

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1. Introduction

High-altitude ecosystems, such as those found on the Tibetan Plateau, remain relatively unexplored in terms of their ant fauna. The extreme environmental conditions of this region, including low temperatures, high solar radiation, and sparse vegetation, present unique challenges and opportunities for insect life. Investigating the adaptations of ants in such environments provides valuable insights into their evolutionary strategies and ecological roles.

During two expeditions investigating grassland biomes of the Tibetan Plateau and conducted in the years 2011 and 2012 (Wang et al. 2018), the authors discovered an unknown ant species of the genus *Formica* Linnaeus 1758 that attracted our attention through its remarkable nest construction. At a north-facing slope at the study site Sazin Gömpa, the soil mounds of these ants showed a completely flat, south-inclined upper plane solidified by a very hard crust of *Kobresia pygmaea* plants and lichens. The mean inclination angle of this plane was determined, showing a value allowing a maximum warming by solar radiation during early spring which is important for rapid brood development. We try to answer how such a plane and immovable solar collector architecture could have developed.

This ant species, described here as *Formica tibetana* n.sp., shows another unusual character: it has a distinct excavation in anteromedian clypeal margin – a rare trait so far known in only two Palaearctic species: *Formica sanguinea* Latreille 1802 and *F. sentschuensis* Ruzsky 1915. Thanks to a loan of a paratype specimen from the holotype locality of *Formica sentschuensis* it became clear that *F. tibetana* n.sp. is a sister species of *F. sentschuensis* and distantly related to *F. sanguinea*.

The ecological role of *Formica sentschuensis* and *F. tibetana* n.sp. in Tibetan grasslands is also remarkable. Li et al. (2023) investigated the ant fauna on eight elevational transects in the central and western parts of the Sichuan Plateau within an area delimited by 31°N, 32°N, 98.5°E and 103.5°E. They reported an ant determined by them as *Formica sentschuensis* to be the eudominant species, representing 37% from a total of 22645 ants collected. According to our information on geographical distribution, the findings of Li et al. may refer to both *Formica tibetana* n.sp. and *F. sentschuensis*.

The purpose of this paper is redescribing the poorly characterized species *Formica sentschuensis*, describing its sister species *Formica tibetana* n.sp. as new and giving information on the biology of the latter including the ontogenesis of its mounds.

2. Material and Methods

Character recording

21 numerically described morphological characters were evaluated in workers. All measurements were made in mounted and dried specimens using a pin-holding stage, permitting full rotations around X, Y and Z axes. Two high-performance stereomicroscopes Leica MZ16A, one equipped with 1.6x and one with 2.0x planapochromatic objective-were used at magnifications of 75-320x. 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 visualisation of silhouette lines. A Schott KL 2500 LCD cold–light source in combination with a Leica coaxial polarised–light illuminator provided optimum 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 the voltage up and down. A Leica cross-scaled ocular micrometer with 120 graduation marks ranging over 65 % of the visual field was used. To avoid parallax error, its measuring line was constantly kept vertical within the visual field.

Setae, also called pilosity or simply ‚hairs‘, are differentiated from pubescence hairs in having at least twice the basal diameter of neighbouring pubescence hairs. All seta counts (acronyms beginning with „n“) are restricted to standing setae projecting >10 µm from cuticular surface as they are seen in a specifically defined view (see below) and are the arithmetic mean of counts from both body halves.

Definition of numeric characters and descriptive terms:

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.

CW: maximum cephalic width; the maximum in *Formica* is found either behind (larger specimens) or across the eyes (smaller specimens).

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

EYE: eye-size index: the arithmetic mean of the large (EL) and small diameter (EW) of the elliptic compound eye.

Full face view: the dorsal aspect of head with both maximum CL and maximum CW in visual plane.

Genae: the lateral part of head delimited by anterior margin of eye and anterolateral corner of head capsule.

GHL: length of longest seta on dorsal plane of first gaster tergite excluding the row of setae immediately anterior of the hind tergite margin.

ML: mesosoma length in the alates; measured in lateral view from the caudalmost portion of propodeum to the frontalmost point of the anterior pronotal slope (i.e. not to the frontalmost point of the whole pronotum that is usually concealed by the occiput).

MtMtP– minimal distance of the bulge margin of the metathoracal spiracle from the most distant caudoventral margin of metapleuron.

MtPpSt – minimal distance between the bulge margins of the metathoracal and propodeal spiracles.

MtSt – minimal distance between the inner margins of the bulges of the metathoracal spiracles.

MW: maximum mesosoma width in the alates, measured before the tegulae.

nGen - with head in full face view, bilateral mean of setae protruding more than 10 µm from genal margin.

nCH: bilateral mean of the number of standing setae protruding more than 10 µm from head silhouette as seen in full face view. Counting begins at the level of anterior eye margin and ends at median occiput. The full depth of focus is used for counting and the parallax error is considered.

nGu: bilateral mean of the number of standing setae protruding more than 10 µm from underside of head (= „gula“) as visible in lateral view.

nHFex: bilateral mean of the number of standing setae protruding more than 10 µm from cuticular surface of the extensor profiles of hind femora. The always present apical setae are not counted.

nHT: bilateral mean of the number of standing setae protruding more than 10 µm from cuticular surface of the extensor profiles of hind tibia. The always present apical setae are not counted.

nMn: bilateral mean of the number of standing setae protruding more than 10 µm from cuticular surface of mesonotum.

nPe: bilateral mean of the number of standing setae protruding in caudal or frontal viewing position more than 10 µm from margin of petiole scale dorsal of spiracle.

nPrMe: bilateral mean of the number of standing setae protruding more than 10 µm from cuticular surface of propodeum and lateral metapleuron (excluding hairs fringing the metapleural gland orifice and those on ventrolateral edge of metapleuron).

nSC: bilateral mean of the number of standing setae protruding more than 10 µm from dorsal plane of scape. Apical setae with direction more or less parallel to longitudinal scape axis are not counted.

OceD: distance between inner margins of posterior (lateral) ocelli.

PeW: maximum width of petiole.

RipD: average distance of transversal microripples on dorsal plane of first gaster tergite. At least three counts along a 90 µm distance on different surface spots are averaged. Counting is performed at magnifications of 256x (RS) or 320x (BS). Use clean surfaces and a lighting best visualizing the ripples.

Setae: all stronger hairs having at least twice the basal diameter of neighbouring pubescence hairs (typical for *Formica* are 3.5 µm diameter for pubescense and >8 µm for setae)

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

sqPDG: square root of pubescence distance on dorsum of first gaster tergite. The number of pubescence hairs n crossing a transverse measuring line of length **L** is counted, hairs just touching the line are counted as 0.5. The pubescence distance PDG is then given by **L/n**. In order to normalise positively skewed distributions, the square root of PDG is calculated. Counting was performed at magnifications of 256x (RS) or 320x (BS). Use a lighting best visualizing pubescence and clean patches of surface but exclude surface parts with detached pubescence. The added length of the counting lines L should be at least in 500 µm in species with low pubescence distance but 2000 µm in species with very dilute pubescence.

The calculation of the daily solar heat input on variably-inclined plane surfaces in dependency from geographical latitude was done by the software Insolation3a1 (Seifert & Pannier 2007). Principal component analysis (PCA) and one-tailed ANOVA tests were performed with the software package SPSS 15.0.

3. Results and Discussion

Phylogenetic placement

We cannot provide a well-founded statement on the phylogenetic placement of *Formica tibetana* n.sp. and *Formica sentschuensis* based on *morphology*. The excavation of antereomedian margin of clypeus in both species is a rare character in the genus *Formica*. This structure is found in no other species group except for members of the *Formica sanguinea* species group (or subgenus *Raptiformica* Forel 1913).

Furthermore, there is in *Formica tibetana* n.sp. and *F. sentschuensis* a strikingly higher distance between the microripples (RipD) and pubescence (sqPDG) on gaster tergites than in *Formica sanguinea* Latreille 1802 and the Nearctic species *F. pergandei* Emery 1893, *F. subintegra* Wheeler 1908, *F. obtusopilosa* Emery 1893, *F. curiosa* Creighton 1935, *F. puberula* Emery 1893, *F. rubicunda* Emery 1893, *F. wheeleri* Creighton 1935 or *F. bradleyi* Wheeler 1913. *Formica manni* Wheeler 1913 combines the presence of a clypeal excavation with high RipD and sqPDG data but shows a strikingly different mesosomal and head microsculpture as well as very different pilosity distribution compared to *F. tibetana* n.sp. and *F. sentschuensis*.

Regarding *Formica sanguinea*, which is the only Palearctic species of the *F. sanguinea* group, a close relatedness to *F. tibetana* and *F. sentschuensis* is extremely unlikely by multiple morphological differences (see Tab. 1). There is almost no overlap in absolute size and *F. sanguinea* shows another allometric rule for eye size.

F. tibetana (and certainly also *sentschuensis*) show an independent single-gyne colony foundation and are not dulotic (see Biology of *F. tibetana*). Absence of these features is a "primordial" trait. In contrast **all** species of the *Formica sanguinea* group known from the Holarctic cannot found their nest independently. This is a derived, "evolved" trait also shown by all species of the evolved Palaearctic subgenera *Formica* s.str. and *Coptoformica*. A thorough whole-genome analysis of the nuclear DNA will be necessary to form more reasonable hypotheses on the phylogenetic placement of our two species. We suppose that *F. sentschuensis* and *F. tibetana* form a unique clade that possibly split off close to the root of the genus *Formica*.

***Formica sentschuensis* Ruzsky 1915**

Formica sentschuensis Ruzsky 1915

This taxon has been described from two locations in NE Tibet. Ruzsky (1915) explicitly gave "1) rechka Sen-chu/ bassein r. Goluboi, 12000', Kam, 2/3. VIII 1900 (gynes, workers). 2) gory Amnen-Kor, 14-15000' abs. vys., VI 1900 (gyne, workers). [translation: (1) rivulet Sen-Chu, basin of Goluba river, 12000 feet, Kam, 2./3. August 1900 (gynes, workers). (2) Amnen-Kor Mountains, 14-15000 feet absolute height, June 1900 (gyne, workers)]. Dlussky (1965) designated a lectotype in a gyne from the first locality for which he published the collecting data in English "Northeast Tibet; river Sen-Chu, bass. of Yangtse, Kam, altitude 3600 m, III 1901 [sic!], coll P. K. Kozlov". A loan of the lectotype from Zoological Institute St. Petersburg was not possible but images of the specimen kindly provided by Dmitry Dubovikoff clearly showed only very few setae on dorsal plane of scape and extensor profile of hind femur. Hence the seta characters of the lectotype gyne are in line with those of the paralectotype worker received as a loan from MCZ Cambridge. This worker is labelled "M.C.Z. Cotype 33835" and "rechka Sen-chu 12T'/ bacc. Goluboi r./ Koslov. nach. III 00" [translation: rivulet Sen-Chu, 12000 feet / basin of Goluba river / Koslov. beginning of March 1900"]. The reasons for the disagreements between the collecting dates at the lectotype locality – August 1900 by Ruzsky, March 1901 by Dlussky and March 1900 on the label of the MCZ Cotype – are perhaps due to writing and or reading errors by Ruzsky and Dlussky. Another possibility is that Kozlov was at the Sen-Chu river both in March (outward bound from Lanshou) and in August (during return). We consider the MCZ cotype worker as true paralectotype since both locality and collecting month are coincident with that of the lectotype. We base our identification of *Formica sentschuensis* on the paralectotype worker and the images of the lectotype gyne.

Formica (*Neoformica* Wh.) *dalailamae Ruzsky 1915*

This taxon has been described in two workers from Amnen-Kor Mountains, collected by the Kozlov expedition in June 1900 at a height of 14-15000 feet. Ruzsky (1915) placed them near to *Formica* (*Neoformica*) *pallidefulva* Latreille 1802. However, Dlussky (1965) recognized *Formica dalailamae* Ruzsky 1915 as junior synonym of *Formica sentschuensis* that was described in the same paper one page before. We follow here Dlussky's concept as he apparently investigated these two specimens. He reported that these were very badly mounted and by no means attributable to North American "*Neoformica*" species near to *Formica pallidefulva* Latreille 1802, because they showed the diagnostic excavation in anteromedian clypeal margin. Furthermore, and important in our context, a senior synonymy of *Formica dalailamae* over *Formica tibetana* n.sp. is unlikely because Ruzsky stated in his rather detailed description of pilosity: "antennal scapes without standing hairs".

Tabele 1. Morphological data of worker individuals; sequence of data – arithmetic mean ± standard deviation [minimum, maximum]. The column in between gives the F values and significance levels of a one-tailed ANOVA. F values of the three most separating characters are given in bold.

	F. sentschuensis n=36	ANOVA $F_{1,117,}$ p	***F. tibetana n.sp*** n=83	***F. sanguinea*** n=43
CS	1157 ±134 [896,1366]	1.30, n.s.	1127 ±131 [876,1462]	1763 ±189 [1438,2189]
CL/CW	1.087 ±0.033 [1.022,1.161]	28.1, 0.000	1.125 ±0.037 [1.009,1.203]	1.032 ±0.022 [0.990,1.080]
SL/CS	1.014 ±0.022 [0.971,1.054]	13.95, 0.000	1.029 ±0.021 [0.981,1.081]	0.969 ±0.026 [0.909,1.034]
OceD/CS	0.195 ±0.012 [0.175,0.224]	0.21, n.s.	0.194 ±0.010 [0.172,0.218]	0.172 ±0.012 [0.172,0.218]
EYE/CS	0.268 ±0.009 [0.250,0.288]	0.56, n.s.	0.267 ±0.010 [0.245,0.291]	0.258 ±0.008 [0.241,0.273]
PeW/CS	0.386 ±0.019 [0.347,0.434]	8.04, 0.005	0.374 ±0.024 [0.330,0.427]	0.455 ±0.022 [0.418,0.508]
MTST/CS	0.143±0.020 [0.109,0.177]	34.21, 0.000	0.124 ±0.015 [0.091,0.168]	
MTPPST/CS	0.340 ±0.012 [0.317,0.363]	13.43, 0.000	0.348 ±0.011 [0.322,0.378]	
MtMTP/CS	0.612 ±0.012 [0.585,0.650]	15.60, 0.000	0.621 ±0.012 [0.588,0.646]	
GHL/CS[%]	12.06 ±1.19 [9.98,14.41]	7.19, 0.008	11.25 ±1.63 [5.69,19.15]	6.85 ±1.27 [3.83, 8.91]
nGen	5.2 ±2.2 [1.3,10.5]	241.29, 0.000	14.3 ±3.2 [7.0,23.5]	0 ± 0
nCH	24.8 ±4.0 [15.5,37.0]	161.44, 0.000	39.9 ±6.6 [23.5,60.3]	0.04 ± 0.08 [0,0.5]
nGu	13.2 ±2.7 [7.8,19.5]	138.73, 0.000	26.5 ±6.6 [13.5,46.0]	0.01 ± 0.08 [0,0.5]
nSC	0.7 ±1.0 [0.0,3.5]	**838.19**, 0.000	25.3 ±5.0 [12.2,39.0]	
nMn	13.9 ±4.7 [1.0,25.0]	89.55, 0.000	25.0 ±6.4 [10.9,38.8]	0.27 ± 0.70 [0,2.0]
nPrMe	25.5 ±6.1 [13.5,41.0]	85.55, 0.000	40.9 ±9.1 [7.0,60.5]	0.14 ± 0.37 [0,2.0]
nHFex	6.2 ±3.5 [1.8,16.5]	**555.83**, 0.000	34.1 ±6.7 [21.0,58.0]	0 ± 0
nHT	5.7 ±3.8 [1.5,17.0]	**628.42**, 0.000	32.0 ±5.8 [12.0,44.0]	0.28 ± 0.48 [0,2.0]
nPe	7.6 ±2.1 [4.5,12.0]	79.87, 0.000	12.5 ±3.0 [7.5,24.3]	0.92 ± 1.00 [0,5.0]
sqPDG	7.24 ±0.70 [5.47,9.02]	59.96, 0.000	8.99 ±1.27 [6.38,12.71]	3.46 ±0.24 [2.96,4.11]
RipD	6.96 ±0.58 [5.8,8.4]	0.94, n.s.	7.06 ±0.50 [6.3,8.4]	5.88 ±0.38 [5.1,7.1]

Material examined. Numeric phenotypical data were taken in 16 worker nest samples with 36 workers. They originated from the Chinese provinces Quinghai (1 sample) and Sichuan (15 samples). For details see supplementary information SI1.

Geographic range. The westernmost known site is the holotype locality Sen-Chu in the province Quinghai (33°N, 97°E, 3900 m). It was not possible to determine more precise coordinates from the data given by Kozlov – the error could be more than 50 km. All remaining samples were collected in the province Sichuan at elevations from 3005 to 4420 m a.s.l. and between 100.0 and 103.5° E, 28.9 and 32.2°N (Fig.1 map).

Diagnosis: --Worker (Tab. 1, Figs. 2-4): All shape ratios given below are primary ratios taken in 36 specimens and all data are given as arithmetic mean ± standard deviation. Verbal statements such as "long", "short", "small" etc. are comparative in relation to the average situation

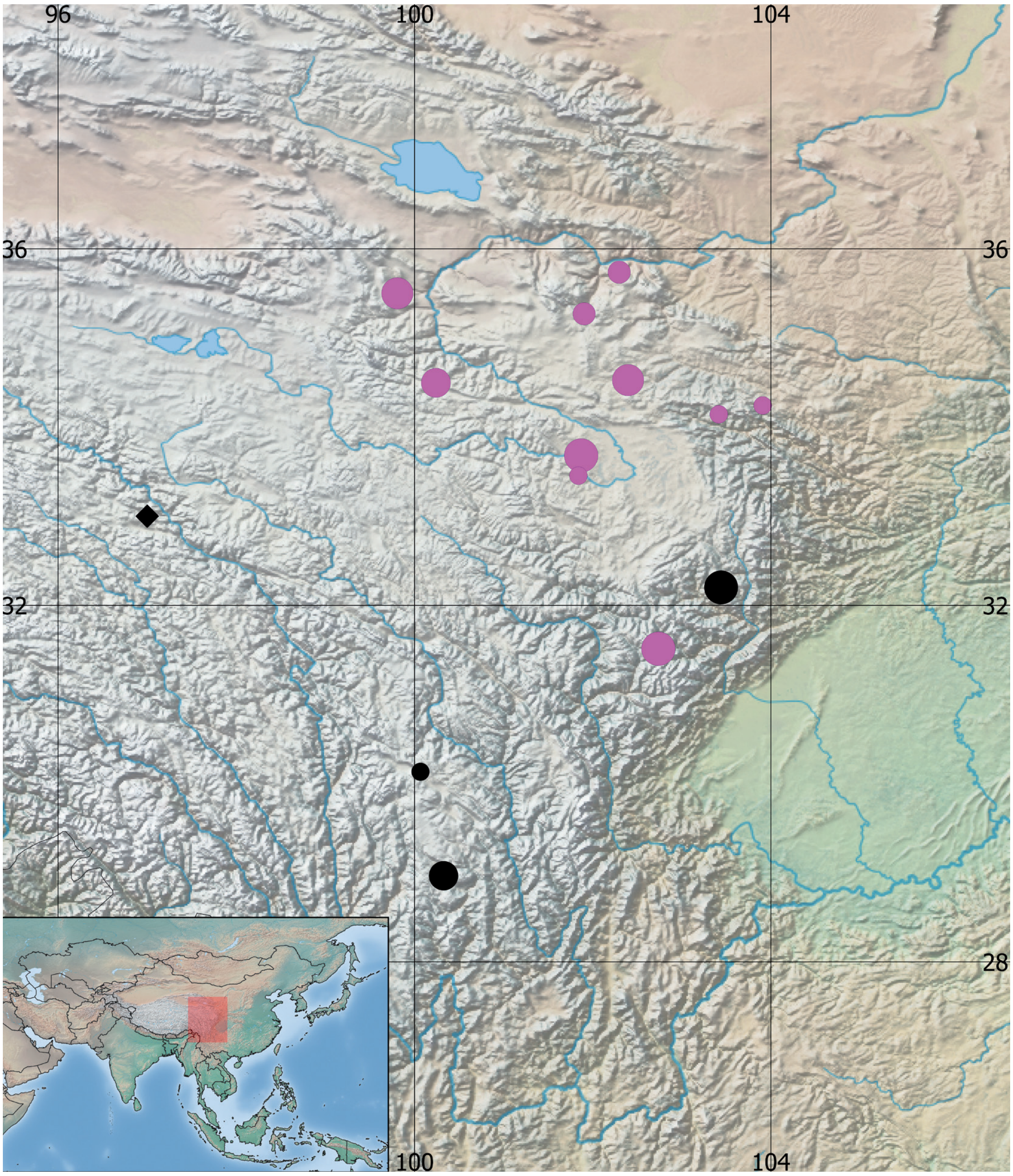

Figure 1. Geographic distribution of *Formica tibetana* n.sp. (pink dots) and of *Formica sentschuensis* Ruzsky, 1915 (black dots, black rhomb type locality) in the Chinese provinces Quinghai, Ganzu and Sichuan. The size of dots is proportional to the number of samples found in a site.

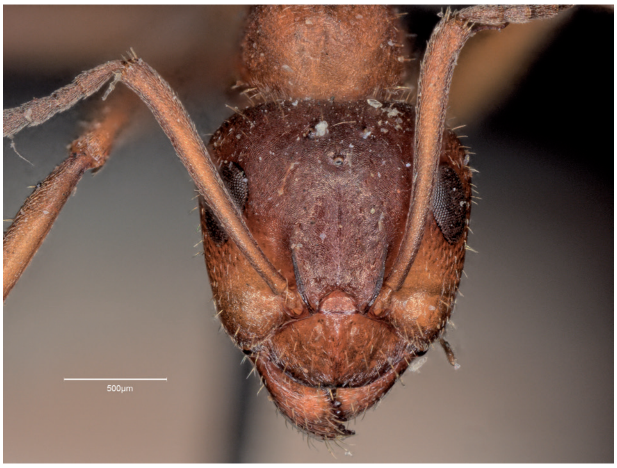

Figure 2. Head of the paralectotype of *Formica sentschuensis* in full face view.

Figure 3. Paralectotype of *Formica sentschuensis* in lateral view.

Figure 4. Clypeus of the paralectotype of *Formica sentschuensis* in frontodorsal view.

in Palaearctic *Serviformica*. Rather small size, CS 1157 ± 134 µm. Head and scape short (CL/CW 1.087 ± 0.033, SL/CS 1.014 ± 0.022). Distance between posterior ocellae moderately large (OceD/CS 0.195 ± 0.012). Eye small (EYE/CS 0.268 ± 0.009). Distance between (a) metathoracal spiracles, (b) between metathoracal and propodeal spiracle and (c) between metathoracal spiracle and caudoventral metapleuron moderately large (MtSt/CS 0.143 ± 0.020, MtPpSt/CS 0.340 ± 0.012, MtMtP 0.612 ± 0.012). Setae on whole body long (GHL/CS 12.06 ± 1.16%). Head, mesosoma, petiole and gaster with numerous setae (nGen 5.2 ±2.2, nCH 24.8 ±4.0, nGu 13.2 ±2.7, nMn 13.9 ± 4.7, nPrMe 25.5 ± 6.1, nPe 7.6 ± 2.1). Extensor sides of femora and tibiae with a lower number of setae (nHFex 6.2 ± 3.5, nHT 5.7 ± 3.8). Dorsal plane of scape without or with only very few short, suberect or subdecumbent setae (nSc 0.7 ± 1.0). Distance of pubescence and of transverse microripples on gaster tergites large (sqPDG 7.24 ± 0.62, RipD 6.96 ± 0.58). Frontal triangle with strong transverse microripples. Clypeus with a sharp median keel stretching over 75% of its length in the largest and over 95% in the smallest workers. The excavation of anteromedian clypeus is conspicuous in frontodorsal view (Fig. 4), but only suggested in full face view. Vertex usually dark brown. Genae, clypeus, mesosoma, legs and scapes usually light reddish brown. Gaster dark reddish brown. Specimens with darker overall pigmentation do occur.

-- Gyne: Compared to *Formica tibetana* n.sp., the images of the lectotype gyne show a strongly reduced pilosity on the dorsal plane of scape, and the extensor profiles of hind femur and hind tibia with nSc about 2, nHFex about 5 and nHT about 5.

Taxonomic comments. For separation from its sister species *Formica tibetana* n.sp. see there.

Biology: There are no reports on biology of this species. All findings are in the montane to subalpine zone at elevations of 3005 to 4420 m. Habitats in Sichuan were stony grassland with scattered conifer trees (5 findings), grassland with shrubs (2), stony grassland (2), light conifer stands (2), a rubble field with sparse vegetation (1) and a grassland (1).

Formica tibetana n. sp.

Etymology: named according to its geographical range.

Type material: Holotype worker labelled „CHI: 34.5406°N, 102.4179°E, Luqy-8.4 km SW, 3296 m, Viehweide, LqA R2, 2011-08-17, Chi 2011 178“ and „Holotype *Formica tibetana* Schultz & Seifert“; two mounted paratype workers on a separate pin plus 8 paratype workers in ethanol with the same collecting data labels; all type specimens from the same nest sample; depository SMN Görlitz.

Material examined. Numeric phenotypical data were taken in 36 nest samples with 83 workers, in one gyne from a nest sample and in one isolated gyne caught walking on ground. Additional 9 nest samples were classified by simple visual inspection. They originated from the Chinese provinces Quinghai, Gansu and Sichuan. For details see supplementary information SI1.

Geographic range. Known from the provinces Quinghai, Gansu and Sichuan in an area delimited by 31.5°N, 35.7°N, 99.8°E and 103.9°E. The altitudinal range extends from 2663 to 3999 m a.s.l. Compared to F. *sentschuensis* it has a more northern distribution (Fig. 1 map) and a lower altitudinal range.

Diagnosis: --Worker (Tab. 1, Figs. 5-7): Rather small size, CS 1127 ± 131 µm. Head more elongated than in *sentschuensis* but scape only slightly longer (CL/CW 1.125 ± 0.037, SL/CS 1.029 ± 0.021). Distance between posterior ocellae moderately large (OceD/CS 0.194 ± 0.010). Eye small (EYE/CS 0.267 ± 0.010). Distance between metathoracal spiracles, slightly smaller than in *sentschuensis* (MtSt/CS 0.124 ± 0.014), distance between propodeal spiracles and between metathoracal spiracle and caudoventral metapleuron larger than in *sentschuensis* (MtPpSt/CS 0.348 ± 0.011, MtMtP 0.621 ± 0.012). Setae on whole body slightly shorter than in *sentschuensis* (GHL/CS 11.25 ± 1.63%). Head, mesosoma, petiole and gaster with more numerous setae than in *sentschuensis* (nGen 14.3 ±3.2, nCH 39.9 ±6.6, nGu 26.5 ±6.6, nMn 25.0 ± 6.4, nPrMe 40.9 ± 9.1, nPe 12.5 ± 3.0). Extensor sides of femora and tibiae with a much larger number of setae than in *sentschuensis* (nHFex 34.1 ± 6.7, nHT 32.0 ± 5.8). Dorsal plane of scape with much more numerous erect and semierect setae than in *sentschuensis* (nSc 23.4 ± 5.2). Distance of pubescence on gaster tergites larger than in *sentschuensis* (sqPDG 8.99 ± 1.27). Distance of microripples on gaster tergites as in *sentschuensis* (RipD 7.06 ± 0.50). Microsculpture of vertex and frontal triangle similar to *sentschuensis*. Clypeus with a sharp median keel stretching over 75% of its length in the largest and over 95% in the smallest workers. The excavation of anteromedian clypeus is conspicuous in frontodorsal view (Fig. 7) but only suggested in full face view. Vertex usually dark to blackish brown. Genae, clypeus, mesosoma, legs and scapes usually light reddish brown. Gaster dark reddish brown to blackish brown. Specimens with darker overall pigmentation do occur.

-- Gyne: The two available gynes have the following data CS 1566, 1724 µm; CL/CW 0.979, 0.955; SL/CS 0.881, 0.899; ML/CS 1.691, 1.679; MW/ CS 1.050, 0.961; PEW/ CS 0.520, 0.511; ML/CS 1.691, 1.679; MW/CS 1.050, 0.961; GHL/CS 15.49%, 17.40%; sqPDG 11.47, 9.57; RipD 8.1, 9.5; nSc 26.0, 14.5; nGen 14.5, 7.5; nGu 30.0, 17.0; nPrMe 41.0, 36.0; nPe 15.5, 10.5; nHFex 30.0, 33.0; nHT 30.5, 20.0. Both show the diagnostic excavation of anteromedian clypeal margin and their seta counts correspond to those of workers.

Taxonomic comments. *Formica tibetana* n.sp. is clearly separable from *F. sentschuensis* on worker individual level alone by the much higher setae numbers on dorsum of scape and extensor profile of hind femur. The maximum nSC and nHFex are 3.5 and 16.5 in *F. sentschuensis* whereas the minima of these characters are 12.2 and 21.0 in *F. tibetana* n.sp. A principal component analysis considering all 20 characters given in Tab. 1 provides two clearly separated clusters (Fig. 8 PCA). Furthermore, there are no mixed nest samples known which excludes that *F. sentschuensis* and *F. tibetana* n.sp. could represent an intraspecific polymorphism. There is no indication that one of the ten taxa of *Formica* described by Chang & He (2002) from China could be a senior synonym of *F. tibetana* n.sp.

Biology. Since we have never observed nests containing workers of *Serviformica* species, *Formica tibetana* n.sp. is undoubtedly not dulotic and colony foundation is obviously independent. The latter becomes clear from nest density data collected during the PaDeMoS project on 19 study plots on grasslands in NE Tibet. Only four *Formica* species were found in these investigations: *Formica picea candida* Smith 1878, *Formica tibetana* n.sp., *Formica* (*Coptoformica*) *brunneonitida* Dlussky 1964 and *Formica* (*Coptoformica) manchu* Wheeler 1929. The mean nest densities on these test plots were 0.42 nests / 100 m² in the temporarily socially parasitic *Coptoformica* species, 8.32 nests / 100 m² in *Formica tibetana* n.sp. and 27.38 nests / 100 m² in *Formica picea candida*. *Coptoformica* was present on 6, *Formica picea candida* on 15 and *Formica tibetana* n.sp. on 6 study plots. The latter two species are apparently highly competitive with strong mutual exclusion showing syntopic occurrence on only two study plots. The realized niche overlap OR as defined by Seifert (2017, p. 25-26) is only 1.9%. These data exclude socially parasitic colony foundation of *Formica tibetana* n.sp. in *F. picea candida*. For comparison: OR is 44.9% between the temporarily socially parasitic *Coptoformica* species and *Formica picea candida* that serves as host for colony foundation in these two *Coptoformica* species (Seifert & Schultz 2021). It appears unlikely that *F. tibetana* n.sp. may serve as host

Figure 5. Head of the holotype of *Formica tibetana* n.sp. in full face view.

Figure 6. Holotype of *Formica tibetana* n.sp. in lateral view.

Figure 7. Clypeus of the holotype of *Formica tibetana* n.sp in frontodorsal view.

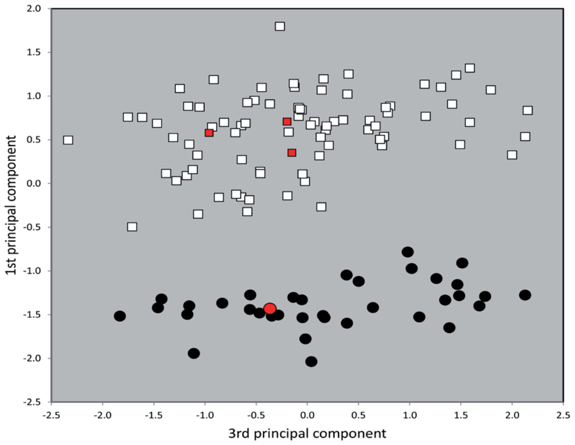

Figure 8. Principal component analysis of worker individuals considering the 21 morphological characters given in Tab. 1. Squares – *Formica tibetana* n.sp., dots – *Formica sentschuensis*; specimens from the holotype samples filled in red.

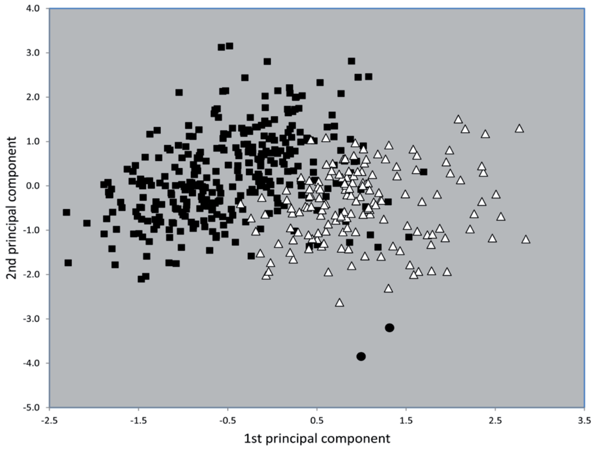

Figure 9. Principal component of gyne individuals of 12 species of Palaearctic *Formica rufa* group species with dependent nest foundation (black squares), of 14 independently founding Palaearctic *Serviformica* species and of *Formica tibetana* n.sp. (black dots) considering head size CS and the shape variables CL/CW, SL/CS, PEW/CS and ML/CS.

Figure 10. Opened *Formica tibetana* n.sp. nest mound. The writing desk-like shape of the mound is clearly visible.

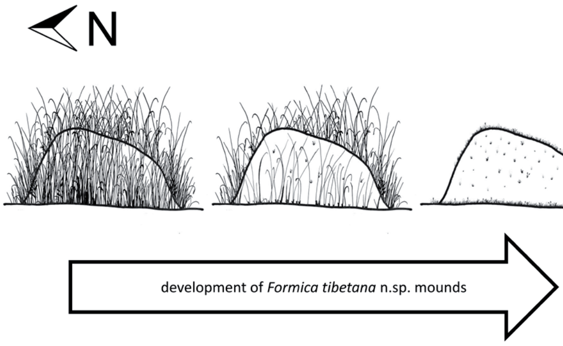

Figure 11. Development of *Formica tibetana* n.sp. nest mound.

of *Coptoformica* because the realized niche overlap OR is only 0.6%. More simply expressed: syntopic occurrence of *Coptoformica* and *F. tibetana* n.sp. was observed only on a single study plot, but here the established host *F. picea candida* was also present.

The second argument against independent colony foundation is gyne morphology. The large gaster size of one single dealate gyne observed walking on ground for colony foundation corresponds to the situation in independently founding *Serviformica* gynes and not to the small gaster of the dependently founding *Formica rufa* group gynes. We have no numeric comparison data on gaster size but we have data on CS, CL/CW, SL/CS, PEW/CS and ML/CS of 327 gynes of 12 species of the *F. rufa* group and of 152 gynes of 14 *Serviformica* species. A principal component analysis run with these data places the two *Formica tibetana* n.sp. gynes widely distant from the *F. rufa* group cluster and closer to *Serviformica* and the diagram also indicates that the character syndrome of *F. tibetana* n.sp. is outstanding (Fig. 9).

The habitats in Sichuan are mainly in the highly montane zone in light conifer stands (6 findings), grassland with few conifers (2) and a rubble field with shrubs (1). Habitats in the eastern part of the Tibetan Plateau (Quinghai and Ganzu) are mainly mesophilic grasslands or pastures (24)), light conifer forest (4), wet grassland (3), stony flood plains (2) and grassland with shrubs (1). *Formica tibetana* n.sp. has been observed to construct nests in the soil, beneath stones, or as soil mounds within areas with dense vegetation. In optimal habitats these ants can reach nest densities ranging from 15 to 36 nests per 100 m^2. In a manner similar to other ant species, such as some *Myrmica*, *Lasius*, and *Formica*, this species constructs earth mounds, referred to as solariums, within dense and tall grassland (Fig. 10). The primary purpose of these mounds is to protrude from the shading vegetation to harness solar energy efficiently. This is particularly important for rapid warming in spring allowing a faster brood development. Observations conducted at the base of a north-facing cattle pasture near the site Sazin Gömpa in Qinghai revealed that *Formica tibetana* n.sp. constructs mounds with southward-facing solar collector surfaces. At the latitude of the Sazin Gömpa site (35.5°n) and during the months of February and March, an inclination of 14° results in 122% of the solar heat input compared to a horizontal plane whereas the advantage in the period April to June is only 102%.

The hypothesized sequence of the development of the writing-desk shape of *Formica tibetana* n.sp. mounds at Sazin Gömpa commences with *Potentilla fruticosa* forming rings around soil nests. These dwarf shrubs are not consumed by grazing cattle hence providing some kind of protective ring against trampling. Subsequently, *Formica tibetana* n.sp. brings up mineral soil to construct a solarium. After a while the *Potentilla* dies off, and the hard *Kobresia* turf begins to spread over the mound. This process is accompanied by the proliferation of crustose lichens, which further contributes to the mechanical stabilization of surface. The shape of the distinctive desk-like mounds is maintained more or less when the nest population of *F. tibetana* n.sp. eventually dies.

A second pathway to form desk-like mounds is their establishment in areas with sparse grazing and dense vegetation. In such environments, *Formica tibetana* n.sp. has been observed to construct soil mounds from the beginning. When grazing increases, the tall grasses gradually disappear while the mounds become covered with *Kobresia pygmaea* and crustose lichens (Fig. 11). The ant population of these mounds dies out after a while and the mounds remain as relicts of a time of less grazing and higher vegetation. Aged mounds are frequently completely overgrown by *Kobresia* and lichens, resulting in the formation of a very hard and felty root-mat of approximately 8-10 cm thickness. These old mounds have diameters of 35 to 90 cm and heights of 30 to 50 cm. These very stable mounds are obviously persisting for a long time – with and without ant populations. Many of these aged mounds are occupied by pikas (*Ochotona*), which cut holes at the mound bases. *Formica tibetana* n.sp. nests restricted to the southern mound side in close proximity to the ground indicate a resettlement of abandoned mounds.

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