



RESEARCH ARTICLE - ANTS

Taxonomic Studies on the Ant Genus *Temnothorax* Mayr, 1861 (Hymenoptera: Formicidae), with the Description of Three New Species from India

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Abstract

The Northeastern Himalaya forms the most significant part of the Indo-Burma hotspot, with many imperative landscapes designed for the region. The region presents an amalgam of Indomalayan, Palearctic, and Sino-Japanese elements, characterized by diverse ecological and altitudinal gradients. The rich faunal and floral diversity can be attributed to tropical rainforests, sub-tropical forests, temperate and alpine forests, which cover more than 60% of the total geographical area. Due to the geographical and cultural proximity of the Southeast Asian countries, the region is of enormous economic importance. The Eastern Himalayas meet the prerequisite criterion of biological commonalities and are designated as a vital eco-region of India. The uplift of the Tibetan Plateau and the rise of the Himalayas as an insurmountable barrier have led to a high degree of endemism in the region. Ant specimens were collected manually. The present study describes three new species, *Temnothorax arunachalensis* sp. nov., *Temnothorax boltoni* sp. nov., and *Temnothorax pangchenensis* sp. nov. from India. An Identification key supplemented with digital images of the known species of this genus, based on the worker caste from India, is also provided.

Zoobank LSID: urn:lsid:zoobank.org:pub:A161321C-BCB8-488C-B728-CCECA992681E

Introduction

Temnothorax Mayr, 1861, is one of the most diverse ant genera in the subfamily Myrmicinae. This genus is currently represented by 504 extant species, 29 extant subspecies, and one fossil species (Bolton, 2025). Species of *Temnothorax* are generally found in various habitats, ranging from deserts to tropical rainforests, and at altitudes from sea level up to 4,000 m (Guénard et al., 2016; Prebus, 2015, 2017a). These tiny creatures inhabit rotten wood, small cavities, under cracks, under rocks, in leaf litter, under twigs, under bark for arboreal species, within hollow nut shells, and directly in the soil where these ants build small nests with a maximum of 200 workers (Beckers et al., 1989; Prebus, 2017b; 2021a). *Temnothorax* ants are sometimes referred to as “rock ants” or “acorn ants” because their nests are frequently located in cracks within rocks and in hollow nut shells (Subedi et al., 2023).

Mayr (1861) described this genus based on the type species *Myrmica recedens*. Historically, *Temnothorax* was placed in different families, subfamilies, and tribes, in Myrmicidae (Emery, 1877), in Myrmicinae (Mayr, 1861; Mayr, 1865; Dours, 1873; Dalla Torre, 1893), in Leptothoracini (Forel, 1917; Emery, 1924; Donisthorpe, 1943), in Formicoxenini (Bolton, 1994; Bolton, 2003). Phylogenetic analysis of the subfamily Myrmicinae has placed the genus in the tribe Crematogastrini (Ward et al., 2015; Blaimer et al., 2018). The genus *Temnothorax* was treated as subgenus of *Leptothorax* (Forel, 1892; Dalla Torre, 1893; Ruzsky, 1905; Wheeler, 1910; Emery, 1915; Forel, 1915; Emery, 1916; Forel, 1917; Bondroit, 1918; Wheeler, 1922; Emery, 1924; Donisthorpe, 1943) and as junior synonym of *Leptothorax* (Forel, 1890; Baroni Urbani, 1971; Brown, 1973; Bolton, 1982; Hölldobler & Wilson, 1990; Ogata, 1991; Bolton, 1994; Bolton, 1995).



Temnothorax as genus: Mayr, 1863; Roger, 1863; Mayr, 1865; Dours, 1873; Forel, 1874; Bernard, 1967; Arnol'di & Dlussky, 1978; Dlussky & Fedoseeva, 1988; Atanassov & Dlussky, 1992; Bolton, 2003).

The significant contributions to the taxonomy of the genus *Temnothorax* include (Emery, 1916; Bondroit, 1918; Emery, 1924; Menozzi, 1931; Bernard, 1967; Kutter, 1973; Kutter, 1977; Buschinger et al., 1987; Agosti & Collingwood, 1987; Buschinger, 1989; Seifert, 1996; Cagniant & Espadaler, 1997; Bolton, 2003; Radchenko, 2004; Radchenko, 2005; Seifert, 2007; Terayama, 2009; Zhou et al., 2010; Eguchi et al., 2011; Czechowski et al., 2012; Bharti et al., 2012; Snelling et al., 2014; Prebus, 2015; Salata & Borowiec, 2015; Radchenko et al., 2015; Csősz et al., 2015; Bharti et al., 2016; Fisher & Bolton, 2016; Galkowski & Lebas, 2016; Radchenko, 2016; Cantone, 2017; Catarineu et al., 2017; Sharaf et al., 2017; Galkowski & Cagniant, 2017; Prebus, 2017a; Csősz et al., 2018; Salata et al., 2018; Fernández & Serna, 2019; Salata & Borowiec, 2019; Sharaf & Aldawood, 2019; Fernández & Serna, 2019; Rasheed et al., 2020; Yusupov et al., 2020a, b; González, 2021; Salata & Borowiec, 2022; Schifani et al., 2022; Salata et al., 2023; Subedi et al., 2023; Hamer et al., 2023; Báthori et al., 2023; Salata et al., 2024; Qian & Xu, 2024; Csősz et al., 2024a, b; Báthori et al., 2024; Wei et al., 2024; Prebus et al., 2024; Borowiec & Salata, 2025; Schifani et al., 2025; Zięcina et al., 2025). Furthermore, Prebus (2017b; 2021a, b) studied the evolution, biogeography, natural history of the acorn ants, investigated the phylogenetic relationships and taxonomic revision of the *Temnothorax salvini* clade. In India, the genus is represented by 12 extant species and one extant subspecies (Yusupov et al., 2020a). Bharti et al. (2012) provided a comprehensive outline of Indian *Temnothorax* by adding three new species from the Northwest Himalayas. Later, Bharti et al. (2016) raised the subspecies *Temnothorax rothneyi simlensis* to *Temnothorax simlensis* and described the reproductive caste along with its plesioibiotic association with Himalayan species of the genus *Myrmica*. Yusupov et al. (2020a, b) described three new species from the Himalayas. Rasheed et al. (2020) recently revised the genus *Temnothorax* and described a new species from the Himalayan range of Pakistan. In the present study, three new species of *Temnothorax* are described from North-East Himalaya, i.e., *T. arunachalensis* sp. nov., *T. boltoni* sp. nov., and *T. pangchenensis* sp. nov. An Identification key supplemented with digital images of the known species of this genus based on the worker caste from India is also provided.

Material and Methods

The specimens were collected manually from the West Kameng district of Arunachal Pradesh. The ground was covered with stones, grasses, bushes, and tall trees. The workers of these species were collected during the post-monsoon season in the months of September and October 2013 and September 2019. Taxonomic analysis was conducted

under a Nikon SMZ 1500 stereomicroscope with a maximum magnification of 112.5x. An MP (Micro Publisher) digital camera attached to the same microscope with Auto-Montage software (Syncroscopy, Division of Synoptics, Ltd.) was used to capture digital images. Later, images were cleaned with Adobe Photoshop CS5 and Helicon Filter 5. Measurements were recorded in millimeters. The standard measurements and indices follow Salata et al. (2024) with some changes as given below: Morphological terminology for measurements and indices is as follows:

EL: eye length; maximum eye length.

EW: eye width; measured along the maximum horizontal diameter of the eye.

HL: Head length; measured in a straight line from the mid-point of the anterior clypeal margin to the mid-point of the posterior margin in full-face view.

HW: Head width; measured directly behind the eyes in full-face view.

ML: Mandible length; The straight-line length of the mandible measured from apex to the lateral base.

PEH: Petiole height; measured in lateral view, the chord of ventral petiolar profile at node level is the reference line perpendicular to which the maximum petiole height is measured.

PEL: Petiole length; measured from the anterior to the posterior inflections of the petiole node in lateral view.

PNW: Pronotum width; maximum width of pronotum in dorsal view (in gyne, maximum width of scutum).

PPL: Postpetiole length; measured from anterior to posterior inflections of the postpetiole node in lateral view.

PPH: Postpetiole Height; measured from sternal process base to postpetiole apex in lateral view.

PPW: Postpetiole width; maximum width of postpetiole in dorsal view.

PSL: Propodeal spine length; measured from the centre of the propodeal spiracle to the top of the propodeal spine in lateral view.

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

WL: Weber's length; measured as the diagonal length from the anterior end of the neck shield to the posterior margin of the propodeal lobe.

TL: The total outstretched length of the ant from the mandibular apex to the gastral apex; when measured in profile, the sum of mandibular length + head length + weber's length + lengths of waist segments + length of gaster.

Ratios

CI: HL/HW

EI1: EL/EW

EI2: EL/HL

SI1: SL/HL

SI2: SL/HW

MI: WL/PNW

PI: PEL/PEH

PPI: PPW/PPL

PSLI: PSL/HW

Depositories:

The type material of the new species has been deposited in PUAC “Punjabi University Patiala Ant Collection” at the Department of Zoology and Environmental Sciences, Punjabi University, Patiala, Punjab, India.

Results

Temnothorax arunachalensis sp. nov. Rilta & Bharti (Figs 1-3)

LSID: urn:lsid:zoobank.org:act:27085150-A880-4CEB-8A77-0250074DC408

Type Material: Holotype (worker) India: *Arunachal Pradesh*: Dirang, 27°21'30.32" N, 92°14'27.67" E, 1634m, 29.ix.2013. Paratype: 14 workers, same data as holotype. Manual collection (coll. J.S. Rilta) [PUAC].

Additional Material: 30 Workers *Arunachal Pradesh*: Dirang, 27°21'18.93" N, 92°14'46.75" E, 1560 m, 03.ix.2019, manual collection (Coll. Tarun Dhadwal).

Worker measurements:

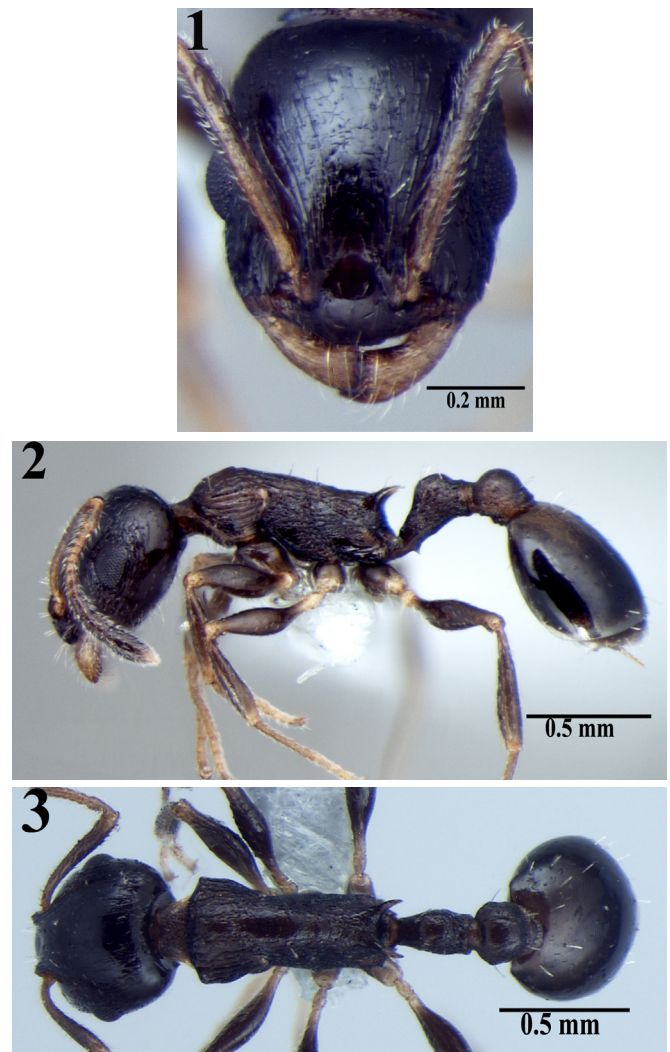
Holotype: HL 0.64; HW 0.56; EL 0.16; EW 14; SL 0.52; ML 0.34; WL 0.78; PNW 0.36; PSL 0.20; PEL 0.34; PEH 0.25; PPL 0.20; PEW 0.14; PPW 0.22; GL 0.66; TL 2.90. CI 1.142; EI1 1.142; EI2 0.25; SI1 0.812; SI2 0.928; MI 2.167; PI 1.36; PPI 1.1; PSLI 0.357.

Paratype: HL 0.64-0.74; HW 0.56-0.64; EL 0.16-0.18; EW 0.14-0.16; SL 0.52-0.54; ML 0.34-0.36; WL 0.78-0.90; PNW 0.36-0.44; PSL 0.20-0.22; PEL 0.34-0.40; PEH 0.25-0.30; PPL 0.20-0.22; PEW 0.14-0.18; PPW 0.22-0.28; GL 0.66-0.78; TL 2.90-3.40. CI 1.142-1.156; EI1 1.125-1.142; EI2 0.24-0.25; SI1 0.729-0.812; SI2 0.281-0.928; MI 2.045-2.167; PI 1.33-1.36; PPI 1.1-1.27; PSLI 0.343-0.357 (n = 10).

Description:

In full-face view, head distinctly longer than broad CI 1.142, posterior head margin almost straight, occipital corners rounded, lateral sides convex; clypeus broad and convex, anterior clypeal margin rounded; mandibles small and triangular, masticatory margin with 5-teeth, apical and preapical teeth larger followed by 3-smaller denticles; antennae 12-segmented with a club of apical 3-larger segments, scape long (SI1 0.812; SI2 0.928) slightly surpassing the posterior head margin; eyes moderate in size (EI1 1.142) and placed laterally at almost mid-length of the head.

Body segment: In dorsal view, mesosoma elongated; promesonotal suture and metanotal groove feebly developed; anterolateral corners of pronotum angular and pronotum convex; dorsal surface of mesonotum and propodeum flat; propodeum armed with a pair of spines and directed inward; petiolar node longer than broad; postpetiole roughly circular in shape; anterior margin of first gastral tergite concave medially and anterolateral corners form obtuse angles; gaster large and oval. In lateral view, the anterior face of the pronotum is steep, the rest of mesosoma slanting; propodeal spines long (PSLI 0.357), acute and slightly curved downward;



Figs 1-3. *Temnothorax arunachalensis* sp. nov. worker. **1.** head in full-face view; **2.** body in profile view; **3.** body in dorsal view.

propodeal declivity feebly concave; propodeal spiracle small and rounded, located far below the basal margin of propodeal spine and propodeal declivity; propodeal lobe large and rounded; petiolar node anteriorly with a long peduncle, petiolar node distinctly longer than high, anterior face of petiolar node feebly concave and dorsal surface rounded; petiole ventrally with a tooth like transparent subpetiolar process; dorsal surface of postpetiole rounded.

Sculpture: Dorsal surface of clypeus, vertex feebly striated, head posterior to vertex smooth and shiny; mandibles very finely striated; anterior and lateral margins of pronotum emarginated; dorsal central surface irregularly striated and coarsely punctated; dorsal central surface of mesonotum smooth and feebly striated; dorsal surface of propodeum longitudinally striated and coarsely punctated; propodeal declivity transversely striated and coarsely punctated; in lateral view, pronotum coarsely and longitudinally striated; mesopleuron and metapleuron irregularly striated and densely punctated; petiole and postpetiole coarsely punctated; dorsal surface of petiole and postpetiole finely punctated; gaster smooth and shiny.

Pilosity and pubescence: Body covered with sparse, erect, sub-erect, stout, and whitish hairs; anterior clypeal margin and mandibles with pale yellow long hairs; decumbent hairs almost wanting on the body but dense on antennae and appendages.

The body is dark brownish; the mandibles and antennae are light brownish; the trochanter, basal portion of the femur, and pretarsi are pale yellowish.

Etymology: The species is named after the type locality.

Biology: The nest of the new species was collected from under a stone in the park of PWD Inspection Banglaw, located in the West Kameng district of Arunachal Pradesh. The ground was covered with grass, and a few flowering plants were planted along the sides of the park. The workers of this species were collected during the post-monsoon season. Another nest of this was collected under a stone from the campus of the National Research Centre on Yak, in the West Kameng district of Arunachal Pradesh. Only workers were reported during the collection survey, while gyne and males were not reported.

Remarks: *Temnothorax arunachalensis* **sp. nov.** is somewhat similar to the Chinese species *Temnothorax angulohumerus* Zhou et al., 2010. It can be distinguished from the latter by the following combination of characters: *Temnothorax arunachalensis* **sp. nov.** dorsal surface of head feebly striated; clypeus, vertex, and head posterior to vertex smooth and shiny; dorsal surface of pronotum irregularly striated and coarsely punctated; mesonotum smooth and very feebly striated; dorsal surface of propodeum finely longitudinally striated and coarsely punctated; laterally pronotum coarsely and longitudinally rugulose; dorsal surface of petiole and postpetiole finely punctated; in dorsal view, propodeal spines curved inward and body dark brownish. In *Temnothorax angulohumerus*, the dorsal surface of the head is finely striated and reticulated; the dorsal surface of the pronotum is smooth medially; mesonotum irregularly striated, and the propodeum transversely striated. The dorsal surface of the postpetiole is smooth; dorsally propodeal spines are curved downward, not inward, and body ochereous yellow. This species is remarkably distinguishable from other Indian species due to the angulated anterolateral corners of the pronotum.

***Temnothorax boltoni* sp. nov. Rilta & Bharti (Figs 4-6)**

LSID: urn:lsid:zoobank.org:act:36DD3713-FB5B-4250-8353-B236DC8AA348

Type Material: Holotype (worker) India: *Arunachal Pradesh*: Tawang, 27°35'43.43" N, 91°52'12.12" E, 2963m, 3.x.2013. Paratype: 2 Workers, same data as holotype. Manual Collection (coll. J. S. Rilta) [PUAC].

Worker measurements:

Holotype: HL 0.66; HW 0.56; EL 0.14; EW 0.12; SL 0.42; ML 0.30; WL 0.84; PNW 0.38; PSL 0.24; PEL 0.32; PEH 0.30; PPL 0.22; PEW 0.16; PPW 0.24; GL 0.78; TL 3.12. CI 1.178; EI1 1.166; EI2 0.212; SI1 0.636; SI2 0.75; MI 2.211; PI 1.067; PPI 1.091; PSLI 0.428.

Paratype: HL 0.66-0.70; HW 0.56-0.60; EL 0.14-0.16; EW 0.12-0.14; SL 0.42-0.50; ML 0.30-0.32; WL 0.84-0.90; PNW 0.38-0.42; PSL 0.24-0.28; PEL 0.32-0.34; PEH 0.30-0.36; PPL 0.22-0.28; PEW 0.16-0.18; PPW 0.24-0.26; GL 0.78-0.80; TL 3.12-3.34. CI 1.167-1.178; EI1 1.142-1.166; EI2 0.212-0.228; SI1 0.636-0.714; SI2 0.75-0.83; MI 2.142-2.211; PI 0.944-1.067; PPI 1.076-1.091; PSLI 0.428-0.466 (n=2).

Description:

In full-face view, the head is roughly rectangular in shape, longer than broad (CI 1.178), posterior head margin feebly convex, occipital corner rounded, lateral sides weakly convex; clypeus sub-quadrate, anterior clypeal margin rounded; masticatory margin with 5-teeth, apical and preapical teeth larger and followed by 3-smaller denticles; frontal carina and antennal scrobe absent; antennae 12-segmented, with a club of apical 3-larger segments, scape long (SI1 0.636; SI2 0.75), slightly falling short to reach posterior head margin; eyes moderate in size (EI1 1.166), placed laterally below the mid-length of the head.

Body Segment: In dorsal view, mesosoma elongated and convex; promesonotal suture and metanotal groove feebly developed; pronotum broader than the rest of mesosoma; propodeal spine long and slightly diverges outward; petiolar node longer than broad; postpetiole distinctly broader than



Figs 4-6. *Temnothorax boltoni* **sp. nov.** worker. **4.** head in full-face view; **5.** body in profile view; **6.** body in dorsal view.

long, anterior face truncate; anterior margin of first gastral tergite concave medially and anterolateral corners form obtuse angles; gaster large and oval. In lateral view, the dorsal surface of mesosoma convex; propodeal spines long (PSLI 0.428) and raised upward; the propodeal declivity concave; propodeal lobe small, translucent, and triangular; propodeal spiracle small and rounded, placed far below the propodeal declivity and basal portion of propodeal spine; petiolar node nodiform, anteriorly with a long peduncle; petiole ventrally with a well-developed translucent tooth like subpetiolar process; dorsal surface of postpetiole rounded; sting present.

Sculpture: Dorsal surface of head feebly striated and punctated up to vertex; in lateral view, head posterior to the vertex, smooth, and shiny; clypeus longitudinally striated; frontal triangle smooth; mandibles longitudinally striated; dorsal surface of mesosoma reticulated and punctated; anterior margin of pronotum emarginated; laterally mesosoma coarsely rugo-reticulated; propodeal declivity smooth; dorsal and lateral surface of petiole finely punctated; postpetiole and gaster smooth and shiny.

Pilosity and Pubescence: Body covered with sparse, erect, sub-erect hairs; anterior clypeal margin and mandibles with few long and fine hairs; decumbent pubescence very sparse all over the body surface but dense on antennae and appendages.

Body dark brownish; mandibles, flagellum, and tarsi light brownish.

Etymology: The species is named after Barry Bolton for his contributions to ant systematics.

Biology: This new species was collected under a stone alongside the road in the West Kameng district of Arunachal Pradesh. The collection site was covered with grass, bushes, and a few tall trees. Only three workers of this species were collected during the collection survey, while gyne and males were not reported.

Remarks: *Temnothorax boltoni* sp. nov. shares most affinities with *Temnothorax nassonovi* (Ruzsky, 1895). The following combination of characters can separate these species: in *Temnothorax boltoni* sp. nov. head feebly striated and punctated up to vertex, posterior to vertex head smooth and shiny; posterior margin of head weakly convex; laterally mesosoma coarsely rugo-reticulate; propodeal spines comparatively short and raised upward; subpetiolar process well developed transparent and tooth like; dorsal surface of petiole feebly punctated, postpetiole smooth and shiny; body dark brownish. While in *Temnothorax nassonovi* dorsal surface of head coarsely rugo-reticulated, posterior head margin concave medially; laterally mesosoma weakly reticulated; propodeal spines long and curved downward; subpetiolar process small and denticle like; dorsal surface of petiole and postpetiole reticulate; head and gaster dark brownish, while mesosoma, pedicel and appendages pale yellowish.

***Temnothorax pangchenensis* sp. nov. Rilta & Bharti (Figs 7-9)**

LSID: urn:lsid:zoobank.org:act:3133B0F8-4D97-4E4E-9981-31389624C0B3

Type Material: Holotype (worker) India: **Arunachal Pradesh:** Zemithang, 27°42'34.69" N, 91°43'43.62" E, 2135m, 8.x.2013. Paratype: 1 Queen, same data as holotype. Manual collection (coll. J.S. Rilta) [PUAC].

Worker measurements:

Holotype: HL 0.76; HW 0.62; EL 0.16; EW 0.14; SL 0.60; ML 0.32; WL 0.90; PNW 0.40; PSL 0.12; PEL 0.34; PEH 0.24; PPL 0.22; PEW 0.14; PPW 0.20; GL 0.86; TL 3.4. CI 1.22; EI1 1.142; EI2 0.210; SI1 0.789; SI2 0.967; MI 2.25; PI 1.41; PPI 0.91; PSLI 0.193.

Description:

In full-face view, head distinctly longer than broad (CI 1.22), posterior head margin straight, occipital corners rounded; clypeus broad and convex, anterior clypeal margin rounded and slightly concave medially; mandibles triangular, masticatory margin with 5-well developed teeth; antennae 12-segmented, scape long (SI1 0.789; SI2 0.967), reaching posterior margin of head; frontal lobe small; frontal carina and antennal scrobe absent; eyes moderate in size (EI1 1.142), placed laterally slightly below the mid-length of the head.



Figs 7-9. *Temnothorax pangchenensis* sp. nov. worker. 7. head in full-face view; 8. body in profile view; 9. body in dorsal view.

Body Segment: In dorsal view, mesosoma elongated and flat; pronotum broader than rest of mesosoma; anterolateral angles of pronotum rounded; promesonotal suture indistinct; metanotal groove feebly developed; propodeum armed with a pair of short spines; petiolar node distinctly longer than broad; postpetiole roughly rectangular; gaster large and oval. In lateral view, dorsal surface of mesosoma almost straight; propodeal spines short (PSLI 0.193) and acute; propodeal declivity weakly concave; propodeal lobes large and rounded; petiolar node anteriorly with small peduncle; anterior face of petiolar node straight and dorsal surface rounded; petiole ventrally with a small denticle like subpetiolar process; dorsal surface of postpetiolar node rounded.

Sculpture: Dorsal surface of head finely microreticulated; clypeus longitudinally striated; mandibles coarsely and longitudinally striated; dorsal surface of mesosoma coarsely reticulated; in lateral view, mesosoma irregularly rugulose and coarsely reticulated; lateral and dorsal surface of petiole coarsely reticulated; dorsal surface of postpetiole feebly reticulated; gaster smooth and shiny.

Pilosity and Pubescence: Head, mesosoma, pedicle, and gaster covered with sparse erect, hairs; anterior clypeal margin and mandibles with long fine hairs; pubescence almost wanting on body surface but abundant on antennae and appendages.

Body dark brownish; mandibles, antennae and appendages light brownish.

Description of Gyne (Figs 10-12):

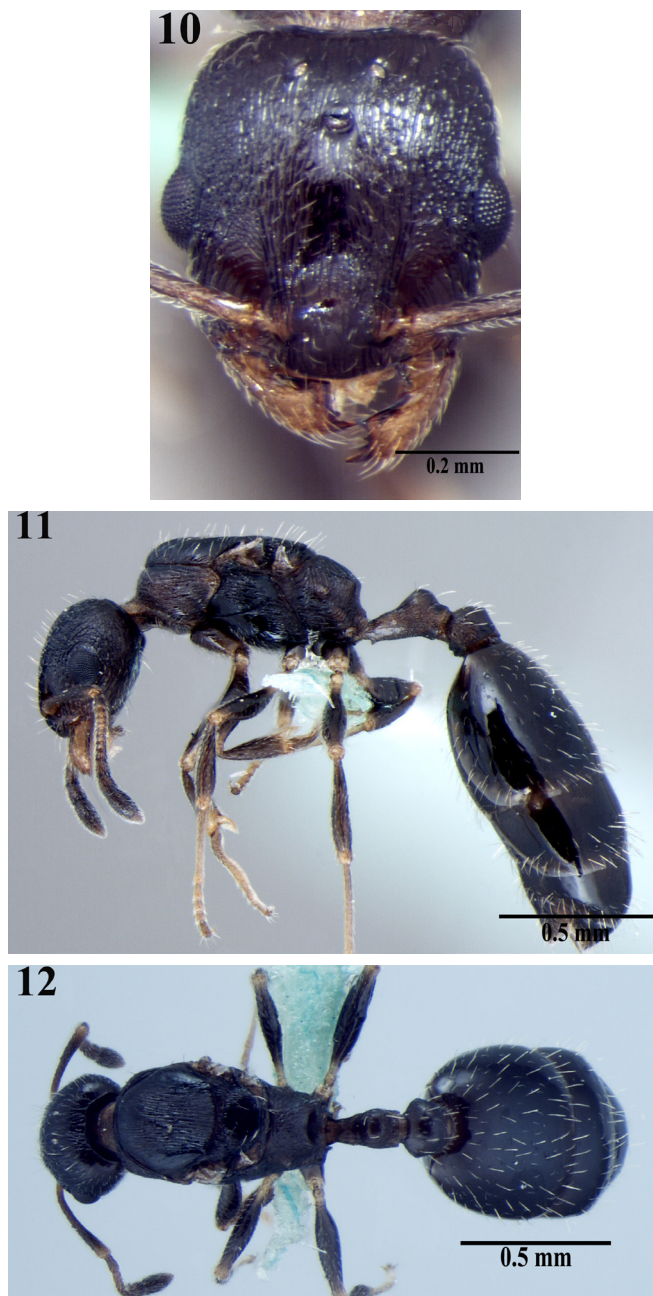
Gyne measurements: HL 0.78; HW 0.70; SL 0.56; EL 0.20; EW 0.16; ML 0.36; WL 1.26; SCW 0.64; PEL 0.46; PEH 0.28; PPL 0.26; PEW 0.22; PPW 0.36; GL 1.70; TL 4.82. CI 1.114; EI1 1.25; EI2 0.26; SI1 0.717; SI2 0.80.

Similar to the worker with some modifications, including larger body size; massive mesosoma and gaster; cephalic dorsum with three prominent ocelli and larger eyes (EI1 1.25); head longitudinally striated; pronotum feebly transversely striated; dorsal surface of scutum flat and longitudinally striated; scutellum smooth; propodeal spine absent; propodeum longitudinally striated and punctated dorsally; laterally mesosoma coarsely longitudinally striated; dorsal surface of petiole and postpetiole smooth.

Body dark brown to blackish.

Etymology: The area is traditionally known as Pangchen, which in the Monpa language means free from all sins. Thus, the Monpa tribes which inhabit the area play a significant role in the conservation of biodiversity in the region. The specific epithet *pangchenensis* embodies the value of conservation in the survival of our planet.

Biology: The specimen of this species was collected under a stone. The collection site was covered with grass, bushes, and very scattered large trees. Only a single worker and a gyne of this new species were collected during the collection survey, while males were not reported.



Figs 10-12. *Temnothorax pangchenensis* sp. nov. queen. 10. head in full-face view; 11. body in profile view; 12. body in dorsal view.

Remarks: *Temnothorax pangchenensis* sp. nov. shares some affinities with *Temnothorax michali* Radchenko, 2004. *Temnothorax pangchenensis* sp. nov. can be distinguished from the latter by the following combination of characters: anterior clypeal margin concave medially; dorsal surface of mesosoma straight; propodeal spines short; anterior face of petiolar node straight; head mesosoma coarsely reticulated and body dark brownish. While, in *Temnothorax michali* the anterior clypeal margin broadly rounded; dorsal surface of mesosoma convex; propodeal spines comparatively longer; anterior face of petiolar node concave; head and mesosoma longitudinally striated and punctated; head dark brownish, mesosoma, pedicle and gaster ochreous-yellow to brownish-yellow.

A revised key to the known Indian species of *Temnothorax* based on worker caste (modified after Yusupov et al., 2020a)

1. In dorsal view, anterolateral corners of pronotum angular (Fig 13A).....*T. arunachalensis* sp. nov.

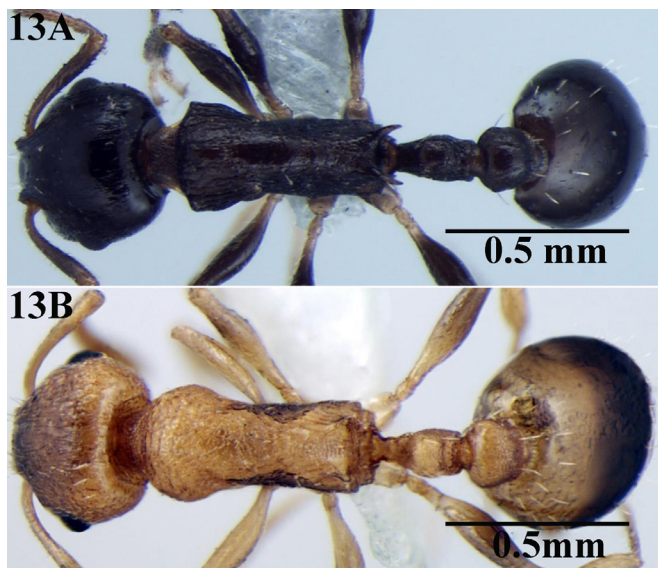


Fig 13: A. Dorsal view of *Temnothorax arunachalensis* sp. nov.; B. Dorsal view of *Temnothorax microreticulatus* Bharti et al., 2012.

— In dorsal view, anterolateral corners of pronotum rounded (Fig 13B).....2

2. Head and thorax brownish; mandibles, antennae, legs, pedicel and abdomen chestnut-brown in color; propodeum without any teeth or spines; (Fig 14A).....*T. inermis* (Forel, 1902)

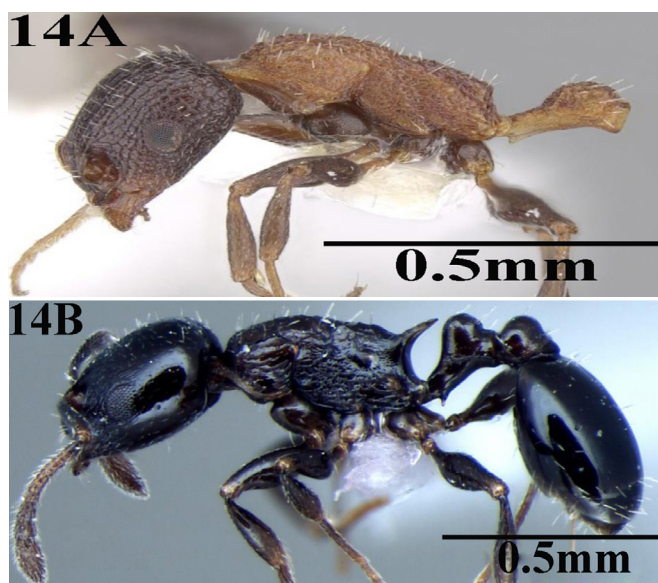


Fig 14: A. Lateral view of *Temnothorax inermis* (Forel, 1902); B. Lateral view of *Temnothorax boltoni* sp. nov.

— Head, thorax and abdomen blackish; mandibles, antennae, legs and pedicel brownish in color; propodeum with well-developed spines; (Fig 14B).....3

3. Dorsal outline of mesosoma in profile, without any impression, mesometanotal groove absent (Fig 15A).....4

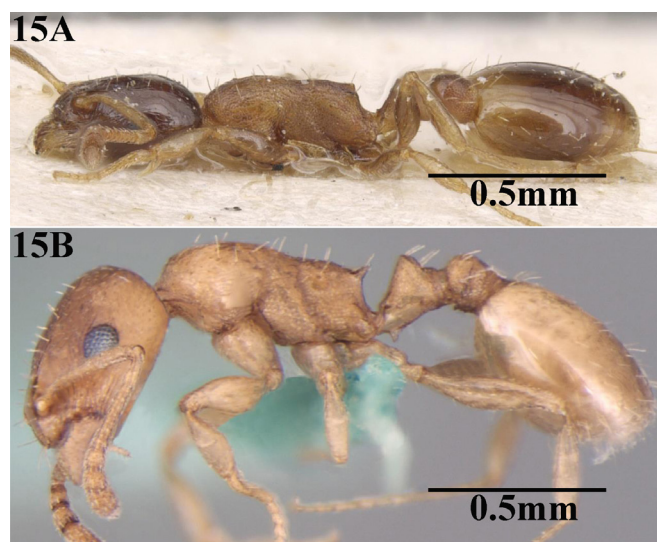


Fig 15: A. Lateral view of *Temnothorax desioi* (Menozzi, 1939); B. Lateral view of *Temnothorax himachalensis* Bharti et al., 2012.

— Dorsal outline of mesosoma in profile, more or less impressed at the mesometanotal groove or behind (Fig 15B).....5

4. Mesosoma, the base of the first gastral segment, petiole, postpetiole, legs, and antennae testaceous yellow to yellowish-brown; head and rest of gaster brown; CI = 122-124; SI1 = 75-78.6 (Fig 16A).....*T. desioi* (Menozzi, 1939)



Fig 16: A. Lateral view of *Temnothorax desioi* (Menozzi, 1939); B. Lateral view of *Temnothorax desioi melanicus* (Menozzi, 1939).

— The colour is uniformly brown; CI = 127-128; SI1 = 73-75 (Fig 16B).....*T. desioi melanicus* (Menozzi, 1939)

5. Either head and mesosoma distinctly sculptured or the head is smooth and mesosoma distinctly sculptured (Fig 17A).....6

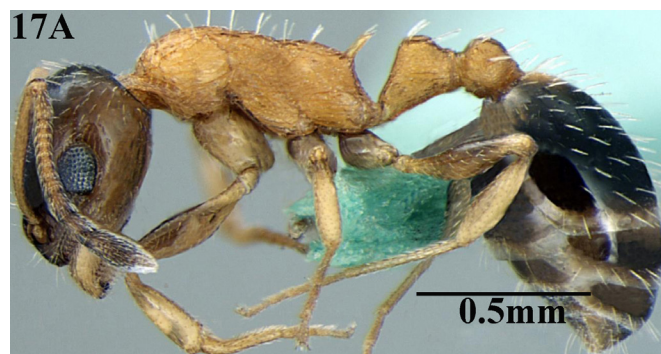


Fig 17: A. Lateral view of *Temnothorax kashmirensis* Bharti et al., 2012; B. Lateral view of *Temnothorax wroughtonii* (Forel, 1904).

— Head and mesosoma smooth and shining with a few rugae (Fig 17B).....14

6. The species is bicoloured, with light to dark brown head and gaster and yellowish to reddish-yellow mesosoma (Fig 18A).....*T. kashmirensis* Bharti et al., 2012

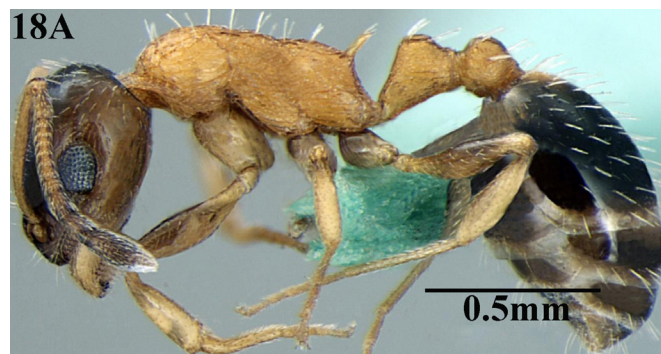


Fig 18: A. Lateral view of *Temnothorax kashmirensis* Bharti et al., 2012; B. Lateral view of *Temnothorax arunachalensis* sp. nov.

— Colour combination different but never as in above (Fig 18B)....7

7. Whole body black or blackish brown; head and mesosoma with coarse longitudinal and reticulate rugosity.....8

— Whole body light yellow to dark brown, never black; head distinctly rugulose and microreticulated.....11

8. Propodeal spines short, strong widened and triangular (Fig 19A).....9



Fig 19: A. Profile view of *Temnothorax schurri* (Forel, 1902); B. Profile view of *Temnothorax microreticulatus* Bharti et al., 2012.

— Propodeal spines long, slightly widened and straight (Fig 19B).....10

9. Head longitudinally rugose, mesosoma and pedicel more densely punctured, anterior clypeal margin convex medially; TL = 2.87 mm, (Fig 20A).....*T. schurri* (Forel, 1902)



Fig 20: A. Lateral view of *Temnothorax schurri* (Forel, 1902); B. Lateral view of *Temnothorax pangchenensis* sp. nov.

— Head finely microreticulate, mesosoma and pedicel coarsely reticulated; anterior clypeal margin concave medially; TL = 3.40mm (Fig 20B).....*T. pangchenensis* sp. nov.
 10. Head posterior to vertex smooth and shiny; petiole; postpetiole smooth and shiny; petiole ventrally with well-developed translucent tooth like subpetiolar process (Fig 21A).....*T. boltoni* sp. nov.

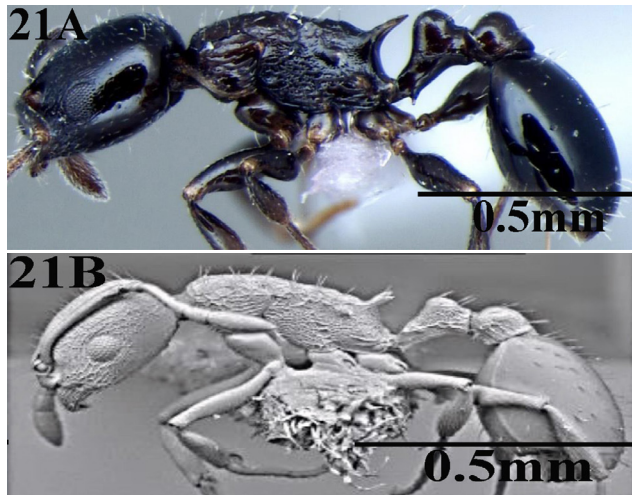


Fig 21: A. Lateral view of *Temnothorax boltoni* sp. nov.; B: Lateral view of *Temnothorax kipyatkovi* Yusupov et al., 2020.

— Head posterior to vertex reticulately rugulose with sinuous longitudinal rugae; petiole; postpetiole rugulose; subpetiolar process reduced (Fig 21B)...*T. kipyatkovi* Yusupov et al., 2020
 11. The color of head distinctly brown (Fig 22A).....12

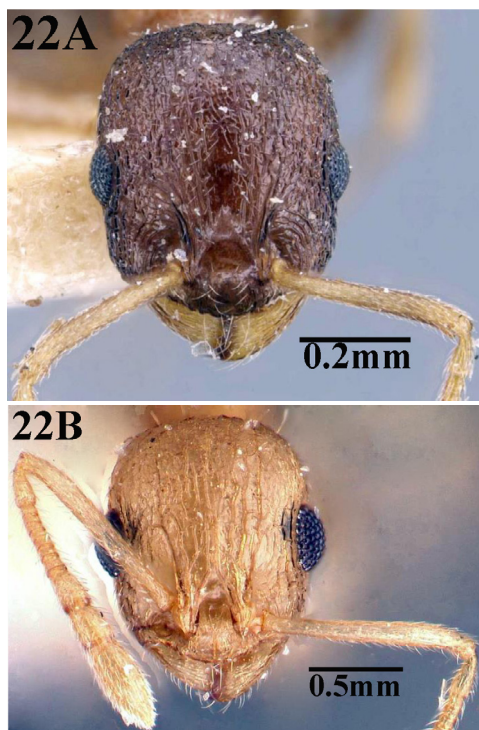


Fig 22: A. Head in Full face view of *Temnothorax rothneyi* (Forel, 1902); B. Head in Full face view of *Temnothorax nordmeyer* (Schulz, 1997).

— The color of head distinctly yellow.....13
 12. Propodeal spines longer, straight, their tips are obliquely cut; ESLI = 11-20 (Fig 23A).....*T. rothneyi* (Forel, 1902)

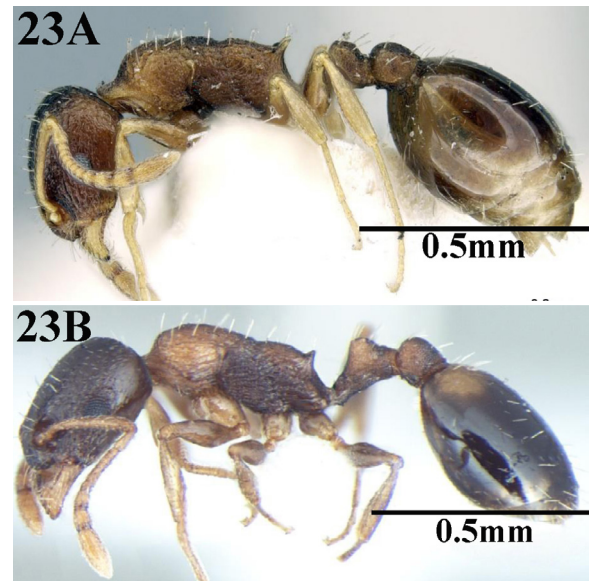


Fig 23: A. Lateral view of *Temnothorax rothneyi* (Forel, 1902); B. Lateral view of *Temnothorax similensis* (Forel, 1904).

— Propodeal spines shorter, triangular, more or less dentate; ESLI = 9-10 (Fig 23B).....*T. similensis* (Forel, 1904)
 13. Scape reaches beyond the posterior margin of the head by 1/6 of its total length; body color uniformly pale yellow; propodeal spines very long (Propodeal spine length PSL = 0.20-0.23mm) (Fig 24A).....*T. nordmeyer* (Schulz, 1997)

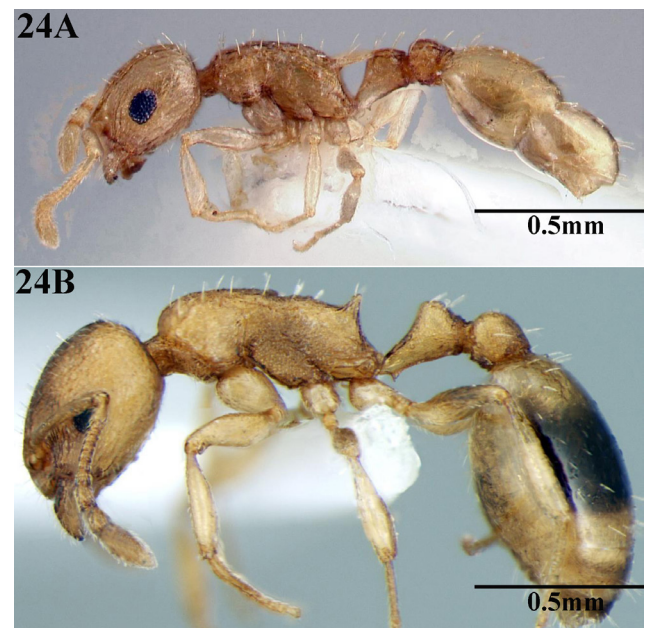


Fig 24: A. Lateral view of *Temnothorax nordmeyer* (Schulz, 1997); B. Lateral of *Temnothorax microreticulatus* Bharti et al., 2012.

— Scape somewhat short not reaching the posterior margin of head; gaster with a brown patch in the middle; propodeal spines short (Propodeal spine length PSL = 0.09-0.11mm) (Fig 24B).....*T. microreticulatus* Bharti et al., 2012

14. Propodeal spines absent, appearing as two small blunt denticles (tubercles) in dorsal view; node of petiole rounded in profile (Fig 25A).....*T. wroughtonii* (Forel, 1902)

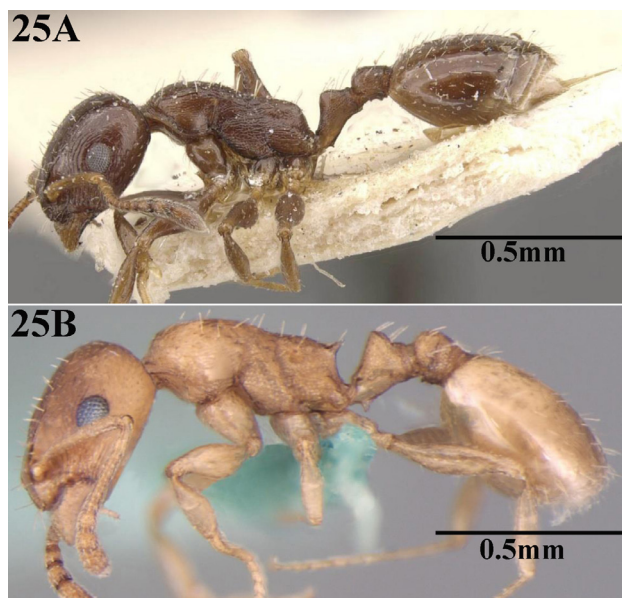


Fig 25: A. Lateral view of *Temnothorax wroughtonii* (Forel, 1904); B. Lateral view of *Temnothorax himachalensis* Bharti et al., 2012.

— Propodeal spines short, as long as 2/3 the range of their bases; node of petiole more or less angular in profile (Fig 25B).....15

15. Head more or less chestnut brown; mesosoma, legs, antennae, petiole and postpetiole more or less yellowish-brown; petiolar node cuneiform; gaster dark brown; CI = 120-139; SI1 = 77-79; SI2 = 94-108 (Fig 26A).....*T. fultonii* (Forel, 1902)

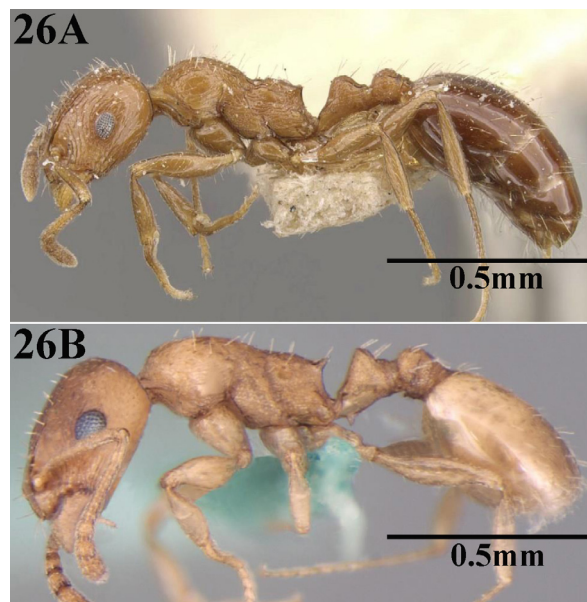


Fig 26: A. Lateral view of *Temnothorax fultonii* (Forel, 1902); B. Lateral view of *Temnothorax himachalensis* Bharti et al., 2012.

— Head light yellow to dark yellow with a brownish tinge; mesosoma light to dark yellow; petiolar node angular at apex;

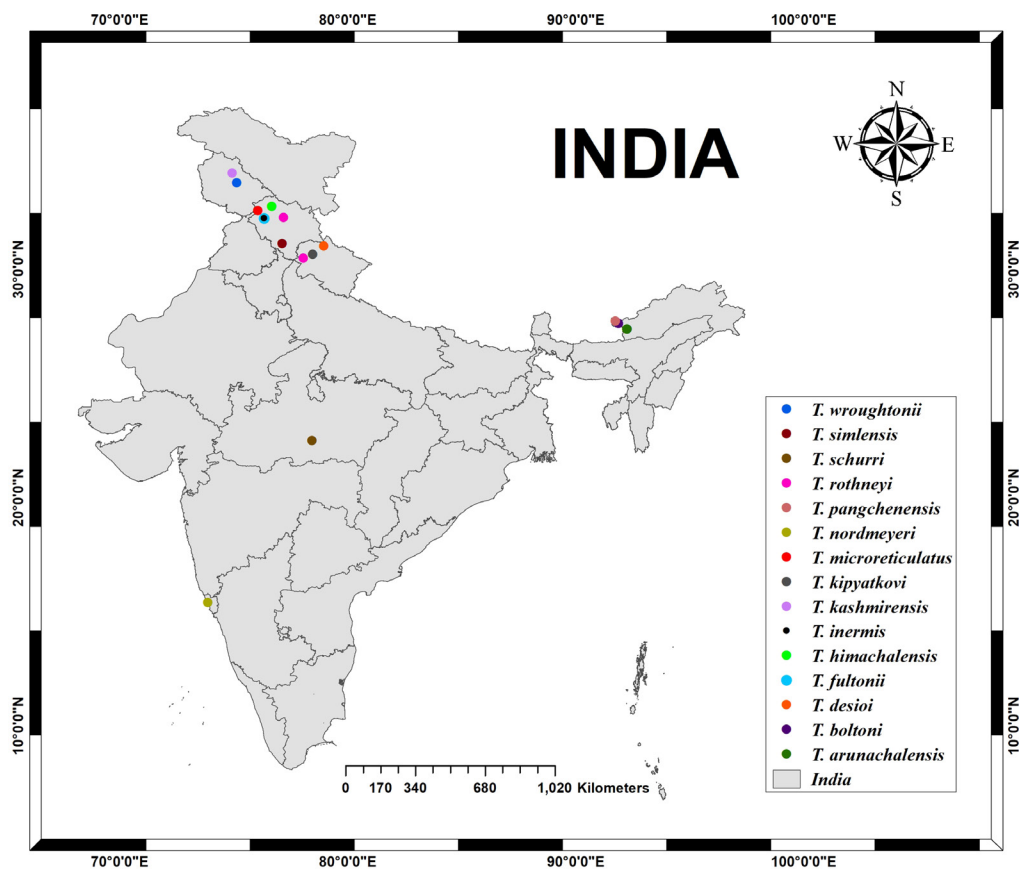


Fig 27. Map showing the Distribution of known *Temnothorax* species across India.

gaster light yellow to dark yellow most often with a brownish patch dorsally in the middle; CI = 113-122; SI1 = 70-76; SI2 = 81-95 (Fig 26B).....*T. himachalensis* Bharti et al., 2012

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Authors' Contribution

JSR: Conceptualization, investigation, writing-original draft, writing-review and editing.

HB: Conceptualization, investigation, writing-original draft, writing-review and editing.

References

Agosti, D. & Collingwood, C.A. (1987). A provisional list of the Balkan ants (Hym. Formicidae) with a key to the worker caste. II. Key to the worker caste, including the European species without the Iberian. Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 60: 261-293.

Arnol'di, K.V. & Dlussky, G.M. (1978). Superfam. Formicoidea. 1. Fam. Formicidae - ants. In G.S. Medvedev (Eds.), Keys to the insects of the European part of the USSR (pp. 119: 3-584) Opredeliteli Faune, SSSR.

Atanassov, N. & Dlussky, G.M. (1992). Fauna of Bulgaria. Hymenoptera, Formicidae. [In Bulgarian.]. Fauna na Bŭlgariya, 22: 1-310.

Baroni Urbani, C. (1971). Catalogo delle specie di Formicidae d'Italia (Studi sulla mirmecofauna d'Italia X). Memorie della Società Entomologica Italiana, 50: 5-287.

Báthori, F., Heinze, J., Trindl, A., Seifert, B., Herczeg, G. & Csősz, S. (2023). Host-switching events are not always the driver of speciation in social parasites: a case study in *Temnothorax* (*Myrmoxenus*) ants (Hymenoptera, Formicidae). Journal of Zoology, 322: 1-11. <https://doi.org/10.1111/jzo.13140>

Báthori, F., Seifert, B., Heinze, J., Kiran, K., Karaman, C. & Csősz, S. (2024). Taxonomy of the Palearctic socially parasitic *Temnothorax* (*Myrmoxenus*) ants (Hymenoptera: Formicidae). PLoS ONE, 19: 1-49. <https://doi.org/10.1371/journal.pone.0308712>

Beckers, R., Goss, S., Deneubourg, J.L. & Pasteels, J.M. (1989). Colony size, communication and ant foraging strategy. Psyche, 96: 239-256. <https://doi.org/10.1155/1989/94279>

Bernard, F. (1967). Faune de l'Europe et du Bassin Méditerranéen. 3. Les fourmis (Hymenoptera Formicidae) d'Europe occidentale et septentrionale. Paris: Masson, 411 p.

Bharti, H., Gul, I. & Schulz, A. (2012). Three new species of genus *Temnothorax* (Hymenoptera: Formicidae) from Indian Himalaya with a revised key to the Indian species. Acta Zoologica Academiae Scientiarum Hungaricae, 58: 325-336.

Bharti, H., Gul, I. & Sasi, S. (2016). Taxonomy of *Temnothorax similensis* stat. nov. (Hymenoptera: Formicidae) with first description of sexual castes along with a mention of its plesiotribic association with Himalayan species of genus *Myrmica*. Sociobiology, 63: 748-754. <https://doi.org/10.13102/sociobiology.v63i2.869>

Blaimer, B.B., Ward, P.S., Schultz, T.R., Fisher, B.L. & Brady, S.G. (2018). Paleotropical diversification dominates the evolution of the hyperdiverse ant tribe Crematogastrini (Hymenoptera: Formicidae). Insect Systematics and Diversity, 2: 1-14. <https://doi.org/10.1093/isd/ixy013>

Bolton, B. (1982). Afrotropical species of the myrmicine ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus* (Formicidae). Bulletin of the British Museum (Natural History). Entomology, 45: 307-370.

Bolton, B. (1994). Identification guide to the ant genera of the world. Cambridge, Mass.: Harvard University Press, 222 p.

Bolton, B. (1995). A new general catalogue of the ants of the world. Cambridge, Mass.: Harvard University Press, 504 p.

Bolton, B. (2003). Synopsis and classification of Formicidae. Memoirs of the American Entomological Institute, 71: 1-370.

Bolton, B. (2025). Bolton's Catalogue and Synopsis Version <http://www.antweb.org>. (Accessed on 10 October, 2025).

Bondroit, J. (1918). Les fourmis de France et de Belgique. Annales de la Société Entomologique de France, 87: 1-174.

Borowiec, L. & Salata, S. (2025). A monographic review of ants of Greece (Hymenoptera: Formicidae) Vol. 2. Review of the subfamily Myrmicinae except the genera *Temnothorax* and *Tetramorium*. Part 1: text. Bytom: Natural History Monographs of the Upper Silesian Museum, 1-476.

Brown Jr., W.L. (1973). A comparison of the Hylean and Congo-West African rain forest ant faunas. In: B.J. Meggers, E.S. Ayensu & W.D. Duckworth (Eds.), Tropical forest ecosystems in Africa and South America: a comparative review (pp. 161-185). Washington, D.C., Smithsonian Institution Press.

Buschinger, A., Fischer, K., Guthy, H.P., Jessen, K. & Winter, U. (1987). Biosystematic revision of *Epimyrma kraussei*, *E. vandeli*, and *E. foreli* (Hymenoptera, Formicidae). Psyche, 93: 253-276.

- Buschinger, A. (1989). Evolution, speciation, and inbreeding in the parasitic ant genus *Epimyrma* (Hymenoptera, Formicidae). *Journal of Evolutionary Biology*, 2: 265-283.
- Cagniant, H. & Espadaler, X. (1997). Les *Leptothorax*, *Epimyrma* et *Chalepoxenus* du Maroc (Hymenoptera: Formicidae). Clé et catalogue des espèces. *Annales de la Société Entomologique de France* (n.s.), 33: 259-284.
- Cantone, S. (2017). Winged ants – The male. Dichotomous key to genera of winged male ants in the world. Behavioral ecology of mating flight. São Paulo: Autopubblicato, 318 p.
- Catarineu, C., Barberá, G.G. & Reyes-López, J.L. (2017). A new ant species, *Temnothorax ansei* sp. n. (Hymenoptera: Formicidae) from the arid environments of south-eastern Spain. *Sociobiology*, 64: 138-145.
<https://doi.org/10.13102/sociobiology.v64i2.1274>
- Csősz, S., Heinze, J. & Mikó, I. (2015). Taxonomic synopsis of the Ponto-Mediterranean ants of *Temnothorax nylanderii* species-group. *PLoS ONE*, 10: e0140000.
<https://doi.org/10.1371/journal.pone.0140000>
- Csősz, S., Salata, S. & Borowiec, L. (2018). Three Turano-European species of the *Temnothorax interruptus* group (Hymenoptera: Formicidae) demonstrated by quantitative morphology. *Myrmecological News*, 26: 101-119.
- Csősz, S., Alicata, A., Báthori, F., Galkowski, C., Schifani, E., Yusupov, Z., Herczeg, G. & Prebus, M.M. (2024a). Integrative taxonomy reveals inflated biodiversity in the European *Temnothorax unifasciatus* complex (Hymenoptera: Formicidae). *Zoologica Scripta*, 53: 1-17.
<https://doi.org/10.1111/zsc.12690>
- Csősz, S., Schifani, E., Seifert, B., Alicata, A. & Prebus, M.M. (2024b). A new species of yellow acorn ant discovered in Italy via integrative taxonomy (*Temnothorax luteus*-complex, Formicidae). *Evolutionary Systematics*, 8: 183-197.
<https://doi.org/10.3897/evolsyst.8.124557>
- Czechowski, W., Radchenko, A., Czechowska, W. & Vepsäläinen, K. (2012). The ants (Hymenoptera: Formicidae) of Poland with reference to the myrmecofauna of Europe. (Fauna Poloniae n.s. 4). Warsaw: Natura Optima Dux Foundation, 496 p.
- Dours, J.A. (1873). Catalogue synonymique des Hyménoptères de France. *Mémoires de la Société Linnéenne de Nord de la France*, 3: 1-230.
- Dalla Torre, K.W. (1893). *Catalogus Hymenopterorum hucusque descriptorum systematicus et synonymicus*. Vol. 7. Formicidae (Heterogyna). Leipzig: W. Engelmann, 289 p.
- Dlussky, G.M. & Fedoseeva, E.B. (1988). Origin and early stages of evolution in ants. In A.G. Ponomarenko (Eds.), *Cretaceous biocenotic crisis and insect evolution*. (pp. 70-144). Moskva: Nauka.
- Donisthorpe, H. (1943). A list of the type-species of the genera and subgenera of the Formicidae. [concl.]. *Annals and Magazine of Natural History*, 10: 721-737.
- Eguchi, K., Bui, T.V. & Yamane, S. (2011). Generic synopsis of the Formicidae of Vietnam (Insecta: Hymenoptera), Part I-Myrmicinae and Pseudomyrmecinae. *Zootaxa*, 2878: 1-61.
- Emery, C. (1877). Saggio di un ordinamento naturale dei Mirmicidei, e considerazioni sulla filogenesi delle formiche. *Bullettino della Società Entomologica Italiana*, 9: 67-83.
- Emery, C. (1915). Formiche raccolte nell'Eritrea dal Prof. F. Silvestri. *Bollettino del Laboratorio di Zoologia Generale e Agraria della Reale Scuola Superiore d'Agricoltura*. Portici, 10: 3-26.
- Emery, C. (1916). Fauna entomologica italiana. I. Hymenoptera-Formicidae. *Bullettino della Società Entomologica Italiana*, 47: 79-275.
- Emery, C. (1924). Hymenoptera. Fam. Formicidae. Subfam. Myrmicinae. [concl.]. *Genera Insectorum*, 174: 207-397.
- Fernández, F. & Serna, F.J. (2019). Subfamilia Myrmicinae. Capítulo 27. In F. Fernández, R.J. Guerrero & T. Delsinne (Eds.), *Hormigas de Colombia*. Bogotá (pp. 791-888), Universidad Nacional de Colombia.
- Fisher, B.L. & Bolton, B. (2016). *Ants of the world. Ants of Africa and Madagascar. A guide to the genera*. Berkeley: University of California Press, 503 p.
- Forel, A. (1874). Les fourmis de la Suisse. Systématique, notices anatomiques et physiologiques, architecture, distribution géographique, nouvelles expériences et observations de mœurs. *Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesamten Naturwissenschaften*, 26: 1-452.
- Forel, A. (1890). Fourmis de Tunisie et de l'Algérie orientale. *Annales de la Société Entomologique de Belgique*, 34: 61-77.
- Forel, A. (1892). Die Ameisenfauna Bulgariens. (Nebst biologischen Beobachtungen). *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 42: 305-318.
- Forel, A. (1915). Fauna insectorum helvetiae. Hymenoptera. Formicidae. Die Ameisen der Schweiz. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft Beilage*, 12: 1-77.
- Forel, A. (1917). Cadre synoptique actuel de la faune universelle des fourmis. *Bulletin de la Société Vaudoise des Sciences Naturelles*, 51: 229-253.
- Galkowski, C. & Lebas, C. (2016). *Temnothorax conatensis* nov. sp., décrite des Pyrénées-Orientales (France) (Hym., Formicidae). *Revue de l'Association Roussillonnaise d'Entomologie*, 25: 80-87.
- Galkowski, C. & Cagniant, H. (2017). Contribution à la connaissance des fourmis du groupe angustulus dans le

- genre *Temnothorax* (Hymenoptera, Formicidae). Revue de l'Association Roussillonnaise d'Entomologie, 26: 180-191.
- González, J.A. (2021). Description of *Temnothorax estel* sp. nov. (Hymenoptera: Formicidae), with a review of the Iberian species of the *sordidulus* species-complex. Zootaxa, 5005: 145-160. <https://doi.org/10.11646/zootaxa.5005.2.2>
- Guénard, B., Shik, J., Booher, D., Lubertazzi, D. & Alpert, G. (2016). Extreme polygyny in the previously unstudied subtropical ant *Temnothorax tuscaloosae* with implications for the biogeographic study of the evolution of polygyny. Insectes Sociaux, 63: 543-551. <http://doi.org/10.1007/s00040-016-0498-7>
- Hamer, M.T., Lee, R.H. & Guénard, B. (2023). First record of the genus *Temnothorax* Mayr, 1861 (Formicidae: Myrmicinae) in Hong Kong, with descriptions of two new species. European Journal of Taxonomy, 879: 116-135. <https://doi.org/10.5852/ejt.2023.879.2165>
- Hölldobler, B. & Wilson, E.O. (1990). The ants. Harvard University Press Cambridge, Massachusetts, 732 p.
- Kutter, H. (1973). Beitrag zur Lösung taxonomischer Probleme in der Gattung *Epimyrma* (Hymenoptera, Formicidae). Mitteilungen der Schweizerischen Entomologischen Gesellschaft, 46: 281-289.
- Kutter, H. (1977). Hymenoptera, Formicidae. Insecta Helvetica. Fauna, 6: 1-298.
- Mayr, G. (1861). Die europäischen Formiciden. Nach der analytischen Methode bearbeitet. Wien: C. Gerolds Sohn, 80 p.
- Mayr, G. (1863). Formicidarum index synonymicus. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien, 13: 385-460.
- Mayr, G. (1865). Formicidae. In Novara Expedition 1865. Reise der Österreichischen Fregatte "Novara" um die Erde in den Jahren 1857, 1858, 1859. Zoologischer Theil. Bd. II. Abt. 1. Wien: K. Gerold's Sohn.
- Menozi, C. (1931). Revisione del genere *Epimyrma* Em. (Hymen. Formicidae) e descrizione di una specie inedita di questo genere. Memorie della Società Entomologica Italiana, 10: 36-53.
- Ogata, K. (1991). A generic synopsis of the poneroid complex of the family Formicidae (Hymenoptera). Part II. Subfamily Myrmicinae. Bulletin of the Institute of Tropical Agriculture Kyushu University, 14: 61-149.
- Prebus, M. (2015). Palearctic elements in the old world tropics: a taxonomic revision of the ant genus *Temnothorax* Mayr (Hymenoptera, Formicidae) for the Afrotropical biogeographical region. ZooKeys, 483: 23-57. <https://doi.org/10.3897/zookeys.483.9111>
- Prebus, M. (2017a). Insights into the evolution, biogeography and natural history of the acorn ants, genus *Temnothorax* Mayr (Hymenoptera: Formicidae). BMC Evolutionary Biology, 17 (250): 1-22. <https://doi.org/10.1186/s12862-017-1095-8>
- Prebus, M. (2017b). Additional file 1: extended taxonomic history and fossil record of *Temnothorax* and relatives. Additional pp. 1-15 from: Prebus, M. 2017a. Insights into the evolution, biogeography and natural history of the acorn ants, genus *Temnothorax* Mayr (Hymenoptera: Formicidae). BMC Evolutionary Biology, 17: 1-22.
- Prebus, M.M. (2021a). Phylogenomic species delimitation in the ants of the *Temnothorax salvini* group (Hymenoptera: Formicidae): an integrative approach. Systematic Entomology, 46: 307-326. <https://doi.org/10.1111/syen.12463>
- Prebus, M.M. (2021b). Taxonomic revision of the *Temnothorax salvini* clade (Hymenoptera: Formicidae), with a key to the clades of New World *Temnothorax*. Peer J, 9: 462 pp. e11514. <https://doi.org/10.7717/peerj.11514>
- Prebus, M.M., Nguyen, N., Doering, G.N. & Booher, D.B. (2024). *Temnothorax caryaluteus* sp. nov. (Hymenoptera: Formicidae): a new ant species from the eastern United States. European Journal of Taxonomy, 970: 175-202. <https://doi.org/10.5852/ejt.2024.970.2757>
- Qian, Y.H. & Xu, Z.H. (2024). Taxonomy of the ant genera *Leptothorax* Mayr, 1855 and *Temnothorax* Mayr, 1861 (Hymenoptera: Formicidae) of China with descriptions of twenty-eight new species and a key to the known Chinese species. European Journal of Taxonomy, 936: 1-97. <https://doi.org/10.5852/ejt.2024.936.2569>
- Radchenko, A.G. (2004). A review of the ant genera *Leptothorax* Mayr and *Temnothorax* Mayr (Hymenoptera, Formicidae) of the eastern Palaearctic. Acta Zoologica Academiae Scientiarum Hungaricae, 50: 109-137.
- Radchenko, A.G. (2005). Monographic revision of the ants (Hymenoptera: Formicidae) of North Korea. Annales Zoologici, 55: 127-221.
- Radchenko, A.G., Yusupov, Z.M. & Fedoseeva, E.B. (2015). Taxonomic notes for some Caucasian *Temnothorax* Mayr, 1861 species, with descriptions of three new species. Caucasian Entomological Bulletin, 11: 161-167. <https://doi.org/10.23885/1814-3326-2015-11-1-161-167>
- Radchenko, A.G. (2016). Ants (Hymenoptera, Formicidae) of Ukraine. National Academy of Sciences of Ukraine. Kiev: I.I. Schmalhausen Institute of Zoology, 496 p.
- Rasheed, M.T., Bodlah, I., Magomedovich, Y.Z., Fareen, A.G., Bodlah, M.A., Prebus, M. & Wachkoo, A.A. (2020). Preliminary contributions toward a revision of the ant genus *Temnothorax* Mayr (Hymenoptera: Formicidae) from Pakistan. Turkish Journal of Zoology, 44: 375-381. <https://doi.org/10.3906/zoo-2003-54>
- Roger, J. (1863). Verzeichniss der Formiciden-Gattungen und Arten. Berliner Entomologische Zeitschrift Beilage, 7: 1-65.

- Ruzsky, M. (1905). The ants of Russia. (Formicariae Imperii Rossici). Systematics, geography and data on the biology of Russian ants. Part I. [In Russian.]. Trudy Obshchestva Estestvoispytatelei pri Imperatorskom Kazanskom Universitete, 38: 1-800.
- Salata, S. & Borowiec, L. (2015). Redescription of *Temnothorax antigoni* (Forel, 1911) and description of its new social parasite *Temnothorax curtisetosus* sp. n. from Turkey (Hymenoptera, Formicidae). ZooKeys, 523: 129-148. <https://doi.org/10.3897/zookeys.523.6103>
- Salata, S., Borowiec, L. & Trichas, A. (2018). Taxonomic revision of the Cretan fauna of the genus *Temnothorax* Mayr, 1861 (Hymenoptera: Formicidae), with notes on the endemism of ant fauna of Crete. Annales Zoologici, 68: 769-808. <https://doi.org/10.3161/00034541ANZ2018.68.4.004>.
- Salata, S. & Borowiec, L. (2019). Preliminary division of not socially parasitic Greek *Temnothorax* Mayr, 1861 (Hymenoptera, Formicidae) with a description of three new species. ZooKeys, 877: 81-131. <https://doi.org/10.3897/zookeys.877.36320>
- Salata, S. & Borowiec, L. (2022). A review of the *Temnothorax anodontoides* species-group (Hymenoptera, Formicidae) from Greece. ZooKeys, 1091: 139-159. <https://doi.org/10.3897/zookeys.1091.79085>
- Salata, S., Środoń, K. & Borowiec, L. (2023). A taxonomic revision of the *Temnothorax graecus* species-group (Hym.: Formicidae) from Greece. Annales Zoologici, 73: 51-68. <https://doi.org/10.3161/00034541ANZ2023.73.1.005>.
- Salata, S., Demetriou, J., Georgiadis, C. & Borowiec, L. (2024). The genus *Temnothorax* Mayr, 1861 (Hymenoptera: Formicidae) in Cyprus. Zootaxa, 5434: 1-69. <https://doi.org/10.11646/zootaxa.5434.1.1>
- Schifani, E., Prebus, M.M. & Alicata, A. (2022). Integrating morphology with phylogenomics to describe four island endemic species of *Temnothorax* from Sicily and Malta (Hymenoptera, Formicidae). European Journal of Taxonomy, 833: 143-179. <https://doi.org/10.5852/ejt.2022.833.1891>
- Schifani, E., Alicata, A., Prebus, M.M. & Csősz, S. (2025). Integrative description of *Temnothorax siculus* sp. n.: a new ant species from Sicily, Italy (Hymenoptera, Formicidae). Diversity, 17: 1-17. <https://doi.org/10.3390/d17040294>
- Seifert, B. (1996). Ameisen beobachten, bestimmen. Augsburg: Naturbuch Verlag, 351p.
- Seifert, B. (2007). Die Ameisen Mittel-und Nordeuropas. Tauer: lutra Verlags-und Vertriebsgesellschaft, 368 p.
- Sharaf, M.R., Akbar, S.A., Al Dhafer, H.M., El-Gharbawy, A. & Aldawood, A.S. (2017). Taxonomy of the myrmicine ant genus *Temnothorax* Mayr, 1861 (Formicidae: Myrmicinae) in the Arabian Peninsula. European Journal of Taxonomy, 280: 1-17. <http://doi.org/10.5852/ejt.2017.280>
- Sharaf, M.R. & Aldawood, A.S. (2019). *Temnothorax almeqeri*, a new ant species (Hymenoptera: Formicidae) from the Asir Mountains, Kingdom of Saudi Arabia, with a key to the Arabian *Temnothorax*. Annales Zoologici, 69: 603-608. <https://doi.org/10.3161/00034541ANZ2019.69.3.009>
- Snelling, R.R., Borowiec, M.L. & Prebus, M.M. (2014). Studies on California ants: a review of the genus *Temnothorax* (Hymenoptera, Formicidae). ZooKeys, 372: 27-89. <https://doi.org/10.3897/zookeys.372.6039>
- Subedi, I.P., Yusupov, Z.M. & Budha, P.B. (2023). Three new species of the ant genus *Temnothorax* Mayr, 1861 (Hymenoptera: Formicidae, Myrmicinae) from Nepal. Far Eastern Entomologist, 475: 6-16. <http://doi.org/10.25221/fee.475.2>
- Terayama, M. (2009). A synopsis of the family Formicidae of Taiwan (Insecta: Hymenoptera). Research Bulletin of Kanto Gakuen University. Liberal Arts, 17: 81-266.
- Ward, P.S., Brady, S.G., Fisher, B.L. & Schultz, T.R. (2015). The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). Systematic Entomology, 40: 61-81. <https://doi.org/10.1111/syen.12090>
- Wei, Y.M., Wu, T.Q., Zhong, Y., Huang, Y.Y. & Nie, G.C. (2024). A new bicolor species of the ant genus *Temnothorax* Mayr, 1861 (Hymenoptera: Formicidae) from Yunnan, China. Journal of the Entomological Research Society, 26: 419-428. <https://doi.org/10.51963/jers.v26i3.2681>
- Wheeler, W.M. (1910). Ants: their structure, development and behavior. New York: Columbia University Press, 663 p.
- Wheeler, W.M. (1922). Ants of the American Museum Congo expedition. New York: Bulletin of the American Museum of Natural History, 1139 p.
- Yusupov, Z.M., Dubovikoff, D.A. & Lopatina, E.B. (2020a). *Temnothorax kipyatkovi* sp. n. – a new species of ants (Hym.: Formicidae) from India. Caucasian Entomological Bulletin, 16: 353-357. <http://doi.org/10.23885/181433262020162-353357>
- Yusupov, Z.M., Lakho, G.M. & Dubovikoff D.A. (2020b). New additions to the fauna of ants of the genus *Temnothorax* Mayr, 1861 (Hymenoptera: Formicidae) of Pakistan. Caucasian Entomological Bulletin, 16: 347-352. <https://doi.org/10.23885/181433262020162-347352>
- Zhou, S., Huang, J., Yu, D. & Liu, Z. (2010). Eight new species and three newly recorded species of the ant genus *Temnothorax* Mayr (Hymenoptera: Formicidae) from the Chinese mainland, with a key. Sociobiology, 56: 7-26.
- Zięcina, D., Salata, S. & Borowiec, L. (2025). Further additions to the taxonomy and distribution of the *Temnothorax graecus* and *T. aveli* species-groups (Hymenoptera: Formicidae) in Greece. Annales Zoologici (Warsaw), 75: 419-435. <https://doi.org/10.3161/00034541ANZ2025.75.2.002>