

## **Additional file 1: extended taxonomic history and fossil record of *Temnothorax* and relatives**

### ***Taxonomic history***

The genus *Leptothorax*, until recently [1], contained most of the species now classified as *Temnothorax*. Established by Mayr [2], the name *Leptothorax* was applied to several different Palearctic species that are now classified as either *Leptothorax* or *Temnothorax*, without a formally designated type species. In 1861, Mayr described the genus *Temnothorax* [3], using this name for a single species with a Mediterranean distribution, *T. recedens* [Figure 1d].

*Temnothorax* was synonymized with *Leptothorax* by Forel [4], but was variously considered a subgenus of *Leptothorax* or a valid genus by others [5-7]. In an effort to provide taxonomic stability for Mayr's original concept of *Leptothorax*, several authors made alternate type designations in parallel, each apparently unaware of the taxonomic changes that the others were proposing, inadvertently compounding the issue. Therefore, while Bingham [8] and Wheeler [9] nominated *L. acervorum* [Figure 2f] as the name bearing species for *Leptothorax*, Emery [10] selected the Palearctic species presently classified as *T. clypeatus* [Figure 1a]; this second genus-concept was then broadly accepted. Around the same time, Ruzsky [11] erected a genus to encompass *L. acervorum* and its close relatives, the genus *Mychothorax*, which is often referred to as *Leptothorax sensu stricto* in the literature. The discrepancies between these parallel taxonomies were noted by M.R. Smith [12], who erected the subgenus *Myrafant* to encompass what he considered to be Emery's concept of *Leptothorax*, distinct from Ruzsky's *Mychothorax*, and subsequently nominated *T. curvispinosus* [Figure 1b], a common Nearctic species, as the type.

This classification scheme remained intact until 2003, when Bolton [1] updated the classification of the tribe Formicoxenini, which in his treatment consisted of twenty-two genera: *Atopomyrmex*, *Chalepoxenus* (= *Temnothorax* [1]), *Cardiocondyla*, *Dilobocondyla*, *Formicoxenus*, *Gauromyrmex*, *Harpagoxenus*, *Leptothorax*, *Myrmoxenus* (= *Temnothorax* [1]), *Nesomyrmex*, *Ochetomyrmex*, *Peronomyrmex*, *Podomyrma*, *Poecilomyrma*, *Protomognathus* (= *Temnothorax* [1]), *Romblonella*, *Rotastruma*, *Stereomyrmex*, *Temnothorax*, *Terataner*, *Vombisidris*, and *Xenomyrmex*. Furthermore, Bolton [1] presented morphological evidence for delineating *Temnothorax* and *Leptothorax s.s.*, observing that the latter is cleanly separated from the former by the presence of a transverse crest on the maxillary stipes [Figure 3b]. As a result, most *Leptothorax* species were transferred to *Temnothorax*. Additionally, Bolton [1] transferred many species to *Nesomyrmex* [Figure 2b] based on clypeal morphology, which in recent studies has been shown to be distantly related to these taxa [13, 14]. Presently, *Leptothorax* consists of nineteen species which vary only slightly from each other morphologically. They are distributed across the boreal habitats of the Northern hemisphere, often nesting in dead wood, under stones, or in close association with other ant species. Closely associated genera include the xenobiotic *Formicoxenus* [Figure 2d] and dulotic *Harpagoxenus* [Figure 2e].

Another former genus that contained many species presently classified as *Temnothorax* was *Macromischa*. Roger [15] established the genus *Macromischa* based, again, on a handful heterogeneous species without designating a type. Wheeler [9] corrected this by naming *T. purpuratus*, the first name appearing in the original article, as the name-bearing species [Figure 4c]. The former genus-or subgenus *Macromischa* was broadly applied to both Baltic amber fossils and extant Neotropical species of *Temnothorax* bearing a peculiar morphological syndrome. The primary diagnostic features of the *Macromischa* syndrome are a thin, elongate

petiole combined with a broad, campaniform post-petiole in dorsal view and a dorsally contiguous, often rounded, mesosoma in profile. Some additional characters that are associated with this syndrome, but not consistently present, are enlarged, spindle-shaped middle and hind femora, and iridescently colored integument. Mann [16] split *Macromischa* into three subgenera to accommodate some of the variation in the group, erecting the subgenera *Croesomyrmex* and *Antillaemyrmex*. Later, Brown [17] provisionally synonymized *Macromischa* with *Leptothorax*, but this name was still in use as a subgenus when Baroni Urbani [18] postulated that *Macromischa* was probably polyphyletic because many of the features that define this syndrome are found independently among clearly different lineages of *Temnothorax*. This taxon name fell out of use when it was formerly synonymized with *Leptothorax* by Snelling [19], who observed that there are many Central American species that are morphologically intermediate between *Leptothorax* and *Macromischa*.

Several subgenera have been proposed specifically for *Temnothorax*: Emery [20] erected the subgenus *Dichothorax* to accommodate the morphologically aberrant ground-nesting Nearctic species *T. pergandei* [Figure 1c]. This species differs from all others in the Nearctic region by its strongly depressed propodeum, massive, rounded promesonotum, and elongate petiole. Several authors have noted that this morphology is also present in several species around the Palearctic Mediterranean and North Africa, namely *T. recedens* [Figure 1d] and *T. schaufussi* [21, 22]. Ashmead [22] raised *Dichothorax* to genus level, but this change was not widely adopted; Hamman & Klemm [23] proposed *Icothorax* for the African species *T. megalops* [Figure 1e]; both names were used as subgenera until Bolton [24] synonymized them with *Leptothorax*. Similarly, Menozzi [25] created the subgenus *Myrmammophilus* to accommodate the Mediterranean *T. finzii* [Figure 1f] because the reproductives lacked a discoidal cell in their forewing, a feature that, in the light of the present study, appears to be plastic within *Temnothorax* and the LGG. This species is not particularly morphologically divergent when the diversity of North African species is considered, and appears to bear close affinities to the *laurae* species group, although it was placed in the *recedens*-group by Salata & Borowiec [26].

As the passages above indicate, the taxonomic history of *Temnothorax* is convoluted: senior synonym of no less than thirteen proposed genera and subgenera, the current definition was only arrived at in 2015 [13], when the species of the erstwhile socially parasitic genera *Chalepoxenus* [Figure 4d], *Myrmoxenus* [Figure 4b] and *Protomognathus* [Figure 4a] were synonymized with *Temnothorax* based on molecular evidence (see [27, 28] for an extensive discussion). Bolton [1, 24] did the bulk of the work updating *Temnothorax* to its modern definition, however, by formally designating the names *Antillaemyrmex*, *Croesomyrmex*, *Dichothorax*, *Icothorax*, *Macromischa*, *Myrafant*, and *Myrmammophilus* as junior synonyms of *Leptothorax* and later *Temnothorax*. Moreover, Bolton [24] provided morphological diagnoses to differentiate *Temnothorax*, the LGG, and the morphologically convergent *Nesomyrmex* [1, Figure 2b] based on mouthpart morphology.

Several large-scale species-level taxonomic revisions have been conducted in recent history: Mackay [29] resurrected and revised the North American subgenus *Myrafant* (i.e. all new world *Temnothorax* species excluding *Macromischa*, *Dichothorax* and *Protomognathus*), and Baroni Urbani [18] revised *Macromischa*, which contains most of the Neotropical species. Similar efforts have been made for the Palearctic taxa, but on a considerably finer geographical scale (e.g. [5, 29-39]). This genus appears to be most species-rich in the Palearctic region, where there are currently 250 described species, as opposed to the 131 known from the Americas (including the Neotropics) and seven described from the depauperate Afrotropical fauna [40].

The disproportionate number of species among these biogeographic areas may be the product of several factors, namely the lack of a large-scale systematic synopsis in the Palearctic, where the large number of small-scale regional revisions has likely inflated the number of species due to undetected synonymies, and the relative paucity of collection efforts in Northern and Central Mexico where *Temnothorax* diversity is likely to be very high based on the number of undescribed species from southern Arizona (Stefan Cover, pers. comm.). Additionally, recent collecting initiatives in Central America, the Baja California peninsula, and the Dominican Republic have recovered many new species, which are currently in the process of being formally described (Prebus in prep.). Many of the authors cited above have offered informal species-group descriptions, but a formal systematic synthesis has not yet been attempted for any biogeographical region, much less on a global scale.

### ***Fossil record***

The fossil record for *Temnothorax* includes one species from Dominican Amber (15-20 Ma) [41, 42, but see 43], six from Baltic Amber (38-47 Ma) [44-48], and eight undescribed species from various European late Eocene and late Oligocene amber deposits (23-47 Ma) [49-51].

*Temnothorax praecreolus* de Andrade 1992, from the Dominican amber, is known from a single worker that exhibits several of the features associated with the *Macromischa* syndrome, including an elongate petiole, a broad, campaniform post-petiole, and enlarged mid and hind femora. While somewhat dorso-ventrally compressed, this fossil still possesses a remarkable number of visible characters. I obtained this fossil for inspection from the Naturhistorisches Museum, Basel, Switzerland [Figure 5a]. Mayr [44] described four species of *Macromischa* and one *Leptothorax* species, *L. gracilis* from Baltic amber [Figure 5d]. Wheeler [53] recognized one of Mayr's *Macromischa* species as *Vollenhovia*, and erected a new genus for the remainder of them, *Nothomyrmica*. Wheeler did not explicitly state his reasoning for this transfer, implying that because these species possess only one of the features of the *Macromischa* syndrome, a pedunculate petiole, that this precludes them from placement in any known genus. Wheeler's [53] treatment also introduced four new fossil species of *Leptothorax* from Baltic amber, noting that several of these species bear a close resemblance to *L. acervorum* in general bauplan, but four of the five fossil species have 12-merous antennae, a condition not found in the extant *Leptothorax* s.s.. Bolton [1] transferred all five of the fossil *Leptothorax* species to *Temnothorax*.

More recently, Dlussky & Radchenko [54] dismantled *Nothomyrmica*, transferring *N. petiolata* to *Temnothorax* [Figure 5b], designating a new genus, *Eocenomyrma* [Figure 5c], for *N. rugostriata* and three newly described fossil species, and subsequently synonymized the remainder of *Nothomyrmica* with *Myrmica* [55]. Dlussky & Radchenko [54] state that *Eocenomyrma*, while clearly separable from *Temnothorax* by clypeal structure, is probably a member the tribe Formicoxenini (*sensu* Bolton [1]). This same treatment did not give an explicit reason for transferring *N. petiolata*, only stating that it is 'indistinguishable by all its characteristic features' from *Temnothorax*, without enumerating the characters that lead them to this conclusion. *Temnothorax petiolata* bears long propodeal spines, 12-merous antennae, a metanotal groove, and a pedunculate petiole. These features in combination do indeed suggest that this species cannot be excluded from the crown group of *Temnothorax*, but I am hesitant to make a positive placement due to the lack of information about mandibular dentition and mouthpart morphology. For example, *T. petiolata* also closely resembles extant species of the Indomalayan and Australasian genus *Vombisidris* Bolton [56], which recent molecular work has

shown to be a close relative of [*Temnothorax* + LGG] [13]. *Vombisidris* has unique mandibular morphology, with a large diastema between the preapical mandibular tooth and the basalmost three. I have not yet been able to personally inspect the Baltic Amber fossils of *Temnothorax*, although images of *T. gracilis* and *T. petiolata* are available on AntWeb (<http://www.antweb.org>) [Figure 5b and d]. In a personal communication with Phillip Barden at the American Museum of Natural History, I inspected images of a Baltic Amber worker specimen identified as *Temnothorax* which had 12 antennomeres and a crest on the maxillary stipes, a condition not known from any extant *Temnothorax* or LGG species [Figure 4d]. This casts considerable doubt on whether *Temnothorax* fossils from Baltic Amber have been accurately identified. Consequently, I conservatively treat all Baltic Amber fossils currently classified as *Temnothorax* as stem lineages of the clade [*Temnothorax* + LGG] until the mouthpart morphology of each described fossil species can be inspected.

### ***Taxonomic results***

The constrained analysis of the Sanger sequencing dataset shown in Figure [2] in the main article. *Temnothorax* is composed of seven well-supported major clades in a pectinate series, which display a high degree of biogeographic structure. Each clade generally corresponds to a clade in the unconstrained Sanger dataset analyses Additional File [3], which is noted at the beginning of the description. Support values are given in posterior probability (PP) from the MrBayes analysis, and in bootstraps (BS) from the IQTREE analysis.

#### *andrei-clade*

The exclusively western and southwestern North American *andrei*-clade forms the first group in the pectinate series, sister to all other crown *Temnothorax*. This clade is composed of the *andrei*-, *nitens*-, as well as *T. gallae* and *T. nevadensis* of the *tricarinatus*-group proposed by Mackay [29]. The *tricarinatus*-group is found to be paraphyletic: *T. nevadensis* and *T. gallae* are more closely related to *T. andrei* than they are to *T. tricarinatus*, which is nested within the *sallei*-clade (see below). *T. nitens* is found to be sister to the *andrei*-group, but with low support (PP 1; BS 68).

#### *sallei-clade*

The *sallei*-clade, found in the southern Nearctic, Neotropics and the Greater Antilles, is the next to branch off. This group shows within-clade geographic structure, with the *sallei* and *iris* subclades distributed among the Greater Antilles and, in the case of *T. allardycei*, southern Florida and the Bahamas. These Caribbean species were informally classified by Baroni Urbani [18] as being members of the *Macromischa allardycei*- (*T. allardycei*), *sallei*- (*T. laetus* and *T. sallei*), *splendens*- (*T. splendens*), *iris*- (*T. gundlachi*), and *versicolor*- (*T. poeyi*) species groups. The *sallei*-group appears to be paraphyletic, with members distributed between the *purpuratus*- and *salvini*-clades (see below). *T. mmp11* and *T. cf. striatulus* form a third distinct group, known only from the cloud forests of Meso-America. The latter is, at first glance, indistinguishable from *T. striatulus*, but the comparative length of the petiolar peduncle and appendages neatly separate the two taxa. The fourth subgroup within the *purpuratus*-clade is the remainder of the *tricarinatus*-group proposed in Mackay [29] (*T. carinatus*, *T. neomexicanus*, *T. obliquicanthus*, *T. punctithorax*, *T. cf. rugithorax*, *T. stenotyle*, and *T. tricarinatus*), within which the *striatulus*- and at least one member of the *andersoni*- species groups arose. This group is broadly distributed

throughout the southern Nearctic, with at least two species (*T. striatulus* and *T. mmp08*) in the cloud forests of Meso-America. Following the *purpuratus*-clade, two smaller clades emerge.

#### *rottenbergi-clade*

The first of the smaller clades is the Palearctic *rottenbergi*-clade, composed of members of the nominal species group *sensu* Cagniant & Espadaler [30] (*T. cabrerae*, *T. formosus*, and *T. semiruber*), which are large, typically ground-nesting species distributed throughout the Mediterranean region, including North Africa and the Canary Islands. Two other species with a Mediterranean distribution are found to be affiliated with the *rottenbergi*-group: *T. cf. flavispinus* of the arboreal *flavispinus*-group (*sensu* Cagniant & Espadaler [30]) and the ground-nesting *T. cristinae*, which has been proposed to be closely related to *T. exilis* [57].

#### *rugatulus-clade*

The second of the smaller clades is the *rugatulus*-clade, which contains a mixture of Palearctic and broadly distributed North American species. The arboreal species *T. clypeatus* and *T. corticalis* (*clypeatus*- and *corticalis*-groups *sensu* Radchenko [32]), which are both rarely collected but apparently widely distributed in the western Palearctic, are contained within this group. The nominal species of this clade is commonly encountered nesting under stones in montane western North America (*longispinosus* group *sensu* Mackay [29]), sister to an undescribed species collected from a mesic mountaintop habitat on the southern Baja California peninsula. *T. schaumii* (*schaumii*-group Mackay [29]) and *T. smithi* (*silvestrii*-group Mackay [29]) are somewhat rarely collected arboreal species from eastern North America. The *longispinosus*- and *schaumii*-groups are polyphyletic as originally described: *T. rugatulus* and *T. schaumii* are more closely related to each other than to the other members of the original groups, all of which are monophyletic and nested within the Palearctic-clade (see below).

#### *salvini-clade*

The Neotropical and Caribbean *salvini*-clade is the next group to emerge, followed by the *obturator* and Palearctic-clades. The members of the *salvini*-clade are morphologically and behaviorally diverse, including many arboreal species from Meso-America and the enigmatic ground-nesting eastern North American species *T. pergandei* (formerly subgenus *Dichothorax*). Species in this clade have been informally classified as members of the *hispidus*-group *sensu* Mackay [29] (*T. sp. nr. peninsularis*), the arboreal mainland Meso-American ‘Macromischa’ species of the *sallei*- species group (*T. aztecus*, *T. salvini* and *T. fuscatus*), and the primarily ground-nesting Meso-American and Caribbean *pulchellus*-group *sensu* Baroni Urbani [18] (*T. augusti*, *T. subditivus*, *T. terricola* and *T. torrei*).

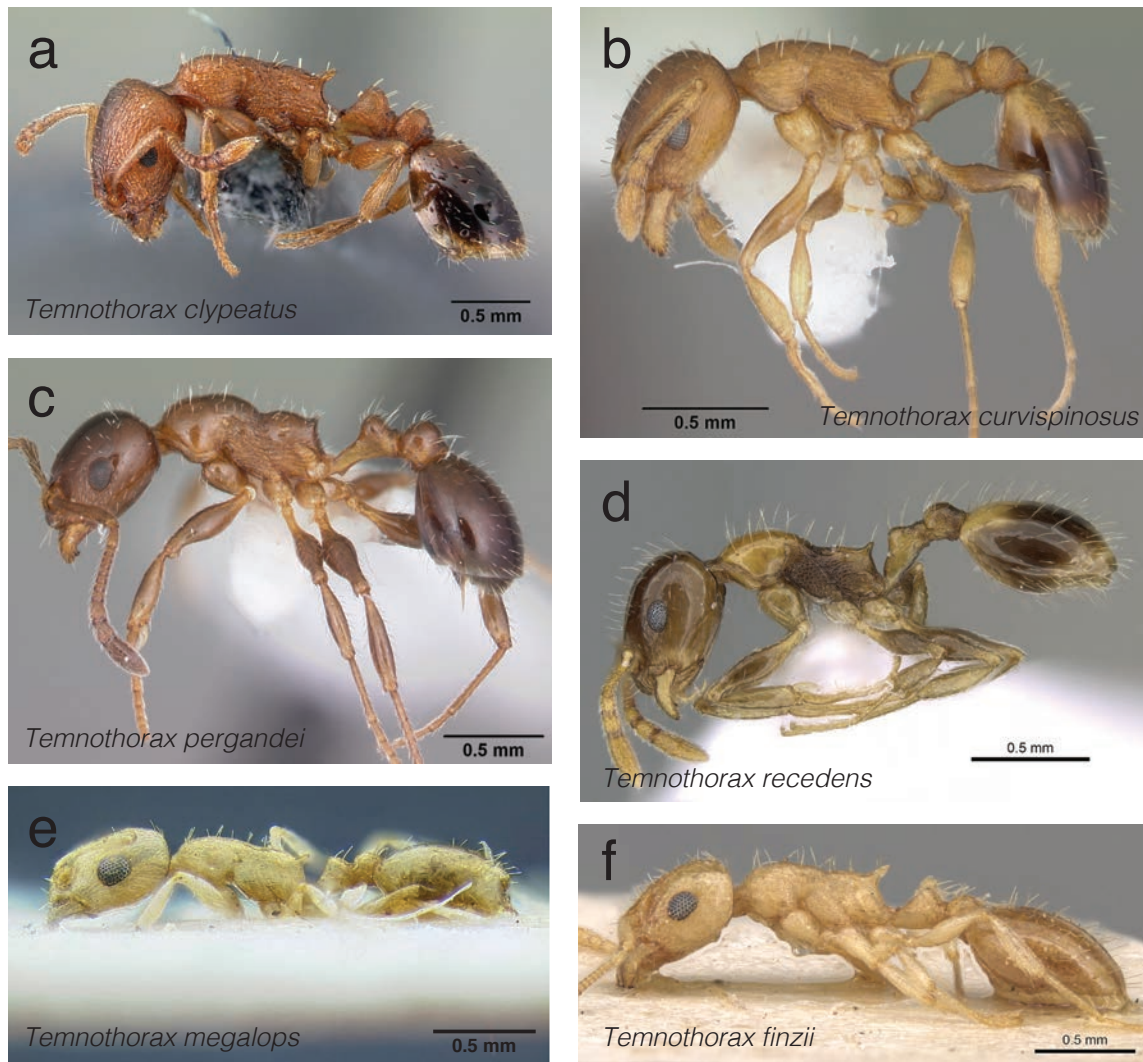
#### *obturator-clade*

The *obturator*-clade is a small group encompassing the *obturator*- and *emmae*- groups *sensu* Mackay [29], and the *creolus*-group *sensu* Baroni Urbani [18]. All known species from this group are arboreal, nesting in dead twigs or galls on live trees. Additional undescribed species were recently collected from Puerto Rico and Meso-American cloud forest. The *obturator*- and *salvini*-clades are both broadly distributed, having ranges like that of the *purpuratus*-clade, with members in the southern Nearctic and the Neotropics, including the Greater Antilles.

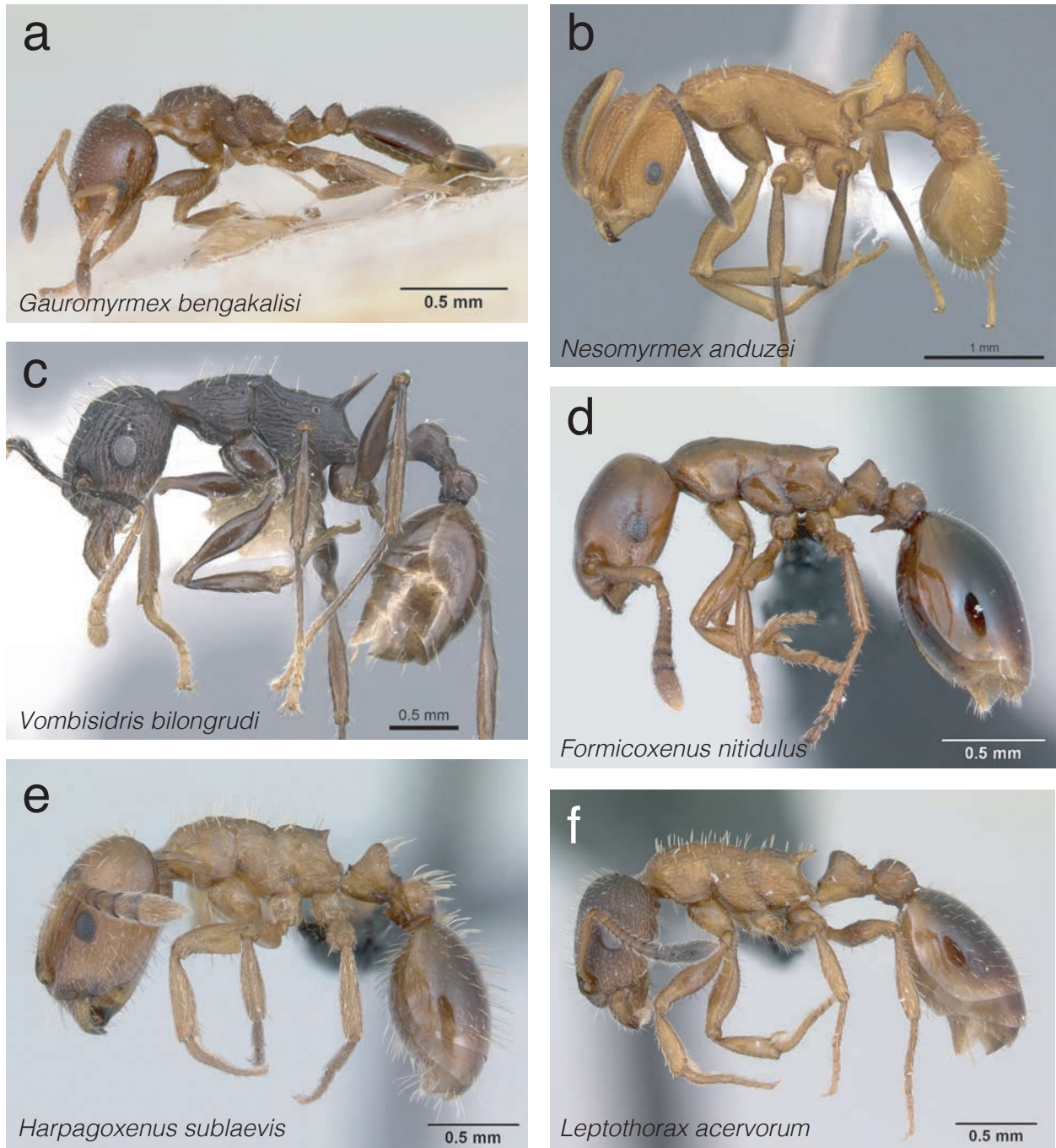
#### *Palearctic-clade*

The Palearctic-clade, as implied by the moniker, is mostly confined to the Palearctic biogeographic realm, with two notable exceptions: the dulotic eastern Nearctic species *T. americanus* (formerly *Protomognathus*) and a group that contains many of its hosts (the remainder of the polyphyletic *longispinosus* and *schaumii*-groups, which will be referred to as the *longispinosus*-group below) are nested within this clade; additionally, the Afrotropical *T. mpala* is nested within the southern Palearctic *laurae*- species group (*sensu* Prebus [40]). The socially parasitic *corsicus*- (formerly genus *Myrmoxenus*) and *muellerianus*- (formerly genus *Chalepoxenus*) species groups are nested within the Palearctic-clade as well, and are sister to [*T. americanus* + *longispinosus*-group] and the *laurae*- species group, respectively. The Palearctic clade is composed of four subclades and is generally, with a few exceptions, ground nesting.

- (I) The first subgroup contains the central Palearctic *T. oxianus* (*bulgaricus*-group *sensu* Radchenko [31]), the *corsicus*-group, *T. americanus* and the *longispinosus*-group.
- (II) A group consisting of eastern and southern Palearctic species, containing *T. nassanowi* (*nassanowi*-group Radchenko [33]), *T. spinosior*, which is a member of the *congruus*-group proposed by Radchenko [34], *T. kubira* and *T. cf. arimensis* from Japan, and *T. rothneyi* from the Himalyas. Two undescribed species are inferred to be members of this subgroup as well: *T. eg01*, collected from southeastern China and northern Vietnam, and *T. ch01*, from southeastern China.
- (III) The third subgroup of the Palearctic-clade comprises species broadly distributed across the Palearctic, including *T. nylanderii* (*nylanderii*-group *sensu* Radchenko [33]), the arboreal *T. congruus* (*congruus*-group *sensu* Radchenko [34]), two members of the *tuberum*-group *sensu* Cagniant & Espadaler [30] (*T. nigriceps* and *T. unifasciatus*), *T. interruptus* of the *unifasciatus*-group *sensu* Bernard [5], *T. exilis* of the *exilis*-group, and *T. turcicus incertae sedis*. The *tuberum*- and *exilis*-groups as most recently described appear to be polyphyletic, with members distributed between this subclade and the Palearctic IV subclade.
- (IV) The last subgroup of the Palearctic-clade contains many species with a circum-Mediterranean, southern Palearctic, and Afrotropical distribution, including members of the apparently polyphyletic *exilis*-group (*T. gredosi* and *T. ibericus*), the *nigritus*-group *sensu* Cagniant & Espadaler [30] (*T. cagnianti*), the *recedens*-group *sensu* Cagniant & Espadaler [30] (*T. recedens*), the polyphyletic *tuberum*-group (*T. algericus trabutii*), the *angustulus*-group *sensu* Cagniant & Espadaler [30] (*T. angustulus*), the *flavicornis*-group *sensu* Bernard [5] (*T. flavicornis*), the former genus *Chalepoxenus*, and members of the *laurae*-group *sensu* Prebus [40] (*T. blascoi* and *T. mpala*).

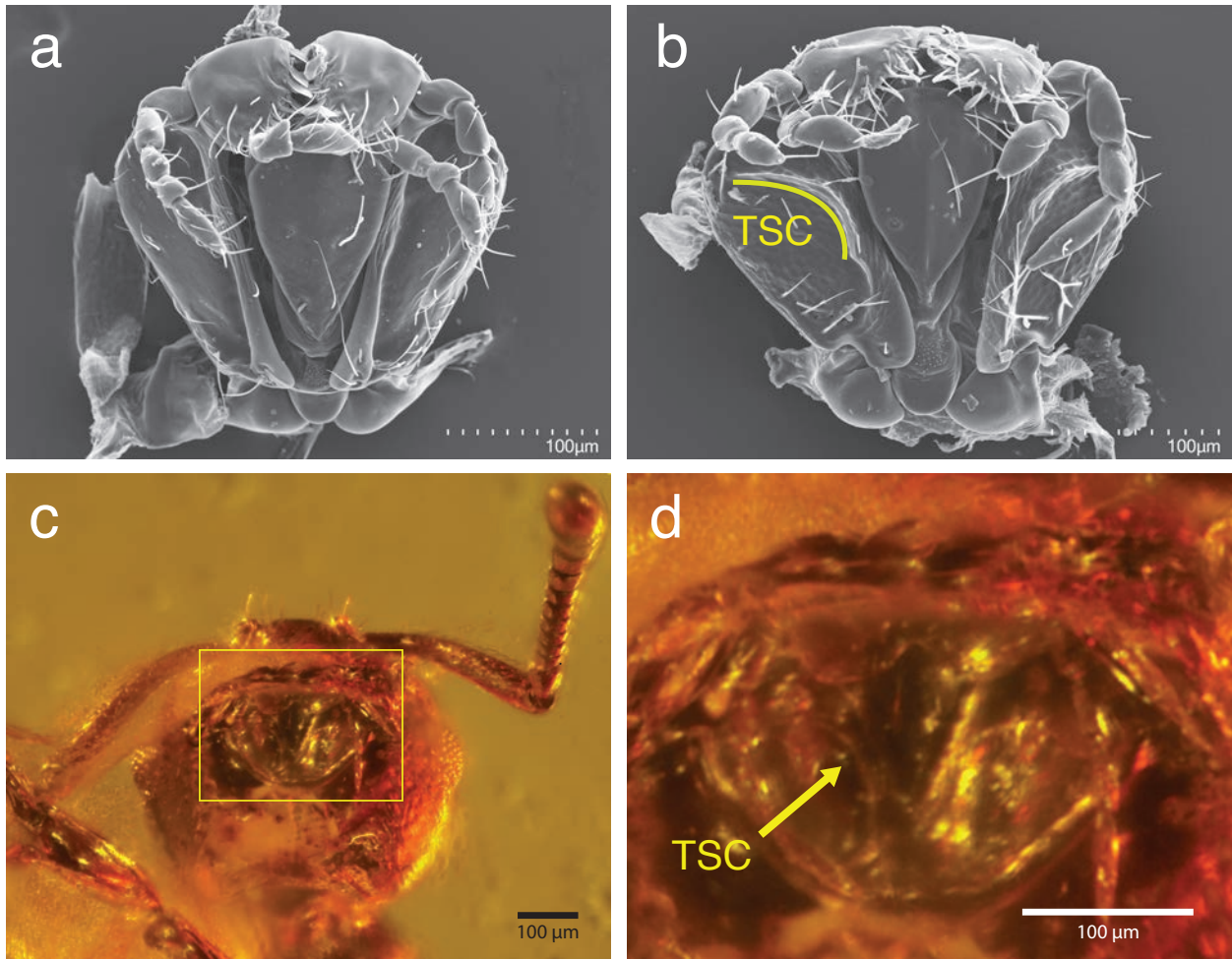


**Figure 1.** Exemplars of the former subgenera of *Temnothorax* discussed in the text. All images can be found on antweb.org (<http://www.antweb.org>) (a) *Temnothorax clypeatus* Mayr 1853, worker, profile view, CASENT0179903, photo: Erin Prado. (b) *Temnothorax curvispinosus* Mayr 1866, worker, profile view, CASENT0104040, photo: April Nobile. (c) *Temnothorax pergandei* Emery 1895, worker, profile view, CASENT0104016, photo: April Nobile. (d) *Temnothorax recedens* Nylander 1856, worker, profile view, CASENT0281561, photo: Estella Ortega. (e) *Temnothorax megalops* Hamann & Klemm 1967, worker, profile view, CASENT0712601, photo: Matthew Prebus. (f) *Temnothorax finzii* Menozzi 1925, worker, profile view, CASENT0904766, photo: Will Ericson.

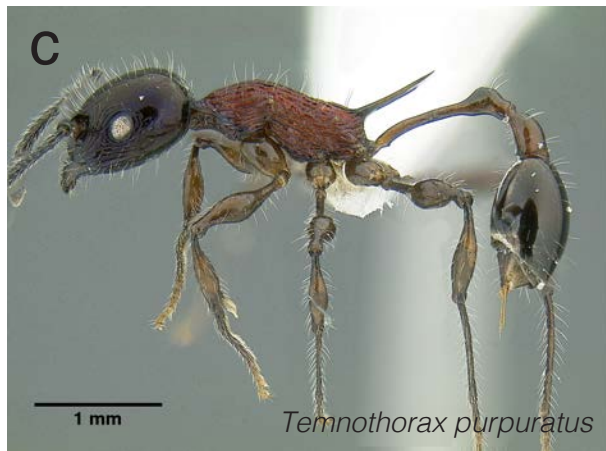


**Figure 2.** Exemplars of some of the outgroups used in the study, and *Nesomyrmex*, a genus that is morphologically convergent with *Temnothorax*. All images can be found on antweb.org (a) *Gauromyrmex bengakalisi* Menozzi 1933, worker, profile view, CASENT0172783, photo: April Nobile. (b) *Nesomyrmex anduzei* Weber 1943, worker, profile view, CASENT0914984, photo: Zach Lieberman. (c) *Vombisidris bilongrudi* Taylor 1989, worker, profile view, CASENT0901985, photo: Will Ericson. (d) *Formicoxenus nitidulus* Nylander 1846, worker, profile view, CASENT0173159, photo: April Nobile. (e) *Harpagoxenus sublaevis* Nylander 1849, worker, profile view, CASENT0178772, photo: April Nobile. (f) *Leptothorax acervorum* Fabricius 1793, worker, profile view, CASENT0173138, photo: April Nobile.

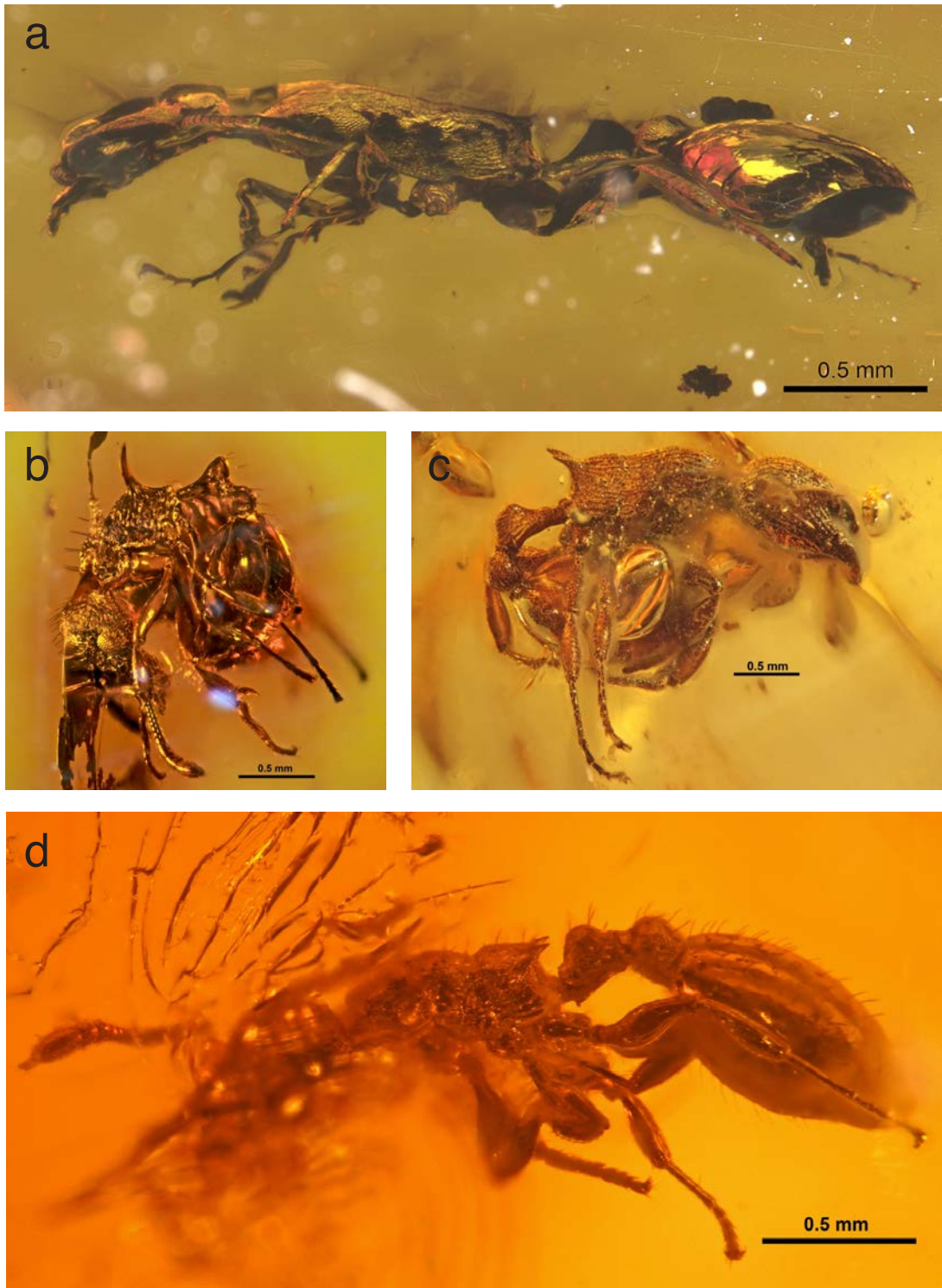




**Figure 3.** Mouthparts of core formicoxenines *sensu* Ward et al. (2016), illustrating absence (a) and presence (b-d) of the transverse crest of the maxillary stipes (TSC). (a, b) scanning electron micrographs of mouthpart dissections: (a) *Temnothorax cf. flavispinus*, photo: Matthew Prebus (b) *Formicoxenus diversipilosus*, photo: Matthew Prebus. (c, d) light microscope images showing the head capsule venter of a Baltic amber specimen AMNH Baltic 40129-511, photo: Phillip Barden: (d) is a magnification of the area highlighted in yellow in (c).



**Figure 4.** Exemplars of *Temnothorax* social parasites and the former subgenus *Macromischa*. All images can be found on antweb.org (a) *T. americanus* Emery 1895, worker, profile view, CASENT0104553, photo: April Nobile. (b) *T. ravouxi* André 1896, worker, profile view, CASENT017641, photo: April Nobile. (c) *T. purpuratus* Roger 1863, worker, profile view, CASENT0732599, photo: Matthew Prebus. (d) *T. muellerianus* Finzi 1922, worker, profile view, CASENT0270722, photo: Shannon Hartman.



**Figure 5.** Images of fossil core formicoxenines *sensu* Ward et al. (2016). All images are found on antweb.org (a) *Temnothorax praecreolus* de Andrade 1992, worker, profile view, CASENT0915320, photo: Zach Lieberman. (b) *T. petiolata* Mayr 1868. Profile view, MBIGK001, photo: Vincent Perrichot. (c) *Eocenomyrma elegantula* Dlussky & Radchenko 2006, profile view, GPIH-BE4505, photo: Vincent Perrichot. (d) *T. gracilis* Mayr 1868, profile view, GZG-BST04661, photo: Vincent Perrichot.

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