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**A PHYLOGENETIC HYPOTHESIS FOR THE *TRACHYMYRMEX* SPECIES GROUPS,  
AND THE TRANSITION FROM FUNGUS-GROWING TO LEAF-CUTTING IN THE  
ATTINI**

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**Abstract**

As part of a series of papers dealing with an ongoing revision of *Trachymyrmex* (Myrmicinae: Attini) ant species, we study here the relationships of its species. The main objective of the series is to reevaluate the taxonomic status of the described taxa and to describe new species. A revision of the *Opulentus* group is the first published paper in the series, followed by a revision of the *Iheringi* group. At the beginning of our work, we accepted the species groups as proposed by authors, but now decided to test this proposal, to avoid major rearrangements in the future. Our parsimony analysis using 50 characters from external worker morphology and 32 taxa (*Mycetarotes parallelus* as outgroup) indicates congruence with unpublished notions of relationships within *Trachymyrmex*, but some important differences as well, and may help to understand the transition from fungus-growing to leaf-cutting in Attini ants.

**Key words:** Hymenoptera, Formicidae, Attini, *Trachymyrmex*, fungus-growing ants, leaf-cutting ants, Neotropics, phylogeny

## Introduction

Reliance on fungi as the dominant food source evolved only once in ants, in the fungus-growing Attini (Myrmicinae), that includes species necessarily dependent on the cultivation of a mutualistic fungus to feed adults and larvae (Mueller *et al.*, 2001). Members of the genus *Megalomyrmex* of the *silvestrii* group, by contrast, are facultative social parasites of attines, consuming fungus grown by their hosts or the hosts' larvae when living inside attine nests (Brandão, 2003).

Until recently, the monophyly of the Attini was supported by their exclusive primary ability to cultivate a basidiomycete fungus in nearly axenic gardens (Mayhé-Nunes, 1995) that, depending on the ant species, are manured with a variety of fresh and dead plant matter, and by three morphological characters of the prepupae (Schultz & Meier, 1995): short, narrow labrum; fleshy, nearly straight, subconical mandibles; and presence of leg vestiges as open slits in the integument. Brandão & Mayhé Nunes (2001) described the first adult female autapomorphy for the tribe: the median clypeal seta in all attines originates from the anteclypeus or at the meeting of the anteclypeus and the clypeal border itself. Thirteen genera with over 210 species are now included in Attini. The Sri Lankan genus *Proatta*, suggested by Moffett (1987) to be possibly an attine, is now placed in Stenammini (Bolton, 2003).

The origin of the attine ant-fungus mutualism has received much attention (see for instance North *et al.*, 1997). Mueller (2002) suggested that the Attini arose at the beginning of the Tertiary, some 45-65 Mya, bracketing the estimate of 50 Mya by Wilson (1971). Mueller *et al.* (2001) summarized the hypotheses for the successive evolution of behavioral elements of attine fungiculture in two main models: 1. the traditional "consumption first" model, in which initial stage fungi growing accidentally in ant nests became part of their diet; subsequently the ants evolved the ability to promote fungal growth, and finally the ants evolved a mechanism to transmit fungi between parent and offspring nests, or 2. the alternative "transmission first" model, where in the initial stage the ants did not feed on fungi, but instead were used by the fungi for dispersion; subsequently the ants incorporate the fungus in their diet, and finally evolved the ability to cultivate and transmit the symbiotic fungus. The exact nature of the ancestral attine-fungus association is difficult to infer, given the long time elapsed and intensive taxon diversification since the origin of the Attini (Mueller, 2002). Also there exist no extant facultative attine-fungus stages of ant-fungus interaction, suggesting transience and instability of non-obligate ant fungus associations and possibly a rapid evolutionary transition from a hunter-gatherer ancestral ant to the derived fungicultural ant.

Most attine fungal cultivars belong to *Leucoagaricus* and *Leucocoprinus* (Agaricales: Basidiomycota: Lepiotaceae: Leucocoprinae), except for some *Apterostigma* ants that secondarily switched to Tricholomataceae (although basal *Apterostigma* cultivate lepiotaceous fungi), and for a subgroup of the *rimosus* species group of *Cyphomyrmex* that secondarily culture their leucocoprineous fungus as yeasts and not as mycelia. Leucocoprineous fungi are common litter decomposers in the moist Neotropics, and have been probably domesticated by the ants repeatedly and independently from free-living populations. Attine fungi are also transferred laterally across nests of even different genera (Adams *et al.*, 2000a; Adams *et al.*, 2000b). Moreover, attine ants combat outbreaks of the potentially devastating microfungal parasite *Escovopsis* using antimicrobial pesticides produced by *Streptomyces* bacteria they grow on specialized regions of their own bodies (Currie *et al.*, 2003). *Escovopsis* phylogeny provides evidence for lateral transfer of the parasite between closely related species. Currie *et al.* (2003) concluded that *Escovopsis* parasitism of the ant-microbe symbiosis likely originated with a parasite of free-living leucocoprineous fungi that invaded the symbiosis along with the domestication of these free-living fungi.

The Attini genera were informally divided by Kusnezov (1964) into two groups: the Paleoattini (also called "apterostigmoid" clade by Schultz & Meier, 1995), encompassing

*Apterostigma*, *Myrmicocrypta*, and *Mycocepurus* (but see Schultz & Meier, 1995 for apparent paraphyly of *Myrmicocrypta* in relation to these lineages), and the Neoattini (correspondingly, the "attoid" clade), for all other genera, including *Sericomyrmex*, *Trachymyrmex* and the polymorphic leaf-cutter ants *Acromyrmex* and *Atta*.

Lower attines and *Trachymyrmex* and *Sericomyrmex* in the higher attines culture their fungus with the type of substrate for which free-living leucocoprineous fungi are specialized: plant detritus, flower parts, seeds and arthropod feces. *Atta* and *Acromyrmex* manure their gardens with fresh leaf material. The fungi cultivated by the lower attines are polyphyletic, probably because of the common horizontal transmission and repeated domestication from free living cultivars. Chapela *et al.* (1994) showed that the fungus cultivated by higher attines is monophyletic, probably because it is vertically transferred, hence clonally, to new colonies. Also, mature cultivars of the higher attines (although literature is not clear on cultivars manured by basal *Trachymyrmex* and *Sericomyrmex* species) produce conspicuous nodules called staphylae, that are clusters of vacuolized hyphal-tip swellings rich in glycogen (gongylidia) (Hölldobler & Wilson, 1990). Stradling and Powell (1986) demonstrated that the fungal symbiont of *Atta* and *Acromyrmex* grows faster than those of *Sericomyrmex* and *Trachymyrmex* and is therefore able to support larger colonies.

*Trachymyrmex* is a key taxon to the understanding of the phylogenetic relationships among the derived Attini. Contrary to the lower attine colonies that number only a few dozen workers, some *Trachymyrmex* and *Sericomyrmex* species live in colonies that can have up to a few thousand workers; in the higher attines *Acromyrmex* colony sizes may reach several hundred thousands or even 5-10 million workers in *Atta*. Also, a sound phylogenetic framework for *Trachymyrmex* may help us to understand the most important transition in attine evolution once their ancestral forms learned how to cultivate fungus, that is, the acquisition of a further specialization of leaf-cutter ants to manure a derived monophyletic staphylae producing cultivar, called Group 1 fungus group by Chapela *et al.* (1994).

*Trachymyrmex* is probably the most derived monomorphic attine ant, with some species showing weak polymorphism (in the sense commonly applied to social insects). *Trachymyrmex* species are widespread in the Neotropical region, with some forms exclusively found in the Nearctic (Kusnezov, 1964; Chapela *et al.*, 1994; Schultz & Meier, 1995; Mayhé-Nunes & Jaffé, 1998). Although abundant in most habitats, most *Trachymyrmex* species are small and inconspicuous foragers on the floor of forests, harvesting opportunistically a wide variety of items used to cultivate symbiotic fungus, including insect frass, plant debris and occasionally freshly cut parts of plants (but see Waller, 1989 for *T. turrifex*). *Trachymyrmex diversus* actively cuts and carries fresh leaves, at least in the laboratory (Schultz & Meier, 1995). Most *Trachymyrmex* workers feign death when disturbed, with the known exception of *T. diversus* (Schultz & Meier, 1995), and are, therefore, easily overlooked on the litter; yet their small to medium sized nests built in the soil are usually conspicuous, because their entrance is normally adorned by tower- or crater-shaped earth mounds (Bhatkar, 1974; Tschinkel & Bhatkar, 1974). *Trachymyrmex* species can collect and disperse seeds, as is the case with different Brazilian Atlantic Forest species that gather seeds of the common tree *Miconia cabucu* (Medeiros & Morretes, 1994). The territorial and nocturnal foragers of *T. urichi* employ chemical communication, laying a trail pheromone released from the poison gland whose concentration regulates the number of workers recruited; nests have a specific odor used in nestmate recognition; and workers secrete a defensive secretion that induces nestmates to attack any object with it, even their gyne (Jaffé & Villegas, 1985). *Trachymyrmex turrifex* individuals show little or no fidelity to food type or foraging routes (Waller, 1989). According to Gallardo (1916), *T. pruinosus* used pieces of orange fruit as substrate to fungus garden in an artificial nest maintained in laboratory. Weber (1945) also has observed workers of *T. cornetzi* gathering orange rind and carrying it to the nest in the field. Torres *et al.* (1999) observed *T. jamaicensis* utilizing a variety of fruits as the substrate for their fungal gardens. *T. holmgreni* collects fresh

leaves of the grass *Paspalum ancyclocarpum* to such a degree that it has been considered an agricultural pest (Gonçalves, 1975). Unidentified species of *Trachymyrmex*, and *T. fuscus*, have also been considered agricultural pests in *Eucalyptus* plantations in Brazil, due to their relatively large populations and relatively high density of nests in these agroecosystems (Oliveira *et al.*, 1998). More recently, however, Araujo *et al.* (2002) have observed that workers of *T. fuscus* transport mainly dry vegetation to the nest. Beshers & Traniello (1994) studied the adaptiveness of worker demography in two populations of *T. septentrionalis*. Army ants are important predators of *Trachymyrmex* brood, and probably also of most attine ant species (LaPolla *et al.*, 2002).

Weber (1972) reported that *Trachymyrmex zeteki* accepted and ate (in laboratory conditions) pieces of fungus taken from nests of other higher attine species, but these ants did not eat the *T. zeteki* fungus. *Sericomyrmex amabilis* ate the fungus of most of these ants, but only two *Atta* species tested ate the fungus of *S. amabilis*. This may indicate that *Acromyrmex* and *Atta* ants and cultivars share characters still more derived in relation to other higher attines and their fungi. Hinkle *et al.* (1994) suggest moreover that cultivars of *Sericomyrmex* and *Trachymyrmex* are different from those cultivated by *Atta* and *Acromyrmex*, and that they are monophyletic. Based on nuclear DNA sequence data, *Escovopsis* parasites living in *Trachymyrmex* nests also represent a specific lineage (Currie *et al.* 2003).

The series of revisionary studies we are publishing aim to reevaluate the taxonomic status of described infraspecies of *Trachymyrmex* and to describe new species. Existing revisionary studies are partial and outdated. When we started the series of revisionary works on *Trachymyrmex*, we decided to accept the proposal of species groups in drafts we found in the Walter W. Kempf personal library, reserving a new classification, based on cladistic approach, to the conclusion the series, when we would be ideally more acquainted with the limits of the taxa within *Trachymyrmex*. However, as our studies proceeded, it became clear that testing Kempf's proposal is now necessary to avoid large taxonomic rearrangements in the future.

Prior to the present work, relationship proposals for *Trachymyrmex* species were mostly based on opinions of describers, and had not been subjected to any formal analysis. However, most authors recognize roughly the same species groups (judging from the comments that follow the species descriptions): Opulentus, Iheringi, Urichi and Septentrionalis groups, with some dispute over the Cornetzi and Farinosus groups, either as independent groups or subgroups of, respectively, Septentrionalis and Urichi groups. Figure 1 summarizes Kempf's ideas on the relationships among *Trachymyrmex* species groups as interpreted from his drafts. Interestingly, if this proposal proves to be right, the most derived clade includes species in Urichi and Septentrionalis groups, that also show the most conspicuous differences in nestmate gyne and workers, the largest size range among worker nestmates, and larger colonies in relation to other *Trachymyrmex*.

The most dramatic evolutionary step in Attini history, after the origin of the fungus-ant symbiosis, was the acquisition of staphylae rich monophyletic cultivars by the higher Attini (the "attoid" clade), in particular *Atta* and *Acromyrmex* that collect only fresh vegetation as a novel form of fungal substrate. Converting vegetation to substrate requires a series of operations and specializations. Vegetation is cut by workers with head width 1.6 mm or greater (other tasks, such as defense, involve workers of even greater size), while the care of the fungus requires very small workers; intervening steps in gardening are conducted by workers of graded intermediate size. We know very little about division of labor in the lower or basal higher attines. *Atta* and *Acromyrmex*, however, show one of the most complicated caste systems found in ants (Hölldobler & Wilson, 1990), although their division of labor is based on an enormous and continuous size variation and alloethism, instead of allometry. Beshers & Traniello (1994) have shown how variation in size can evolve in the context of life history strategies and how this variation may serve as a preadaptation for division of labor.

On the ant side, this major evolutionary change seems to have put the higher Attini on a course resulting in much larger colonies, by the increase in size differences between gynes and daughter workers, and hence increase in ovariole counts, allowing rapid colony growth, and by the increase in size variation among worker nestmates, able to execute all activities involved in fungus cultivation. *Atta* species represent an extreme in this tendency because their single queen per nest is huge in relation to the workers (even the extremely large majors), with ovaries composed of hundreds of ovarioles that individually produce relatively more eggs than do ovarioles of lower attine gynes (Weber, 1972), resulting in mature colonies that can attain millions of individuals. The question is when in attine evolution these characters started to change. There are no *Atta* or *Acromyrmex* species showing incipient stages in worker size variation, while *Trachymyrmex* species commonly show a variation in these features. A study on the evolution of polymorphism in basal “attoids” within a phylogenetic framework may be therefore an interesting way to understand the origin of the world’s most powerful herbivores.

Wilson (1987) studied the then known Cretaceous ant species, concluding that females appear to have differentiated as queen and worker castes belonging to the same colonial species, instead of winged and wingless solitary females belonging to different species. He based his study on the fact that gasters of workers of modern and extinct Miocene ant species are smaller relative to the rest of the body than is the case for modern wingless solitary wasps. The wingless Cretaceous formicoids conform to the proportion of ant workers rather than to those of wasps, and hence are reasonably interpreted to have lived in colonies.

Inspired by Wilson’s (1987) work, we studied size differences between reproductive and sterile females and size ranges among workers of different *Trachymyrmex* species and species groups, superimposed on a new phylogenetic hypothesis based on a parsimony analysis of worker external morphological characters.

### SUMMARY OF TAXONOMIC HISTORY

*Trachymyrmex* was proposed by Forel (1893) as a subgenus of *Atta* Fabricius, when he described and compared *T. urichi* with two species originally described in *Atta* (*Acromyrmex*) and *Oecodoma*, respectively *T. saussurei* (Forel) and *T. tardigrada* (Buckley); the latter now is considered unrecognizable and *incertae sedis* in *Atta* (Bolton, 1995). Two other species now included in *Trachymyrmex*, *T. jheringi* (Emery) and *T. jamaicensis* (André), were also described as *Atta* (*Acromyrmex*). After 1893, the subgenus *Atta* (*Trachymyrmex*) was adopted almost universally, but surprisingly Forel (1914a, b) described two *Atta* species in *Acromyrmex* (*Trachymyrmex*) and Bruch (1921) proposed *Acromyrmex* (*T.*) *tucumanus cordovanus*, ignoring the raising of *Trachymyrmex* to generic rank by Wheeler (1916). In the same year, Santschi (1916) described *T. fiebrigi*, considering *Trachymyrmex* as a subgenus of *Cyphomyrmex*, following Emery’s (1913) ideas. Mann (1922) proposed *Myrmicocrypta cucumis*, now a junior synonym of *T. bugnioni*, and *T. opulentus* in *Sericomyrmex*; Weber (1937) also described a species in the latter genus, later recognized as *Trachymyrmex*. From 1930 on, a relatively large number of taxa were described in *Trachymyrmex*, making it today the second richest genus in the Attini; exceeded only by *Acromyrmex*. The striking morphological resemblance between some *Trachymyrmex* and other attines can explain, however, descriptions of species now accepted in *Trachymyrmex* in different taxa, supporting also the impression shared by several myrmecologists that *Trachymyrmex* may not be a natural group (see comments by Schultz & Meier, 1995 and references). Notwithstanding, reproductive and sterile females of all *Trachymyrmex* share the presence of microtuberculated mesosomal projections, an exclusive and hence apomorphic trait of the genus (Mayhé-Nunes & Brandão, 2002)—a character already noticed by Forel when he choose the name (from Greek, *trachis*, coarse), although overlooked in the recent literature (but see Gallardo, 1916 comments on *T. pruinosus* Emery).

## MATERIALS AND METHODS

We measured head width in frontal view and the largest diameter of gasters in dorsal view of workers and dealated gynes of all *Trachymyrmex* species for which we found gynes and workers on the same pin in the collection of the Museu de Zoologia, Universidade de São Paulo, that is collected at the same time, hence probably from the same colony, and probably representing gynes not founding new colonies at the time of their collection, but instead from mature colonies. In so doing, we could also study size distributions among workers of different *Trachymyrmex* species.

We found 41 pairs of *Trachymyrmex* gynes and workers on the same pin. We list below the species from which we took measurements and to which group we consider them to belong:

Septentrionalis group: *T. septentrionalis* (6 pairs), *T. diversus* (one pair), *T. smithi* (4 pairs), and *T. arizonensis* (2 pairs);

Cornetzi (as subgroup of Septentrionalis): *T. cornetzi* (one pair), *T. bugnioni* (one pair), and *T. levis* (one pair);

Iheringi group: *T. holmgreni* (one pair), and *T. kempfi* (7 pairs);

Opulentus group: *T. relictus* (5 pairs), and *T. opulentus* (one pair);

Urichi group (includes the Farinosus subgroup): *T. urichi* (one pair), *T. farinosus* (one pair), *T. ruthae* (one pair), *T. oetkeri* (one pair), and *T. turrifex* (8 pairs).

The measurements were submitted to regression analysis by caste, by species, and by species groups.

## PHYLOGENETIC ANALYSIS

The character matrix (Table 2, Appendix) for 50 external morphological worker characters compiled from 32 attine species, including *Mycetarotes parallelus* (Emery) as the outgroup, was subjected to unweighted parsimony analysis using the computer programs NONA (Goloboff, 1993) and WinClada version 1.00.08 (Nixon, 2002). Characters were treated as unordered. The data matrix was generated with the NEXUS Data Editor version 0.5.0 (Page, 2001). We searched for trees using the following NONA parameters: hold 1000 (maximum trees to keep), mult\*N 100 (number of replications), hold/ 5 (starting trees per rep), with mult\*max\* (multiple TBR+TBR) as search strategy; the strict consensus was calculated for the obtained trees.

**Table 1.** List of worker morphological characters and character coding for the genus *Trachymyrmex*.

1. Pilosity of the gaster and femora: (0) only hairs, without fine pubescence; (1) dense, long dark hairs mixed with an extremely low, fine and abundant light pubescence.
2. Discal area of mandibles: (0) smooth; (1) finely striated; (2) coarsely striated.
3. Lateral borders of frontal lobes: (0) semicircular; (1) sub-triangular; (2) triangular.
4. Accessory lobes or teeth at the base of frontal lobes: (0) absent; (1) present.
5. Anterior border of frontal lobes: (0) straight; (1) convex; (2) concave.
6. Posterior border of frontal lobes: (0) straight; (1) convex; (2) concave.
7. Lateral borders of frontal lobes: (0) smooth; (1) crenulated.
8. Frontal carina: (0) not reaching the preoccipital (posterior) margin of head; (1) reaching the preoccipital margin.
9. Frontal and preocular carina: (0) ending separated; (1) ending together.
10. Preocular carina: (0) strongly curved; (1) vertical.
11. Preocular carina: (0) unique; (1) double.

12. Scrobe: (0) absent; (1) present.
13. Scrobe: (0) opened; (1) closed.
14. Apical tubercle of the antennal scrobes: (0) absent; (1) present.
15. Basal lobes of the antennal scapes: (0) absent; (1) present.
16. Basal lobes of antennal scapes: (0) not transversely broadened; (1) transversely broadened pointing mesad (2) transversely broadened pointing to both sides.
17. Anterior surface of antennal scapes: (0) smooth; (1) weakly microtuberculate; (2) notably microtuberculate.
18. Length of antennal scapes: (0) surpassing weakly the posterolateral corners of head; (1) surpassing notably the posterolateral corners; (2) not surpassing the posterolateral corners.
19. Preoccipital (posterior) margin of head: (0) distinctly notched; (1) almost straight.
20. Preoccipital spines: (0) larger than the tubercles of the preoccipital lobes; (1) nearly the length of the tubercles of the preoccipital lobes; (2) absent or vestigial.
21. Supraocular projections: (0) absent or vestigial; (1) present.
22. Supraocular projections: (0) tooth or spine-like; (1) microtuberculate swelling.
23. Dorsal projections of mesosoma: (0) smooth spine- or tooth-like; (1) microscopically multituberculate swelling, tooth- or spine-like.
24. Median pronotal projections: (0) present; (1) absent or vestigial.
25. Number of median pronotal projections: (0) two; (1) one.
26. Lateral pronotal projections: (0) spine-like; (1) tooth-like; (2) microscopically multituberculate or multidentate swelling.
27. Lateral pronotal projections in frontal view: (0) directed upwards and outwards; (1) laterally directed.
28. Inferior pronotal corner: (0) unarmed, obtusely angulate or rounded; (1) armed with a tooth or spine.
29. Size of projection on the inferior pronotal corner: (0) weakly projected; (1) notably projected.
30. Shape of projection on the inferior pronotal corner: (0) triangular; (1) spine-like; (2) rounded.
31. Anterior mesonotal projections: (0) nearly of the length of the pronotal lateral ones; (1) notably shorter than pronotal lateral ones; (2) notably longer than pronotal lateral ones.
32. Apex of projection on the inferior pronotal corner: (0) blunt; (1) acute.
33. Anterior mesonotal projections: (0) spine-like; (1) microscopically multituberculate or multidentate swelling; (2) semicircular multidentate ridge from above.
34. Shape of median pronotal projections: (0) spine-like; (1) ridge or multituberculate swelling.
35. Posterior mesonotal projections: (0) present; (1) absent or vestigial.
36. Shape of posterior mesonotal projections: (0) spine-like; (1) ridge or multituberculate tumulus.
37. Pilosity of mesopleura: (0) vestigial or absent; (1) present.
38. Projection on the inferior margin of mesopleura: (0) absent; (1) present.
39. Projection on the superior margin of mesopleura: (0) absent; (1) present.
40. Shape of projection on the superior margin of mesopleura: (0) small tooth or triangular spine; (1) large lobe.
41. Projections at the meeting of basal and declivous faces of propodeum: (0) as long as the larger projections of promesonotum; (1) shorter than promesonotal projections; (2) longer than promesonotal projections.
42. Projections at the meeting of basal and declivous faces of propodeum: (0) as long as the projections of basal face; (1) longer than the projections of basal face; (2) tooth-like, nearly of the length of pronotal lateral ones.
43. Petiolar node: (0) unarmed; (1) with a pair of teeth; (2) with two pairs of teeth.
44. Petiolar node from above: (0) longer than broad; (1) as long as broad.

45. Postpetiole from above: (0) distinctly transverse; (1) as long as broad.
46. Posterior border of postpetiole: (0) straight; (1) superficially excised; (2) notably excised.
47. Hairs of the first gastric tergite: (0) strongly curved, hook-like; (1) in two shapes: straight or weakly curved medially and hook-like; (2) straight.
48. Tubercles on the basal third of the first gastric tergite: (0) clearly in four longitudinal rows; (1) more or less in four longitudinal rows; (2) randomly distributed; (3) inconspicuous, but with notable ridge on each side.
49. Large welt on each side of lateral posterior region of the first gastric tergite: (0) absent; (1) present.
50. First gastric sternite: (0) without hook-like hairs; (1) with hook-like hairs; (2) in two shapes: straight or weakly curved medially and hook-like.

## RESULTS

The tree presented in Fig. 3 is the strict consensus (L 323; CI 21; RI 38) of the 68 equally parsimonious trees (L 259; CI 27; RI 54) resulting from the analysis, showing 15 unresolved terminal branches, but keeping the Iheringi and “Cornetzi” species groups, and the clades *jamaicensis-zeteki* and *arizonensis-nogalensis*. One of the 68 trees is presented in Fig. 2, as it shows the species groups in *Trachymyrmex* proposed by Kempf in his manuscripts (Fig. 1), with the following differences:

1. Urichi group: In our analysis it includes *T. phaleratus*, that Kempf included in the Septentrionalis species group. By contrast, *T. oetkeri* appeared in our analysis out of this group, where it has been traditionally included. Two character states are at the base of the Urichi clade: 8.1. frontal carinae reaching the preoccipital margin and 17.1. anterior scape surface weakly microtuberculate. However, 8.1 reverts to 8.0 in *T. ruthae* and in the clade *T. agudensis* – *T. isthmicus*; in *T. jamaicensis* character 17 appears in state 2. In this particular tree, these characters are thus not synapomorphic for the group and generate homoplasies within the group.

2. Septentrionalis group: The major problem here is the lack of sound characters at the base of the largest clade in the *T. septentrionalis* – *T. levis* branch (with nine species) and the fact that *T. mandibularis* and *T. saussurei* appeared outside the species group. As said before, in our analysis *T. phaleratus* is nested within the Urichi group.

3. We based our analysis on worker characters only, because we did not have enough information on sexuals and/or immatures. However, Schultz & Meier (1995) studied larval characters and found an apparent apomorphy shared by members of the Cornetzi group they studied, *T. bugnioni* and *T. cornetzi*, supporting this clade. Only larvae of these species are entirely devoid of hairs on the ventral region of the body. These two species are also the only ones among *Trachymyrmex* larvae Schultz & Meier (1995) studied having only two subantennal (genal) setae.

4. *Trachymyrmex relictus* does not belong to the Opulentus species group clade in the consensus, but in 60 of the 68 trees (88%) it is nested within the species group we assigned.

## DISCUSSION

As far as informed by external characters of workers, *Trachymyrmex* seems to be a monophyletic taxon, including species that share unique microtuberculate mesosomal projections.

We found only four characters that can clearly differentiate monophyletic groups within *Trachymyrmex*. The Opulentus group females present pilosity interspaced with fine decumbent pubescence, more clearly visible at the hind femora (Mayhé-Nunes & Brandão, 2002). Female specimens in the Iheringi group (Mayhé-Nunes & Brandão, 2005) are easily recognized by the presence of a lobe at the base of the antennal scapes.



We were not able to find synapomorphies to support the two larger species groups, Urichi and Septentrionalis, and have also doubts of an Arizonensis subgroup, but we did not include all species of these groups in our analysis. Apparently, females in the Urichi group have the posterolateral corners of the head angulate, while in the Septentrionalis group these corners are rounded. In each of these two large groups, we identified two possible subgroups: Farinosus with exclusive and very conspicuous posterolateral gastral protuberances and Cornetzi with low promesonotal projections. However, our study supports a Cornetzi group, as it consistently showed a clade formed by *T. cornetzi*, *T. bugnioni*, *T. ingardae* and *T. levis*. Also, all trees show a clade formed by *T. arizonensis* and *T. nogalensis*, traditionally assigned, however, to the Septentrionalis group. The same is true for the clade *T. jamaicensis* and *T. zeteki*, assigned by most authors to the Urichi group.

When we superimpose the data on size differences between gynes and workers of *Trachymyrmex* on our preferred tree (Fig. 4), members of the Septentrionalis group show the greatest differences. *Trachymyrmex* species reported as agricultural pests also belong to this species group, possibly meaning that mated queens can produce more workers in a shorter time and that their relatively larger gasters support more and/or more productive ovarioles.

Members of the Septentrionalis and Urichi groups show also the largest size range among workers. Our proposal suggests the Septentrionalis group as the basal *Trachymyrmex* group. However, our morphological analysis indicates a derived position for species in this group. In any topology, Urichi and Septentrionalis groups never came up together.

Analysis of measurements taken from pairs of nestmate gynes and workers of different *Trachymyrmex* species indicates that worker and gynes appear clearly differentiated, with very little overlap. Although the differences among species, within groups or even between species (workers and gynes taken separately) are not statistically significant, our results suggest secondary departures from the strict monomorphic state of basal *Trachymyrmex* and lower attines, and moreover, that the increase in size differences between worker and gynes and the increase in size range among workers occurred independently in the main *Trachymyrmex* clades.

The two major groups of *Trachymyrmex* species, Urichi and Septentrionalis, are mostly distributed in southern and central-North America, respectively. Of the 12 extant species that seem to belong to the Septentrionalis group, six are endemic to the Nearctic region (Mayh -Nunes, 1995); the others are widespread in northern South America, above parallel 10 S. The Dominican amber fossil *T. primaevus* seems to belong to this group.

The majority of the species of the Urichi group are also found in northern South America, but two of them occur in Central America (*T. isthmicus* and *T. zeteki*) and other two are found between the parallels 10 -25 S (*T. agudensis* and *T. fuscus*); there is also an endemic Nearctic species, *T. turrifex*. However, *T. jamaicensis*, a species widely distributed in the Caribbean, also occurs in Florida. The Opulentus group has three species widespread in northern South America, with a unique species (*T. opulentus*) found in Central America, and another (*T. dichrous*) that seems to be a typical inhabitant of the vast savannas of Central Brazil. Contrary to other groups, Iheringi is restricted to the southern Neotropical region, although some species are widespread in South America (as *T. holmgreni* and *T. kempfi*), the distribution of the group does not cross the parallel 10 S.

The topology of the species groups cladogram is partially congruent with a pattern explained by vicariant events of speciation. Particularly, by a first split in Nearctic and Neotropical clades, probably due to repeated breaks between North and South America during the Cenozoic Era, until the definitive formation of the Isthmus of Panama (3-5 Mya). The close proximity among the clades *T. arizonensis* - *T. nogalensis* and *T. cornetzi* - *T. levis* (see also the consensus in Fig. 3) can indicate shared ancestral lineages from the north of South America that migrated to Central America, with some of them later established in the Nearctic region. Another example of probable vicariance is the clade *T. jamaicensis* - *T. zeteki*. In spite of our insufficient knowledge on the geographic distribution of *T. zeteki* (known only from type-locality, Panama),

it possibly shared an ancestor with *T. jamaicensis*, that in the past was able to cross the passage between Yucatan and Cuba. On the other hand, the limited distribution of the Iheringi group is sufficient to postulate that its component species shared an ancestor that lived in the southern Neotropical region. In some cladograms *T. papulatus* is the nearest species to the clade *T. pruinosus* - *T. tucumanus*, although it does not belong to the Iheringi group because it lacks lobated antennal scapes; it is found only in southern South America (Argentina).

Baroni Urbani (1980) said that some questions could be solved with a reasonable phylogenetic proposal for *Trachymyrmex*, and we can, hopefully start to answer them now: The Miocene-Oligocene Dominican amber fossil *T. primaevus* does not seem to be the sister species of recent Antillean *Trachymyrmex*, so we may assume that the Antilles were colonized more than once by *Trachymyrmex*. *T. primaevus* belongs to a primarily Nearctic clade, but other Septentrionalis group species occur in the Caribbean islands, strongly suggesting multiple arrivals of *Trachymyrmex* in the islands.

Our studies indicate independent origins of polymorphism and rapid colony growth in the higher attines, or “attoids”, and may help to devise the evolutionary steps and their sequence in the attine evolution.

### CONCLUSIONS

Our phylogenetic analysis of *Trachymyrmex* is congruent in many ways with relationships proposed informally by other authors, especially ideas presented in Walter W. Kempf's unpublished drafts. Contrary to some opinions, however, *Trachymyrmex* is accepted as monophyletic, composed of six recognizable species groups. Size differences between nestmate gynes and workers and size range among nestmate workers of different *Trachymyrmex* species depart from monomorphism independently in the two main *Trachymyrmex* clades, suggesting at least two origins for rapid colony growth, increased polymorphism, and large colony populations in the genus.

### ACKNOWLEDGMENTS

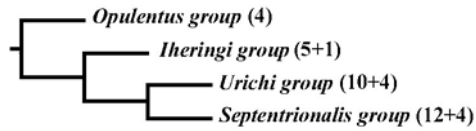
It is a pleasure and an honor for us to participate in this homage to Edward Wilson. Ed has been a continuous source of inspiration for all of us, and instrumental in bringing myrmecology to the scientific center stage. We heartily thank the organizers of the book for the invitation. Rodrigo M. Feitosa helped with measurements, Rogerio Rosa da Silva with the statistics, and Mirian D. Marques and Alexandre P. Aguiar with the text.

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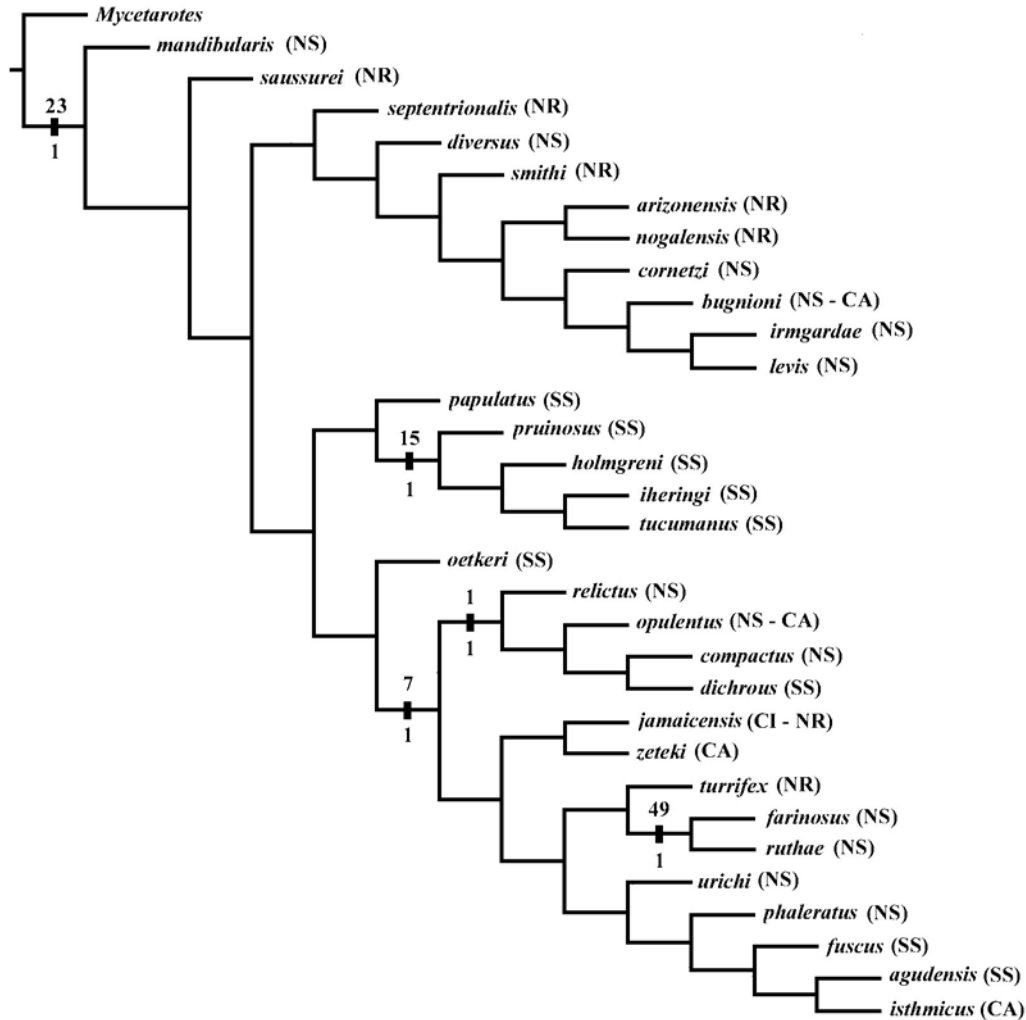
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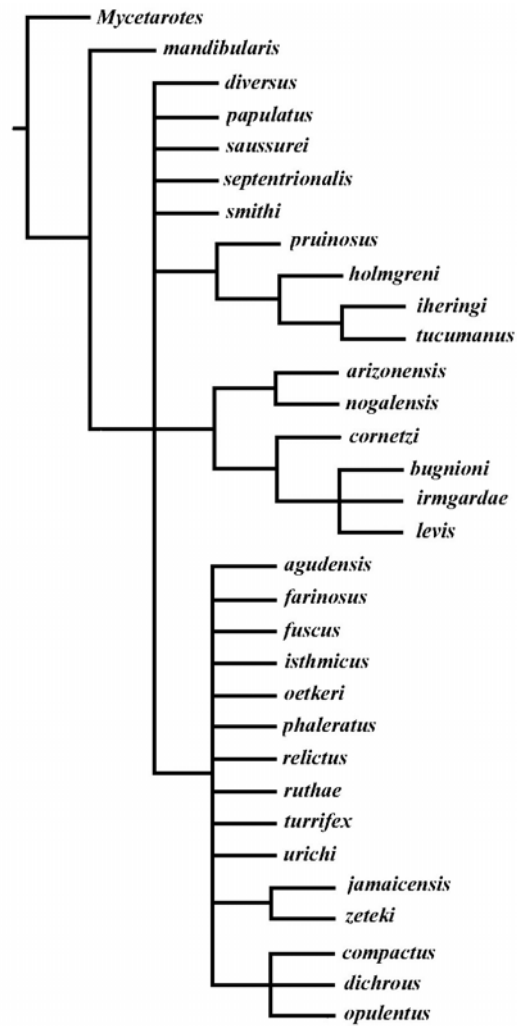
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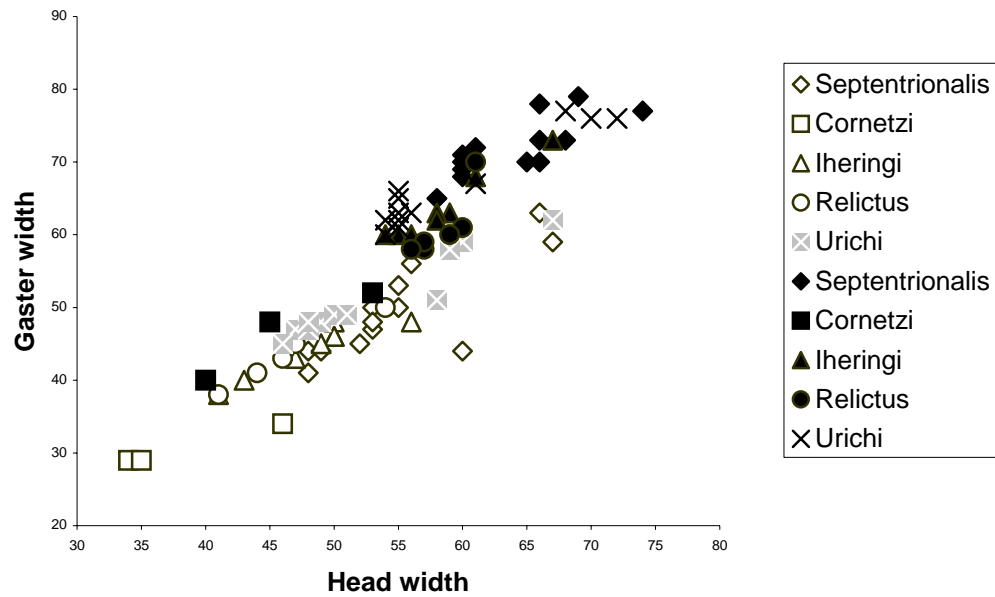
**Figure 1.** Sketch of Kempf's ideas on the relationships among main species groups of *Trachymyrmex* Forel. Numbers between parentheses represent respectively described and undescribed species.



**Figure 2.** One of the 68 equally parsimonious trees for the data matrix (L 259; CI 27; RI 54). Numbers in branches correspond to synapomorphies: characters above and state below, respectively (see list of characters in table 1). CA, Central America; CI, Caribbean islands; NR, Nearctic region; NS, northern part of South America (above parallel 10°S); SS, southern part of South America (below parallel 10°S).



**Figure 3.** Strict consensus cladogram for *Trachymyrmex* species relationships obtained from the 68 equally parsimonious trees, using the data matrix presented in Table 2 in the appendix. L 323; CI 21; RI 38.



**Figure 4.** Head and gaster widths of nestmate workers (open symbols) and dealated gynes (filled symbols) of several *Trachymyrmex* species groups (see Material and Methods for explanation). Measurements were not transformed into mm.

## APPENDIX

**Table 2.** Data matrix of thirty-one taxa of *Trachymyrmex* (outgroup *Mycetarotes parallelus*) and fifty morphological characters of workers.

											1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5		
<i>Mycetarotes</i>	0	1	0	0	0	0	0	1	0	0	0	0	-	1	0	-	0	0	0	0	0	-	0	0	0		
<i>T. agudensis</i>	0	0	2	0	0	0	1	0	1	1	1	1	0	1	0	-	1	0	0	0	1	1	1	0	1		
<i>T. arizonensis</i>	0	2	1	0	2	2	0	0	0	0	0	0	-	0	0	-	0	1	1	1	0	-	1	1	0		
<i>T. bugnioni</i>	0	2	0	0	2	0	0	0	0	1	0	1	0	0	0	-	0	0	0	1	0	-	1	0	0		
<i>T. compactus</i>	1	0	0	0	1	1	1	0	1	1	0	1	0	1	0	-	0	0	0	2	1	1	1	1	-		
<i>T. cornetzi</i>	0	0	1	0	0	0	0	0	0	1	0	0	-	0	0	-	0	0	1	1	0	-	1	0	0		
<i>T. dichrous</i>	1	0	1	0	0	0	0	0	0	1	0	0	-	0	0	-	0	0	0	2	1	1	1	1	-		
<i>T. diversus</i>	0	1	1	0	0	0	0	0	0	0	0	0	-	0	0	-	0	1	1	0	1	1	1	0	0		
<i>T. farinosus</i>	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0	-	1	2	0	0	1	0	1	0	1		
<i>T. fuscus</i>	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0	-	1	0	0	0	1	0	1	0	1		
<i>T. holmgreni</i>	0	1	1	0	0	2	0	0	0	1	0	1	0	0	1	1	2	1	0	0	1	1	1	0	0		
<i>T. iheringi</i>	0	1	2	0	2	0	0	0	0	1	0	1	0	0	1	2	2	1	1	0	1	1	1	0	1		
<i>T. irmgardae</i>	0	2	1	0	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	2	0	-	1	1	-		
<i>T. isthmicus</i>	0	1	0	1	1	1	1	0	0	1	0	1	0	1	0	-	0	0	0	0	1	0	1	0	0		
<i>T. jamaicensis</i>	0	0	0	0	2	1	1	1	0	1	0	1	0	1	0	-	2	1	0	0	1	0	1	0	1		
<i>T. levis</i>	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	-	0	0	1	1	0	-	1	0	0		
<i>T. mandibularis</i>	0	2	2	0	0	0	0	0	0	0	0	0	-	0	0	-	0	1	0	0	0	-	1	0	0		
<i>T. nogalensis</i>	0	2	2	0	2	0	0	0	0	0	0	0	-	0	0	-	0	1	1	1	0	-	1	1	-		
<i>T. oetkeri</i>	0	0	0	0	1	1	0	0	0	1	0	1	0	1	0	-	0	1	1	0	1	0	1	0	1		
<i>T. opulentus</i>	1	2	0	0	0	1	1	0	1	1	0	1	0	1	0	-	0	0	0	2	1	0	1	0	1		
<i>T. papulatus</i>	0	0	1	0	0	2	0	0	1	1	0	1	0	0	0	-	1	1	0	1	1	0	1	0	1		
<i>T. phaleratus</i>	0	1	0	0	1	1	1	1	1	1	0	1	1	0	0	-	1	0	1	0	1	1	1	0	0		
<i>T. pruinus</i>	0	0	2	0	0	0	0	0	0	1	0	1	0	0	1	0	2	1	0	0	1	0	1	0	0		
<i>T. relictus</i>	1	1	0	0	1	1	1	0	0	1	0	1	0	1	0	-	0	0	1	2	1	0	1	1	-		
<i>T. ruthae</i>	0	0	0	1	1	1	1	0	1	1	0	1	0	1	0	-	1	2	0	0	1	0	1	0	0		
<i>T. saussurei</i>	0	2	2	0	0	0	0	0	0	0	0	0	-	0	0	-	0	1	1	1	1	0	1	0	0		
<i>T. septentrionalis</i>	0	2	1	0	0	0	0	0	0	0	0	0	0	-	0	0	-	0	1	1	0	1	0	1	0		
<i>T. smithi</i>	0	2	0	0	0	0	0	0	0	0	0	0	-	0	0	-	0	0	1	1	0	-	1	0	0		
<i>T. tucumanus</i>	0	0	1	0	2	2	0	0	0	1	0	1	0	0	1	2	1	1	0	0	1	1	1	0	0		
<i>T. turrifex</i>	0	0	0	0	1	1	1	1	1	1	0	1	1	1	0	-	1	2	1	0	1	0	1	0	1		
<i>T. urichi</i>	0	0	0	0	1	1	1	1	1	1	0	1	1	1	0	-	1	1	1	0	1	0	1	0	1		
<i>T. zeteki</i>	0	0	0	1	1	1	1	1	0	1	0	1	0	1	0	-	1	2	0	0	1	0	1	0	1		



**Table 2** (continued)

	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	5		
	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
<i>Mycetarotes</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-	0	1	1	0	1	1	2	3	0	0				
<i>T. agudensis</i>	0	0	1	1	1	0	0	0	0	1	0	0	0	1	1	1	1	0	0	1	0	1	0	0	1					
<i>T. arizonensis</i>	0	0	1	1	1	0	0	0	0	1	-	0	0	0	-	1	1	2	1	0	0	1	2	0	1					
<i>T. bugnioni</i>	1	1	1	1	1	0	0	1	0	1	-	0	0	0	-	0	0	1	1	1	0	0	2	0	1					
<i>T. compactus</i>	0	0	0	-	-	1	-	1	1	1	-	1	0	0	-	1	1	0	0	0	2	2	2	0	1					
<i>T. cornetzi</i>	1	1	1	1	1	0	1	1	0	1	-	0	1	0	-	1	1	1	1	1	1	1	0	0	1					
<i>T. dichrous</i>	2	0	0	-	-	2	-	0	0	0	0	1	0	0	-	1	2	0	0	0	2	2	3	0	0					
<i>T. diversus</i>	0	1	1	1	2	1	0	1	0	1	-	0	0	1	0	1	0	1	1	0	1	0	2	0	1					
<i>T. farinosus</i>	0	0	1	1	1	0	1	0	0	0	0	0	0	0	-	0	0	2	1	0	0	1	2	1	1					
<i>T. fuscus</i>	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	2	0	2	0	1	0	1	0	0	1					
<i>T. holmgreni</i>	0	1	1	1	1	0	1	0	1	1	-	0	0	1	0	2	1	1	1	1	0	1	1	0	1					
<i>T. iheringi</i>	0	0	1	1	0	1	0	1	0	1	-	0	0	1	0	0	1	2	1	0	0	1	3	0	1					
<i>T. irmgardae</i>	1	1	1	1	1	1	0	1	1	1	-	0	0	0	-	1	0	1	1	1	0	0	2	0	1					
<i>T. isthmicus</i>	0	0	0	-	-	0	-	0	0	0	0	1	0	0	-	1	1	2	0	1	0	1	0	0	1					
<i>T. jamaicensis</i>	0	0	1	1	1	0	0	0	0	1	-	0	0	0	-	0	0	1	1	1	0	0	1	0	1					
<i>T. levis</i>	1	1	1	0	0	1	0	1	1	1	-	0	0	1	0	1	1	1	1	1	0	0	2	0	1					
<i>T. mandibularis</i>	1	1	1	0	0	2	1	0	0	0	0	0	0	0	-	0	0	2	0	1	0	0	2	0	1					
<i>T. nogalensis</i>	0	0	1	1	1	0	1	0	0	0	1	0	0	0	-	1	1	2	0	0	1	1	2	0	1					
<i>T. oetkeri</i>	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	2	1	0	0	0	2	0	1					
<i>T. opulentus</i>	1	1	1	1	0	2	1	0	0	0	1	1	0	0	-	1	0	0	0	0	0	2	2	0	0					
<i>T. papulatus</i>	0	1	1	1	0	1	1	1	1	1	-	0	0	1	0	0	0	2	1	0	0	1	2	0	1					
<i>T. phaleratus</i>	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	0	0	2	0	1	0	1	1	0	1					
<i>T. pruinus</i>	0	1	1	0	0	1	1	1	0	1	-	1	0	1	0	0	1	2	1	0	0	1	1	0	1					
<i>T. relictus</i>	0	0	1	1	0	1	1	1	0	0	0	0	0	0	-	0	0	2	1	0	0	2	0	0	0					
<i>T. ruthae</i>	0	0	1	1	0	1	1	2	0	1	-	0	0	0	-	0	0	2	0	0	1	2	2	1	2					
<i>T. saussurei</i>	0	0	1	1	1	0	1	0	0	0	0	0	0	1	0	0	0	2	1	1	1	0	2	0	1					
<i>T. septentrionalis</i>	0	0	1	0	0	0	1	0	0	1	-	0	0	1	0	0	0	2	1	0	1	0	2	0	1					
<i>T. smithi</i>	0	1	1	1	0	1	1	1	0	1	-	0	0	1	0	0	0	2	1	0	1	0	3	0	1					
<i>T. tucumanus</i>	0	0	1	1	1	1	0	1	0	1	-	1	0	1	0	0	1	2	1	0	0	1	3	0	1					
<i>T. turrifex</i>	0	0	1	1	0	1	1	1	0	1	-	0	0	0	-	0	0	2	1	0	0	1	2	0	1					
<i>T. urichi</i>	0	1	1	1	0	0	1	0	0	0	0	0	0	1	0	2	0	2	1	0	0	1	0	0	1					
<i>T. zeteki</i>	0	0	1	1	1	0	1	0	0	1	-	0	0	0	-	0	0	2	0	0	0	0	1	0	1					