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Morphology and Foraging Behavior of Oklahoma's Grass-Feeding Termite: *Gnathamitermes tubiformans* (Isoptera: Termitidae)

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ABSTRACT: Grass-feeding termites, *Gnathamitermes* sp., can be considered beneficial in pastureland, where they aerate topsoil, recycle nutrients from grasses and forbs, and excavate and redistribute soil. The primary objective of this report is to illustrate and determine the average physical dimensions of *Gnathamitermes tubiformans* soldiers by measuring key body parts, including left mandible length, as well as discuss observed foraging behavior. *G. tubiformans* soldiers have unique mandibles that can be used for accurate identification. Workers are morphologically similar compared with some other arid-land termite species, thus soldier characteristics are used for identification. The secondary objective is to describe observations of *G. tubiformans* foraging behavior. This report also provides detailed line drawings and a watercolor illustration for aid in identification. Termites were collected near Temple, Cotton County, Oklahoma, and measured with high precision microscopy. To ensure accurate identification, fourteen different soldier body measurements were determined. The ability to identify termites that are potentially beneficial or detrimental to forage grass biomass production may aid efforts to enhance livestock production on pastures.
KEY WORDS: Desert termites, grass forage damage, pasture desertification

Termites are eusocial insects that exhibit a caste system consisting of soldiers, reproductives, and workers. Workers comprise the majority of a termite colony, building mud foraging tunnels and nest workings, as well as searching for cellulose food resources in their environment. Generally, the most common indigenous Oklahoma subterranean termite encountered in grasslands is *Reticulitermes flavipes* (Kollar), who's soldiers measure 5.58 $\pm$ 0.27-mm overall length including mandibles (Brown *et al*., 2005; Shelton *et al*., 2010). This overall length is one characteristic that can be used to separate visibly smaller *Gnathamitermes tubiformans* (Buckley) (Isoptera: Termitidae) soldiers that average 4.89 $\pm$ 0.14-mm overall length including mandibles from *R. flavipes* soldiers. *G. tubiformans* soldiers tend to be larger than their workers, and use their large, heavily sclerotized head and mandibles to guard the colony against invading predators such as ants and beetles. Alates are solely responsible for establishing new colonies and for steady production of brood.

Worldwide, there are 3138 termite species currently described (Harris 1961; Weesner 1965; Engel *et al*., 2009; Krishna *et al*., 2013; American Museum of Natural History 2011). Generally, species are differentiated by unique morphological characteristics as well as feeding preferences and foraging behavior (McDonald *et al*., 2010). For example, drywood termites are structural pests found in dead trees and limbs, and also above-ground, infesting homes and wooden structures in coastal areas of the southern and western United States. In arid, temperate, and tropical climates, subterranean termites live in the soil and build mud foraging tunnels as they search for food resources.

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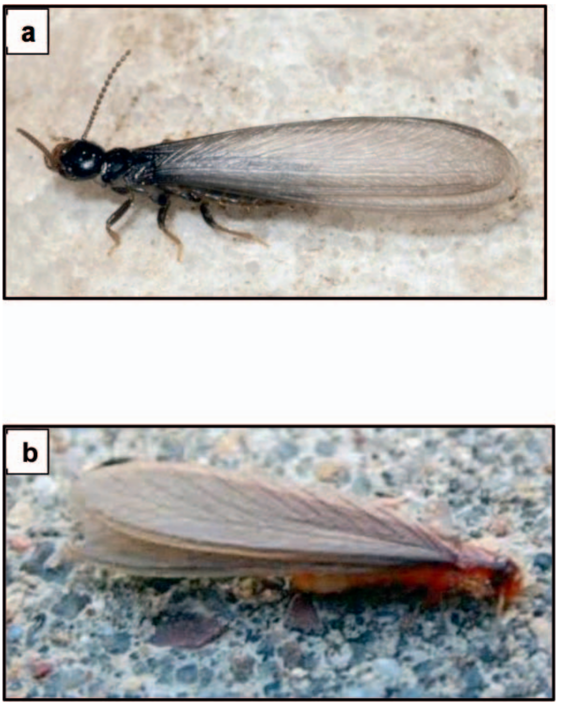

Fig. 1. Primary reproductives. a. The eastern subterranean termite, *Reticulitermes flavipes*, ubiquitous in Oklahoma (Courtesy S. Ellis). b. *Gnathamitermes tubiformans*. Note pale rusty-tan body color and non-transparent brownish-grey wing color (Courtesy McDonald *et al*., 2010). Average overall length including wings: *R. f.* = 10.2 mm; *G. t.* = 14.3 mm. (Antennas not included).

*G. tubiforman*s is an arid-climate, grass-feeding subterranean termite that is not classified as a structural pest. It provides benefits to soil due to tunneling activities that enhance nutrient cycling and soil aeration (Schaefer and Whitford 1981; McDonald *et al*., 2010; Lamoureux and O'Kane 2012). Alate flights by *G. tubiforman*s occur following first summer rainstorms. These flights are timed with precipitation because surrounding pasture areas briefly have increased growth of grasses (Schaefer and Whitford 1981).

Alate bodies are pale rusty-tan in color, in contrast with most native Oklahoma subterranean termite alates that have dark brown-to-black bodies (Fig. 1). This termite is commonly found in the driest areas of Texas, Arizona, and New Mexico (McDonald *et al*., 2010), but is sporadic in southwest Oklahoma arid grassland environments. It prefers to eat red threeawn (*Aristida purpurea* Nutt.), buffalograss (*Bouteloua dactyloides* Nutt.), and blue grama (*Bouteloua gracilis* Willd. ex Kunth.) during spring and summer. During fall it consumes standing dead grass and plant litter (McDonald *et al*., 2010), and also feeds on non-digested grass in livestock manure (Fuchs *et al*., 1990).

For this study, specimens of *G. tubiformans* were collected in southwest Oklahoma (Brown *et al*., 2004) (Fig. 2). *G. tubiformans* resembles *G. perplexus* (Banks), a closely related desert-dwelling termite. Soldiers of these two species are morphologically separated by the unique inward notched tooth of *G. tubiformans* located centrally along the inside margin of each mandible (Fig. 3); soldiers of *G. perplexus* lack this notched tooth.

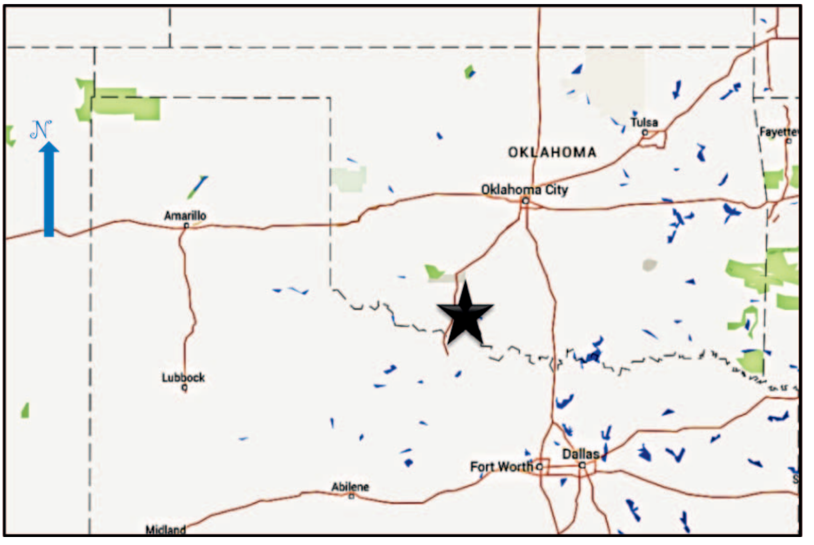

Fig. 2. Star (★) indicates location of the *G. tubiformans* pasture study site near Temple, Cotton County, southwest Oklahoma. (Courtesy Google Maps)

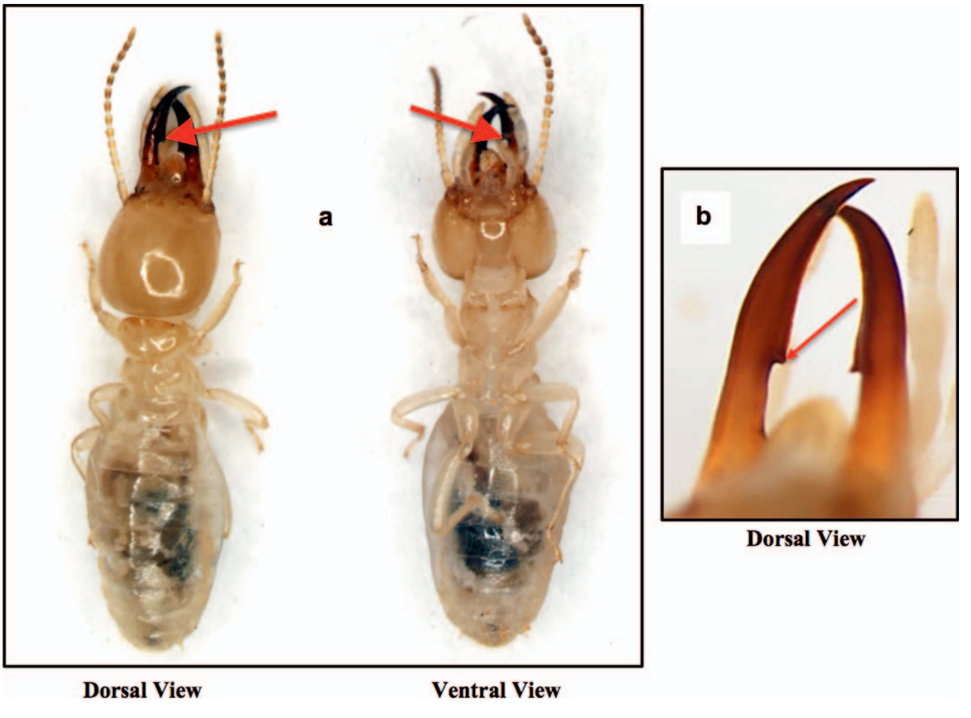

Fig. 3. a. *Gnathamitermes tubiformans* soldier. Average overall body length including mandibles = 4.89 ± 0.14 mm (Antennas not included). b. Soldier mandibles with centrally located, inward-notched tooth.

Fig. 4. *Gnathamitermes tubiformans* constructed mud tubing encasing grass stems.

Termites adapt by creating a stable, cryptic environment that protects them from inclement weather as well as predators. They build structures such as mounds and mud tubes, or protective carton nests made of saliva, soil, cellulose, and frass. These workings stabilize moisture and temperature, which are important factors within termite habitat because termites rapidly dehydrate if exposed to hot, dry conditions. For some *Reticulitermes* sp., Williams (1934) found they preferred a relative humidity (RH) of nearly 100%, and that this RH was normal inside their soil tunnels and cavities. In another observation, Ueckert *et al*. (1976) noted that during warm weather most *G. tubiformans* were located from the soil surface down to 59-cm deep. However, when outside air temperatures dropped to 10°C or less, termites were found as deep as 12-cm below the soil surface. By moving vertically within the soil profile, termites avoid extreme temperature and moisture variations. Although *G. tubiformans* creates foraging tubes and mud plastering on the soil surface, the colony lives below ground.

By modifying their soil environment, termites also improve soil nutrient conditions favorable for plant growth. When termites create mud tunnels and plastering, they transport deeper soil components and nutrients to the surface as observed in the pasture sites used for this study. *G. tubiformans* plasters muddy soil over its soil-surface food sources. Dried mud plastering completely encases grass stems and leaves, thereby allowing foragers to feed within protected areas (Fig. 4). Mud plastering is found covering food resources such as grass, cacti, manure, wooden twigs and small branches, and around bases of wooden structures such as fence posts (Fig. 5). Mud tunnels and plastering appear as a 'spider webbed' network on the soil surface, spreading across rangeland and pastures as termites expand their foraging area (Fig. 6).

G. tubiformans is designated a 'keystone' species due to its impact on soil quality (Whitford 1991). Topsoil is enhanced with essential plant nutrients from disintegrating soil plastering and mud tubes caused by wind and rainfall or other disturbances. These weather factors cause a "patchy mosaic" of nutrient-rich soil areas preferable for plant growth (Smith and Yeaton 1998; Eldridge *et al*., 2001; Masanori and Tohru 2004). When nutrient-rich soil is packed inside woody materials and termite galleries below the soil

Fig. 5. Mud plastering deposited by *G. tubiformans* on a tree limb fence post.

surface or other locations protected from water and wind erosion, it can take several years to fully erode this mud and soil plastering to disperse these nutrient-rich materials into the topsoil.

Fig. 6. Mud tubes and plastering constructed by *G. tubiformans* 'spider-webbed' across denuded pasture surface in southwest Oklahoma.

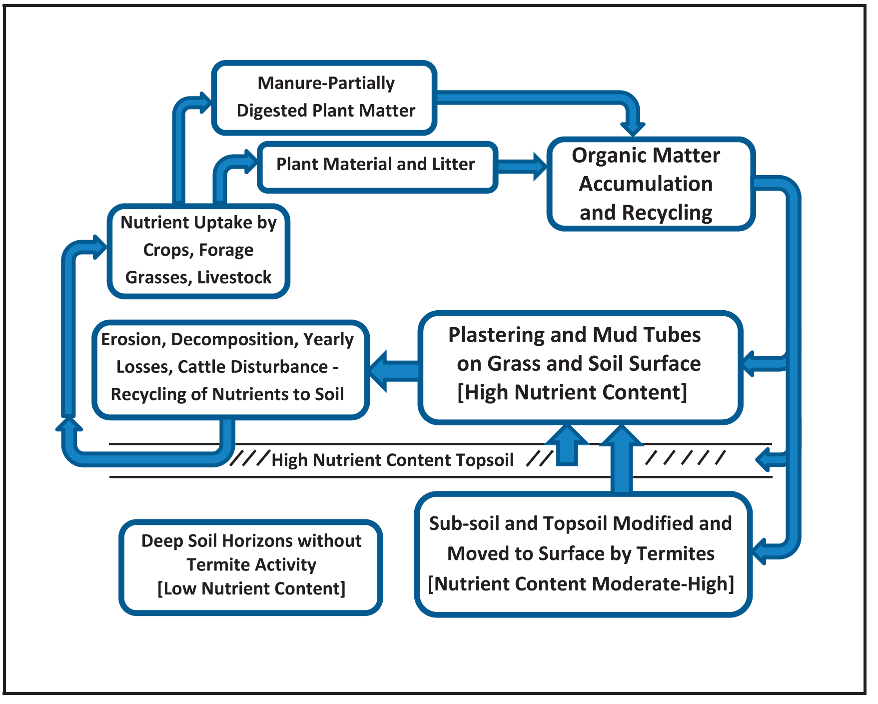

Fig. 7. Soil and nutrient cycling enhanced by termites in a field habitat. (Modified from Coventry *et al*., 1988)

In the southwestern USA Sonoran desert, a closely related termite, *G. perplexus*, exhibits a similar behavior compared with *G. tubiformans* in Oklahoma. *G. perplexus,* and *Heterotermes aureus* (Snyder), another common species of termite in the Sonoran desert, are primary soil movers (Haverty *et al*., 1975). Combined, they move nearly 0.75 metric tons of sub-soil per hectare per year to the surface. It was also shown that *G. perplexus* soil surface plastering and mud tubes disperse relatively quickly compared with *H. aureus* (Nutting *et al*., 1987; Miguelena and Baker 2012). *G. tubiformans* mud tubes and plastering that are exposed on the soil surface are similarly fragile with low density and rapidly break down and disperse in the same manner as *G. perplexus*. When *G. tubiformans* plastering and mud tubes encase grass stems or extend across the soil surface, they are subject to erosion by wind and rain. Due to rapid decomposition of exposed *Gnathamitermes* sp. mud tubes and plastering during periods of monsoon rains in southwest USA deserts, there are concomitant pulses of higher nutrient content in the topsoil (Fig. 7).

Plastering and mud tube disintegration and runoff from *G. perplexus* are rich in clay, and raise soil pH levels in the immediate area. There are also increases in sodium, magnesium, phosphate, and soluble salts added to topsoil (Nutting *et al*., 1987). *G. perplexus* activity in soil produces measurable effects on nitrogen, phosphorus, and sulfur nutrient cycles (Schaefer and Whitford 1981). Similar effects on soil characteristics can be expected to result from *G. tubiformans* tunneling and plastering activities.

In areas with populations of *Gnathamitermes* sp., aeration of the soil due to their foraging activity affects soil-water relationships (Spears *et al*., 1975). Tunneling by *G. tubiformans* is common down to 7-cm-deep below the soil surface. These tunneling activities increase aeration of soil, similar to effects of earthworms (Ueckert *et al*., 1976). A grassland field study where *G. tubiformans* foragers were killed with insecticides resulted in an increase in biomass of forbs, grasses, and plant litter, and also affected the dominance of annuals (Ueckert *et al*., 1976). During droughts, termites can remove enough soil surface litter to influence rainfall infiltration rates (McDonald *et al*., 2010). Spears *et al*. (1975) showed that controlling *G. tubiforman*s resulted in better watershed value with improved moisture retention in the soil. Termite-free soils also exhibited above-average pore space. When termites were eliminated, soil-water relationships of forage plants on a shortgrass prairie improved (Ueckert *et al*., 1976).

Description

Limited work exists on a detailed physical description of *G. tubiforman*s. Full body and body part measurements with detailed illustrations are needed for improved description. Roonwal (1970) compiled a list of standards for consistent measuring of termites, facilitating morphological comparisons for differentiation between termite species. Before this list was created, termite measurements lacked standardization and comparisons between termite species were inconsistent. It was not until Light (1927) set standard measurement parameters that a series of consistent specific body part dimensions appeared in morphological publications (Roonwal 1970). These parameters and those of Brown *et al.* (2005) were used for body measurements in this study.

Detailed illustrations of *G. tubiforman*s are few, and mainly consist of the defining trait of a single notched tooth on the inside margin of each mandible. By illustrating full body morphology and detailed morphological characteristics of *G. tubiformans*, this study provides an improved, more complete description of this species. It is also interesting to observe the foraging behavior of this desert termite because some ranchers consider it a pest of grass forage, but are not aware of its positive effects on soil aeration, improved water infiltration, plant-soil nutrient enhancement and cycling, and increased soil fertility.

Objectives

To improve our knowledge of *G. tubiformans* morphology, the first objective was to accurately and precisely measure and illustrate major body parts. The second objective was to collect and validate the location and identity of *G. tubiformans* in SW Oklahoma, and observe its foraging behavior and characteristics.

Materials and Methods

Termites

Workers and soldiers of *G. tubiformans* were collected on a farm and cattle ranch near the town of Temple, Cotton County, Oklahoma. Using shovels and hand trowels, clumps of soil were extracted intact to a depth of 5- to 10-cm in areas of sandy-loam topsoil where foraging mud tubes and plastering were evident on the pasture surface. Termites were collected from this soil and from within foraging tubes that were constructed on the soil surface and plastered over clumps of grass, as well as under cattle manure and within mud plastering on wooden fence posts (Figs. 4, 5, 6). The majority of mud tubes revealed workers, with the most termites collected along the edge of the pasture where cattle disturbance was reduced (Fig. 8a, b). The greatest numbers of soldiers were collected from within mud plastering on wood fence post bases and immediately adjacent soil. Soldiers and workers were immediately placed in labeled vials containing 100% ethyl alcohol. Alates were not encountered.

Fig. 8. Collection site near Temple, Cotton County, southwest Oklahoma. Arrows indicate denuded areas due to *G. tubiformans* feeding accompanied by cattle grazing. Pasture elevation: 279-m above mean sea level (AMSL). (Courtesy Google Earth images) a. Denuded circular pasture areas (photo elevation 3095-m AMSL; March 2013); b. Denuded pasture with mud plastering (photo elevation 1218-m AMSL; July 2015).

Measurements

Digital images and morphological measurements were acquired using a programmable Olympus SZ61 microscope with an Insight™ Firewire® Spot-2 'mega sample' camera Model #18.2 with $2\times$-2 magnification. Measurements from five soldiers were taken, including pronotal width, head posterior width, length of head with mandibles, length of head without mandibles, length of thorax plus abdomen, total length of termite (tip of mandibles to tip of abdomen), gula at broadest and narrowest points, labral width and length, and length of excised left mandibles. Subsequently, the gular ratio (broadest:narrowest), total

Table 1. *Gnathamitermes tubiformans* soldier standard measurements, mm.

Characteristic*	Soldier** I	II	III	IV	V	Mean ± SEM
Pronotal Width	0.77	0.75	0.75	0.74	0.67	0.74 ± 0.02
Length Thorax + Abd	2.66	2.68	2.51	3.07	2.60	2.70 ± 0.10
Length of Head w/ Mds	2.24	2.33	2.13	2.30	1.86	2.17 ± 0.09
Total Body Length	4.92	5.05	4.65	5.36	4.49	4.89 ± 0.14
Length of Head w/o Mds	1.18	1.23	1.24	1.23	1.01	1.18 ± 0.04
Head Posterior Width	1.16	1.20	1.19	1.26	1.21	1.20 ± 0.02
Labral Width	0.33	0.32	0.26	0.32	0.28	0.30 ± 0.01
Labral Length	0.39	0.41	0.28	0.30	0.21	0.32 ± 0.04
Gula Width Broad, B	0.34	0.37	0.35	0.37	0.38	0.36 ± 0.01
Gula Width Narrow, N	0.19	0.20	0.19	0.20	0.24	0.20 ± 0.01
Gula Ratio [B : N]	1.79	1.85	1.84	1.85	1.58	1.78 ± 0.05
Total Length ÷ Head	2.20	2.17	2.18	2.33	2.41	2.26 ± 0.05
Length of Left Md	1.22	1.15	1.22	1.18	1.20	1.19 ± 0.01
Head Length ÷ Width	1.02	1.03	1.04	0.98	0.83	0.98 ± 0.04

Abd: abdomen; Md(s): mandible(s); w/o: without.
* Based on Brown *et al*., 2005.
** n = 5. Five soldier termites total dissected and measured from three different sites.

body length divided by head length, and the head length without mandibles divided by the head posterior width were calculated. The camera and microscope were calibrated to ensure measurement accuracy (Table 1).

Photographs

High resolution photographs were acquired with a Nikon Digital Sight DS-5M camera attached to an Olympus SZX16 microscope and Epson Perfection V550 photo scanner using a 'photo-stacker' program (Combine ZP®), and edited through Jasc Paint Shop® Pro 7. Dorsal and ventral sides of the head, total body, and mandibles were photographed.

Illustrations

The photos along with a dissecting microscope were used to create detailed line drawings of the right lateral view (Fig. 9), mandibles (Fig. 10), ventral head without mandibles (Fig. 11), and dorsal body view (Fig. 12) of *G. tubiformans* soldiers. Using a calibrated microscope with a modified lens grid-micrometer ensured accurate and proportional drawings. Dimensions of original line drawings were created on 35.6-cm-wide by 43.2-cm-tall paper sheets. This paper size allowed for illustrations that were large enough for minute detail but that also fit on a computer scanner. Initial drafts were outlined in pencil on a paper drawing pad to allow for revision, and then tracing paper was taped over the drawing and outlined with indelible ink. Additional shading was then done by stippling on the tracing paper. The tracing paper was removed and scanned, creating a digital copy that could be cleaned and edited using the photo manipulation program Jasc Paint Shop® Pro 7. For fine details such as hairs and spines, another layer of tracing paper was overlaid onto the original draft and traced over. This sheet was also scanned, then using the photo editor it was layered over the first scan. Creating a colored plate using watercolor was done by first tracing the original pencil sketch onto heavyweight (136-kg cold press) watercolor paper using graphite paper to transfer the image. Several cylindrical brushes of various sizes

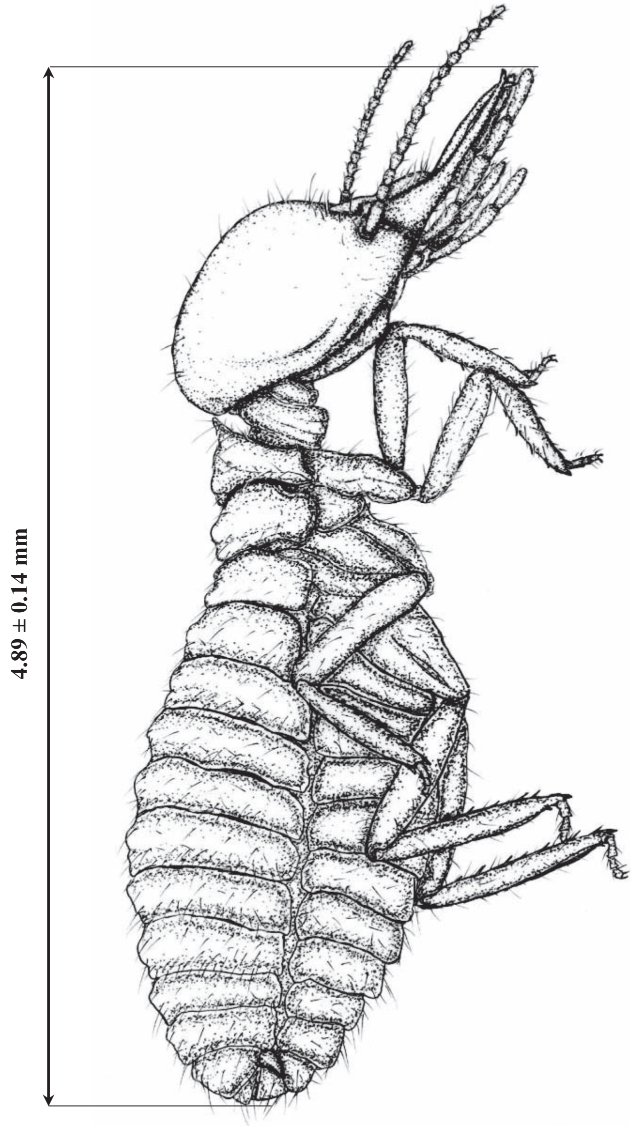

Fig. 9. Right lateral aspect, *G. tubiformans* soldier (11 abdominal segments).

(1- to 5-mm diameter) were used along with masking fluid to create detailed coloring with shading and highlights. A calligraphy holder with nibs was used for drawing hairs and outlining using watercolor paint instead of ink. Future drawings could be done using an electronic, computer drawing pad and digital art program that would aid in making quick adjustments and revisions.

Results

Measurements of *G. tubiformans* soldiers were accurately determined at 0.01-mm precision, and means and standard errors (SEM) calculated (Table 1). Measurements $\pm$ SEM:

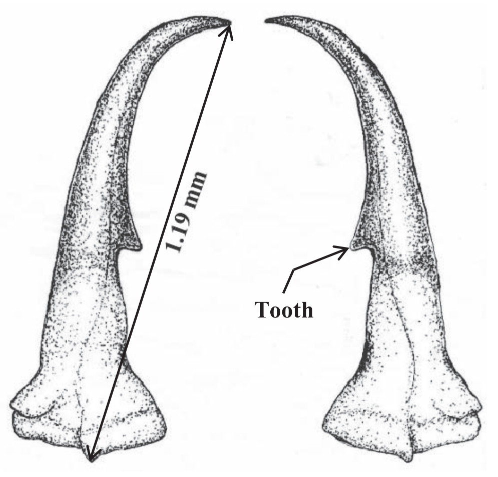

Fig. 10. Mandible dorsal view, *G. tubiformans* soldier. Note unique characteristic tooth near middle of inside margin.

pronotal width, 0.74 ± 0.02 mm; length of thorax plus abdomen, 2.70 ± 0.10 mm; length of head with mandibles, 2.17 ± 0.09 mm; total length, 4.89 ± 0.14 mm; length of head without mandibles, 1.18 ± 0.04 mm; head posterior width, 1.20 ± 0.02 mm; labral width, 0.30 ± 0.01 mm; labral length, 0.32 ± 0.04 mm; gular width at the broadest and narrowest locations, 0.36 ± 0.01 mm and 0.20 ± 0.01 mm, respectively; gular ratio: 1.78**:**1.00; total body length ÷ head length, 2.26 ± 0.05 mm; length of left mandible, 1.19 ± 0.01 mm; and length of head divided by its width, 0.98 ± 0.04 (Table 1).

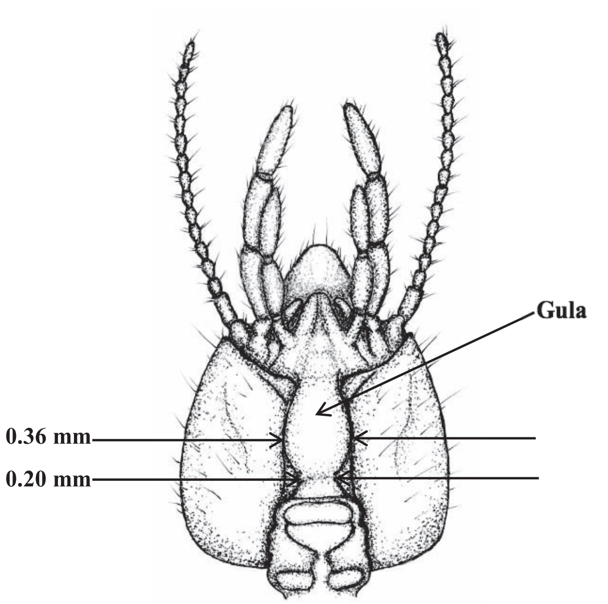

Fig. 11. Ventral head with mandibles removed showing gula dimensions, *G. tubiformans* soldier.

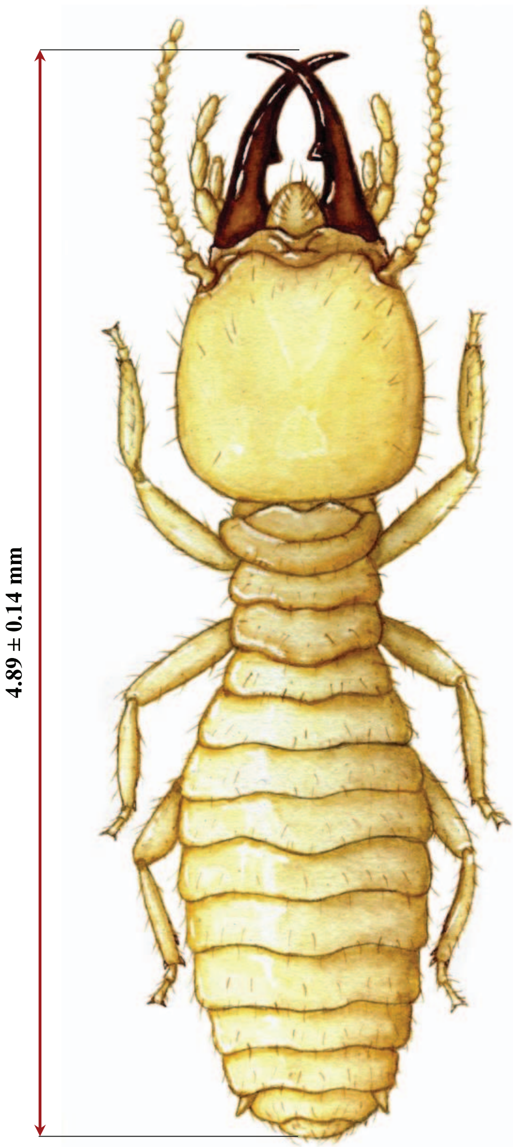

Fig. 12. *Gnathamitermes tubiformans* soldier, dorsal view. Natural pigmentation.

Mud plastering on the soil surface and mud tube construction encasing grass forage was apparent and extensive in pasture areas. This plastering and tubing behavior demonstrates the ability of *G. tubiformans* to excavate and move soil both vertically and horizontally within soil horizons, affecting soil fertility and nutrient cycling (Fig. 7). Mud tubing and plastering, and feeding and foraging behavior is diagnostic for *G. tubiformans* identification, and pasture desertification was so extensive on the study site it was clearly visible in satellite images (Fig. 8a, b).

Discussion

When measuring *G. tubiformans* soldiers, overall length dimensions were more variable compared with width measurements, which were more consistent for each body part. This is because relatively rigid sclerotized cuticle comprises the mandibles, head capsule, and gula, keeping their widths stable, whereas fleshy membranes of the abdomen can extend or contract in length, especially when stored in ethyl alcohol. Additional measurements of freshly collected termites before preserving in alcohol will help further validate morphological dimensions.

It is difficult to capture high resolution photographic images because of the small termite size and bland, creamy body coloration. Pale rusty-tan color, sclerotized body parts provided clearer details in photographs. Termites became more translucent after storage in alcohol, thereby obscuring some details such as setae numbers and joint articulations and sutures. Using a photo-stacker program improved resolution, but when the area needed to be photographed was relatively minute, a photograph lacked the fine resolution needed for use as a descriptive tool. Therefore, creating line drawings and watercolor images was important to illustrate fine details. Line drawings made while viewing through a microscope show fine details that a photograph does not capture. For example, the ventral side of the head capsule contains a complex gula. A line drawing clearly illustrates its shape and dimensions whereas a photograph does not. Drawings also allow for adjustments to improve accuracy and clearly define the number of segments.

G. tubiformans is considered beneficial for its positive effects on soil composition and its reducing-decomposing and recycling of surface plant litter. In one study, soil was enriched 1.5 times its normal nutrient concentration when termite foraging activity was present, compared with termite-free soils (Coventry *et al*., 1988). The beneficial effects of nutrient turnover from soil dwelling animals such as earthworms and a wide diversity of arthropods that are generally found in moist habitats are not present in arid environments (La Fage *et al*., 1976).

Earthworms are one of the more numerous soil aerators in tropical and temperate climates. However, in arid grassland environments where earthworms are scarce, *G. tubiformans* is one of the few animals to fill that role by turning over soil and improving aeration and rainfall infiltration, and adding nutrient-rich frass to the soil. Therefore, foraging termites are one of the primary contributors of soil nutrient fluctuation that brings nutrients to upper soil horizons. Such activity has proven to be a lead factor of plant growth stability (Coventry *et al*., 1988; Silenshi *et al*., 2010).

In addition to the morphological observations of *G. tubiformans,* future studies of its ecology and behavior would be beneficial. Currently, this termite is found in southwest Oklahoma pastures and native grasslands. It also inhabits arid grasslands and cattle grazing areas of Texas and New Mexico. In high population densities its damage to pastures is clearly apparent. However, due to its current limited territory in Oklahoma it affects relatively few Oklahoma ranchers.

When collecting *G. tubiformans*, foraging and mud plastering and tunneling activity was widespread, but breaking open most mud tubes and plastering revealed only workers. Soldiers were collected from only one area along the fence line separating grazed and non-grazed pasture in the southeast quadrant of the ranch (Fig. 8a, b). Hoof damage and soil disturbance and compaction from grazing cattle may have decreased soldier numbers on areas of open pasture denuded soil. With cyclic grass seed drilling and regular grazing activities, disturbance on the pasture surface could push soldiers deeper into their colony workings, making them less available for collection. There was reduced soil disturbance immediately under fence lines, and fence posts were the few standing woody materials along the pasture boundary. A colony established near standing wood posts may receive some protection from foraging cattle. When a soldier was found, there were always three-to-eight more in the same location near the surface. This indicates that *G. tubiformans* soldiers may aggregate in small numbers to protect the colony workings rather than being evenly distributed within the colony.

Termites were present where mud tubing was found on the soil surface and where grass stems were abundant. Soil collected within denuded areas where mud tubing was found across bare pasture surface produced the fewest numbers of termites. Foraging termites damage grass stems and leaves, and when accompanied by cattle grazing this resulted in denuded circular areas of soil (2- to 3-m diameter), thereby reducing forage for livestock. Within livestock pasture, termite damage to grass stems and roots was accompanied by grazing cattle that uprooted and dislodged weakened and damaged grass, creating the denuded areas. Loss of normal forage density in this manner led to overgrazing damage (Fig. 8a, b). However, from an ecological perspective, in arid locations *G. tubiformans* performs a beneficial role that earthworms and numerous soil-dwelling arthropods perform in temperate climates. This trade-off between being considered a detrimental forage grass damaging pest, contrasted with acting as a soil improvement benefactor makes this termite an interesting social insect within a grassland forage environment.

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