Article

Description of a novel termite ectoparasite, *Termitaria hexasporodochia sp. nov.* (Kathistaceae), presenting an unusual six-sectioned infestation, and a key to the fungal family Kathistaceae

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Abstract

Termites, an economically significant group of eusocial cockroaches, are host to a variety of ectoparasitic fungi. Here, we provide up-to-date morphological and geographic data for fungal ectoparasites described belonging to the family Kathistaceae and describe *Termitaria hexasporodochia sp. nov.*, a species observed to form lesions on its host in an unusual hexad arrangement. To date, the family Kathistaceae comprises 4 genera (*Kathistes, Mattirolella, Termitaria*, and *Termitariopsis*) and 11 valid species. Two genera we focus on in this paper, *Termitaria* and *Mattirolella*, are asexual ectoparasitic fungi that form sporodochia on the eusocial insects, termites. Morphological data collected via Micro-CT, SEM, and confocal microscopy confirms that this is a new fungal species belonging to the genus *Termitaria.* A comparison chart and dichotomous key are provided to distinguish all members of the family, Kathistaceae, to which the new species belongs.

Keywords: Ascomycote, asexual, fungi, ectoparasite, social insects, termites

Introduction

In 1920, the genus *Termitaria* was erected to describe two new species of ectoparasitic fungi (Thaxter 1920) that form conspicuous lesions called sporodochia on the exoskeleton of termites. To date, two genera (*Termitaria* and *Mattirolella*), have been documented forming sporodochia on termites, (Blackwell & Rossi 1986). Due to their highly similar morphology, sporodochia development and asexual conidia spore production, both genera were grouped into an artificial classification referred to as "Termitariales" (Kimbrough & Lenz 1982; Khan & Kimbrough 1974a). Seven species have been previously described infesting termites: *Mattirolella silvestri* (Colla 1929: page)*, Mattirolella crustosa* (Khan & Kimbrough 1974a: 396)*, Termitaria snyderi* (Thaxter 1920: 8)*, Termitaria coronata* (Thaxter 1920: 8)*, Termitaria longiphialidis* (Kimbrough & Lenz 1982: 266)*, Termitaria macrospora* (Kimbrough & Lenz 1982: 263) and *Termitaria rhombicarpa* (Kimbrough & Lenz 1982: 266). It is important to note that two additional species have been proposed, *Termitaria thaxteri* by Reichensperger (1923: 103) and *Termitaria pacadensis* by Pickens (1952: 134)*, but their validity was never established.

Termitaria is placed in the family Kathistaceae, belonging to the order Ophiostomatales, class Sordariomycetes (Benny & Kimbrough 1980). Fungi from this group are commonly associated with wood-infesting insects, often termites and bark beetles although they can cause human disease as well (Lumbsch & Huhndorf 2007; Wingfield *et al.* 1993). This order exhibits approximately 11 ascospore morphotypes defined by de Beer & Wingfield (2013) and asexual morphs presenting five conidiophore types (de Beer *et al.* 2022). A defining feature of the family Kathistaceae is its spherical asci borne uniformly in the centrum (Malloch & Blackwell 1990). Kathistaceae is comprised of 4 genera (*Kathistes*, *Termitaria, Mattirolella*, and *Termitariopsis*), and 12 species typically saprophytic on herbivore dung and insects (Maharachchikumbura *et al.* 2016b; Malloch & Blackwell 1990). The sexual morph of Kathistaceae

is characterized by globose to subglobose ascomata with parallel hyphae, a long neck, and straight curved ostiolar setae (adapted from Maharachchikumbura *et al.*, 2016b). Kathistaceae lacks paraphyses, and the asci bear 8 clavate to falcate ascospores (Malloch & Blackwell 1990). The asexual morph resembles the spherical sexual ascomata; this form is enteroblastic, phialidic, and exhibits a conidiomatal wall composed of flattened cells of textura angularis. The conidia are released in a continuous chain through the ostiolar neck (adapted from Maharachchikumbura *et al.* 2016b; Malloch & Blackwell 1990).

The type genus, *Kathistes,* is named after the Greek word for "rider" in reference to its use of arthropods as ascospore dispersers (Malloch & Blackwell 1990). *Kathistes* differs morphologically from other genera within Kathistaceae and is characterized by its globose to subglobose ascomata, long-necked perithecia with setose ostioles, and ascospore production that resembles budding yeast (Malloch & Blackwell 1990). The sporidia-producing structure called a sporidiomata is diagnostic for all three species of *Kathistes,* and has not been reported for any other fungal genera (Malloch & Blackwell 1990). *Kathistes calyculata*, the type species for Kathistaceae, is named for the termination of its reddish-brown ascomotal neck into a cuplike apex or "kalyx" (Malloch & Blackwell 1990). *Kathistes analemmoides* is named after the Greek word for sundial, analemma, because the ascomata remains buried in the substrate with their necks extending to cast a shadow (Malloch & Blackwell 1990). **Kathistes fimbriata** (Barrasa & Moreno) is similar in form to *K. calyculata*, however its ascomycota are larger and the ostiolar seta differ in form as they are straight to slightly spreading (Malloch & Blackwell 1990; Barassa & Moreno 1982). *Kathistes* is the only sexual genus in Kathistaceae, while *Mattirolella*, *Termitaria*, and *Termitariopsis* are described by their asexual forms (Maharachchikumbura *et al.*, 2015).

Termitaria and *Mattirolella* fungi share many unique traits, the most visibly obvious being sporodochia; lesions consisting of tight columns of phialides with asexual conidia spores produced endogenously in basipetal succession into collarettes at a spore-producing region known as the conidigenous locus (Khan & Aldrich 1973, Khan & Kimbrough 1974b). In its mature condition, each sporodochium exhibits a pigmented, sterile ring around its periphery in which no conidia are present. Water and nutrient absorption are done via root-like protrusions called haustoria into the host cuticle (Kimbrough & Lenz 1982; Thaxter 1920) and despite the presence of hyper-trophied host tissues at the protrusion sites, *Termitaria* fungi do not directly kill their host (Thaxter 1920). Although direct harm is rare, swelling caused by lesions has been observed to negatively affect survivorship in older individuals and cause a reduction in wood consumption (Hojo *et al.* 2002; Colla 1929; Khan & Kimbrough1974b; Lenz & Kimbrough 1982). The genus *Mattirolella* differs from *Termitaria* most evidently in its formation of a superficial sterile crust called an epihymenium over the columns of phialides, which are compartmentalized into alternating sterile and spore-bearing regions. *Termitariopsis cavernosa,* a parasite on *Neivamyrmex* ants, forms sporodochia with black excipular cells, haustoria, and a pseudoparenchymatous sub-hymenia closely resembling termitophilous genera *Termitaria* and *Mattirolella* (Colla 1929; Khan & Kimbrough, 1973a, 1974b, Khan & Aldrich, 1973, 1975). *Termitariopsis* can be discerned from all other genera by its thick-walled basal layer cells, the lack of the epihymenial layer which characterizes *Mattirolella*, and the presence of macroconidia arising from a low hymenial layer sporodochia. Additionally, the presence of phialoconidia in some exicipular cells, and the absence of them within the exicipular cavity in *T. cavernosa,* further discerns this species from those of the other two genera (Blackwell 1980).

Species from the genera *Termitaria* and *Mattirolella* are readily distinguished by the size, shape, and location of sporodochia lesions on their hosts, which are exclusively termites. The following forms, illustrated in Fig. 1, have been observed; circular/discoid, rhomboid, ellipsoid, stellate, beaked, and elongate. Additional diagnostic features include shape, size, and number of conidia, phialide length, the location of the conidiogenous zone, the morphology of the haustoria, the dimensions of the sporodochium, and pigmentation of various structures (Kimbrough & Lenz 1982; Thaxter 1920, Reichensperger 1923; Feytaud 1927). Most *Termitaria* and *Mattirolella* species develop randomly on the legs, antennae, and abdominal cuticle of their host, however *T. hexasporodochia*, *sp. nov.* infests the host cuticle in a very specific pattern. A key to the genus *Termitaria* based on morphological characters was created by Kimbrough & Lenz in 1982. Here, we produce an updated key to include all species of the family Kathistaceae, a host-species checklist, geographical locations (Table 1) (Blackwell & Rossi 1986), and the major diagnostic characters of all species from the family Kathistaceae, Table 2. Additionally, we provide high-resolution evidence of structures via uCT, confocal microscopy and scanning electron micrographs, to describe the new species, *Termitaria hexasporodochia sp. nov.* from Guyana, which infests termites in a rare hexad arrangement.
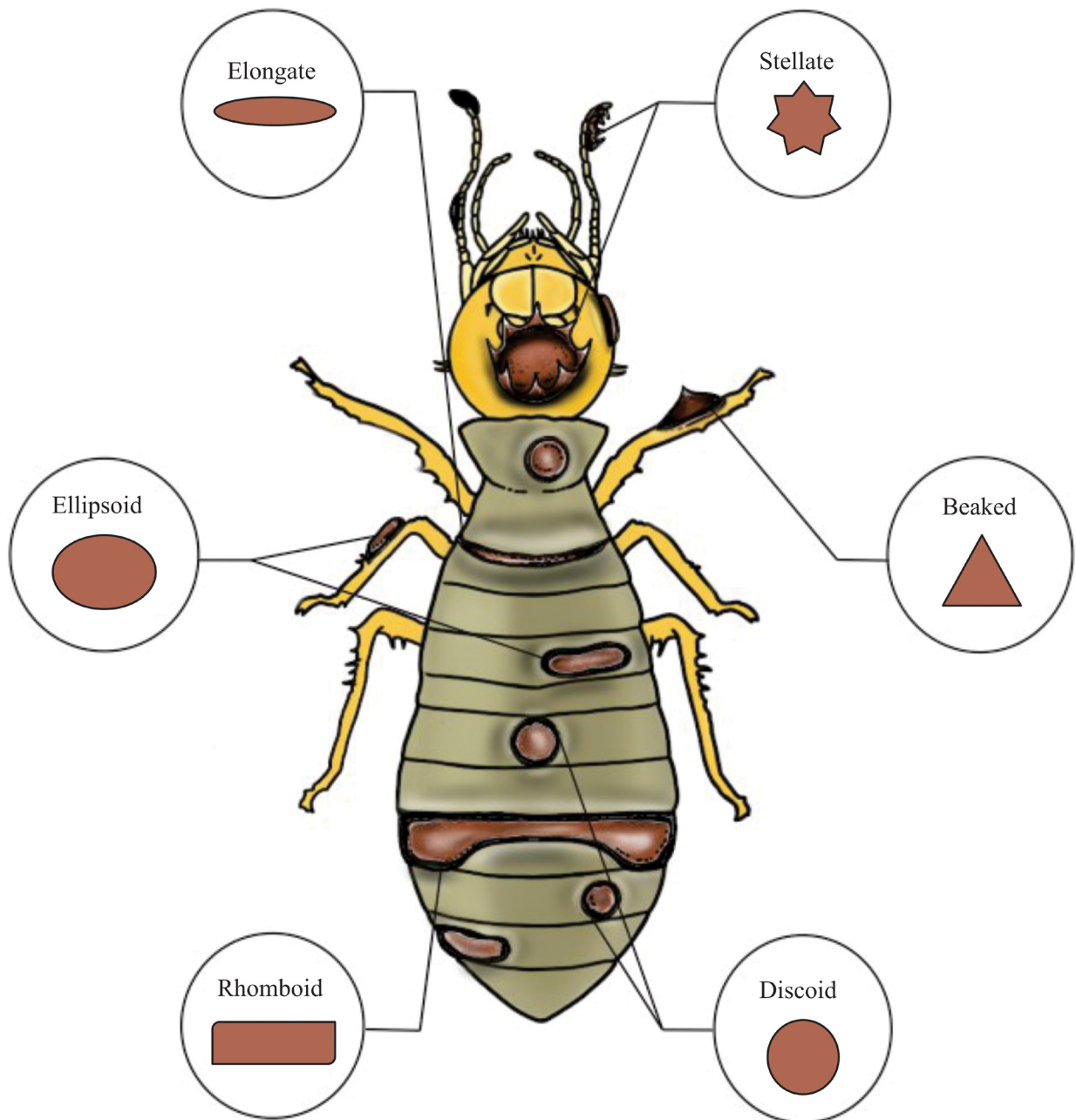
FIGURE 1. Sporodochia forms. Schematic of various sporodochia lesions and positions. Representative forms are not exclusively found on these positions on the host, lesions can form on any external surface. Illustrated by Megan Wilson .

Materials and methods

Imaging

Whole mount SEM images of *Termitaria hexasporodochia sp. nov.*, and host *Amitermes sp.* were taken using a Zeiss Evo-60 VPSEM under low vacuum without sputter coating or critical point drying. A Hitachi S-4700 FESEM was used to image dissected organ tissue, which was first sputter coated with Au-Pd and mounted on Al stubs.

Confocal light microscopy was performed on a dissectedsporodochia using a Zeiss LSM 710. Blue, green, and red spectra from autofluorescence of the cuticle were collected using 405, 488, and 633 nm wavelength laser lines, respectively. Light photomicrographs were taken using a Leica MZ16 stereomicroscope, and a DFC 480 camera with software version LAS V4.4 and on Nikon SMZ18 stereomicroscope. Illustrations were done using SketchBook (Autocad)

software on an Apple iPad Pro and Corel Draw on a desktop computer. All measurements taken for sporodochia size analysis were undertaken using "ImageJ" (NIH) software. Micro-CT X-ray reconstructions of the entire infested worker abdomen were generated at the New Jersey Institute of Technology Otto H. York Center for Environmental Engineering and Science. Scanning of a semi-wet worker specimen (specimen was placed into a microcentrifuge tube after soaking in 95% ethanol) was performed with a Bruker SkyScan 1275 at 25kV and 125µA with an effective voxel size of 6.01µm. A Z-stack reconstruction of the resulting 600 images was generated and reconstructed with 3D Slicer.

Sampling—Of the 64 colonies of wood and soil dwelling termites collected from Guyana, South America, one *Amitermes* colony (identified using Emerson 1925; Scheffrahn & Su 1987)was infested with *Termitaria* fungi. Individuals were collected from an arboreal mound (Fig. 2) using aspirators and stored in spirits temporarily (cane-sugar based "high wine") then transferred to 95% ethanol for long-term storage. All termite specimens were later analyzed using light microscopy, and seven individuals were identified as exhibiting *Termitaria* infestations. Each of the seven individuals were infested with six *Termitaria hexasporodochia sp. nov.* lesions from which morphological measurements were taken (N=42) (Fig. 3) and identification of material confirmed (Kimbrough & Lenz 1982). The holotype is currently deposited in the American Museum of Natural History. Isotype specimens are registered for deposition at Newark Museum Herbarium (NEMU).

FIGURE 2. Locality images and map, for termite host and fungi. Type- habitat, and map of Rupununi River Region locality. Photographed by Megan Wilson .

Results

Like the typical infestation rate of other described *Termitaria* species, the infestation rate of *T. hexasporodochia sp. nov.* is very low. We collected 64 colonies of termites from the Rupununi Region of Guyana, and only 1 colony of *Amitermes sp.* was observed to be infested with *T. hexasporodochia sp. nov.* Museum collections (AMNH) of *Amitermes* termites from this region were examined in addition to field caught specimens, but no other infested termites were found. The infestation rate within the colony is extremely low (>3%); 7 out of 231 termite workers from a single colony were infested, and no infestations were found on soldiers or reproductive caste members (Fig.3). Sporodochia do not extend into the termites' abdominal cavities, instead resting on the surface of the cuticle causing longitudinal muscles to become slightly distended and arch over lesions(Fig. 3, Fig. S1). All sporodochia were found in sets of six, paired on ventral abdominal segments 4, 5, and 6 (Fig. 2). No infestations were found in any other arrangement on the termite hosts and has never been reported for any other ectoparasitic termite fungi.
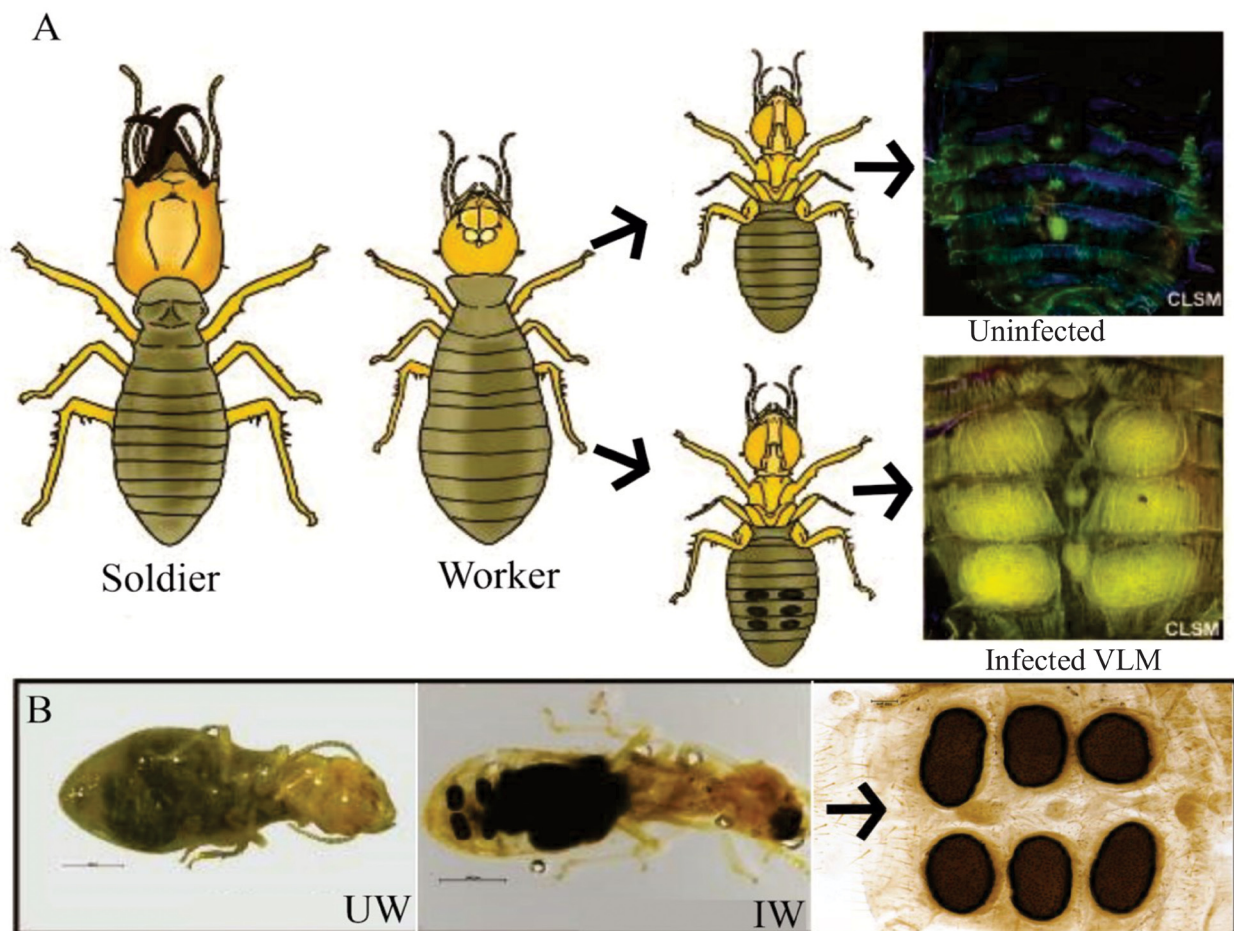

FIGURE 3. *T. hexasporodochia sp. nov.* **host**. A. Dorsal view of soldier and worker caste morphology useful in termite species identification. Ventral view of un-infested worker and location of paired sporodochia on abdominal segments 4-6 on infested workers (rare). Corresponding confocal images of longitudinal abdominal muscles included on far right of figure, with apparent abdominal swelling in infested worker muscle. B. Light microscope images of intact un-infested termite worker and infested termite worker intact. Scale bars: 500 µm, 500 µm, 100 µm. Photographed by Steve Davis. Illustrated by Megan Wilson.

Taxonomy

Family: Kathistaceae, Order: Ophiostomatales, Subclass: Diaporthomycetidae, Phylum: Sordariomycetes, Subphylum: Pezizomycotina, Phylum: Ascomycota, Kingdom: Fungi

Genus Termitaria, Thaxter 1920
Species: Termitaria hexasporodochia Wilson, Emam, Davis, Barden, Hall, Ware. *sp. nov.*
Mycobank ID : MB832822
Newark Museum Herbarium, Newark, NJ (NEMU)
American Museum of Natural History, NYC, NY (AMNH)

Type Specimens

Locality: South America, Guyana: Rupununi River Region, Karanambu Ranch, Capuchin trail, elevation: 100km, 03°44.85' N ,059°19.13' W, tropical rainforest surrounded by open savannah, on host termite in an arboreal soil mound, 11, January 2016, Collected by M. Wilson, J. Ware, P. Barden, S. George. L. Johnson, S.T. Mafla-Mills.

On *Amitermes* sp., preserved in ethanol. Deposited at AMNH and registered at NEMU Herbarium (NEMU), labeled: South America, Guyana: Rupununi River Region, Karanambu Ranch, Capuchin trail, elevation: 100km, 03°44.85' N ,059°19.13' W, collected 11, January 2016, (holotype: T1-P1S7S3! , isotypes:T2-P1S7S3!,T2-P2S7S3!).

Diagnosis—*Termitaria hexasporodochia sp. nov.* exhibits a unique phenotype, exclusively forming six moderately sized black rimmed, elliptical sporodochia on the ventral abdominal segments (4–6) of its host. *Termitaria hexasporodochia sp. nov.* exhibits 8–9 conidia per collarette, is 116–120 μm thick, elliptical in shape, has a conidiogenesis zone location 20μm–25μm from the sporodochium base, and thick-walled, lobate haustoria. The dimensions of the sporodochia range from 256 μm–609μm to 102–218 μm, the phialides are 110–115 μm in length, and the expiculum is the only pigmented region noted.

Description of the holotype—Entomogenous: Sporodochium thallus is 116 μm thick, 256 μm long, 102 μm wide, and ellipsoid in shape. At the basal layer, haustoria are initially formed from thick-walled haustorial mother cells at the base of the sporodochium and appear thick and lobular. Haustoria range from 19–23μm in length, and 1.7–2.4 μm in width. Superficial to this layer is the sporogenous hymenium layer composed of a mass of tight columnar phialides 110–115 μm thick. Each individual phialide ranges from 1.5–2.2 μm in diameter, terminating in two flat rounded tips. Endogenously-formed conidia originate from long rod-shaped conidiogenous cells at the conidiogenous locus, located 20–25 μm from the base of each phialide. Conidial spores are rectangular and catenate, 1–1.3 μm in width and 3–4 μm in length. 8–9 spores were found in each collarette and 11–13 in each phialide. Spores break off simultaneously as they reach the sporodochium surface. The surface of each sporodochial lesion appears perforated, bearing a hexagonal pattern referred to as "textura angularis", with pores being larger in diameter along the rim preceding the sterile expiculum. The expiculum forms a smooth black crust with no apparent openings. The holotype selected for description was one of the six lesions found infesting the 4th ventral abdominal segment of an *Amitermes* termite worker T1-S7S3!.

Etymology—*Termitaria* is the established generic name, and *hexasporodochia* is an adjective referring to the hexad arrangement of sporodochia exhibited on the type-host, *Amitermes*.

Ecology and host species—*Amitermes sp.* found to be infested with *Termitaria* were collected from large arboreal mounds constructed on sandpaper trees (*Curatella americana*) growing at the interface between open savannah and rainforest (Fig. 2). The mounds were found during the dry season (January) in regions surrounding the Rupununi River that flood during the annual wet season (May-August). It was found only on worker caste termite hosts, never on soldiers or reproductives.

Differential diagnoses—*Termitaria hexasporodochia sp. nov.* exhibits a unique arrangement phenotype, forming six moderately-sized, black-rimmed, elliptical sporodochia on the ventral abdominal segments (4–6) of its host. This fungus belongs to the genus *Termitaria* and is readily distinguished from two described members of the genus *Mattirolella*. It lacks a major generic character shared amongst *Mattirolella*, the sterile hyphae separating fertile hyphae in the hymenium is not present in the new species. The maximum lengths of *T. hexasporodochia sp. nov.* sporodochia are less than half the size of those described for Australian species, *T. macrospora* and *T. rhombicarpa* (Table 1; Kimbrough & Lenz 1982). Additionally, *T. rhombicarpa* can be distinguished by the rhomboid shaped sporodochium it typically forms on the host as opposed to the elliptical/circular lesion formed on *T. hexasporodochia sp. nov.*, shorter phialide lengths (Table 1, 100–105 μm vs. 110–115μm), longer conidiogenous locus (Table 1. 30–35 μm vs. 20–15 μm from phialide base) and haustoria penetrating twice as deep into the host cuticle (TABLE 1. 50–55 μm vs. 20–23 μm). *T. hexasporodochia sp. nov.* spores are easily distinguished from those produced by *T. macrospora*.

As its name suggests *T. macrospora* produces 4–5 massive spores per collarette (app 3.8–9.1 μm) whereas *T. hexasporodochia sp. nov.* produces 8–9 spores per collarette (app 1–1.3 × 3–4 μm). Another Australian species, *T. longiphialidis*, is best identified by its small circular sporodochia and having the longest phialides of any *Termitaria*

species (Table 1. 160–180 µm vs. 110–115 µm; Kimbrough & Lenz 1982). *T. hexasporodochia sp. nov.* is readily distinguished from the commonly described *T. snyderi*, by phialide length. *T. hexasporodochia sp. nov.* possesses a much thicker sporodochium, with phialides double the length of those found in *T. snyderi* (Table 1, 110–115 µm vs. 50–60 µm). *T. coronata* can be distinguished from all *Termitaria* species, *T. hexasporodochia sp. nov.* included, in the appearance of its sporodochium, with its echinulate surface and the high position of its conidiogenous locus (Table 1, 50–60 µm vs. 20–25 µm).

TABLE 1. Natural history summary. Locations and described hosts of *Termitaria* and *Mattirolella* from this study and pre-existing literature.

Kathistes Species	Host	Geographic location	Reference
Termitaria hexasporodochia sp. n.	Termite: *Amitermes sp.*	Rupununi region, Guyana	This paper
Termitaria rhombicarpa	Termite: *Porotermes adamsoni*	ACT, Australia	Kimbrough& Lenz 1982
Termitaria macrospora	Termite: *Mastotermes darwiniensis*	Queensland, Australia	Kimbrough & Lenz 1982
Termitaria longiphialidis	Termite: *Coptotermes lacteus, C. aciniformis*	Australia	Kimbrough & Lenz 1982
Termitaria snyderi	Termite: *Reticulitermes flavipes, R. virginicus, R.lucifigus, Rhinotermes marginalis, Porotermes quadricollis, Neotermes somoanus*	USA-Washington DC,FL,CA,GA ,Guyana, Guadeloupe, Italy, Chile, Samoa	Thaxter 1920, Khan &Kimbrough 1974a, Blackwell 1980, Blackwell 1986, Colla 1929, Rossi & Cesari-Rossi 1977b, Tate 1927
Termitaria coronata	Termite: *Nasutitermes costalis, N. corniger, N.guayanae, N.kempe, N.exitosus, N.surinamensis, N.fumigatus,N.longipennis, Amitermes evuncifer, Cryptotermes sjostedt, Microcerotermes fuscotibialis, Odontotermes badius, Allodontermes schultzei, A.rhodesiensis, Porotermes adamsoni, Coptotermes lacteus, C. aciniformis*	Panama	Khan & Kimbrough 1974, Kimbrough & Thorne 1982
Mattirolella crustosa	Termite: *Nasutitermes corniger, N. ephratae, N. columbicus*	Guyana	Colla 1929
Mattirolella silvestri	Termite: *Rhinotermes marginalis*	Canada, New Brunswick. Canada, Nippissing district Ontario	Malloch & Blackwell 1990
Kathistes calyculata	Dung: Moose	Canada, New Brunswick. Canada, Nippissing district Ontario	Malloch & Blackwell 1990
Kathistes fimbriata	Dung: Cow : *Bos bovis*	Rupe Lecanda, Spain	Barrasa & Moreno 1982; Malloch & Blackwell 1990.
Kathistes analemmoides	Dung: Moose	Algonquin provincial park, Nipissing district Ontario, Canada	Malloch & Blackwell 1990
Termitariopsis cavernosa	Army ants: *Neivamyrmex opacithorax, N. pilosus*	Manhattan, Kansas, Panama Canal Zone, Barro Colorado Island	Blackwell *et al.*, 1980

Ultrastructure of T. hexasporodochia sp. nov.—The complete sporodochium (Fig.4) is composed of many tightly aligned vertical columns. We group the sporodochia layers into three major regions (Fig.5A); the basal region (Fig. 5) most closely appressed to the insect cuticle, the sporogenous hymenial region (Fig. 6), and the upper region (Fig.7) filled with conidia and phialides terminating into flaps.

The basal region—This region of the sporodochium is approximately 4–5 rows and 8.5–12.5 μm thick. It is comprised of haustorial mother cells that give rise to a subcuticular layer of haustoria that penetrates the host (Fig. 5). The thin-walled cells composing the upper layer of the basal region have been referred to in previous studies as the "subhymenial layer" and gives rise apically to the hymenial phialides (Kimbrough and Thorne 1982). Haustoria aggregate towards and penetrate the host via tetra ocular channels in its cuticle. We observe 12+ major penetration points between the fungal body and its host (Fig.5 B), extending below the cuticle to thick-walled lobular haustoria ranging from 19–23 μm in length and 1.7–2.5 μm in width. We do not refer to this "haustorial region" as an internal region within the sporodochium because it lays below the cuticular layer of its host (Fig.6E–F). Additionally, its penetration into the host cuticle does not change the classification of this fungus as an ectoparasite, in that it does not invade the host cytoplasm. Each sporodochia appears to be formed from major infestation sites with cells growing upward from the basal layer, with approximately 160–240 openings per sporodochium (size dependent) that appear dark in photomicrographs (Fig.5C).

The sporogenous hymenium region—This region consists of a thick hymenium of tightly appressed phialides (Fig.6A), comprised of long rod-shaped conidiogenous cells 14–22 μm in length, which differentiate into asexual conidia at a fixed conidiogenous locus (Fig 6B–C). The phialides are approximately 1.5–1.2 μm in diameter and the conidiogenous locus (Fig.6D), the initial point of asexual spore differentiation, occurs 20–25μm, from the base of each hymenial phialide. Each collarette contains 8–9 rectangular, catenate conidia (Fig.7B–C), and approximately 11–13 spores can be found in the phialide during this time. Under high-definition microscopy, the internal surface of the hymenial phialides are coated with a dense mat of minute filaments that appear to be restricted to the upper 3/4th of the secondary canals (Fig.7A).

The upper region—At the superficial level of the sporodochia, a dark, peripheral expiculum surrounds a region resembling a hexagonal honeycomb (Fig.7A,C). This pattern is formed by fields of terminating phialides (Fig.3B) of elongate tubes referred to as *textura angularis*, the apices of which are bivalved (Fig 7B–D). The apical valves are formed by two isosceles trapezoidal flaps that fit closely together to form a large circular pad of thousands of hexagons (Fig.7D). Visible from confocal stack images just below the pad surface, each sporodochia appears densely populated with hexagonal pores, with the conidial spores visible within each tubular hymenial channel leading to the apical pore valves (Fig.7B). On average, a sporodochia contains approximately 12,000–14,000 phialides.

Overall, the most striking feature of *Termitaria hexasporodochia sp. nov.* is apparent in the arrangement and ultrastructure of the six moderately-sized, black-rimmed, elliptical sporodochia it forms on its termite host. Of all members of the family Kathistaceae, the formation of sporodochia on termites is diagnostic for members of the genera *Termitaria* and *Mattirolella*, hence why we focus on those two genera in assessing the new species. *Termitariopsis* is the only remaining member of Kathistaceae which forms sporodochia, although it does not use termites as a host and exhibits sporodochial features absent in the other two genera (Table 2a). *Kathistes* genera do not form sporodochia and are described instead off of their sexual form, whereas *Termitaria hexasporodochia sp. nov.* is described by its asexual sporodochia form. The genus *Ectomyces calotermi*, described on termites to form sporodochial lesions, has been synonymized with *Termitaria snyderi* (Tate 1928), a species described in this article. No further examination is needed on this genus as its synonym *T. snyderi* is examined here. We place the new species in *Termitaria* because it lacks the defining features of *Mattirolella*: sterile hyphae interspersed with fertile hyphae and an epihymenium (Table 2a). The new species can be differentiated from other *Termitaria* species by sporodochial length (*T. macrospora* and *T. rhombicarpa),* sporodochial shape (*T. rhombicarpa),* phialide lengths (*T. longiphialidis, T. snyderi*), location of conidiogenous locus, spore size, and haustorial depth (Table 2a).
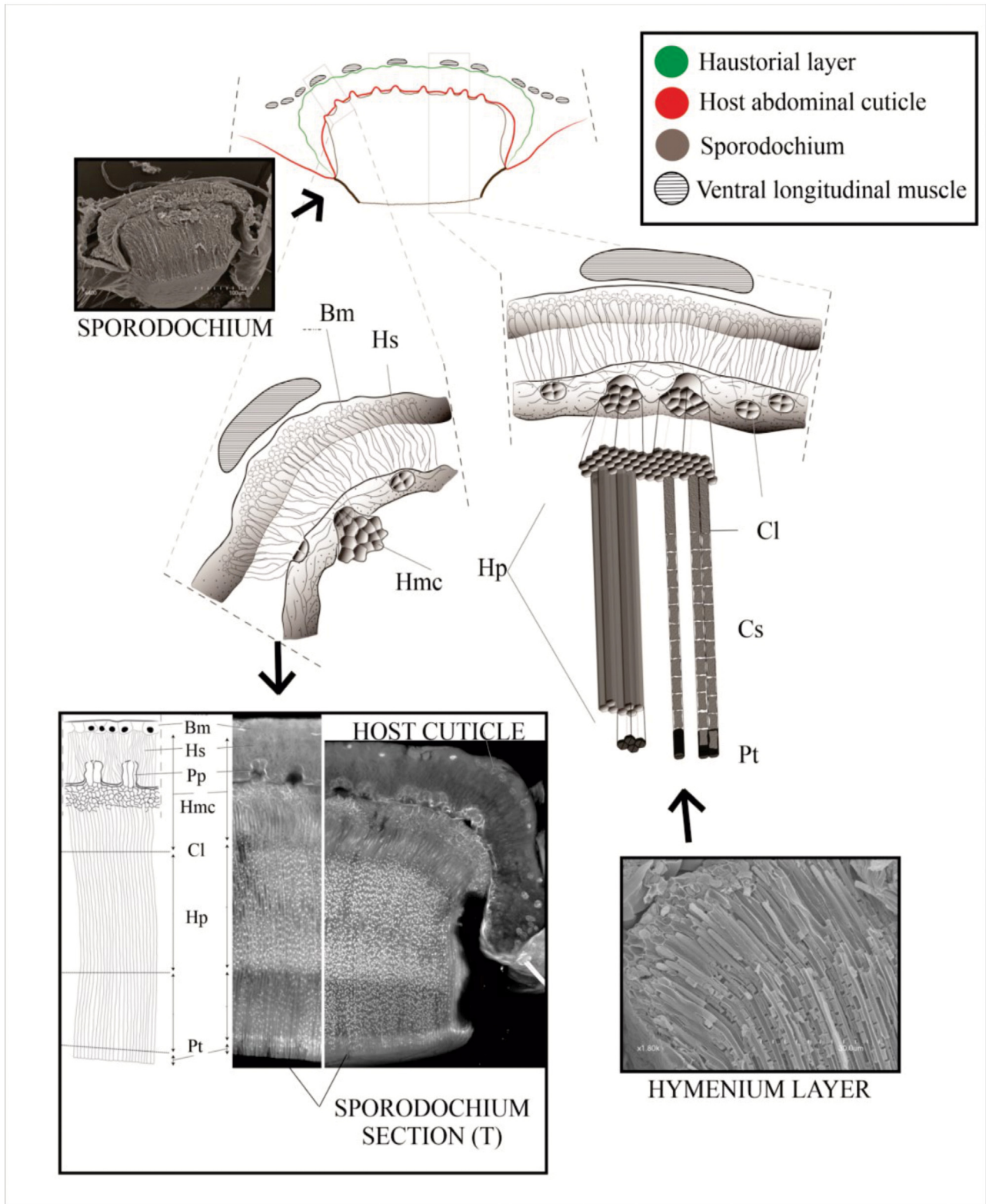
FIGURE 4 Structural schematic of _T. hexasporodochia sp. nov._ Sporodochium section, (T=Transverse) in situ on its _Amitermes_ host. SEM and Confocal images included for reference. Abbreviations used; Bm—Basement membrane, Hs—Haustoria, Hmc—Haustorial mother cells, Hp—Hymenial phialides, Cl—Conidigenous locus, Conidial spores, Phialide tips. Scale bars: sporodochium: 100 μm, hymenium: 30 μm. Illustrated by Steve Davis.
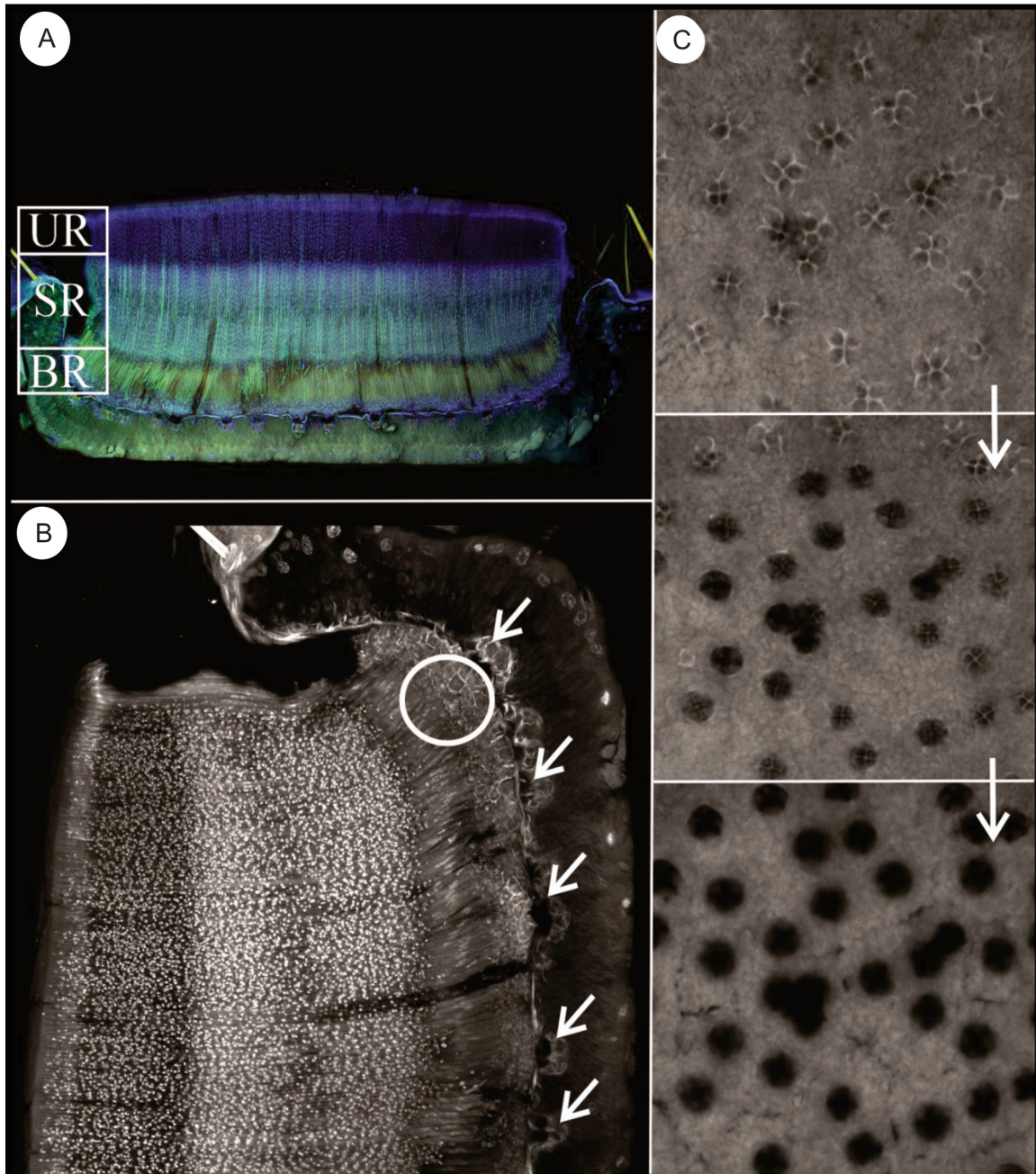
FIGURE 5. Sporodochial layers CLSM. A. Upper region (UR), Sporogenous Region composed of a phialidic hymenium (SR), Basal region (BR) composed of haustorial mother cells and subhymenial layer that gives rise to SR. B. Basal most layer above insect cuticle 4-5 rows thick. White circle indicates thick haustorial mother cells that give rise to a subcuticular layer of haustoria that penetrates the host cuticle. White arrows indicate major penetration points between *T. hexasporodochia sp. nov.* and host cuticle. C. Confocal stack of tetralocular junctures between host cuticle and parasite. Photographed by Steve Davis.
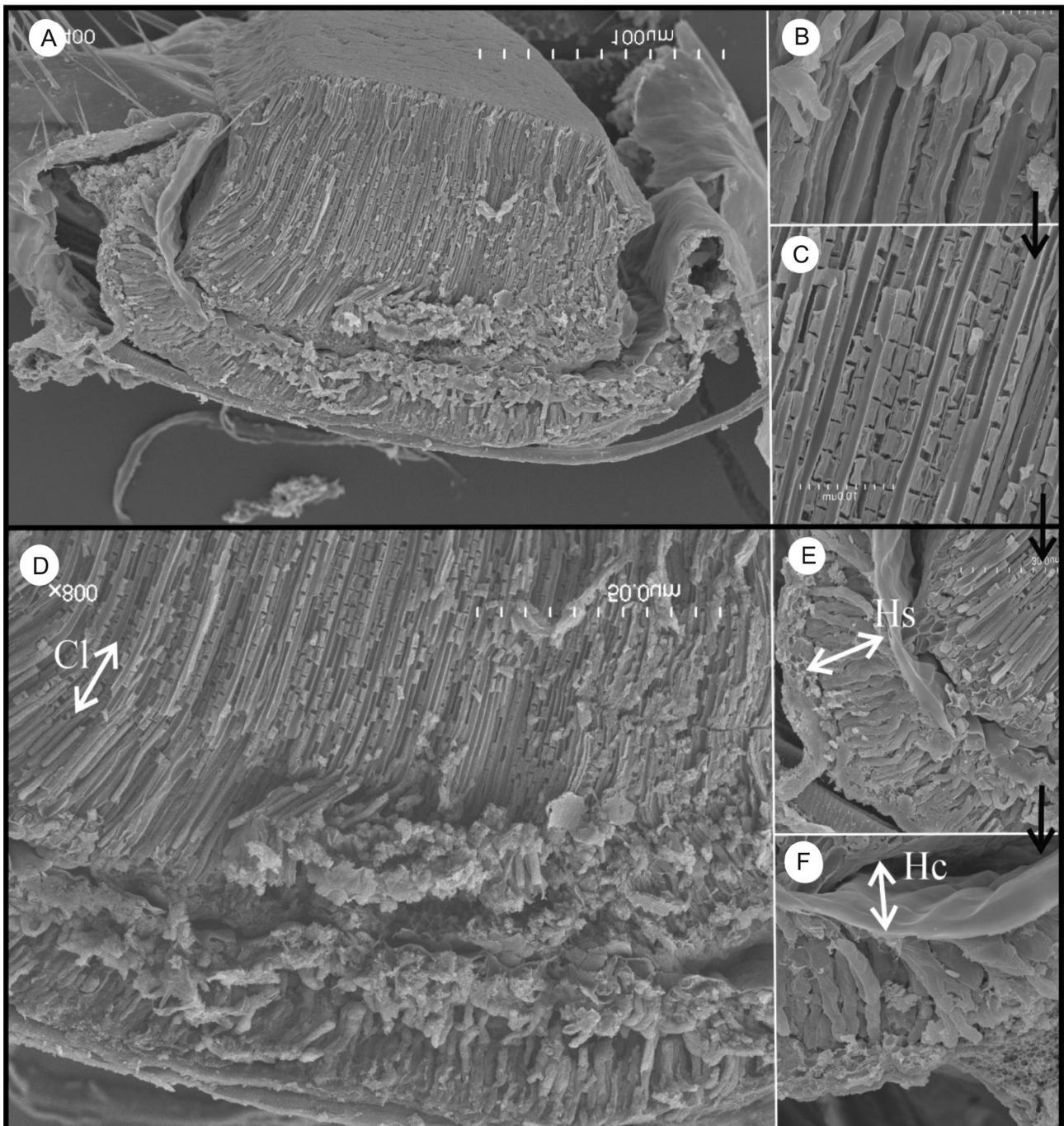
FIGURE 6. Microscopic ultrastructure of *T. hexasporodochia sp. nov.* sporodochium.
A. Transverse section of a single sporodochium resting upon the cuticle of the host. B. Transverse view of the bivalve flap terminations of the phialides. C. Rectangular conidia assemblage within the phialide are formed endogenously and in basipetal succession D. Fixed conidiogenous locus in which spore differentiation occurs (Cl) E. Basal region of the sporodochium in right corner of image showing initial phialidic growth, and left bottom of image shows thick haustorial layer (Hs) extending below the host cuticle (termite). F. Host cuticle (Hc) with underlaying haustoria. Scale bars: A—100 µm, B—5 µm, C—10 µm, D—50 µm, E—30 µm. Photographed by Steve Davis.
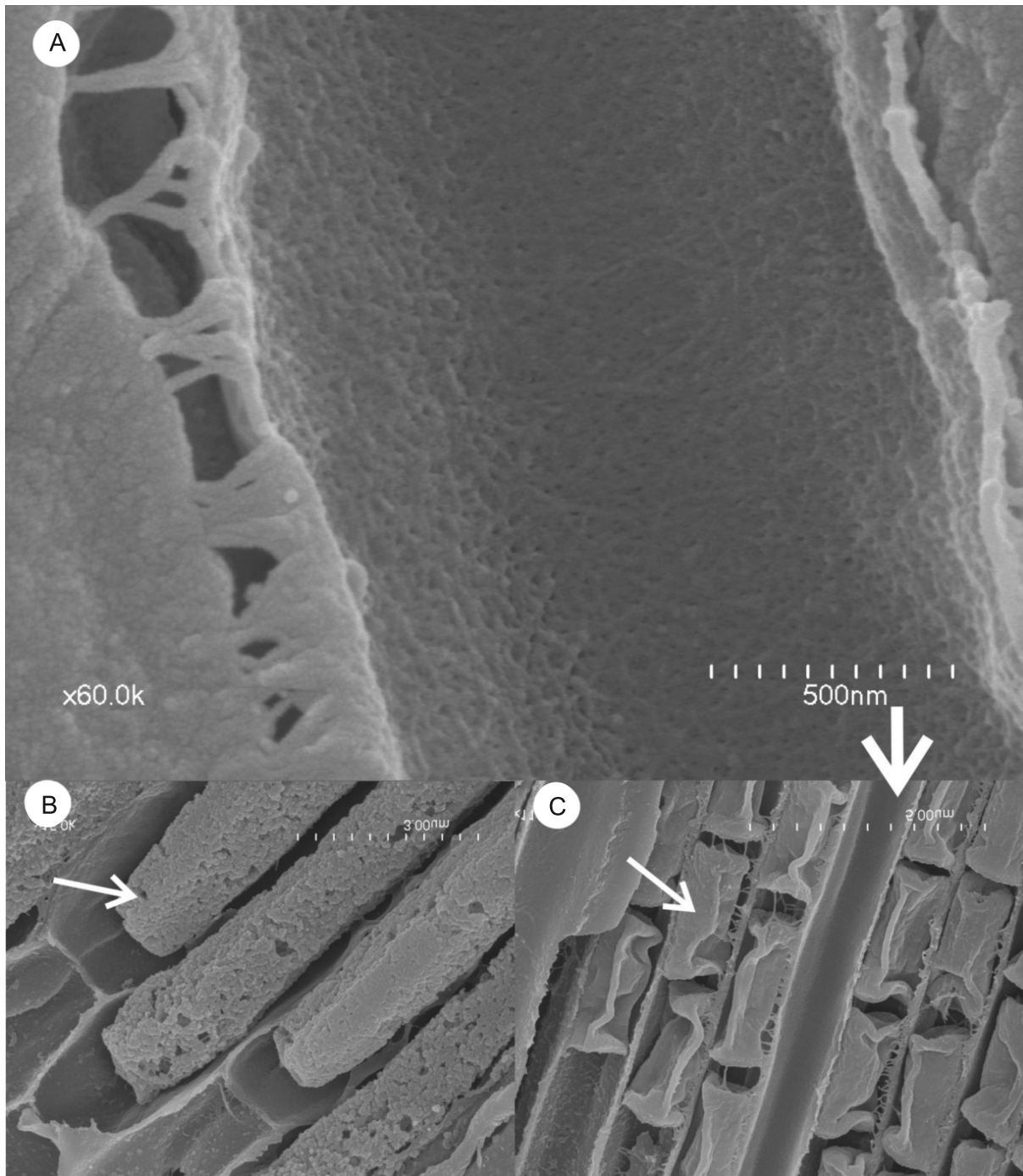
FIGURE 7. Phialide and spores SEM. A. internal surface of the hymenial phialide, with dense minute filamentous coating B. Sporogenous structure prior to endogenous division at conidiogenous loci. C. Rectangular, catenate conidial spores located beyond the conidiogenous locus indicated by arrow. Scale bars: A—500 nm , B—3.0 μm, C—2 μm . Photographed by Steve Davis.

TABLE 2a. Sporodochia-forming fungi (Kathistaceae) identification summary. Significant characters and morphological measurements of asexual features of *Termitaria* and *Mattirolella* from this study and pre-existing literature included.

Feature	Measure (µm)	*Termitaria hexasporodochia* sp. nov.	*Termitaria rhombicarpa*	*Termitaria macrospora*	*Termitaria longiphialidis*	*Termitaria snyderi*	*Termitaria coronata*	*Mattirolella crustosa*	*Mattirolella silvestri*	*Termitariopsis cavernosa*
Sporodochium	length	250–610	5,000–6,000	2,000–3,000	375–425	400–1000	>300	800–1200	200-802	700
	width	100–200	400–500	500–600	375–425	37	>300	250–300 um	365–800	200
	thickness	116–120	125–140	120–140	190–200	70–80	80–100	80–90	60–70	100 expiculum
	location on host	Ventral abdomen: sternites 4,5,6	Thorax, abdomen	Thorax, abdomen	Head, abdomen, legs	All body parts	All body parts	All body parts	Thorax, abdomen, legs	Leg on *Neivamyrmex opacithorax*
	shape	Ellipsoid, circular	Ellipsoid, Rhomboid	Ellipsoid, Circular	Circular	Ellipsoid, circular	Circular	Ellipsoid, circular, beaked	Ellipsoid, star-shaped	Ellipsoid
	CG locus	20–25	30–35	-	-	30–35	50–60	12–15	52	-
Conidia	width	1–1.3	1.2–1.8	3.8–4	1.9–2.2	1.5–2.0	2.0–2.1	1.5–1.8	1.5	Macroconidia: 20-30 Microconidia: 2.0
	length	3–4	3.6–4	8.8–9.1	4.25	3.5–4.5	3.5–4	3–3.5	2.5–3	Macroconidia:40-60 Microconidia: 2.0
	# per collarette	8–9	8–10	4–5	8–10	4–5	10–12	10–12	10–12	-
	shape color	Rectangular, catenate hyaline	Rectangular, catenate hyaline	Rectangular, catenate hyaline	Rectangular, catenate hyaline	Cylindrical, catenate hyaline	Rectangular, catenate hyaline	Cylindrical, catenate hyaline	Cylindrical, catenate hyaline	Macroconidia: multicellular,appendaged Microconidia: spherical
	length	110–115	100–105	90–95	160–180	50–60	90–95	50–55	37–40	100
	width	1.5–2.2	-	-	4.5–5	2–2.5	2–2.5	4.5–5.5	4–5.5	3.0
	arranged	Tight columns	Tight columns	Loose columns	Tight columns	Tight columns	Tightly appressed	Compartments w/ sterile hyphae	Compartments w/sterile hyphae	Present in some expicular cells and absent in expicular cavity
Phialides	tips	Blunt rounded, flat	Blunt,rounded,flat	Pointed, minute	Blunt,rounded	Blunt,flat	Thick,rounded	Below expicular crust	Below expicular crust	-
	texture	Perforate, light, textura angularis	Perforate, light, textura angularis	Echinulate, light, textura angularis	Perforate, dark, textura angularis /prismatica	Perforate, light Textura angularis	Echinulate, dark, textura prismatica	Reticulate,dark pycnidium/ ostiole	Arched, dark epihymenium	-
	length	19–23	50–55	20–25	15–20	-	-	7.5–8	-	5.0 (mother cells)
	width	1.7–2.4	10–15	12.5–15	3–4	-	-	8–10	-	10.0 (mother cells)
Haustoria	appears	Thick walled, Lobate	Thick walled elongate, branched	Thick walled, Lobate	Thick walled short, lobate branched	Thick walled, Lobate	Thick walled, lobate	Finely branched, compact	Finely branched, compact	Arise from dark thick-walled cells
	pigmentation	Expiculum	Expiculum	Phialide wall: CL to base expiculum	Mid CL walls expiculum	Mid phialide walls, expiculum	Tip of phialide expiculum	Epihymenium	Epimhymenium Haustorial mother cells	Expiculum
	references	This report	Kimbrough &Lenz 1982	Kimbrough & Lenz 1982	Kimbrough& Lenz 1982	Kimbrough & Lenz 1982 Thaxter 1920, Khan &Aldrich 1974 Khan&Kimbrough 1974b	Kimbrough & Lenz 1982 Thaxter 1920 Colla 1929, Ensaf et al. 2006	Khan&Kimbrough 1974a, Kimbrough &Thorne 1982	Khan &Kimbrough 1974a Colla 1929	Blackwell et al., 1980

TABLE 2b. Non-sporodochia forming fungi (Kathistaceae) identification summary. Significant characters and morphological measurements of sexual features of Kathistaceae fungi compared and described.

| Features	Measure(µm)	Kathistes calyculata	Kathistes fimbriata	Kathistes analemmoides
Ascomata	length	26–62	70–110	50–120
	width	26–62	70–110	50–120
	color	hyaline/transparent	hyaline/transparent	hyaline/transparent
	shape	spherical to subspherical	spherical to subspherical	spherical to subspherical
Ascomata neck	length	80–120	220–310	140–150
	width	6–11	11–14	10–18
	color	dark reddish brown	dark reddish brown	dark reddish brown
	length	13–22	40–50	54–64
	width	6.5–10.2	10–15	9–11
Asci	spore number	8	4	8
	shape	ellipsoidal, clavate, short stipitate	clavate, short stipitate	fusoid, subcylindrical, stipitate
	arrangement	basal fascicle	basal fascicle	basal fascicle
	length	13–20	38–43	32–42
	width	2.3–2.9	3.5–4	2.5–4.3
Ascospores	color	hyaline	hyaline to pale brown	hyaline
	shape	falcate/clavate, narrow below	falcate/clavate, narrow below	falcate/clavate, narrow below
	septa	unicellular at first, develops 3+ septa	unicellular at first, develops 3+ septa	unicellular at first, develops 5 septa
	location	in substrate	in substrate	in substrate
Sporodiomata	association	ascomata	ascomata	ascomata
	appears	spherical, similar to ascomata	spherical, similar to ascomata	spherical, similar to ascomata
References		Malloch & Blackwell 1990	Malloch & Blackwell 1990; Barrasa & Moreno 1982	Malloch & Blackwell 1990
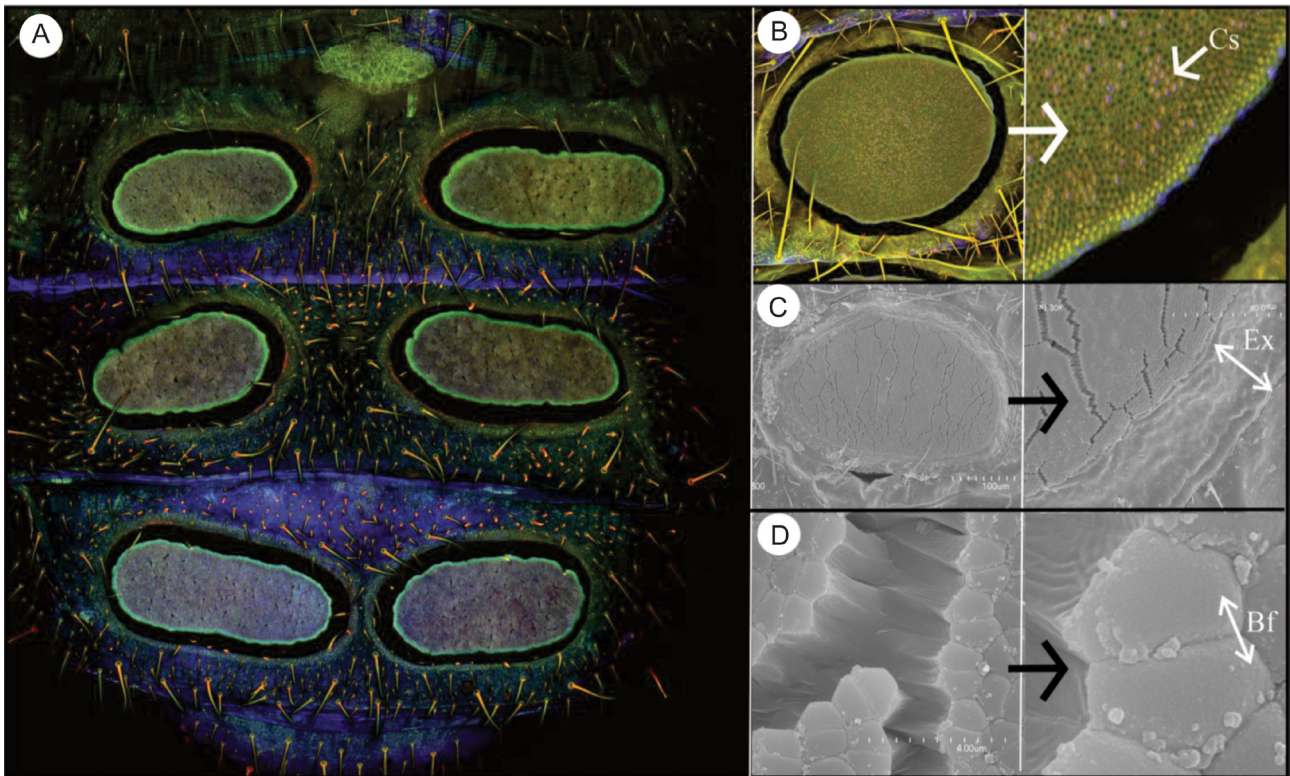
FIGURE 8. Upper region structure of *T. hexasporodochia sp. nov.* A. Confocal stack image showing position of sporodochia on the ventral surface of *Amitermes* worker abdomen with six prominent elliptical sporodochia of *T. hexasporodochia sp. nov.* on ventral sternites 4, 5, and 6. Thick dark expiculum present along the periphery of each lesion. B. Confocal stack image just below the pad surface, showing sporodochia appears densely populated with 12,000–14,000 hexagonal pores (textura angularis), with the conidial spores (Cs) visible within each tubular hymenial channel leading to the apical pore. C. SEM image showing apical most surface of the hexagonal honeycomb of phialides, in contrast to the smooth, crust like expiculum (Ex) 4- Phialides terminate in two blunt bivalved flaps (Bf) that appear as two isosceles trapezoidal flaps that combine to form a hexagonal unit. Scale bars: C-100 μm, D-4 μm. Photographed by Steve Davis.

Discussion

Remarks—The accepted current classification of *Termitaria* is in the family Kathistaceae, in the order Ophiostomatales. It is important to distinguish this grouping from the old, artificial classification, 'Termitariales', erected to contain the genera *Termitara* and *Mattirolella*, as a result of the highly similar morphology, sporodochia development and asexual conidia spore production (Blackwell & Rossi 1986) (Kimbrough & Lenz 1982; Khan & Kimbrough 1974a). In 1990, it was determined by Malloch and Blackwell that Kathistaceae has sufficient taxonomic distance from Pyxidiophoraceae, therefore, it was reported as its own family in the order Ophiostomatales. Due to lack of adequate sample sizes and ability to culture fungi in laboratory settings, molecular data are rarely included in studies of fungi that infest termites, and morphological evidence is still widely used for species delimitation. Past work provides molecular evidence that the most observed *Termitaria* fungus, *T. snyderi*, is closely related to the Ascomycote fungi from the genus *Kathistes* (Blackwell *et al.* 2003). Based on similar morphology and its close association with termites, however, we suspect *Mattirolella* is likely most closely related to *Termitaria* although it has never been sequenced. Attempts to extract and amplify DNA from most ectoparasitic termite fungi have yet to produce successful amplification results (Guswenrivo *et al.* 2018); for instance, amplification attempts of the fungus *Coreomycetopsis oedipus* were unsuccessful due their scarcity (Blackwell *et al.* 2003). We describe this new species based on key morphological characteristics differentiating it from all currently described Kathistaceae species: sporodochium size, arrangement, phialide length, and haustoria length. Unfortunately, due to our limited sample size and an inability to culture this fungus in a laboratory setting, we faced similar difficulties in extracting useful molecular information. To date, morphological evidence has been exclusively used for all novel species descriptions of *Termitaria* and *Mattirolella* fungi.

The infestation rate of this fungus is extremely low across termite colonies we collected from this region of Guyana (>1.5% infestation rate) and individuals belonging to the colony from which it is described (>3% infestation rate). The low infestation rate of *Termitaria* is initially difficult to explain; cold climates serve as barriers to infestation, however rates should be expected to be higher within a humid and enclosed colony setting where food sharing and grooming behaviors of the host facilitate spore release and infestation (Hojo *et al.* 2001, Kramm *et al.*, 1982; Blackwell & Rossi, 1986; Myles *et al.* 1998). The number of individuals infested by *Termitaria* within a single colony typically falls far below 10%, with most termite colonies lacking infestation altogether (Khan & Kimbrough,1974b; Blackwell 1980; Lenz & Kimbrough,1982; Hojo, unpublished data). The phenomenon we observe here perhaps is best explained through the lens of Van Valen's "Red Queen Hypothesis" (1973), in which host and parasite populations undergo antagonistic coevolution due to selective pressures they place on one another. Evidence exists to suggest that although the parasite often does not directly cause lessened survivorship, it does so indirectly via swelling of tissues around haustoria protrusions and a reduction in vigor and wood consumption (Hojo *et al.* 2001, Colla 1929; Khan & Kimbrough, 1974b; Lenz & Kimbrough, 1982). In this study, we observed swelling in muscular tissues of the termites, but the full extent of the damage is yet to be determined.

When considering the evidence of harm to its host, the low infestation rate of *Termitaria hexasporodochia* makes this fungus a poor candidate for biocontrol. Past work has indicated mixed to low success for fungi used in biocontrol of termites (Chouvenc and Su, 2010). To start, many impactful termite pest species build diffuse subterranean nests making fungal application difficult to administer effectively since transmission does not occur between members of extended colonies (Chouvenc and Su, 2010; Rath, 1995; Milner *et al.*, 1998a; Mburu *et al.*, 2009). Behavioral constraints contribute as well; deceased termites infested with fungal spores are not effective vectors for transfer of spores (Grace & Zoberi, 1992), termites perform allogrooming activities to remove fungal spores from nestmates (Liu *et al.*, 2019), and termites are capable of "learned avoidance" of nest regions infested with fungi (Rath 2000). The sporodochia of *Termitaria* grow largest on older individuals which no longer molt. It is possible that this fungus can be impactful in a way similar to *Antennopsis*, another ectoparasitic fungi that infests termites; mortality rate of termites infested by *Antennopsis* in large well-established colonies is low; (Gouger & Kimbrough 1969, Myles 1998, Guswenrivo *et al.* 2017), whereas it is high in small and founding colonies (Buchli 1960; Buchli 1966) It is suspected that this fungus is kept in check when the termite molts its exoskeleton and sheds traces of fungal forms and that the remaining terminal caste members (no longer molt) tolerate the remaining fungi without any discomfort (Buchli 1960). Perhaps with more study of this fascinating fungal group, we can discover mechanisms in which to surpass the organization of termites and take advantage of *Termitaria* in fungal control.

Conclusion

The most unusual feature of *T. hexasporodochia sp. nov.* is the hexad arrangement that the infestation forms on its host. We hesitate to describe this fungus based on the hexad sporodochial arrangement alone, but little has been shown in past studies to indicate strong directionality of sporodochial arrangement on the hosts of all described *Termitaria* species. Still, even with a host sample size (n=7) and a parasite sample size (N=42), we stress how unique this arrangement is, with all six lesions always presenting as pairs on ventral abdominal segments 4, 5, and 6. For this pattern to mirror itself, on seven distinct individuals, is highly unlikely to have occurred by chance. We hypothesize that perhaps a predisposition shared amongst worker siblings to becoming infested at weak cuticular intersegmental regions of the host may cause the pattern we observe. At the same time, it is possible this parasite may be more tightly associated with its hosts' behaviors or morphology than formerly believed. Without more samples of this rare and intriguing fungus, it is yet unclear whether the arrangement of sporodochia lesions varies among instars, castes, and colonies as we can only analyze the individuals at hand.

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Conceptualization: Wilson, Barden, Ware
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Methodology: Wilson, Davis, Hall
Formal analysis: Wilson, Barden, Ware, Davis, Hall
Investigation: Wilson, Barden, Ware, Davis, Hall
Resources: Ware, Hall, Davis
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Writing: original draft preparation: Wilson, Barden, Ware, Davis
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FIGURE S1. Movie showing uCT reconstruction movie of *Termitaria* lesions on host. Photographed by Phillip Barden.

Diagnostic key for the Kathistaceae

1.	Sexual morph present with sporodiomata	10
-	Asexual morph present with sporodochium	2
2.	The production of microconidia and macroconidia appendages	*T. cavernosum*
-	Microconidia produced at conidiogenous locus	3.
3.	Phialide tips echinulate and pigmented	*T. coronata*
-	Phialide tips flat and unpigmented	4.
4.	Phialides greater than 160 µm in length	*T. longiphialidis*
-	Phialides less than 120 µm in length	5.
5.	Conidia are large; dimensions ~ 8 µm × 4 µm	*T. macrospora*
-	Conidia are small; dimensions ~4 µm × 2 µm	6.
6.	Large rhomboid or ellipsoid sporodochia; 5–6 mm in diameter	*T. rhombicarpa*
-	Circular or ellipsoid sporodochia; less than 1 mm in diameter	7.
7.	Maximum of 5 conidia per collarette	*T. snyderi*
-	Minimum of 8 conidia per collarette	8.
8.	Phialides tips exposed at surface of sporodochium and terminate in flaps; phialides are fertile and not arranged into compartments	*T. hexasporodochia* sp. nov.
-	Phialide tips covered at surface of sporodochium by superficial epihymenium; phialides arranged into sterile and fertile compartments	9.
9.	Sporodochia exhibit a beak-like pycnidium and ostiole and are ellipsoid in shape; conidiogenous locus ~15 µm from base	*M. crustosa*
-	Sporodochia lack pycnidia and ostiole; sporodochia are stellate or ellipsoid in shape; conidiogenous locus ~ 50 µm from base	*M. silvestri*
10.	4 ascospores produced in ascus	*Kathistes fimbriata*
-	8 ascospores produced in ascus	11
11.	Ascospores develop with 3 septa	*Kathistes calyculata*
-	Ascospores develop with 5 septa	*Kathistes analemmoides*