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Compositermes vindai (Isoptera: Termitidae: Apicotermitinae), a new genus and species of soldierless termite from the Neotropics

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Abstract

The New World *Anoplotermes* group is a common and diverse clade of soil-dwelling soldierless termites that is undergoing needed taxonomic reclassification. Based on robust worker gut morphology centered near the enteric valve, a new genus and its singular species, *Compositermes vindai*, are described from collections encompassing a massive expanse of tropical America. The enteric valve armature is thought to enhance inoculation of the food stream with symbiotic bacteria.

Key words: French Guiana, Panama, Paraguay, Trinidad and Tobago, *Anoplotermes* group, enteric valve seating, proctodeal segments

Introduction

In his treatise on the gut anatomy of the higher termites, Noirot (2001) divided the subfamily Apicotermitinae into three taxonomic groups based on the gut morphology of the worker caste. His *Apicotermes* group includes species with soldiers from tropical Africa, the *Speculitermes* group includes species with soldiers from tropical Asia, and the *Anoplotermes* group consists of soldierless species from both the American and African tropics (Noirot 2001). The molecular and morphological phylogeny elucidated by Inward *et al.* (2007) confirms monophyly for the Apicotermitinae, but provides evidence that the neotropical *Anoplotermes* s.l. forms a separate clade from the more basal African Apicotermitinae. Those who have studied the soldierless termites of the Neotropics (e.g. Bourguignon *et al.* 2010, Davis 2002, Fontes 1992, Mathews 1977) agree that the genus *Anoplotermes* is in dire need of revision and at present constitutes a superficially cryptic, yet diverse group. The five other *Anoplotermes*-group genera, *Aparatermes*, *Grigiotermes*, *Longustitermes*, *Ruptitermes*, and *Tetimatermes*, also need reevaluation as a whole using current morphological and molecular techniques.

In the Neotropics, only *Longustitermes manni* (Synder 1922) and *Tetimatermes oliveirae* Fontes (1986) were described from the worker caste alone; the former having an unusually small and elongate body, and the later possessing a deep concavity of the fore tibia. In a landmark discovery, Grassé and Noirot (1954) found that the worker gut of higher termites contains robust morphology that is useful for taxonomic comparisons. Noirot (2001) refers specifically to the enteric valve of the *Anoplotermes* group as having “great systematic value”. Sands (1972) was the first to embrace these gut characters in large scale for his landmark revision of the soldierless termites of Africa. Sands (1972, 1998) photomicrographs of enteric valves from African termite workers are often diagnostic at the species level because of their complex, yet intraspecifically stable nature. But even so, Sands (1972) included the imago in all of his generic and specific descriptions, no doubt leaving taxa without accompanying imagos undescribed.

For soldierless termites, it has been customary to use the winged imago as the primary, often sole, morphological basis for taxonomic descriptions. However, imagos of this group are rarely collected. The University of Florida Termite Collection (Davie, Florida) alone has over 2,000 colony samples of neotropical soldierless termites of which only 5% contain imagos. The shortcomings of using solely imago characters and overlooking the worker enteric valve armature in the *Anoplotermes*-group taxonomy were made most evident by

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Bourguignon *et al.* (2010). They reexamined the enteric valve of workers in types of three of Snyder's (1922, 1926) and one of Emerson's (1925) neotropical *Anoplotermes* species. Bourguignon *et al.* (2010) found all of these to be conspecific with *A. parvus* Snyder. *A. parvus* has an unmistakable pectinate crown capping the posterior end of the enteric valve (Fig. 1) that was unknown to Emerson and Snyder. Bourguignon *et al.* (2010) also synonymized *A. linearis* Snyder (1926) from Bolivia with *L. manni* (Snyder 1922) originally described from Honduras, because of congruency of their distinct enteric valve armature (Fig. 1). The only other depictions of enteric valves from Neotropical Apicotermitinae include *Grigiotermes* nr. *metoecus* and *Grigiotermes metoecus* Mathews (1977), *G. bequaerti* (Snyder & Emerson in Snyder, 1949) in Godoy and Torales (1999), *A. bahamensis* Scheffrahn & Křěcěk and *A. opinatus* Scheffrahn & Křěcěk (Scheffrahn *et al.* 2006), and *A. banksi* Emerson, *A. janus* Bourguignon & Roisin, and *A. pacificus* Müller (Bourguignon *et al.* 2010).

In the first morphological comparison of the five soldierless neotropical genera recognized at the time (the above genera minus *Longustitermes*), Fontes (1992) produced an illustrated key of the workers using digestive tube architecture, mandible dentition, salivary gland volume, and fore leg and head capsule characters. Fontes (1992) omitted the enteric valve and its seating (*sensu* Sands 1972). Although the relative length and position of the worker gut compartments have some taxonomic utility (Noirot 2001), the circuitous route of the gut and variable volume in each compartment (depending on food content) makes detailed comparison, even as line drawings, rather difficult. The mandibular dentition among genera and species of the *Anoplotermes* group varies only slightly and its utility is further challenged as a result variability from feeding erosion. The relative phylogenetic importance of these worker characters, in addition to those reported by Noirot (2001), remain open to debate. But, for explicit morphological diagnoses, the enteric valve is by far the most robust character in many higher termites, especially those that are geophagus. Enteric valve architecture may even surpass genital "lock and key" morphology in complexity and intraspecific uniformity used extensively in species discrimination of other insect groups (Eberhard 1985). In the current paper, I describe *Compositermes vindai*, a new genus and its singular species based primarily on the unique morphology of its enteric valve region.

Material and methods

Specimens of *Compositermes vindai* were collected in French Guiana, Panama, Paraguay, the island of Trinidad, and the island of Tobago (Fig. 2). Photos in Figs. 3 and 4 (top) were taken as multi-layer montages using a Leica M205C stereomicroscope controlled by Leica Application Suite version 3 software. Preserved specimens were taken from 85% ethanol and suspended in pool of Purell® Hand Sanitizer to position the specimens over a transparent Petri dish background. The enteric valve and mandible photographs (Figs.1, 4 bottom, 5, and 6) were taken from slide mounts using a Leica CTR 5500 compound microscope with phase-contrast optics and the same montage software. The field habitus (Fig. 5) was taken with a Nikon 7SC digital camera in macro flash mode. Terminology of the worker gut follows that of Sands (1972) and Noirot (2001).

Compositermes gen. nov.

Type-species: *Compositermes vindai* sp. nov.

Imago unknown.

Worker (Figs. 3–6). Monomorphic. Fore tibia moderately inflated (ratio length/width 3.98). Ventral surfaces of fore tibiae with four or five thin longer spines. Mesenteron (M) and first proctodeal segment (P1) tubular with simple diagonal connection forming a very short or absent intervening mixed segment; M forming complete 360° loop. P1 "C" shaped, beginning with anterior connection to M and ending with posteriolateral connection to enteric valve (P2). Enteric valve seating (S) without lobes, yellowish, subtubular; S very long and wider than P2 except near P3 connection; curving anteriodorsally about 90° where it meets dorsal center of paunch (P3). Fourth proctodeal segment (P4) long; anterior loop partly surrounding dorsum of P3and paralleling M; posterior portion winding behind M to emerge ventrally and curving near S before joining rectum (P5). Enteric valve constriction in

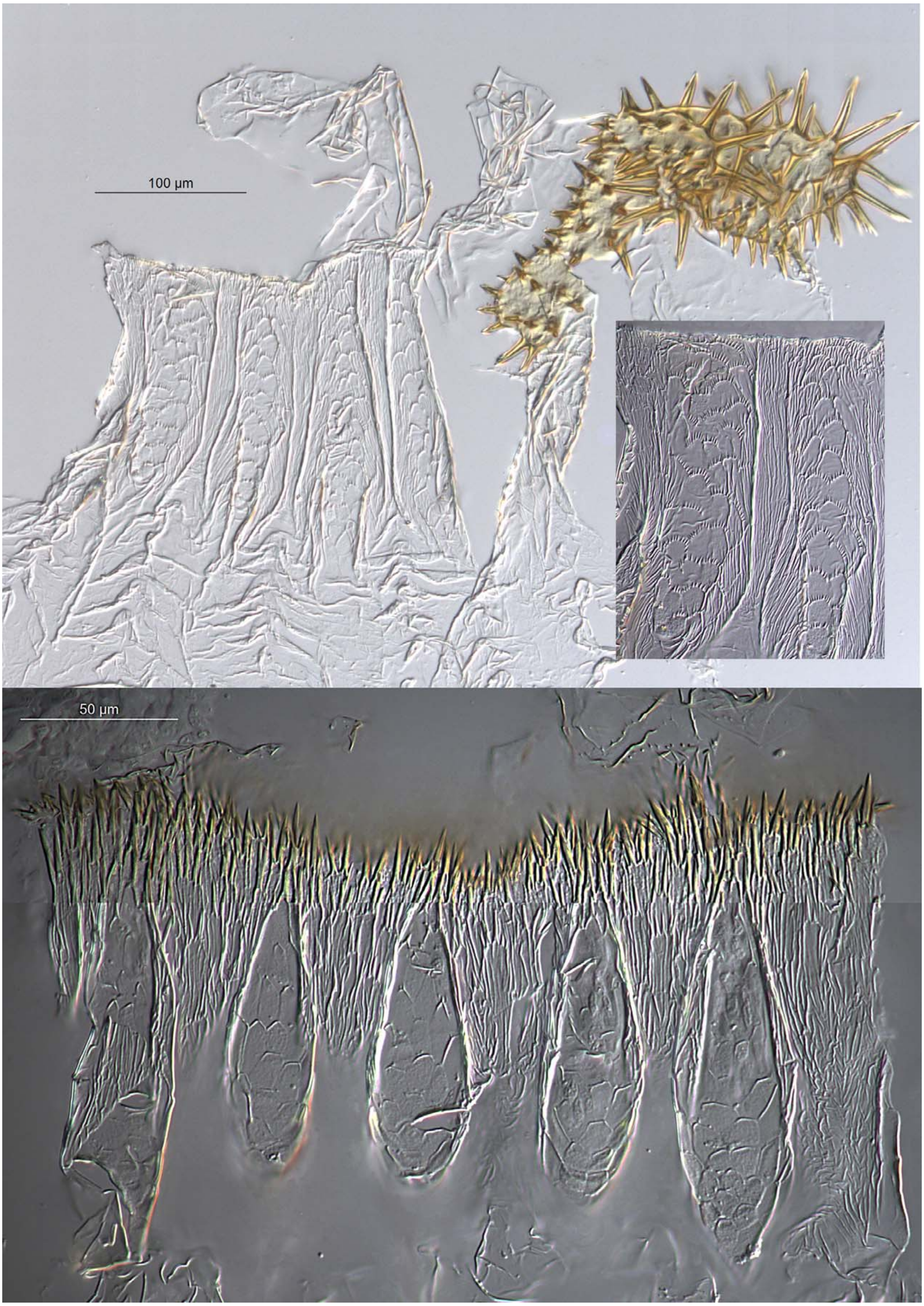

FIGURE 1. Top: *Anoplotermes parvus* (EC431) enteric valve pads anterior to pectinate crown (inset showing texture of pads). Bottom: *Longustitermes manni* enteric valve showing both spines and texture of anterior cushions (PN741).

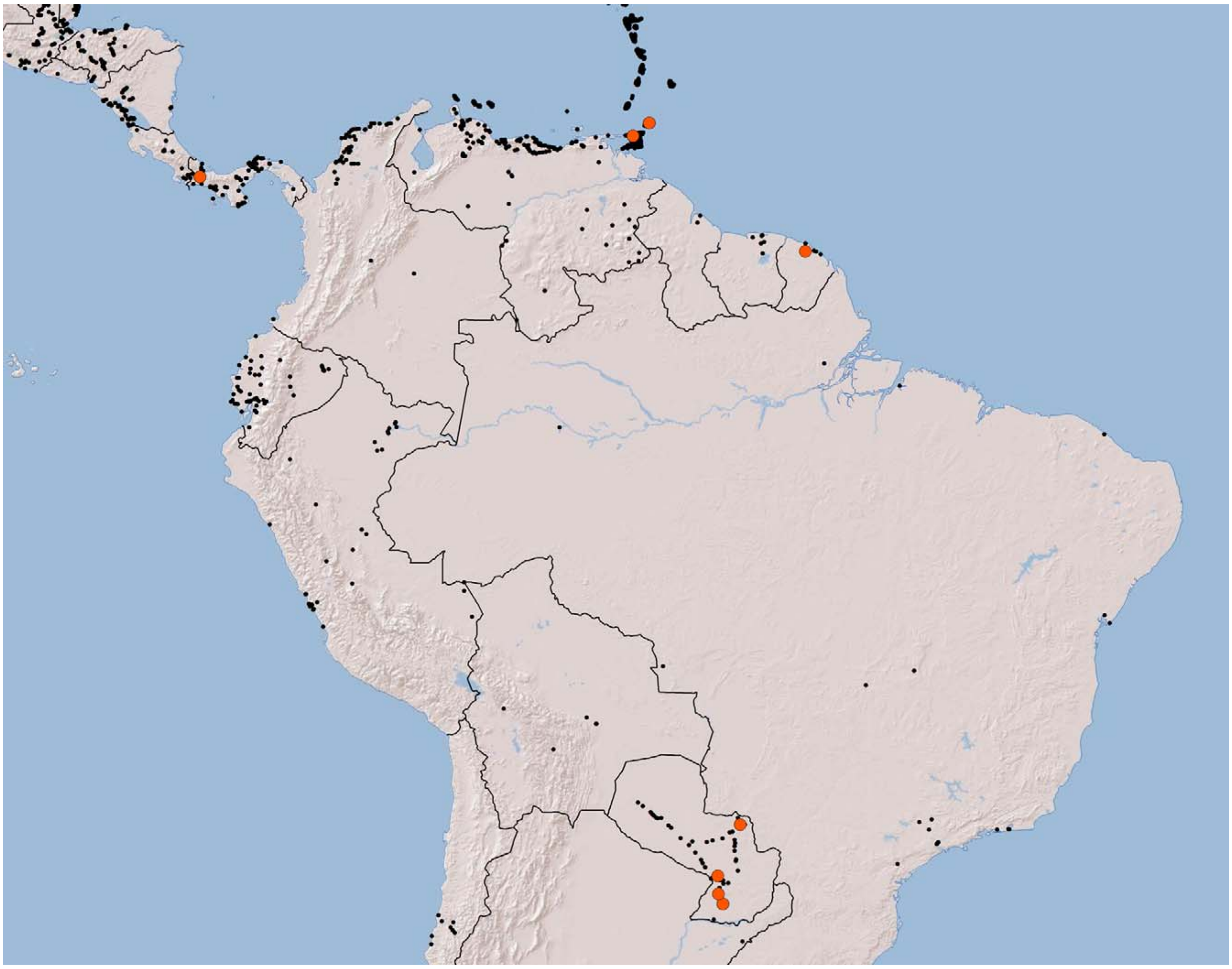

FIGURE 2. Collection localities of *Compositermes vindai* (red dots) and UF collection localities (small black dots).

P2 formed by six slightly incongruent, egg-shaped cushions. Intersection of S and P3 embellished with 15–20 small pectinate paddles visible externally *in situ* under microscope when abdominal integument removed. Apical and marginal teeth of both mandibles sharply triangulate and well-defined from each other; dentition as in Fig. 6.

Diagnosis. The enteric valve cushions, much enlarged and tubular enteric valve seating, and the sclerotized pectinate paddles at the S/P3 junction are unique among all termite workers.

Comparison. *Compositermes* **n. gen.** workers have a long P4 similar to that of *Grigiotermes* Mathews, but the enteric valve cushions of the latter have posterior pectinate pads and no seating. The mandibles of *Compositermes* are most similar to *Ruptitermes* Mathews but workers of the latter genus have short trilobed enteric valve seatings. Unlike *Compositermes*, neither genus has a ring of pectinate paddles at the S/P3 junction.

Etymology. From Latin “compositus” which means an aggregation; made up of parts. This refers to the 15 or more pectinate paddles that form a circular ring around the S/P3 junction.

Compositermes vindai sp. nov.

Holotype: worker, 25MAY2003, Univ. Florida collection no. TT1136.

Type locality. Trinidad: Mount Saint Benedict (10.66630, -61.40126).

Imago unknown (brachypterous nymph shown in Fig. 6).

Worker (Figs. 3–6). Medium to medium-large in size. Head capsule and antennae light yellowish; pronotum and legs hyaline; abdominal integument transparent with no fat body. Antennal articles gradually more pigmented toward distal end. Antennae with 14 articles; 2>3=4<5. Head capsule and pronotum with long scattered setae,

FIGURE 3. *Compositermes vindai* (PA1139) top to bottom: worker in dorsal, right, ventral, and left view. C=crop, M= mesenteron, P1=first proctodeal segment, P2=enteric valve, S=enteric valve seating, P3= third proctodeal segment or paunch, P4=forth proctodeal segment, and P5= fifth proctodeal segment or rectum. Abdominal integument removed and P4-P5 extended out to expose S (S outline highlighted in left view). Approximate juncture of M and P1 shown as black line in ventral view.

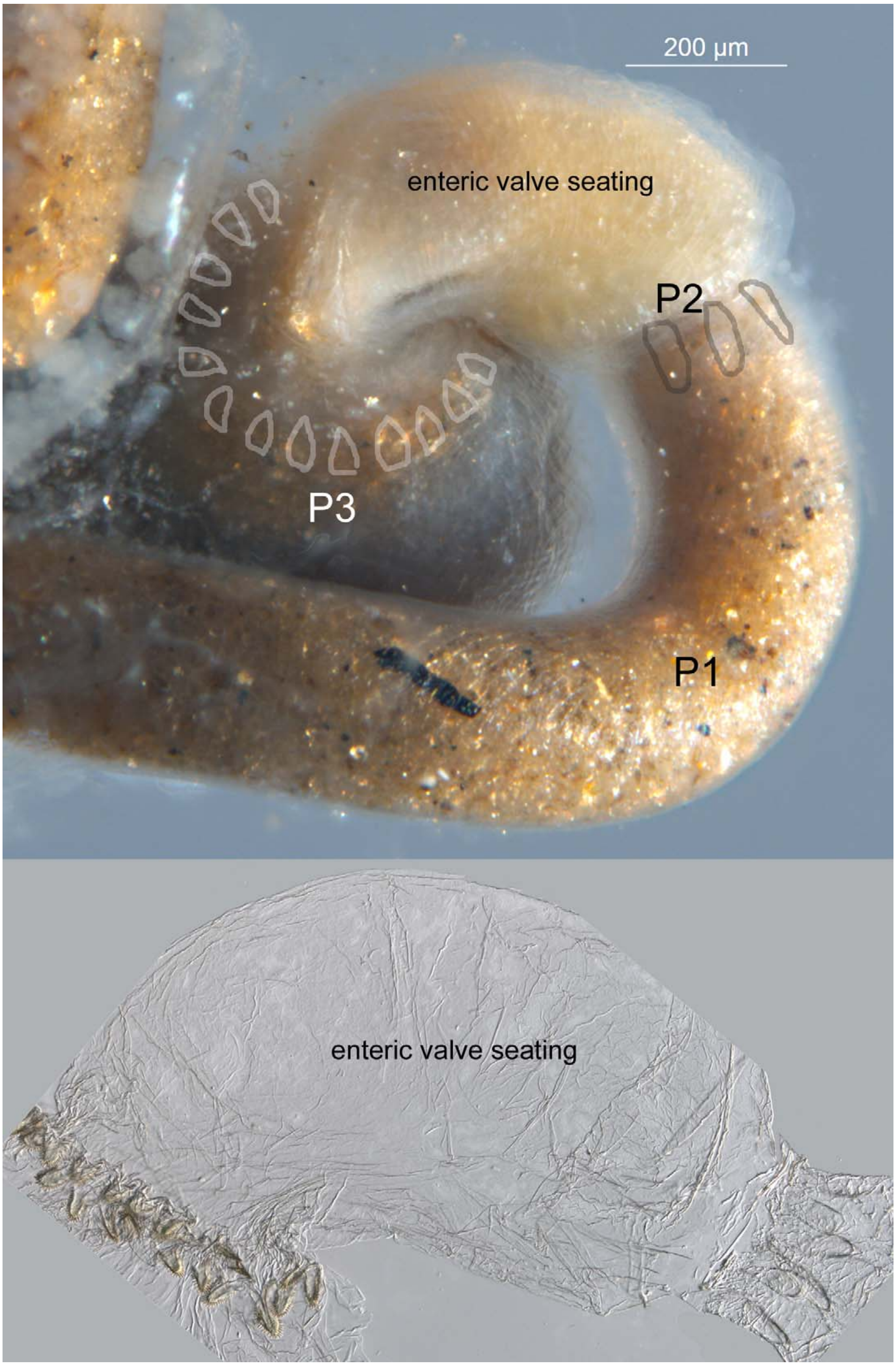

FIGURE 4. Top: dorsolateral view of *Compositermes vindai* (PA1139) worker gut section from the posterior of P1 to the anterior of P3. Enteric valve seating filled with bacteria. Locations of enteric valve cushions (P2) and pectinate paddles at the junction of S and P3 are highlighted diagrammatically. Bottom: P2 to S-P3 (TT618) section with musculature removed and emptied of food to show *in situ* arrangement of enteric valve cushions and pectinate paddles.

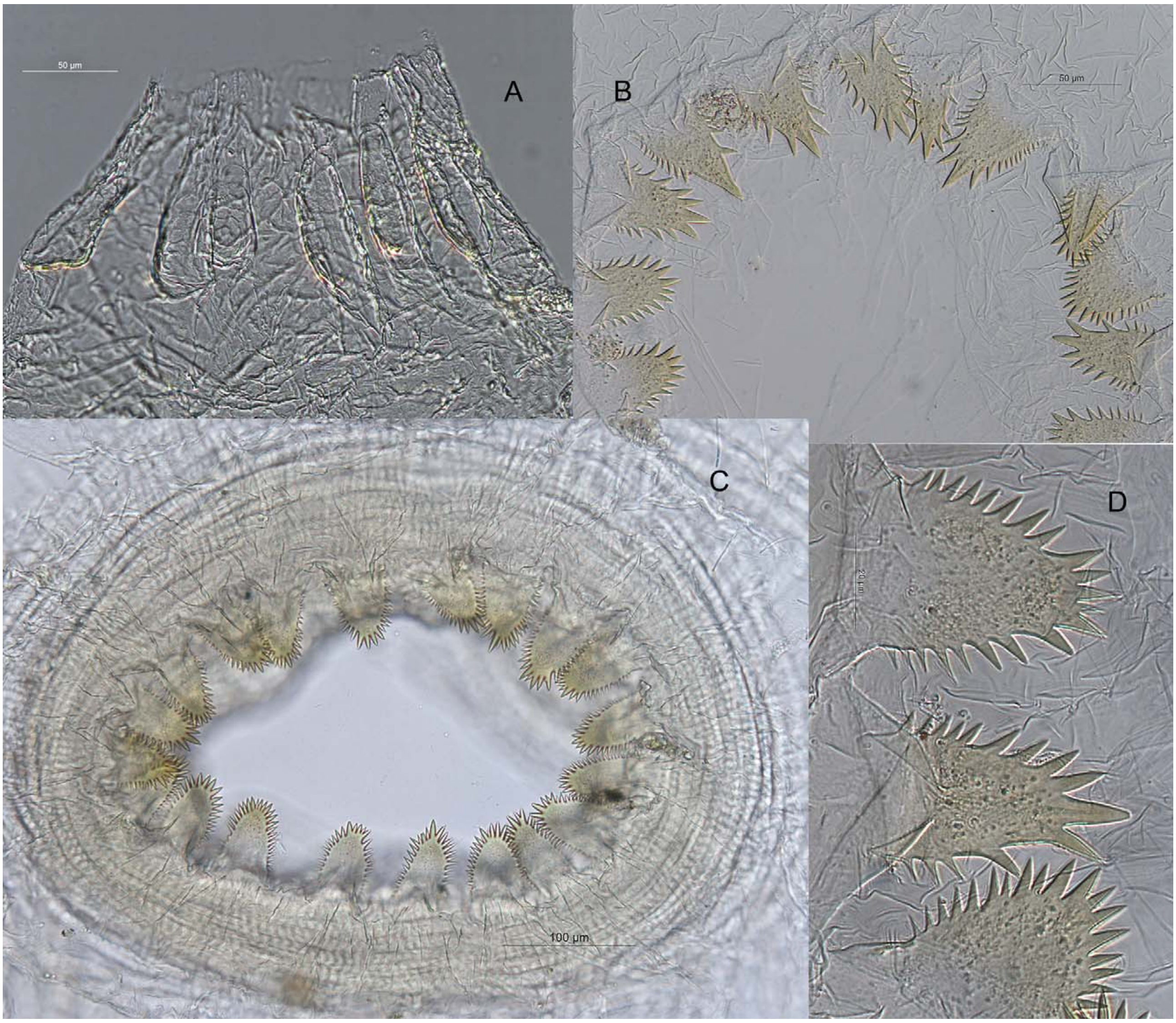

FIGURE 5. A. Worker enteric valve cushions of *Compositermes vindai*, overlapping lateral view (TT618). B. Partial ring of pectinate S-P3 paddles, muscle removed (PN1064). This specimen has 18 paddles. C. Whole ring of S-P3 paddles with muscle, view from P3 lumen. This specimen has 20 paddles (TT618). D. S-P3 paddles showing granular surface, possibly adhering bacteria (PN1064).

pronotum steeply bilobate in lateral view. Postclypeus and fore tibia moderately inflated. Mandibular dentition as in Fig. 6. Gut structure as in generic description and Fig. 3. Six enteric valve cushions in hexaradial arrangement; subequal, 60–80 µm long (Fig. 5A); egg-shaped and distinctly aculeate at posterior (direction of gut contents movement); surface of cushions with 5–10 reticulate polygons. Lining of enteric valve seating (S) smooth, sac-like. Seating surrounded by circular muscles; thicker toward posterior. Intersection of S and P3 embellished with a circular chain of 15–20 pectinate, dome-shaped paddles, each paddle ca. 15µ long; teeth on paddles acutely triangular; 15–30 teeth per paddle depending somewhat on width of individual teeth and width of paddle.

Measurements in mm, (mean±standard deviation, range; n=1, 1 each from 11 samples): FG811, PA1137, PA1140 l, PA1215, PN1064, PN1065, TT616.2, TT618, TT620, TT1136.1, TT1137): maximum head width 0.90±0.06, 0.84–1.01; maximum pronotum width 0.57±0.04, 0.52–0.64; hind tibia length 0.77±0.05, 0.69–0.84; fore tibia length 0.54±0.06, 0.47–0.67; fore tibia maximum width 0.14±0.01, 0.12–0.15; fore tibia length/width ratio 3.98±0.58, 3.17–5.20. Specimens from Tobago (TT616.2, TT618, TT620) proportionally larger in all measurements corresponding to the maximum in each range.

Diagnosis. The intersection of S and P3 in the worker gut is embellished with 15–20 pectinate, dome-shaped paddles each with 15–30 acutely triangulate teeth. In this respect, *C. vindai* does not, even distantly, resemble any other known termite worker.

Comparison. See genus comparison above.

Etymology. *Compositermes vindai* is named in honor of Boudanath (Vinda) Maharajh (1950–2009) who first joined our termite diversity survey team in 1996 at his homeland of Trinidad and Tobago. Vinda participated in another 23 expeditions until his last in 2008 to Venezuela. Vinda's enthusiasm, collecting skills, and automobile driving style will not be forgotten.

Material examined (workers only). French Guiana: Forest W Petit Saut Dam (5.06754, -53.0592), 22 NOV2010, col. J. Krěcěk, UF collection no. FG811; Panama: NE Caldera (8.67241, -82.35207), 31MAY 2010, PN1063-PN1065; Paraguay: Depto. Amanbay, Hwy 5 E at Hwy 3 (-22.68366, -56.21476) 29MAY2012, PA388; Depto. Misiones, San Miguel (-26.52573, -57.04178) 4JUN2012, PA1137-PA1139-PA1141; Depto. Paraguari, Ruta Lago Ypoa (-26.05232, -57.26914) 4JUN2012, PA1215; Depto. Cordillera, Nueva Colombia (-25.17472, -57.28762) 5JUN2012, PA1267; Tobago: Roxborough Rd., NW Roxborough (11.28467-60.60133), 31MAY1996 TT616, TT618, TT620; Trinidad: Forest Trail W. Mount Saint Benedict (10.66630, -61.40126) 25MAY2003, TT1136-TT1137 (holotype and paratype series). All samples collected by those mentioned in the acknowledgments. **Other material examined for Fig. 1**: *Anoplotermes parvus* Ecuador: Francisco de Orellana, Yasuni station area (0.67177, -76.39793), 28MAY2011, EC431, col. R. Scheffrahn. *Longustitermes manni* Panama: Colon, Sierra Llorona, Los Monos trail (9.34321, -79.77535), 4JUN2005, PN741, col. J. Krěcěk, in soil mound with *Coatitermes clevelandi*. All material deposited in the University of Florida Termite collection, Davie, Florida.

Discussion

In the Neotropics, only a few *Anoplotermes*-group species build epigeal (e.g. *A. pacificus*, Fontes 1992) or arboreal (e.g. *A. banksi*, Bourguignon *et al.* 2010) nests, and only species of *Ruptitermes* s.l. forage in the open (Mathews 1977). The great majority of *Anoplotermes*-group species do not build nests or foraging galleries on or above the ground and their workers, like most higher termites, leave the soil only briefly to escort and defend alates emerging for dispersal flights (Scheffrahn *et al.*, unpublished). Workers of non-nest building *Anoplotermes*-group species are found in soil galleries underneath rocks or stones, in and under cow pats, or beneath rotting logs. Some soldierless species also build galleries and nests within the epigeal mounds of other termites. *Compositermes vindai* workers have been collected under stones, and in Paraguay, in the soil nests of *Cornitermes* spp. (Fig. 6). Its gut contents (Fig. 4) contain decomposing organic debris and some silica particles typically ingested by soil-feeding termites.

The area of distribution for *C. vindai* is enormous (Fig. 2) and includes northern Amazonia *sensu lato* (French Guiana, Peres *et al.* 2010). Although we did not find this species during our 2010 expedition to Amazonian Ecuador (Parque Nacional Yasuni), *C. vindai* probably occurs throughout Amazonia, in addition to its circum-amazonian range extending west to Panama, north to Tobago, and south into Paraguay. The encounter of *C. vindai* at latitude -26.5, our southernmost survey site in Paraguay, was unexpected as low temperatures in the winter can occasionally dip below 0°C there. Where it does occur, *C. vindai* tends to be locally abundant; of its eight collection localities, four yielded between two and four separate colonies. The occurrence of some "local endemic" species (really an artifact of limited survey areas) are now known to be widespread (e.g. *A. parvus* Bourguignon *et al.* 2011, and *C. vindai*) and lend support to the findings that Amazonia was broadly forested and had a stable wet climate throughout the Pleistocene (Kastner and Goñi 2003) allowing for slow-dispersing, K-selected organisms, like termites, to expand their range extensively across tropical America.

As with *C. vindai*, all Apicotermitinae and other higher termite subfamilies show a hexaradial arrangement of their enteric valve cushions even though in some species, especially those that feed on soil, the soft cushions are adorned with a striking variety of armatures. The enteric valve cushions and ultrastructure of the enteric valve armatures from selected African apicotermitines are most recently depicted by Donovan (2002) using light and scanning electron microscopy. Her figures demonstrate the uniform hexaradial (*Phoxotermes*), subhexaradial (*Machadotermes*), bilateral (*Jugositermes*), moderate (*Allognathotermes*), and extreme (*Ateuchotermes*) asymmetry of the armature of African soil feeders. In an example of asymmetry in the New World, the *A. parvus* armature inverts into the paunch, posterior to the hexaradial orientation of its enteric valve cushions (Fig. 1). Because the S/PS3 armature of *C. vindai* lacks a hexaradial arrangement and is spatially removed from the enteric valve by its long and tubular seating, it may have evolved as an analogous character to serve the function of the enteric valve armature.

FIGURE 6. Left: dorsal view of *Compositermes vindai* worker mandibles (PA247). Right: field habitus of *C. vindai* workers and nymph in gallery of *Cornitermes* sp. mound (PA1139).

Donovan (2002) hypothesized that the pectinate structures associated with the enteric valve are adaptations to soil feeding. She suggested that the enteric valve armatures filter and channel gut contents based on particle size and food flow. I argue that such “soil fractionation” is not the primary function of this armature. Unlike Bignell (2011), I have yet to observe particle-class sorting in any gut compartment. I suggest an alternative hypothesis: these structures enhance microbial inoculation of ingested material before entry into the paunch. The paunch is the site of greatest microbial fermentation (Tholen & Brune 1999) by a complement of highly diverse and novel symbiotic bacteria (Schmitt-Wagner *et al.* 2003). Noirot (2001) notes that dense bacterial growth occurs in the seating and aptly gives this compartment the alternate name, “bacterial pouch”. I have also observed a dense microbial slime filling the seating as well as bacteria adhering to the armature surfaces of soil feeding species, including *C. vindai* (Fig. 5D). The anterior proximity of the seating allows the armature to impel the inoculum into the stream of food entering the paunch. Mixing of food and bacteria is aided with contraction of thick radial musculature in the area (Fig. 4). Further inference by Donovan (2002) that antiperistalsis, observed in *Cubitermes* by Bignell (2011), enhances particle sorting is also hard to envision based on existing morphology. In the Cubitermitinae, the enteric valve armature consists of mats of spines which angle with the food stream at the entrance to the P3 (Sands 1998). Should an antiperistaltic contraction move the food bolus toward these spines they would resist anterior flow which “goes against the grain” of the spines. Under the inoculation hypothesis, anterior flow, although impeded by the armature, would force the spines into the food, thus facilitating mixing and inoculation. Each termite species has evolved its own design for an inoculation device, either as part of the enteric valve proper, or, in the case of *C. vindai*, as a specialized structure of the enteric valve seating. In addition to sclerotized armature, the enteric valve cushions of almost all soil feeders are lined with thin cuticle in the form of unidirectional scales, spines, and other overlapping plates (Fig. 1, *A. parvus* inset). This lining also resists food particles from flowing backwards.

The described diversity of neotropical Apicotermitinae (Constantino 2012, Bourguignon *et al.* 2011, herein) now stands at 36 species in seven genera. Based on unpublished enteric valve morphology, the UF termite collection has over 80 species and many new genera in this group. Considering the role of termites as decomposers (Lee & Wood 1971), and their dominant biomass (1 g Apicotermitinae/m^2 Brazilian forest (Vasconcellos 2010) vs. 0.4 g primates/m^2 western Amazonia (Peres 1997) and 0.04 g litter frogs/m^2 central Brazil (Deichmann *et al.* 2010), it is hoped that studies on these termites advance at a rate that reflects their ecological status.

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