



Efficient capture of natural history data reveals prey conservatism of cryptic termite predators[☆]



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ABSTRACT

Stenophagy, specialization of a clade on a narrow range of taxa, has not been well studied in speciose clades of predators, principally due to the difficulty of obtaining adequate natural history data. The pantropical Salyavatinae (Hemiptera: Reduviidae; 17 genera, 107 species) contains members with enigmatic morphology and specialized behavior for feeding on termites. All Salyavatinae are suspected specialist termite predators; however, existing observations are limited to seven species. Prior analyses indicate that Salyavatinae may be paraphyletic with respect to another subfamily, Sphaeridopinae, also hypothesized to feed on termites. A molecular phylogeny of these putative termite assassins is here constructed using seven loci from 28 species in nine genera and is used in a dating analysis to shed light on the timing of Neotropical colonization by this primarily Old World clade. DNA extracted from gut contents of 50 individuals was assayed using PCR with prey-specific primers. Molecular assays, along with recent photographs and observations, provide substantial evidence that this clade feeds specifically upon termites, documenting 28 new individual associations. Our phylogeny supports a sister group relationship of the Neotropical genus *Salyavata* with Sphaeridopinae. Termite association data combined with our phylogeny provide evidence of previously unknown prey conservatism among clades of one of the most diverse groups of specialist termite predators.

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1. Introduction

Specialization is widespread in arthropod herbivores (Bernays and Graham, 1988), parasites, parasitoids and provisioners (Price, 1980), but prey specificity in predators is less common. Arthropod predators tend to have less intimate predator–prey relationships than comparable trophic associations of other guilds because predatory relationships are often primarily governed by ecological factors, not intrinsic traits of prey, thus specialization may develop more rarely (Albuquerque et al., 1997). Yet, narrow specialization on groups of typically related prey species, a phenomenon known as stenophagy, does occur, especially within speciose clades of primarily generalist arthropod predators. Specialization of predators involves evolution of one or a series of behavioral, morphological or physiological adaptation(s) for predation, mandating stronger associations between predator and prey (Albuquerque et al., 1997; Darst et al., 2005; Symondson, 2004). It has been shown that specialization enhances efficiency feeding on certain taxa but decreases efficiency on others and evolutionary success depends on either

continued abundance of specific organisms or adaptability to thrive on others (Albuquerque et al., 1997; Futuyma and Moreno, 1988; Rana et al., 2002). Thus, narrow specialization could doom species to extinction. Conversely, narrow host ranges may cause specialists to be more prone to speciation via adaptive radiation or coevolution (Cruaud et al., 2012; Futuyma and Moreno, 1988). Stenophagy of predators may influence diversification rates but few existing studies have found mixed results (e.g., “increased” in Coccinellidae, no formal analysis (Seago et al., 2011); decreased in spiders, not statistically different (Pekár et al., 2012)). Furthermore, well-studied herbivorous and parasitic specialists are frequently coarsely specialized, with a clade-for-clade correspondence tracking subclades of hosts (termed host conservatism), indicating ancient and seemingly irreversible adaptation to one progenitorial taxon with host switching among descendants (Forister and Feldman, 2011; Murray et al., 2013; Percy et al., 2004). Adaptation to subclades of a broader prey taxon (here called prey conservatism) is unknown or undocumented in large clades of specialized predators, potentially because adequate study of stenophagy in predators has been impeded by lack of phylogenetic and biological data. Crucially, reports of prey taxa are rare, anecdotal or unavailable for most potential specialist arthropod predators, especially those native to tropical regions.

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Termites (epifamily Termitoidae; 9 families; 2,933 extant species; [Krishna et al., 2013]) are the most ancient (crown termite divergence dates range from ~150–230 mya (Thorne et al., 2000; Ware et al., 2010) and the second most speciose group of eusocial animals, outnumbered only by ants. Colonies of these two successful eusocial lineages are prevalent in temperate ecosystems but remarkably prolific in tropical environments where they total up to 30% of all animal biomass (Fittkau and Klinge, 1973; Jones and Eggleton, 2000; Wood and Sands, 1978). Considering the antiquity, abundance and ubiquity of termites, specialists exploiting these organisms as food sources are relatively rare. Hypotheses explaining the dearth of natural enemies include stringent defense of termite colonies by soldiers, and cryptic, often subterranean, domiciles (Grace, 1997). However, members of several arthropod groups have managed to evolve strategies overcoming these defenses and are adapted to feed exclusively on termites (Deligne et al., 1981; Disney et al., 2009; Kistner, 1982; Pekár et al., 2012; Wedmann et al., 2013). Although some termites belong to relict lineages such as Mastotermitidae that have existed since the Jurassic (Legendre et al., 2015), termite specialists have a tendency to be associated with members of the more recently derived Termitidae. Termitidae (8 subfamilies, 2072 living species; Krishna et al., 2013), make up the bulk of the diversity of Termitoidae and two groups, in particular, are frequently the targets of termite specialists, Macrotermitinae and Nasutitermitinae. Macrotermitinae (12 genera, 373 living species), the Old World fungus-growing termites, are sister to all other Termitidae and are thought to have originated ~62 mya in Africa having since dispersed to the Oriental region (Aanen and Eggleton, 2005; Brandl et al., 2007). Nasutitermitinae are characterized by soldiers with nozzle-like structures that expel defensive compounds and are the single largest monophyletic termite subfamily (76 genera, ~600 species; Krishna et al., 2013). This abundant pantropical group is thought to be relatively recently derived with the first fossils (e.g., *Nasutitermes* spp.) documented from Mexican and Dominican amber (estimated age 15–20 mya [Iturralde-Vinent and MacPhee, 1996; Krishna, 1996; Coty et al., 2014]).

Reduviidae, or assassin bugs, are the most speciose clade of non-holometabolous insect predators (Froeschner and Kormilev, 1989; Maldonado Capriles, 1990). With the exception of blood-feeding Triatominae (Lent and Wygodzinsky, 1979), reduviids feed on other arthropods, mostly as generalists although several groups are thought to specialize on specific groups of prey e.g., some Holoptilinae on ants (Weirauch et al., 2010; Bulbert et al., 2014), *Phonoctonus* (Harpactorinae) on pyrrhocorids (Stride, 1956; Schaefer, 1987), some Emesinae on spiders (Wygodzinsky, 1966; Soley et al., 2011) and presumably all Ectrichodiinae on millipedes (Forthman and Weirauch, 2012). Certain groups of reduviids also contain suspected specialist termite predators. Nymphs of *Micrauchenus lineola* (Harpactorinae) are inquilines and specialist predators of *Nasutitermes* species in the Neotropics (Bérenger and Pluot-Sigwalt, 2009). Tegeini (Harpactorinae) may all be obligate termite predators as species of *Phonolibes*, *Lophocephala*, and particularly *Tegea* have been observed to prey on termites, specifically *Nasutitermes*, in the Old World (Miller, 1953; Casimir, 1960; Ravichandran, 1988). Some genera of Cetherinae have fed on unspecified termites in captivity e.g., *Eupheno* and *Cethera* (Haviland, 1931; Miller, 1956). *Neivacoris steini* (Reduviinae) have been found in Brazilian termite nests (probably *Cornitermes* [Nasutitermitinae]; Lent and Wygodzinsky, 1947) and two species of *Acanthaspis* (Reduviinae) have been observed to feed on termites but not exclusively (Odhiambo, 1958; Anwar, 1970).

Termite stenophagy has been postulated for all members of Salyavatinae (Weirauch, 2003), a group of 107 described cryptically-colored tropical species in 17 genera (Maldonado Capriles, 1990; van Doesburg and Forero, 2012), although only

seven species have been previously documented in association with termites (see Table A4). *Salyavata mcmahanae*, a species of the only Neotropical genus of Salyavatinae, is the best-documented example. The nymph, camouflaged with the same mix of excrement and saliva that termites use to build domiciles, is reported to reside on nests of *Nasutitermes corniger* (McMahan, 1982). When openings are introduced by falling debris or colony expansion, the bug will seize a termite and feed, unnoticed by soldiers (McMahan, 2005). Exploiting eusocial hygienic behavior, the bug lures additional termites by rhythmically vibrating the first carcass over the breach in the nest and inserting its labium behind the head capsule of the next termite (McMahan, 1983). Nymphs have been observed to feed for up to three hours, successively killing 31 workers with remarkable efficiency (McMahan, 1982). This behavior has been called a “bait and capture” or “fishing” strategy and is considered by some to be one of few examples of tool use in insects (Pierce Jr., 1986). Species of four other genera in Africa and Asia, some of which have enigmatic inflated pro-tibial structures, have also been observed to prey on termites although “fishing” has not been reported for any other species (Ambrose and Ravichandran, 2007; Miller, 1953; Sheppe, 1970). One member of another subfamily, the exclusively Neotropical Sphaeridopinae (6 species), preyed on termites in captivity after collection near a termite nest (P. Wygodzinsky pers. comm. in McMahan [1982]) and these two subfamilies were postulated to be close relatives by Usinger (1943). Based on a morphology-based cladistic analysis of Reduviidae (75 taxa; 162 characters), and despite dramatically different general appearances of these groups, Weirauch (2008) found strong support for a clade comprising Salyavatinae and Sphaeridopinae, based on two male genitalic characters and virtually identical mouthparts in the two groups. In that analysis, the Neotropical genus *Salyavata* was supported as sister clade to the Sphaeridopinae, based on four mouthpart, antennal, head and female genitalic characters, rendering Salyavatinae paraphyletic (Weirauch, 2008).

To clarify relationships of these putative termite assassins, we construct the first comprehensive molecular phylogeny of Salyavatinae and Sphaeridopinae with inclusion of data from eight additional genera, including the first molecular data available for Sphaeridopinae. Furthermore, we address the issue of lacking natural history data concerning this infrequently observed tropical group with molecular techniques (i.e. PCR with newly developed termite-specific primers on reduviid gut contents), used here for the first time in a phylogenetic context on species of hypothesized specialist predators. These data are supplemented with recent observations and crowd-sourced photographic evidence of Salyavatinae species in close association with termites and this information is used to document prey conservatism of clades of Salyavatinae to groups of termite prey. Lastly, a divergence-dating analysis is conducted to elaborate evidence-based hypotheses relating to the pantropical distribution of this group and integrate observed biogeographic patterns with those of their prey taxa.

2. Materials and methods

2.1. Natural history data reports

Images of live Salyavatinae were collected through popular photo-sharing websites (Flickr, iSpot, Project Noah, Facebook) as well as from communications with various scientists. More than 125 images of identified Salyavatinae representing at least 17 species are now catalogued and publicly available by means of a Flickr account (<https://www.flickr.com/people/102169367@N08>). Termites were identified to genus, when possible, using separate photographs of conspecific soldiers. Images documenting very

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