



A call to termitologists: it is time to abandon the use of “lower” and “higher” termites

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Received: 16 June 2023 / Revised: 31 July 2023 / Accepted: 8 August 2023

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Abstract

This commentary paper addresses the outdated and misleading terminology used to categorize termites into “higher” and “lower”. These terms perpetuate a linear progression view of evolution, which is both inaccurate and detrimental to our understanding of the diversity of life. We trace the historical origins of these terms and highlight their flawed interpretation of evolutionary relationships. We advocate for the adoption of Termitidae (or termitid), rather than “higher termites”. As for the paraphyletic group of “lower termites”, we recommend refraining from grouping them together, unless specifically referring to their symbionts. In such cases, we propose “protist-dependent termites” or “non-Termitidae termites”.

Commentary

Biological evolution has always been subject to denial and misunderstanding in our society. One of the most adverse misconceptions is the notion of a linear progression from simple to complex organisms, often represented by the “march of progress” image, leading inevitably to *Homo sapiens* (Gould 1989; Minelli 2008; Santos et al. 2019). This concept is reminiscent of the *Scala Naturae* or “chain of being”, which traces its origins back to Plato and Aristotle, although significantly revised and promoted by medieval

Christian scholars (Lovejoy 1964). It stems from the intuitive belief that all living organisms on Earth can be arranged in a hierarchical order of complexity, with our species occupying the highest position and the most “primitive” forms of life at the bottom (Lovejoy 1964). The conventional understanding of the evolutionary process, influenced by the “march of progress” and the *Scala Naturae*, presents an oversimplified and flawed depiction of the natural world (Minelli 2008). This viewpoint categorizes extant organisms as “primitive” or “advanced” and assigns hierarchical positions of “lower” or “higher” to different groups, and along with these labels a flood of false connotations tied up in such terms. However, this interpretation not only misunderstands and obscures the nature of evolution, but also perpetuates harmful notions of human presumption of superiority and undermines the intricate complexity and interconnectedness that characterizes the diversity of life.

Charles Darwin, in a note scribbled on the margin of his copy of Robert Chamber's *Vestiges of the Natural History of Creation*, wisely advised himself to refrain from using the terms “higher” or “lower” (Gould 1977). However, despite recognizing the limitations of a linear portrayal of evolution, specific segments of the scientific community persist in labeling biological groups as such, perpetuating the use of vestigial terms that have been carried over during history. The initial misconceptions about the fundamental concept of common descent, which forms the basis for constructing evolutionary trees, i.e., phylogenies (Gregory 2008),

Appendix for the full list of supporting signatories.

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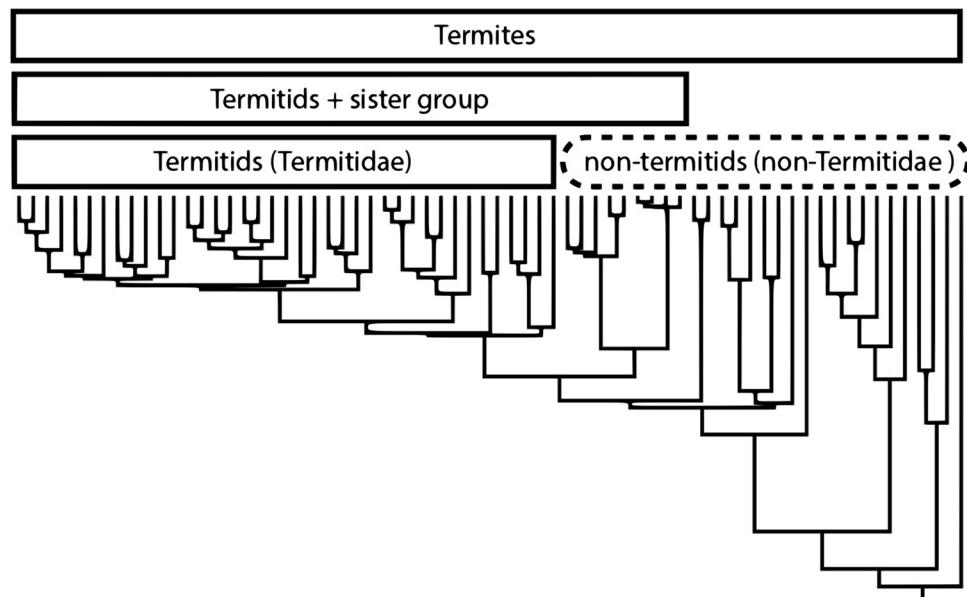
irrevocably seeded its persistent erroneous interpretation. The continuation of the use of terms that could now be considered as anachronistic may also be out of convenience for many, despite an acknowledgement that such terms are problematic. However, in a phylogeny of extant species, which evolved for an equal time from a common ancestor, comparisons made between sister lineages should be preferable to comparisons made between a taxon and the paraphyletic group composed of its relatives (Minelli 2008; Omland et al. 2008).

In the study of social insects, a long list of terms commonly used in insect sociobiology remains problematic for their underlying connotation and historical use (Breed 2020). Among termitologists, there is an extensive history of using the terms "lower termites" and "higher termites" (Fig. 1). The so-called "higher termites" encompass termites belonging to the monophyletic family Termitidae, which exhibit the most remarkable species diversity and a wide range of lifestyle habits. These termites have lost their flagellated protist symbionts (Parabasalia and Oxymonadida). Conversely, the term "lower termites" represents a non-monophyletic group (i.e., a grade) that includes all remaining families of Isoptera to the exclusion of Termitidae, and also exhibits a wide range of lifestyle traits. The dependence on unicellular eukaryotic symbionts in their hindguts, which play a vital role in lignocellulose digestion, is a plesiomorphic trait of the termites and is shared with the cockroaches of the genus *Cryptocercus*, sister group of all termites (Cleveland 1934; Krishna et al. 2013).

The categorization of termites into "higher" and "lower" likely originated with Foggatt's studies on *Mastotermes darwiniensis* Foggatt (1896, 1897, 1898). During the late nineteenth century, all termites were grouped under the

family Termitidae and Foggatt further divided them into subfamilies, perceiving certain groups as relatively "primitive" compared to the more "advanced" forms. Among these, *M. darwiniensis* was considered the most primitive termite species (Krishna et al. 2013). Such notions were further codified by Holmgren (1911, 1912) who created three families specifically to emphasize the linear progression of evolutionary "advance" in Isoptera: the "primitive" Protermitidae, the slightly more "advanced" Mesotermitidae, and ultimately the more "advanced" Metatermitidae. Snyder (1924) then recognized Mastotermitidae as "the most primitive termite" (p. 76) and classified the remaining Isoptera into three families: Termitidae (referred to as "higher termites"), Kalotermitidae (referred to as "lower termites"), and Rhinotermitidae (considered "intermediate"), setting the basis for modern family-level termite classification (Bourguignon et al. 2017). The presence of plesiomorphic "cockroach-like" traits (e.g., large pronotum, conspicuous styli, mandibular dentition, and wing venation), in *Mastotermes*, *Hodotermopsis*, *Zootermopsis*, *Archotermopsis*, *Stolotermes*, and *Porotermes* has long perpetuated the interpretation that such termites were "primitive", "archaic", or "living fossils" (an oxymoronic term) (Grassé 1986; Holmgren 1911; Howse 1968; Imms 1919; Martynov 1937; Thorne and Carpenter 1992; Wier et al. 2002; but for a different perspective on using "living fossil", see Cavin and Guinot 2014). Ultimately, the term "lower termite" was generally adopted in the mid-twentieth century as a convenient way to represent all non-termitid taxa. This oversimplification often resulted in lumping termite groups with widely different biologies, behaviors and ecologies such as *Mastotermes*, *Hodotermes*, *Cryptotermes*, and *Coptotermes* in the same basket, under the argument that they all "still" possess protists in their guts.

Fig. 1 Termite phylogeny showing the monophyletic family Termitidae (traditionally referred to as "higher termites") and the paraphyletic group of non-termitid termites (traditionally: "lower termites"). The sister group of Termitidae is a clade composed of the genera *Coptotermes*, *Heterotermes*, and *Reticulitermes*. Phylogenetic tree based on Buček et al. 2019



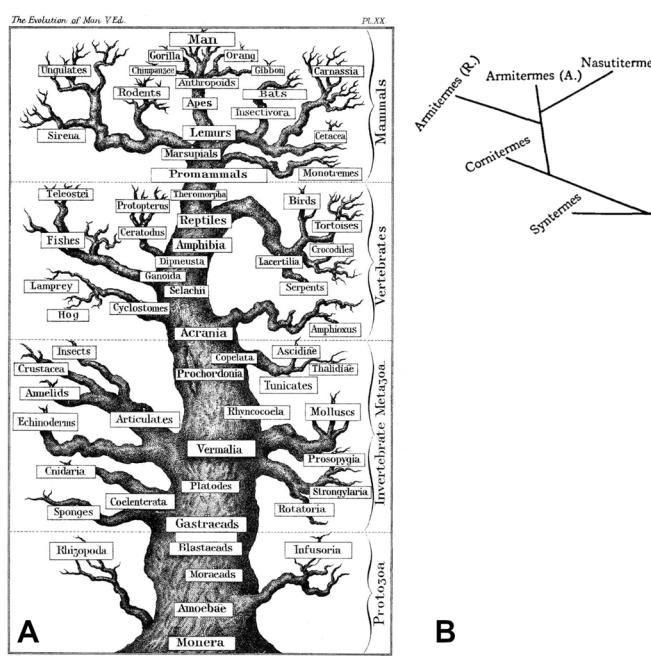
Similarly, the use of “highly evolved” or “evolutionary advanced” terms to describe Termitidae became accepted, as exemplified by Ahmad (1950, p. 95): “The Termitidae are the (...) most highly evolved family” and derived from an ancestor within Rhinotermitidae. Such interpretative shortcut was common before Hennig's work on *Phylogenetic Systematics* (1966), where phylogenetic diagrams often depicted groups in a linear sequence, with the more “primitive” groups (i.e., early diverging) positioned at the bottom and progressing to the supposedly more “evolved” groups in a chain-like arrangement (Fig. 2). After Hennig, however, the three-taxon statement—a taxon A is more closely related to a taxon B than a taxon C, since A and B share a most recent common ancestor that is not shared by C, which made A the “sister group” of B—became the standard for comprehending evolutionary relationships. This three-taxon statement replaced the ancestor–descendant representation advocated by systematists in the era of the Modern Synthesis (Santos 2008).

The acknowledgment of the problematic nature of ranking extant termites in terms of supposed advancement is not a recent development (Eggleton and Tayasu 2001; Emerson 1938; Nalepa 2011; Roisin 1999). However, despite the establishment of phylogenetic systematics and the widely accepted usage of the term “sister group” since the 1980s, the terms “higher termites” and “lower termites” have persisted in the scientific literature (e.g., Bai et al. 2022; Bourguignon et al. 2017; Chouvenc et al. 2021; Hellemans et al. 2019; Korb and Hartfelder 2008; Marynowska et al.

2023; Noirot 2001). Such persistence most likely stems from its historical use and its perpetuation across academic generations, but also out of convenience, in the absence of universally accepted alternatives. While many authors use quotation marks around these terms to indicate their inadequacy, it is worth considering moving away from such terms altogether.

The most suitable term to replace “higher termites” is Termitidae itself. This family is monophyletic (Bucek et al 2019), and while there has been some debate about potentially reclassifying it as a subfamily (Eggleton et al. 2007; Lo et al. 2007), there is currently a consensus to retain its classification as a family.

Regarding the designation of “lower termites”, as all Isoptera except Termitidae, the recommended approach is to avoid treating it as a distinct grouping. Phylogenetically speaking, the “lower termites” form a paraphyletic grade, which means it is not a natural (sensu Hennig 1966) or cohesive unit (i.e., it is not a formal taxon). While we acknowledge that this terminology is not a formal classification, the indiscriminate practice of grouping all termite families except Termitidae into a single “lower termite” category, emphasizes their shared characteristics, which are not extensive (aside from the plesiomorphic presence of obligate flagellated symbionts). As an example, it is not uncommon to see authors generalizing traits of non-termitid termites, indicating that all have a linear developmental pathway, with pseudergates (e.g. Korb and Hartfelder 2008), while many different lineages have a bifurcated pathway, with true



B



Fig. 2 Examples of pre-Hennigian phylogenetic diagrams. Haeckel's (1874) tree of life (A) and Hare's (1937) phylogeny of termites (B)

workers (e.g. *Mastotermes*, *Coptotermes*, *Hodotermes*, *Rhinotermitidae*) (Roisin 2000; Roisin and Korb 2011). Thus, maintaining the use of a paraphyletic group distorts the exploration of unique traits and obscures homology inferences and significant trait gain or loss (Chouvenc et al. 2021). On the other hand, named paraphyletic groups can eventually serve a purpose. In this case, “non-Termitidae” (and its common name equivalent “non-termitid”) is a non-stigmatized term previously used to refer to the “lower termites” (Eggleton and Tayasu 2001; Roisin 1999) which meets the minimal goal of this commentary: to retire the evolutionary misleading “lower” term.

Since the presence or absence of flagellated nutritional symbionts is the only trait that creates a dichotomy between Termitidae and the rest of termites, an alternative solution would be to state this information directly. Therefore, the terms “protist-dependent” and “protist-independent” could be used. These terms have begun to appear in the literature (Velenovsky et al. 2023). It is important to note that the term “protist” is also a non-monophyletic group because it includes all eukaryotes except for animals, plants, and fungi. However, there are many such informal terms for organisms that do not indicate relatedness (e.g., “tree”), and the term “protist” does not carry the same type of misleading connotation as “higher” or “lower”. As an alternative, “flagellate-dependent” and “flagellate-independent” could be used, since the protist symbionts of non-termitid termites have often been referred to generally as “flagellates” in the literature. Flagellates are not a monophyletic group either, but the term is more specific than “protist” while still being accessible to non-protistologists. Moreover, the protist symbionts of termites are not themselves a monophyletic group; multiple lineages of flagellates have colonized the termite hindgut independently and become dependent on their hosts. If we wished to use a clade name to denote the flagellates, the most inclusive clade that includes all termite symbionts is Metamonada. This is not a familiar term outside of protistology and therefore is not likely to be adopted as a replacement, i.e., “Metamonada-dependent” instead of “lower”.

In conclusion, termite researchers should discard the outdated terminology of “higher” and “lower” (as well as “basal”, “derived”, “ancestral”, “primitive”, “advanced”, or “living fossil”) termites, when referring to extant taxa or groups. These terminologies only reinforce misconceptions about inherent superiority or inferiority among different taxa and perpetuates the misguided belief that certain lineages are more advanced or evolved than others. In reality, all extant species have gained and lost many unique traits since the divergence from a common ancestor. Moreover, the antiquated concept of a linear ladder of nature, advocated by early naturalists, was replaced more than six decades ago by understanding a branching tree of life that does not endorse any progressive view of evolution.

Researchers and scientific communities are responsible for embracing the transformative impact of phylogenetic systematics on our understanding of evolutionary relationships among organisms. This entails promoting accurate communication and facilitating a more profound comprehension of evolution within scientific circles and for non-academic audiences. To promote a comprehensive understanding of organisms' evolutionary relationships and characteristics, it is essential to employ precise and descriptive terminology that strikes a balance between accessibility to a broad audience and meeting the needs of experts in the field. Let us endeavor to develop a more inclusive and nuanced understanding of evolution that acknowledges the intricate interconnectedness of life and celebrates the rich diversity of the natural world. As mentioned earlier, we strongly advocate for the adoption of the name Termitidae or its common name/adjectival version, termitid, rather than using the term “higher termites”. As for the “lower termites”, we recommend refraining from grouping them together, unless specifically referring to their symbionts. In such cases, we propose “protist-dependent termites” or “non-Termitidae termites” (or its common name/adjectival equivalent “non-termitid termites”). A “paraphyletic group of” can be added to further emphasize that such a group is not a formally recognized taxon.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00040-023-00929-0>.

Acknowledgements Authors are thankful to all the participants of the ‘2022 International Termite Course’ (Ft Lauderdale, FL, USA), the event that nurtured this collaboration. We are grateful to the São Paulo Research Foundation (FAPESP) for grants #2020/06041-4 (TFC), #2017/11768-8 (CMDS), #2014/11982-1 (JPC), #2020/08121-5 (IH), and #2018/22839-6 (AA); and to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for grants #304027/2022-7 (CMDS) and #308408/2019-5 (EMC).

Data availability There is no data available.

References

- Ahmad M (1950) The phylogeny of termite genera based on imago-worker mandibles. *Bull Am Mus Nat Hist* 95:37–86
- Bai ZD, Shi CY, Sillam-Dussès D, Wang RW (2022) Elusive workers are more likely to differentiate into replacement reproductives than aggressive workers in a lower termite. *Curr Zool*. <https://doi.org/10.1093/cz/zoac040>
- Bourguignon T, Lo N, Šobotník J, Ho SYW, Iqbal N, Coissac E, Lee M, Jendryka MM, Sillam-Dussès D, Křížková B, Roisin Y, Evans TA (2017) Mitochondrial phylogenomics resolves the global spread of higher termites, ecosystem engineers of the tropics. *Mol Biol Evol* 34(3):589–597. <https://doi.org/10.1093/molbev/msw253>
- Breed MD (2020) The importance of words: revising the social insect lexicon. *Insectes Soc* 67(4):459–461. <https://doi.org/10.1007/s00040-020-00783-4>
- Bucek A, Šobotník J, He S, Shi M, McMahon DP, Holmes EC, Roisin R, Lo N, Bourguignon T (2019) Evolution of termite

- symbiosis informed by transcriptome-based phylogenies. *Curr Biol* 29(21):3728–3734. <https://doi.org/10.1016/j.cub.2019.08.076>
- Cavin L, Guinot G (2014) Coelacanths as “almost living fossils.” *Front Ecol Evol* 2:49. <https://doi.org/10.3389/fevo.2014.00049>
- Chouvenc T, Šobotník J, Engel MS, Bourguignon T (2021) Termite evolution: mutualistic associations, key innovations, and the rise of Termitidae. *Cell Mol Life Sci* 78(6):2749–2769. <https://doi.org/10.1007/s00018-020-03728-z>
- Cleveland LR (1934) The wood feeding roach *Cryptocercus*, its protozoa, and the symbiosis between protozoa and roach. *Mem Am Acad Arts Sci* 17:185–342
- Eggleton P, Tayasu I (2001) Feeding groups, lifetypes and the global ecology of termites. *Ecol Res* 16:941–960. <https://doi.org/10.1046/j.1440-1703.2001.00444.x>
- Eggleton P, Beccaloni G, Inward D (2007) Response to Lo et al. *Biol Lett* 3:564–565. <https://doi.org/10.1098/rsbl.2007.0367>
- Emerson AE (1938) Termite nests — a study of the phylogeny of behavior. *Ecol Monographs* 8(2):247–284
- Froggatt WW (1896) Australian termitidae, part I. Proceed Linn Soc New South Wales. <https://doi.org/10.5962/bhl.part.24356>
- Froggatt WW (1897) Australian termitidae, part II. Proceed Linn Soc New South Wales. <https://doi.org/10.5962/bhl.part.8483>
- Froggatt WW (1898) Australian termitidae, part III. Proceed Linn Soc New South Wales. <https://doi.org/10.5962/bhl.part.12741>
- Gould SJ (1977) Ever since Darwin: reflections on natural history. W.W. Norton, New York
- Gould SJ (1989) Wonderful life: the Burgess Shale and the nature of history. W.W. Norton, New York
- Grassé PP (1986) Termitologia, Vol III. Comportement - Socialité - Ecologie - Evolution - Systematique. Masson, Paris
- Gregory TR (2008) Understanding evolutionary trees. *Evol Educ Outreach* 1:121–137. <https://doi.org/10.1007/s12052-008-0035-x>
- Haeckel E (1874) Anthropogenie: oder, Entwicklungsgeschichte des Menschen: gemeinverständlich wissenschaftliche Vorträge über die Grundzüge der menschlichen Keimes- und Stammes-Geschichte. Engelmann, Leipzig
- Hare L (1937) Termite phylogeny as evidenced by soldier mandible development. *Entomol Soc Am* 37:459–486. <https://doi.org/10.1093/esa/30.3.459>
- Hellemans S, Dolejšová K, Křivánek J, Fournier D, Hanus R, Roisin Y (2019) Widespread occurrence of asexual reproduction in higher termites of the *Termitidae* (Termitinae). *BMC Evol Biol*. <https://doi.org/10.1186/s12862-019-1459-3>
- Hennig W (1966) Phylogenetic systematics. University of Illinois Press, Urbana
- Holmgren N (1911) Termitenstudien. 2. systematik der termiten die familien mastotermitidae, protermitidae und mesotermitidae. *Kungliga Sven Vetensk Akademiens Handl* 46(6):1–86
- Holmgren N (1912) Termitenstudien. 3. systematik der termiten die familie metatermitidae. *Kungliga Sven Vetenskaps-Akademiens Handl* 48(4):1–166
- Howse PE (1968) On the division of labour in the primitive termite *Zootermopsis nevadensis* (Hagen). *Insectes Soc* 15:45–50
- Imms AD (1919) On the structure and biology of *Archotermopsis*. *Isoptera Philos Trans Roy Soc Lond Ser B* 209:75–180
- Korb J, Hartfelder K (2008) Life history and development—a framework for understanding developmental plasticity in lower termites. *Biol Rev Camb Philos Soc* 83:295–313. <https://doi.org/10.1111/j.1469-185X.2008.00044.x>
- Krishna K, Grimaldi DA, Krishna V, Engel MS (2013) Treatise on the Isoptera of the world. *Bull Am Mus Nat Hist* 371:1–2704
- Lo N, Engel MS, Cameron S, Nalepa CA, Tokuda G, Grimaldi D, Kitade O, Krishna K, Klass KD, Maekawa K, Miura T, Thompson GJ (2007) Save Isoptera: a comment on Inward et al. *Biol Lett* 3:562–565. <https://doi.org/10.1098/rsbl.2007.0264>
- Lovejoy AO (1964) The great chain of being. Harvard University Press, Cambridge, MA/London
- Martynov AV (1937) Wings of termites and phylogeny of Isoptera and of allied groups of insects. *Acad Sci USSR, N.Y.*, Moscow (N.Y. Nassanov memorial vol.) 83–150.
- Marynowska M, Sillam-Dussès D, Untereiner B, Klimek D, Goux X, Gawron P, Roisin Y, Delfosse P, Calusinska M (2023) A holobiont approach towards polysaccharide degradation by the highly compartmentalised gut system of the soil-feeding higher termite *Labiotermes labralis*. *BMC Genom* 24:115. <https://doi.org/10.1186/s12864-023-09224-5>
- Minelli A (2008) Perspectives in animal phylogeny and evolution. Oxford University Press
- Nalepa CA (2011) Body size and termite evolution. *Evol Biol* 38(3):243–257. <https://doi.org/10.1007/s11692-011-9121-z>
- Noirot C (2001) The gut of termites (Isoptera) comparative anatomy, systematics, phylogeny. II.-higher termites (Termitidae). *Ann Soc Entomol Fr* 37:431–471
- Omland KE, Cook LG, Crisp MD (2008) Tree thinking for all biology: the problem with reading phylogenies as ladders of progress. *BioEssays* 30:854–867. <https://doi.org/10.1002/bies.20794>
- Roisin Y (1999) Philopatric reproduction, a prime mover in the evolution of termite sociality? *Insectes Soc* 46:297–305. <https://doi.org/10.1007/s000400050149>
- Roisin Y (2000) Diversity and evolution of caste patterns. In: Abe T, Bignell DE, Higashi M (eds) Termites evolution, sociality, symbioses, ecology. Springer, Dordrecht, pp 95–119. https://doi.org/10.1007/978-94-017-3223-9_5
- Roisin Y, Korb J (2011) Social organisation and the status of workers in termites. In: Bignell DE, Roisin Y, Lo N (eds) Biology of termites: a modern synthesis. Springer Press, Heidelberg, pp 133–164. https://doi.org/10.1007/978-90-481-3977-4_6
- Santos CMD (2008) Os dinossauros de Hennig: sobre a importância do monofiletismo para a sistemática biológica. *Sci Stud* 6(2):179–200. <https://doi.org/10.1590/S1678-31662008000200003>
- Santos PS, Pugliese A, Santos CMD (2019) A iconografia linear da evolução na perspectiva de docentes que atuam na Educação Básica. *Ens Pesqui Educ Ciênc* 21:e10594. <https://doi.org/10.1590/1983-21172019210117>
- Snyder TE (1924) “Adaptations” to social life: the termites (Isoptera). *Smithson Misc Collect* 76:1–14
- Thorne BL, Carpenter JM (1992) Phylogeny of the dictyoptera. *Syst Entomol* 17:253–268
- Velenovsky JF, De Martini F, Hileman JT, Gordon JM, Su NY, Gile GH, Chouvenc T (2023) Vertical transmission of cellulolytic protists in termites is imperfect, but sufficient, due to biparental transmission. *Symbiosis*. <https://doi.org/10.1007/s13199-023-00917-9>
- Wier A, Dolan M, Grimaldi D, Guerrero R, Wagensberg J, Margulies L (2002) Spirochete and protist symbionts of a termite (*Mastotermes electrodominicus*) in Miocene amber. *PNAS* 99:1410–1413. <https://doi.org/10.1073/pnas.022643899>