Fungal Ecology xxx (xxxx) xxx

Contents lists available at ScienceDirect

Fungal Ecology

journal homepage: www.elsevier.com/locate/funeco

On interactions, associations, mycetangia, mutualists and symbiotes in insect-fungus symbioses

Fernando E. Vega [a, *], Peter H.W. Biedermann [b]

[a] Sustainable Perennial Crops Laboratory, U. States Department of Agriculture, Agricultural Research Service, Beltsville, MD, 20705, USA
[b] Research Group Insect-Fungus Symbiosis, Department of Animal Ecology and Tropical Biology, University of Wuerzburg, Germany

ARTICLE INFO

Article history:
Received 28 October 2019
Received in revised form
14 December 2019
Accepted 17 December 2019
Available online xxx

Corresponding Editor: Lynne Boddy

Keywords:
Etymology
Mutualism
Scientific terms
Semantics
Symbiotic
Terminology

ABSTRACT

There is some confusion in the scientific literature concerning terms involving insect-fungus symbioses, including associations vs. interactions, mycetangia vs. mycangia, symbiote vs. symbiont, and symbiosis vs. mutualism. We present a rationale that demonstrates the difference between an association and an interaction, and why the correct term for exoskeletal cavities that harbor fungi should be mycetangia. In addition, symbiote should be used over symbiont due to its etymology. Precise, common use of terms is important in scientific communication.

Published by Elsevier Ltd.

1. Introduction

In “Advice to a Young Scientist,” P.B. Medawar (1981) writes: “Another little rule (for medical scientists especially) is that mice, rats, and other laboratory animals should never be injected. Few hypodermic needles are large enough for even the smallest mouse to pass through, especially if it is injected with something. (“Mice were injected with rabbit serum albumin mixed with Freund's adjuvant,” we read. “Ah, but what into?” the cry goes up.) Mice should receive injections, or substances should be injected into them.” This is a humorous example of imprecise scientific writing, and many papers have been published on the importance and need for defining and using precise terminology, e.g., ecological terms (Jax et al., 1992), parasitism and symbiosis (Lewin, 1982), symbiosis (Martin and Schwab, 2013), psychology and psychiatry (Lillenfeld et al., 2015), kairomones (Ruther et al., 2002), microbiome studies (Tipton et al., 2019), sustainability (Glavič and Lukman, 2007), and endophytism (Wilson, 1995), among others.

To better understand insect-fungus symbioses, it is important to define the use of various terms commonly used in the scientific literature, associations vs. interactions, mycetangia vs. mycangia, symbiote vs. symbiont, and symbiosis vs. mutualism. Our goal is to encourage scientists to use a common and correct terminology.

2. Associations vs. interactions

In a biotic association (co-occurrence), the specific effects of two dissimilar organisms on each other might or might not be known and could also be referred to as a symbiosis. In contrast, use of the term interaction, implies, by definition, a reciprocal action or influence (The New Shorter Oxford English Dictionary, 1993), i.e., a particular effect of “organism A” on “organism B” has been determined, and *vice versa*. It is quite common to see the term “interaction” in the scientific literature, when “association” would be more appropriate, as reciprocal effects (interspecific interactions) have not been elucidated. In other words, “An interaction wouldn't *be* an interaction if it had no effect, because we're *defining* interactions by their effects …” (Malcolm, 1966).

3. Refer to them as symbiotes, not symbionts

The term “symbiosis” originates from the Greek συμβιώσεως

* Corresponding author.
E-mail address: Fernando.Vega@ars.usda.gov (F.E. Vega).

https://doi.org/10.1016/j.funeco.2019.100909
1754-5048/Published by Elsevier Ltd.

(sumbíōsis), meaning "living together." In 1879, the German scientist Heinrich Anton de Bary (1831–1888), gave the word a biological context, defining it as "dissimilarly named organisms that live together, in symbiosis, as we can call these associations" (de Bary, 1879; Oulhen et al., 2016). This definition was influenced by the German botanist Albert Bernhard Frank's (1839–1900) previous use of the word "symbiotismus" (Sapp, 1994; Oulhen et al., 2016): "We must bring all the cases where two different species live on or in one another under a comprehensive concept which does not consider the role which the two individuals play but is based on the mere coexistence and for which the term symbiotismus is to be recommended" (Frank, 1877; translation by Sapp, 1994). Thus, symbiosis simply means an association, the living together (co-occurrence, co-existence) of two dissimilar organisms. The "members of the symbiotic association" (Hertig et al., 1937) have been referred to as symbiotes or symbionts. We submit that using symbiote is more appropriate than symbiont because as stated by Hertig et al. (1937), the former "definitely has a Greek original and is correctly formed in English", in contrast to the latter, which "has no Greek original."

4. If the beneficial effect is known, they are mutualists, not symbiotes

The term "mutualism" was coined in the early 1870s by the Belgian zoologist Pierre-Joseph van Beneden (1809–1894), when he classified species interactions as mutualistic, parasitic or commensalistic (van Beneden, 1873, 1876). He defined mutualisms as species that live in close proximity and render each other mutual services (van Beneden, 1876; Sapp, 2010). The close proximity also defines symbiosis (see above) and this shared character with mutualism was probably the reason for "the greatest quandary in the history of biological terminology" (Martin and Schwab, 2013). Some biologists began to restrict the original definition of symbiosis by de Bary (1879), which included mutualism, parasitism and commensalism, to the restricted definition of symbiosis equals mutualism (Sapp, 1994, 2010; Douglas, 2010; Martin and Schwab, 2013; Bronstein, 2015). The term "symbiont" has been used liberally in the scientific literature for cases in which a beneficial effect on the host might or might not be known. A famous example in the insect-fungus-symbiosis literature includes ectosymbioses between bark and ambrosia beetles and their ambrosia fungus symbionts (e.g., Francke-Grosmann, 1967; Hulcr and Stelinski, 2017). Referring to ambrosia fungi as "symbionts" (or symbiotes) is imprecise, because a mutualistic role has been demonstrated for most of the primary fungal symbiotes of primary ambrosia beetles (e.g., Biedermann et al., 2013; Kirkendall et al., 2015; Biedermann and Vega, 2020).

We propose that (i) "fungal mutualists" should replace "fungal symbionts" (or "fungal symbiotes") whenever a beneficial interaction with the host is known; (ii) the term "symbiote" can be useful for microorganisms as long as their fitness effects on their hosts have not been determined (e.g., gut symbiotes); and (iii) as long as there is so much confusion in the literature about the use of "symbiote" and "symbiosis", these terms need to be defined whenever used (Bronstein, 1994; Martin and Schwab, 2013).

In closing, it is also important to point-out that parasites are symbiotes, and were described by van Beneden (1876) as follows: "The parasite is he whose profession it is to live at the expense of his neighbour, and whose only employment consists in taking advantage of him, but prudently, so as not to endanger his life." The term parasite is sometimes incorrectly used in the entomological literature to describe parasitoids, a term coined by Reuter (1913). Parasitoids include some insects in the Hymenoptera, Strepsiptera, and Diptera (Vinson, 1976) that oviposit in other insects, eventually killing them. The distinction is that a parasite will not kill its host, while a parasitoid will (Wheeler, 1923).

5. Do bark beetles have mycetangia or is it mycangia?

Two terms have been used in the scientific literature to refer to cuticular invaginations that carry fungal spores in bark beetles: mycetangia and mycangia. Before these terms were coined, the structures in ambrosia beetles were referred to as "holes" and "openings" (Nunberg, 1951), "skin-gland organs" (translated from the German "Hautdrüsenorgane"; Francke-Grosmann, 1956), "fungal storage sac" (Fernando, 1959), and "specialized areas", "well defined sacs" and "fungus-carrying structure" (Farris, 1963). Batra (1963) coined the term mycangia to refer to these structures.

In a discussion with scientists attending a meeting in Berlin, Giese (1965) made a proposal "for consistency of nomenclature regarding the storage-transmission organ of ambrosia beetles. The term mycetangium (mycetangia) was selected as the most reasonable member of the family of similarly derived words already in use (e.g. mycetome and mycetocyte[1]) and should replace the often used mycangium." Thus, mycetangia originates from the Greek μύκης (múkēs), meaning "fungus" and the Greek ἀγγεῖον (angeîon), meaning "vessel". We propose that scientists working on this topic follow Giese (1965) and Francke-Grosmann (1965, 1967) suggestion, and use the term mycetangium or its plural form, mycetangia, instead of mycangium or its plural form, mycangia, as is done by most scientists nowadays, despite the correct use of the term in many papers, most of them published prior to the mid-1990s (Giese, 1967; MacLean and Giese, 1968; Schneider and Rudinsky, 1969a, 1969b; Nakashima, 1971, 1972, 1975, 1982; Francke-Grosmann, 1975; Schneider, 1975; Nakashima et al., 1982, 1987; Aksent'ev and Uchastnova, 1986; Sawada and Morimoto, 1986; Schneider, 1987, 1991; Uchastnova, 1987, 1988; Wood, 1993; Tío et al., 1995; Biedermann and Vega, 2020). Another term for "spore-carrying structures", i.e. sporotheca, was coined by Moser (1985) for mites; a sporothecum is "similar to the mycangium described from bark beetles, but differs in that no gland cells are present and the fungal spores do not multiply in the structure." There is really no need for such terminology, as six different types of mycetangia have been described by Six (2003), including glandular and nonglandular pits, sacs, and setal brushes. Even though exoskeletal pits in more than 22 coleopteran families have been assumed to possibly serve as mycetangia, definitive evidence is only available for Scolytinae and Platypodinae (Curculionidae) and Attelabidae (Grebennikov and Leschen, 2010).

6. Conclusions

According to Browne (1853), "it is wisdom to profit by the errors of others." We provide evidence as to why there is an important difference between an association and an interaction, mycetangia vs. mycangia, symbiote vs. symbiont, and symbiosis vs. mutualism. There is no justification for using incorrect or imprecise scientific terminology. It is time to profit from the errors of others.

Acknowledgements

Comments by Meredith Blackwell, Lynne Boddy, Henrik H. De Fine Licht, Sarah Emche, Chase G. Mayers, George O. Poinar, Jr., and Ann Simpkins on a previous version of this manuscript are greatly

[1] "In various invertebrate animals, the structure or organ which houses symbiotes. The cells making up the mycetome and containing the symbiotes are known as mycetocytes" (Steinhaus and Martignoni, 1970).

Please cite this article as: Vega, F.E., Biedermann, P.H.W., On interactions, associations, mycetangia, mutualists and symbiotes in insect-fungus symbioses, Fungal Ecology, https://doi.org/10.1016/j.funeco.2019.100909

appreciated. Special thanks to Wayne Olson (USDA, National Agricultural Library) for literature searches. Peter Biedermann was funded by the German Research Foundation (DFG Emmy Noether Grant BI 1956/1–1).

References

Aksent'ev, S.I., Uchastnova, L.N., 1986. The problem of the symbiosis of xylophagous beetles and ambrosia fungi. Nauchnye Dokl. Vysshei Shkoly Ser. Biol. Nauki (Moscow) 8, 5–22 (In Russian).

de Bary, A., 1879. Die Erscheinung der Symbiose. Karl J. Trübner, Strassburg (In German).

Batra, L.R., 1963. Ecology of ambrosia fungi and their dissemination by beetles. Trans. Kans. Entomol. Soc. 66, 213–236.

van Beneden, P.-J., 1873. Un mot sur la vie sociale des animaux inférieurs, 2me Série Bull. Acad. R. Sci. Lett. Beaux-Arts Belg. 36, 779–796 (In French).

van Beneden, P.-J., 1876. Animal Parasites and Messmates. Henry S. King & Co., London.

Biedermann, P.H.W., Klepzig, K.D., Taborsky, M., Six, D.L., 2013. Abundance and dynamics of filamentous fungi in the complex ambrosia gardens of the primitively eusocial beetle *Xyleborinus saxesenii* Ratzeburg (Coleoptera: Curculionidae, Scolytinae). FEMS Microbiol. Ecol. 83, 711–723.

Biedermann, P.H.W., Vega, F.E., 2020. Ecology and evolution of insect-fungus mutualisms. Annu. Rev. Entomol. 65 (in press).

Bronstein, J.L., 1994. Our current understanding of mutualism. Q. Rev. Biol. 69, 31–51.

Bronstein, J.L. (Ed.), 2015. Mutualism. Oxford University Press, Oxford.

Browne, P.A., 1853. Trichologia Mammalium; A Treatise on the Organization, Properties and Use of Hair and Wool. J. H. Jones, Philadelphia.

Douglas, A.E., 2010. The Symbiotic Habit. Princeton University Press, Princeton.

Farris, S.H., 1963. Ambrosia fungus storage in two species of *Gnathotrichus* Eichhoff (Coleoptera: Scolytidae). Can. Entomol. 95, 257–259.

Fernando, E.F.W., 1959. Storage and transmission of ambrosia fungus in the adult *Xyleborus fornicatus* Eich. (Coleoptera: Scolytidae). J. Nat. Hist. 2, 475–480.

Francke-Grosmann, H., 1956. Hautdrüsen als Träger der Pilzsymbiose bei Ambrosiakäfern. Z. Okol. Morphol. Tiere 45, 275–308 (In German).

Francke-Grosmann, H., 1965. Ein Symbioseorgan bei dem Borkenkäfer *Dendroctonus frontalis* Zimm (Coleoptera Scolytidae). Naturwissenschaften 52, 143 (In German).

Francke-Grosmann, H., 1967. Ectosymbiosis in wood-inhabiting beetles. In: Henry, S.M. (Ed.), Symbiosis. Academic Press, New York, pp. 141–205.

Francke-Grosmann, H., 1975. Zur epizoischen und endozoischen Übertragung der symbiotischen Pilze des Ambrosiakäfers *Xyleborus saxesenii*. Entomol. Ger. 1, 279–292 (In German).

Frank, A.B., 1877. Über die biologischen Verhältnisse des Thallus einiger Krustenflechten. Beitr Biol. Pflanz. 2, 123–200 (In German).

Giese, R.L., 1965. The bioecology of *Corthylus columbianus* Hopkins. Holz Org. 1, 361–370.

Giese, R.L., 1967. The Columbian timber beetle, *Corthylus columbianus* (Coleoptera: Scolytidae). V. A description of the mycetangia. Can. Entomol. 99, 54–58.

Glavič, P., Lukman, R., 2007. Review of sustainability terms and their definitions. J. Clean. Prod. 15, 1875–1885.

Grebennikov, V.V., Leschen, R.A.B., 2010. External exoskeletal cavities in Coleoptera and their possible mycangial functions. Entomol. Sci. 13, 81–98.

Hertig, M., Taliaferro, W.H., Schwartz, B., 1937. Supplement to the report of the twelfth annual meeting of the American Society of Parasitologists. J. Parasitol. 23, 325–329.

Hulcr, J., Stelinski, L.L., 2017. The ambrosia symbiosis: from evolutionary ecology to practical management. Annu. Rev. Entomol. 62, 285–303.

Jax, K., Zauke, G.-P., Vareschi, E., 1992. Remarks on terminology and the description of ecological systems. Ecol. Model. 63, 133–141.

Kirkendall, L.R., Biedermann, P.H.W., Jordal, B.H., 2015. Evolution and diversity of bark and ambrosia beetles. In: Vega, F.E., Hofstetter, R.W. (Eds.), Bark Beetles: Biology and Ecology of Native and Invasive Species. Academic Press, San Diego, pp. 85–156.

Lewin, R.A., 1982. Symbiosis and parasitism – definitions and evaluations. Bioscience 32, 254–260.

Lillenfeld, S.O., Sauvigné, K.C., Lynn, S.J., Cautin, R.L., Latzman, R.D., Waldman, I.D., 2015. Fifty psychological and psychiatric terms to avoid: a list of inaccurate, misleading, misused, ambiguous, and logically confused words and phrases. Front. Psychol. 6, 1100.

MacLean, D.B., Giese, R.L., 1968. Fungi associated with *Xyloterinus politus* (Say) (Coleoptera: Scolytidae). J. Invertebr. Pathol. 10, 185–189.

Malcolm, W.M., 1966. Biological interactions. Bot. Rev. 32, 243–254.

Martin, B.D., Schwab, E., 2013. Current usage of symbiosis and associated terminology. Int. J. Biol. 5, 32–45.

Medawar, P.B., 1981. Advice to a Young Scientist. Harper Colophon Books, New York, p. 128.

Moser, J.C., 1985. Use of sporothecae by phoretic *Tarsonemus* mites to transport ascospores of coniferous bluestain fungi. Trans. Br. Mycol. Soc. 84, 750–753.

Nakashima, T., 1971. Notes on the associated fungi and the mycetangia of the ambrosia beetle, *Crossotarsus niponicus* Blandford (Coleoptera: Platypodidae). Appl. Entomol. Zool 6, 131–137.

Nakashima, T., 1972. Notes on the mycetangia of the ambrosia beetle, *Platypus severini* Blandford and *P. calamus* (Coleoptera: Platypodidae). Appl. Entomol. Zool 7, 217–225.

Nakashima, T., 1975. Several types of the mycetangia found in platypodid ambrosia beetles (Coleoptera: Platypodidae). Insecta Matsumurana 7, 1–69.

Nakashima, T., 1982. Function and location of mycetangia in ambrosia beetles. In: Akai, H., King, R.C., Morohoshi, S. (Eds.), The Ultrastructure and Functioning of Insect Cells. The Society for Insect Cells, Japan, pp. 87–90.

Nakashima, T., Iizuka, T., Ogura, K., Maeda, M., Tanaka, T., 1982. Isolation of some microorganisms associated with five species of ambrosia beetles and two kinds of antibiotics produced by XV-3 strain in these isolates. J. Fac. Agric. Hokkaido Univ. 61, 70–72.

Nakashima, T., Goto, C., Iizuka, T., 1987. The primary and auxiliary ambrosia fungi isolated from the ambrosia beetles, *Scolytoplatypus shogun* Blandford (Coleoptera: Scolytidae) and *Crossotarsus niponicus* Blandford (Coleoptera: Platypodidae). J. Fac. Agric. Hokkaido Univ. 63, 185–208.

Nunberg, M., 1951. Contribution to the knowledge of prothoracic glands of Scolytidae and Platypodidae (Coleoptera). Ann. Mus. Zool. Pol. 14, 261–265.

Oulhen, N., Schulz, B.J., Carrier, T.J., 2016. English translation of Anton de Bary's 1878 speech, '*Die Erscheinung der Symbiose*' ('*De la symbiose*'). Symbiosis 69, 131–139.

Reuter, O.M., 1913. Lebensgewohnheiten und Instinkte der Insekten bis zum Erwachen der sozialen Instinkte. R. Friedländer & Sohn, Berlin.

Ruther, J., Meiners, T., Steidle, J.L.M., 2002. Rich in phenomena-lacking in terms. A classification of kairomones. Chemoecology 12, 161–167.

Sapp, J., 1994. Evolution by Association. A History of Symbiosis. Oxford University Press, New York.

Sapp, J., 2010. Saltational symbiosis. Theor. Biosci. 129, 125–133.

Sawada, Y., Morimoto, K., 1986. Mycetangia and the mode of the fungus transmission in the weevil genus *Euops* (Coleoptera: Attelabidae). Sci. Bull. Fac. Agric. Kyushu Univ. 40, 197–205.

Schneider, I., 1975. Untersuchungen über die biologische Bedeutung der Mycetangien bei einigen Ambrosiakäfern. Mater. Org. (Berl.) 3, 489–497 (In German).

Schneider, I., 1987. Verbreitung, Pilzübertragung und Brutsystem des Ambrosiakäfers *Xyleborus affinis* im Vergleich mit *X. mascarensis* (Coleoptera: Scolytidae). Entomol. Gen. 12, 267–275 (In German).

Schneider, I., 1991. Einige ökologische Aspekte der Ambrosiasymbiose. Anz. Schaedlingskd. Pflanzenschutz Umweltschutz 64, 41–45 (In German).

Schneider, I., Rudinsky, J.A., 1969a. Mycetangial glands and their seasonal changes in *Gnathotrichus retusus* and *G. sulcatus*. Ann. Entomol. Soc. Am. 62, 39–43.

Schneider, I., Rudinsky, J.A., 1969b. Anatomical and histological changes in internal organs of adult *Trypodendron lineatum, Gnathotrichus retusus*, and *G. sulcatus* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Am. 62, 995–1003.

Six, D.L., 2003. Bark-beetle fungus symbioses. In: Bourtzis, K., Miller, T.A. (Eds.), Insect Symbiosis. CRC Press, New York, pp. 97–114.

Steinhaus, E.A., Martignoni, M.E., 1970. An abridged glossary of terms used in invertebrate pathology, Second ed. U.S. Department of Agriculture, Forest Service, p. 39. Pacific Northwest Forest and Range Experiment Station.

The New Shorter Oxford English Dictionary, 1993. Oxford University Press, Oxford.

Tío, R. del, Soria, F.J., Ocete, M.E., 1995. Micetangio y aparato estridulador de *Platypus cylindrus* Fabricius, 1801 (Coleoptera: Platypodidae). La Nouv. Rev. Entomol. 12, 197–204 (In Spanish).

Tipton, L., Darcy, J.L., Hynson, N.A., 2019. A developing symbiosis: enabling cross-talk between ecologists and microbiome scientists. Front. Microbiol. 10, 292.

Uchastnova, L.N., 1987. Scolytids as disease-spreading organisms. Zashchita Rastenii (Mosc.) 8, 44–45 (In Russian).

Uchastnova, L.N., 1988. Some data on the of bark and ambrosia beetles. Nauchnye Dokl. Vysshei Shkoly Ser. Biol. Nauki (Moscow) 8, 38–41 (In Russian).

Vinson, S.B., 1976. Host selection by insect parasitoids. Annu. Rev. Entomol. 21, 109–133.

Wheeler, W.M., 1923. Social Life Among the Insects. Harcourt, Brace and Company, New York.

Wilson, D., 1995. Endophyte – the evolution of a term, a clarification of its use and definition. Oikos 73, 274–276.

Wood, S.L., 1993. Revision of the genera of Platypodidae (Coleoptera). Great Basin Nat. 53, 259–281.

Please cite this article as: Vega, F.E., Biedermann, P.H.W., On interactions, associations, mycetangia, mutualists and symbiotes in insect-fungus symbioses, Fungal Ecology, https://doi.org/10.1016/j.funeco.2019.100909