Insect–bryophyte interactions: a little explored territory in the domain of insect–plant interactions

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Many plant-feeding insects have evolved as generalists, living and feeding on plants. Insects have existed from the Devonian (410–355 million years ago [mya]) synchronizing with the diversification of woody angiosperms[1]. Sometime between the Devonian and the Carboniferous, utilization of sori of early Filicophyta as food existed concurrently in extinct groups of insects[2]. This could also be the period when a majority of the phloem-feeding Hemiptera evolved. Insect-feeding damage, possibly caused by hemipteroids, has been known in the fossil specimens of *Metzgeriothallus sharonae* (Marchantiophyta: Metzgeriales) of the Middle Devonian[3]. An extensive volume of publications explains the dynamics of insect–plant interactions, customarily the term 'plant' implying angiosperms. However, our knowledge of insects that live and feed on lower plants, such as bryophytes, is limited. This note aims to provide a brief review on the subtlety of interactions between bryophytes and insects, as much as known.

In the context of land-plant evolution, bryophytes are critical organisms, which represent key stages of transition. Evolutionary relationships between bryophytes and pteridophytes have been demonstrated extensively[4,5]. Therefore, a brief consideration of insect–pteridophyte interactions would be appropriate. The pre-1990 literature on insect–pteridophyte interactions explained that only a few insects live and feed on pteridophytes, especially on ferns[6,7]. The attributed reasons were that the pteridophytes include higher quantities of insect-defence compounds – polyphenols and alkaloids – than what usually occur in angiosperms. The other complicating factor in insect–pteridophyte relations is that the ferns include high doses of moulting-hormone analogues, e.g. ecdysone, 20-ecdysterone[8–10], which have been implicated as the principal reasons for insect avoidance of pteridophytes. However, the alleged reasons for fewer insects on ferns in the pre-1990s are being challenged presently, because more numbers of both generalist and specialist Coleoptera, Hemiptera and Lepidoptera living and feeding on ferns are being discovered; symbiotic and facultative relationships have also been shown in insects living on ferns[11]. Mehltreter[11] disputes the claim of fern secondary metabolites restricting insect feeding. Using radioactive tracers, Gay[12] has established that nutrients of an ant source get incorporated into *Lecanopteris* (Polypodiaceae). Five species of *Iridomyrmex* and *Crematogaster* (Hymenoptera: Formicidae) that nest in the hollow rhizomes and accumulated debris in a species of *Lecanopteris* benefit it by supplying nutrients through root absorption of carbon and uptake of solutes from ant faeces and debris. Nectar secretion by species of Polypodiopsida and its role in attracting *Brachymyrmex minutus*, *Crematogaster formosa*, *Paratrechina longicornis*, *Solenopsis geminata*, *S. picea*, and *Wasmannia auropunctata* (Hymenoptera: Formicidae) too have been demonstrated[13]. Jasmonic acid-induced emission of volatile organic compounds has been shown in *Pteridium aquilinum* (Dennsteadtiaceae)[14]. Radhika *et al.*[14] tested this behaviour of *P. aquilinum* by subjecting its foliage to feeding by the generalist *Spodoptera littoralis* (Lepidoptera: Noctuidae) and the specialist *Strongylogaster multifascinata* (Hymenoptera: Tenthredinidae). They found that *S. multifasciata* and *S. littoralis* feeding did not induce adequate levels of jasmonic acid necessary for activating the methylerythritol 4-phosphate and mevalonate pathways and subsequent volatile emission[14].

Bryophytes represent a specialized balance between water economy and light-related activity on the one hand, and carbon and mineral nutrient acquisition on the other. Bryophytes include high doses of lipophilic sesqui- and diterpenoids, phenols and polyketides. A few mosses and liverworts include high levels of riboflavin, tocopherols and prostaglandin-like unsaturated fatty acids[15]. Some liverworts and mosses include weakly conjugated cytokinins and auxins, *cis* Z-type cytokinins and abundant 2-oxindole-3-acetic acid. Stress hormones such as abscisic, jasmonic and salicylic acids are not known in bryophytes[16]. Analyses of bryophytes[17] have revealed the presence of sitosterol, campesterol and stigmasterol. Sterols such as 22-dihydrobrassicasterol, clionasterol, cholesterol, 24-methyl-5,22-cholestadienol and 24-methyl-5,7,22-cholestatrienol have been isolated from *Conocephalum conicum* (Conocephalaceae), *Marchantia diptera* (Marchantiaceae), a species of *Bazzania* (Lepidoziaceae), *Mastigophora diclados* (Mastigophoraceae), *Plagiomnium succulentum* (Mniaceae) and *Sphagnum palustre* (Sphagnaceae). Cycloartenol has been shown in Hepaticae[18]. In 16 species of mosses, C29-sterols that commonly occur in microalgae, such as dinoflgellates, occur as predominant constituents[19,20].

Bryobionts (organisms that live on bryophytes), bryophiles (those that primarily live on bryophytes, but could also live elsewhere), bryoxenes (those that spend a part of their lifecycle on bryophytes), and occasionals (those that associate with bryophytes casually and not bryobionts) are terms used in designating categories of bryophyte-associated animals, including insects[21]. The Ephemeroptera, Plecoptera and Odonata are well-known bryoxenes, since many of them occur proximally to bryophytes, usually feeding on detritus[22]. Grylloblattodea (Notoptera) are indicated to use mosses for oviposition[22]. *Bryopsocus angulatus*, *B. townsendi* (Psocoptera: Bryopsocidae), and *Echmepteryx madagascariensis* (Psocoptera: Lepidopsocidae) live associated with epiphyllous mosses in New Zealand[23]. *Sphagnum*-feeding (Sphagnaceae) *Neonemobius palustris* (Orthoptera: Gryllidae) are known in Canada[24]. A few Chrysomelidae (Coleoptera) have been indicated as moss-inhabiting organisms[25]. Konstantinov *et al.*[25] allude to feeding on mosses by these Chrysomelidae and polyphagous. A curious relationship between some extinct bryophytes and some extinct species of Collembola and Oribatidae has been shown[26].

A report on 'gall' induction by an undescribed species of *Aphelenchoides* (Nematoda: Tylenchida: Aphelenchoididae) on the shoot terminals of *Cheilolejeunea* cf. *giraldiana* (Lejeuneaceae) exists[27]. Glime[23] provides several examples of nematode-induced 'galls' on different bryophytes.

A relatively less-known group of Hemiptera, the Peloridiidae (Coleorrhyncha: Peloridomorpha; popularly 'moss bugs') includes the best examples that feed only on bryophytes, particularly on mosses. Helmsing and China[28] established that the Peloridiidae feed and live on mosses. Close proximity to moss populations in permanently wet environments is indicated as the critical factor for the Peloridiidae[28,29]. These are cryptically coloured bugs, 2–5 mm long and have been found in New Caledonia, New Zealand, southeastern Australia, and southern South America. They lack hind wings and cannot fly[30].

Although the known Peloridiidae (17 genera, 32 species) are Gondwana elements[31], curiously, none is known from the Indian subcontinent and Africa. This pattern of distribution is highly similar to that of *Nothofagus* (Nothofagaceae), which occur in the cooler rain forests of Australasia and southern Chile[32]. Similar to other Hemiptera, 'Candidatus Evansia Muelleri' (Gammaproteobacteria) have been shown in the South American, Australian (Tasmanian), and New Zealand populations of Peloridiidae[33]. Details of the mouthparts of *Xenophyes cascus* (Peloridiidae), which feed on *Notoligotrichum crispulum* (Polytrichaceae) from the wet forests of New Zealand, are available[34]. Based on details of distribution and types of sensilla on the rostrum and cross-sectional details of the labium, Brożek[34] explains how the Peloridiidae are a unique hemipteran group and how they derive from the Heteroptera.

The Tetrigidae, a primitive cohort of plant-feeding caeliferan Orthoptera, considered related to the Acrididae on the one hand and the Tridactilidae on the other[35] are known to feed on the algae and bryophytes[36]. *Tetrix bolivari* (Orthoptera: Tetrigidae) feeds on *Bryum caespiticium* and *B. argenteum* (Bryaceae)[37]. Dwelling on the correlation between nutrition and reproduction in *Euscelimena harpago* (Tetrigidae: Scelirneninae) and *Potua sabulosa* (Tetrigidae: Cladonotinae) in India, Bhalerao *et al.*[35,38] report that these two taxa feed on mosses.

A single record of a cavernicolous *Kunstidamaeus langersorfi* (Oribatida: Damaeidae) feeding (indicated as 'intentional consumption) of the spores of *Schistostega pennata* (Schistostegaceae) exists[39]. Haines and Renwick[40] explored bryophytes as food for insects, using caterpillars of generalist *Trichoplusia ni* (Lepidoptera: Noctuiidae), feeding them experimentally on *Bryum argenteum* (Bryaceae), *Climacium americanum* (Climaciaeae), *Leucobryum glaucum* (Leucobryaceae) and *Sphagnum warnstorfi* (Sphagnaceae) by integrating bryophyte materials in the synthetic diets best known for artificial culturing of *T. ni*. In no-choice trials, *T. ni* consumed less of moss-based diet than the controls tested with wheat germ and lettuce. The only moss-based diet consumed by *T. ni* in reasonable quantities was that of *C. americanum*. Haines and Renwick's[40] conclusions provoke interest, since they mention that the digestibility, assimilation and overall utilization efficiency of *C. americanum* is not starkly different from that of lettuce, although the ethanol extract of *L. glaucum* is a deterrent, implying that chemical defences play a critical role. They conclude that pre-ingestive mechanisms are more important than post-ingestive mechanisms in discouraging herbivory on mosses; also, mosses are not simply nutrient-poor.

A novel, but one-off approach exploring insect-resistant proteins in bryophytes has been attempted in India[41]. Here representative bryophytes were screened for protein-based insecticidal activity. The researchers tested this capacity against *Helicoverpa zea* and *Spodoptera litura* (Lepidoptera: Noctuidae), which usually do not naturally feed on bryophytes. Protein profiles from the chosen bryophytes were compared with those from a lepidopteran-susceptible *Glycine max* cultivar in laboratory assays. Protein extracts from *Octoblepharum albidum* (Calymperaceae), *Fissidens asperifolius* (Fissidentaceae), *Bryum argenteum* (Bryaceae), and *Marchantia linearis* (Marchantiaceae) produced the 'greatest decrease in damage' in leaf-disc assays. A reduction in efficiency of conversion of ingested food and digested food, and an increase in approximate digestibility and metabolic cost are indicated as key reasons.

Close to 2500 species of bryophytes are known in India as of 2011: mosses – 1786 species, 355 genera; liverworts – 675 species, 121 genera; hornworts – 25 species, six genera[42]. Based on what we presently know, no Coleorrhyncha occurs in India, and considerable confusion prevails with those Tetrigidae known in India, whether they feed solely on bryophytes or on lichens and detritus as well. Except for scattered remarks on a few occasionals on bryophytes, we have no precise knowledge on Indian insects feeding exclusively on bryophytes. Questions regarding whether any exclusive bryophyte-feeding insects occur in India, and if so, how do they feed, are they specific to certain bryophyte taxa, or do they feed as generalists, what ecological factors regulate their interaction, and what kind of nutrition do they gain by feeding on bryophytes are daunting. Similar to moulting hormone analogues isolated from some of the pteridophytes and the implicated reasoning that could be vital for insect avoidance of pteriophytes, whether moulting hormone analogues occur in the bryophytes either preventing or favouring their feeding, also remains a question. Overall, a literally unexplored field of insect–plant interactions and an exciting field of research remain wide open for Indian entomologists, because of a staggering range of bryophytes in the Indian subcontinent.

1. Garrouste, R. *et al.*, *Nature*, 2012, **488**(7409), 82–85.
2. Bernays, E. A., *BioScience*, 1998, **48**, 35–44.
3. Labandeira, C. C., Tremblay, S. L., Batrowski, K. E. and Hernick, L.V-A., *New Phytol*., 2014, **202**, 247–258.
4. Bennici, A., *Commun. Integr. Biol*., 2008, **1**, 212–218.
5. Patiño, J., Carine, M., Fernandez-Palacios, J. M., Otto, R., Schaefer, H. and Vanderpoorten, A., *New Phytol*., 2014, **201**, 305–311.
6. Hendrix, S. D., *Am. Nat.*, 1980, **115**, 171–196.
7. Cooper-Driver, G. A., *Am. J. Bot.*, 1985, **72**, 921.
8. McMorris, T. C. and Voeller, B., *Phytochemistry*, 1971, **10**, 3253–3254.
9. Canals, D., Irrure-Santilari, J. and Casas, J., *FEBS J.*, 2005, **272**, 4817–4825.
10. Sláma, K. and Williams, C. M., *Nature*, 1966, **210**, 329–330.
11. Mehltreter, K., In *Fern Ecology*, (eds Mehltreter, K., Walker, R. and Sharpe, M.), Cambridge University Press, Cambridge, USA, 2010, pp. 220–254.
12. Gay, H., *Biol. J. Linn. Soc*., 1993, **50**, 221–233.
13. Koptur, S., Palacios-Rios, M., Díaz-Castelazo, C., Mackay, W. P. and Rico-Gray, V., *Ann. Bot*., 2013, **111**, 1277–1283.

14. Radhika, V., Kost, C., Bonaventure, G., David, A. and Boland, W., *PLoS ONE*, 2012; https://doi.org/10.1371/journal.pone.0048050
15. Shaw, A. J., Szövényi, P. and Shaw, B., *Am. J. Bot*., 2011, **98**, 352–369.
16. Asakawa, Y. and Ludwiczuk, A., *J. Nat. Prod*., 2016; doi:10.1021/acs/natprod.6b01046.
17. Drábková, L. Z., Dobrev, P. I. and Motyka, V., *PLoS ONE*, 2015; https://doi.org/10.1371/journal.pone.0125411
18. Chiu, P.-L., Patterson, G. W. and Fenner, G. P., *Phytochemistry*, 1985, **24**, 263–266.
19. Toyota, M. T., Omatsu, I., Braggins, J. and Asakawa, Y., *J. Oleo Sci*., 2009, **11**, 579–584.
20. Matsuo, A. and Sato, A., *Phytochemistry*, 1991, **30**, 2305–2306.
21. Gerson, U., In *Bryophyte Ecology* (ed. Smith, A. J. E.), Chapman & Hall, London, 1982, pp. 291–332.
22. Capinera, J. L. (ed.), In *Encyclopedia of Entomology*, Springer, Dordrecht, 2008, p. 3202.
23. Glime, J. M. (ed.), In *Bryophyte Ecology, Volume 2, Bryological Interaction*, Ebook sponsored by Michigan Technological University and the International Association of Bryologists, 2017; http://digitalcommons.mtu.edu/bryophyte-ecology2/
24. Vickery, V. R., *Ann. Entomol. Soc. Que*., 1969, **14**, 22–24.
25. Konstantinov, A., Chamorro, M. L., Prathapan, K. D., Ge, S.-Q. and Yang, X.-K., *J. Nat. Hist*., 2013, **47**, 2459–2477.
26. Cronberg, N., *Lindbergia*, 2012, **35**, 76–85.
27. Asthana, G. and Srivastava, S. C., *Lindbergia*, 1993, **18**, 94–96.
28. Helmsing, I. W. and China, W. E., *Ann. Mag. Nat. Hist*., 1937, **19**, 473–489.
29. China, W. E., *Trans. R. Entomol. Soc. London*, 1962, **114**, 131–161.
30. Evans, J. W., *Rec. Aust. Mus*., 1982, **34**, 381–406.
31. Burckhardt, D., *Deutsch. Entomol. Z.*, 2009, **56**, 173–235.
32. Heads, M., *Biogeography of Australasia: A Molecular Analysis*, Cambridge University Press, Cambridge, UK, 2013, p. 493.
33. Kuechler, S. M., Gibbs, G., Burckhardt, D., Dettner, K. and Hartung, V., *Environ. Microbiol*., 2013, **15**, 2031–2042.
34. Brożek, Y., *Aphid. Hemipt. Ins*., 2007, **13**, 35–42.
35. Bhalerao, A. M., Naidu, N. M. and Paranjape, S. Y., *Proc. Indian Acad. Sci. (Anim. Sci.*), 1986, **96**, 323–327.
36. Gupta, S. K., *Zootaxa*, 2016, **4097**(1), 118–124.
37. Kuřavová, K., Šipoš, J., Wahab, R. A., Kahar, R. S. and Kočárek, P., *Zool. J. Linn. Soc.*, 2017, **179**, 291–302.
38. Kočárek, P., Holuša, J., Grucmanová, S. and Musiolek, D., *Cent. Eur. J. Biol*., 2011, **6**, 531; https://doi.org/10.2478/s11535-011-0023-y
39. Ignatov, M. S., Sidorchuk, E. A. and Ignatova, E. A., *Bryoph. Divers. Evol*., 2017, **39**, 2017; doi:http://dx.doi.org/10.11646/bde.39.1
40. Haines, W. P. and Renwick, J. A. A., *Entomol. Exp. Appl*., 2009, **133**, 296–306.
41. Krishnan, R. and Murugan, K., In *Prospects in Bioscience: Addressing the Issues* (eds Sabu, A. and Augustine, A.), Springer India, New Delhi, 2013, pp. 19–32.
42. Dandotiya, D., Govindapyari, H., Suman, S. and Uniyal, P. L., *Arch. Bryoph*., 2011, **88**, 1–126.

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Veterinarians as scientific contributors in mainstream biomedical research

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Arguably, veterinarians belong to one of the most respected professions owing to their significant contribution in protecting global food supply, uplifting public health and being the custodians of more number of species than any other professional can claim. The curriculum of veterinary sciences includes knowledge of anatomy and physiology of a variety of animals, pathobiology of developmental, metabolic and degenerative diseases, the epidemiology of zoonotic diseases and reverse zoonosis, in addition to basic sciences and extension-related subjects. Therefore the unique set of skills acquired by veterinarians who choose to become biological scientists makes them better contributors in biomedical research as well. However, their potential remains unharnessed, particularly in India, to fulfil unmet challenges in an ever-changing climate that is bound to impend the ecosystem and pose an unheard scale of public health problems in the not-so-distant future.

Approximately 60% of the pathogens infecting humans originate from animals, which also serve as a reservoir or mixing vessel for emerging pathogens. Therefore, knowledge of disease pathogenesis in animals can be useful for devising interventions to ameliorate human sufferings. Veterinarians are trained to handle and treat animals, and therefore are aptly trained to measure and intervene in normalizing vital parameters during animal experimentation. This suitably prepares them to add value to biomedical research endeavours as well. If such parameters were not factored in during analyses, the outcome of experiments would have limited, if any, translational value. However, if their contributions are relegated to mere caregivers, the whole concept of mutual collaboration would be jeopardized only to significantly halt progress in biomedical science. In the past, veterinarians-turned-scientists have contributed immensely to our understanding of the fundamental phenomena in biology (Table 1). From India also we do have notable contributions in vaccines, diagnostics and mammalian cloning by veterinary scientists. In countries like India