Epichloë evolution: What ChatGPT won't tell you

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Sexual *Epichloë* species were described by Persoon in 1798, Fries in 1849 and the Tulasne brothers in 1865, whereas strictly seed-borne grass-*Epichloë* symbioses were first reported in separate 1898 papers by P. Guerín, A. Vogl and A. Nester, then by K. Sampson in 1933 and J.C. Neill in 1941. However, it was the watershed paper by Bacon et al. in 1977 that linked them to livestock toxicoses and sparked the major international research activities that continue today. Amazingly, without having the advantages of well-known model organisms, the *Epichloë* species have nevertheless provided outstanding examples of numerous evolutionary processes.

That said, I asked ChatGPT to give me a short abstract, which I minimally corrected to give the following paragraph. *Epichloë* species (fam. Clavicipitaceae) are endophytic fungi that form symbiotic relationships with cool-season grasses (Poaceae subfamily Poöideae), playing a crucial role in the ecology and evolution of grassland ecosystems. Over time, the genus has diversified through both sexual and asexual lineages, with many asexual species arising via hybridization events. These fungi are notable for producing a diverse array of alkaloid compounds—such as ergot alkaloids, lolines, peramine, and indole-diterpenes—that provide chemical defences to host grasses against herbivores. The evolution of these alkaloid pathways is complex, involving gene duplication and neofunctionalization, gene losses and perhaps horizontal gene transfer (HGT), and shaped by selective pressures from plant-herbivore interactions. Comparative genomics has revealed a dynamic and modular organization of alkaloid biosynthetic gene clusters that seemingly facilitates diversification of alkaloid profiles. This chemical diversity contributes to the ecological success of both the fungi and their hosts. Understanding the co-evolution of *Epichloë* species and their alkaloids sheds light on symbiotic innovation, adaptation, and the evolutionary mechanisms underlying mutualistic interactions in plant-microbe systems.

It is a credit to the current, vibrant research community that the above paragraph requires updating.

One area of new knowledge concerns the diversity of alkaloids and underlying genetics and biosynthetic pathways. Ergot alkaloids of *Epichloë* species include ergovaline, a complex ergopeptine that is highly toxic to livestock, simpler lysergyl amides that are psychotropic but not as acutely toxic, and chanoclavine, long considered an early intermediate but now recognized as a pathway end-product in several strains, but one that has little or no effect on mammals. Similarly, some *Epichloë* species or strains produce *exo*-1-acetamidopyrrolizidine (AcAP) rather than lolines in the 1-aminopyrrolizidine class of alkaloids. Also recently discovered is an array of pyrrolopyrazines, making that class much richer than just peramine, and adding allelic trans-species polymorphism among the evolutionary mechanisms known to enhance chemotypic diversity. Finally, among the highly diverse indole-diterpene class, recent focus has led to newly identified genes for biosynthesis and diversification of the highly complex epoxyjanthitrems, which can help protect against insects.

Host specificity is evident in associations of *Epichloë* species with particular grass genera or tribes, but underlying mechanisms are only beginning to be revealed (with discovery of *afpA*), and it is unknown how such specificity is overcome to allow hybrid formation. For example, *Epichloë bromicola* strains that produce *N*-formylloline were discovered in Isfahan Province of Iran and are, or are closely related to, the contributors of *LOL* clusters in ca. half of the known loline-producing hybrid *Epichloë* species. Those same populations had dramatically broader host ranges for both *E. bromicola* and *Epichloë festucae* than previously known. These findings suggest that hybridization of *Epichloë* species

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may occur in geographical hotspots where local grasses may have been selected for broaden compatibility with *Epichloë* species.

Other recent findings indicate rare but important HGTs, including a trichothecene detoxification gene originating from *Epichloë* that acts as a disease resistance gene in a wild relative of wheat.

Thus, recent findings in the *Epichloë* evolutionary "model" involve host specificity, polyploidy and hybridization hotspots, and gene dynamics such as duplications, rearrangements, selective losses, trans-species polymorphisms, and even inter-kingdom HGT.