Clavicipitalean Fungi

Evolutionary Biology, Chemistry, Biocontrol, and Cultural Impacts

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Clavicipitaceous Anamorphs

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1. INTRODUCTION

Asexual states (anamorphs) play prominent roles in the life cycles of clavicipitaceous fungi. Most are presumed to be parts of the life cycles of sexual species, but relatively few have been linked to their sexual states, especially among the insect pathogenic species. This creates a problem of naming, as fungi are formally classified based on the features of their sexual (teleomorphic) states. Anamorphs are classified based on the morphology of structures associated with spore production. They are named under the aegis of Article 59 of the International Code of Botanical Nomenclature (Greuter et al., 2000), which permits the assignation of multiple names to the same organism (among extant organisms, this practice is unique to fungi). When the sexual state (teleomorph) is known, the name of that state is preferred, but in practice the names of asexual or anamorphic states are frequently used to describe the anamorph when it occurs alone.

In general, the anamorphs of clavicipitaceous fungi are hyphomycetes that bear a close resemblance to the anamorphs of other hypocrealean fungi. Their pale or sometimes brightly colored conidiogenous structures produce ameroconidia in dry chains or slimy drops, and conidiogenesis is typically phialidic or sympodial. Many exceptions to these general rules exist, and these are discussed below under individual genera. Modern studies have revealed new connections by both cultural

not generally needed; wet mounts can be prepared according to standard methods described by Humber (1997a,b), Malloch (1981), and other authors. Endophytes can be visualized inside plant hosts using a simple staining protocol (Clark et al., 1983), but generally spore-forming structures are needed for identification, and these are best examined from host surfaces or artificial culture. General identification guides that cover the full range of fungi discussed here are lacking. Pertinent literature of use in identification is listed under individual genera, below.

6. KEY TO CLAVICIPITACEOUS GENERA

1. Forming synnemata on the host 2
1′. Not forming synnemata on the host 18
2. Conidia green in mass . . . . . 21. *Metarhizium*
2′. Conidia some other color 3
3. Conidia produced on Aspergillus-like conidiophores that arise from the synnemata 4
3′. Not as above 5
4. Conidiogenous cells phialidic; on spiders . . . . . 12. *Gibellula*
4′. Conidiogenous cells polyblastic, producing ameroconidia singly on short denticles . . . . . 30. *Pseudogibellula*
5. Conidiogenous cells occurring in a compact hymenial layer on well-formed, discrete synnemata 6
5′. Synnemata loosely arranged, often with a fluffy appearance 10
6. Conidiogenous cells phialidic 7
6′. Conidiogenous cells polyblastic 9
7. Conidia in dry chains. Conidiogenous cells with very short or absent necks, sometimes ornamented . . . . . 1. *Akanthomyces*
7′. Conidia held in slime, conidiogenous cells with distinct necks . . . 8
8. Conidiogenous cells with inflated base and a pronounced, usually elongate neck; conidia often held in a discrete slime droplet . . . . . 17. *Hirsutella*
8′. Conidiogenous cells tapering, conidia produced in slime that may coalesce with that of adjacent conidiogenous cells . . . . . 29. *Polycephalomyces*
9. Conidiogenous cells irregularly cylindrical or convoluted; on spiders, usually co-occurring with *Gibellula* synanamorph . . . . . 13. *Granulomanus*
9′. Conidiogenous cells cylindrical to clavate, bearing multiple apical or subapical denticles; well organized in a hymenial layer on synnema . . . . . 18. *Hymenostilbe*
10. Conidiogenous cells phialidic 11
10′. Conidiogenous cells polyblastic? 16

11. Conidia produced in dry chains 12
11′. Conidia produced in slime 15
12. Conidiogenous cells tapering into a short apical neck 13
12′. Conidiogenous cells with a blunt or slightly clavate apex 14
13. Conidiophores with a central axis bearing multiple levels of whorls of short branches, each bearing 3–7 conidiogenous cells . . . . . 24. *Nomuraea*
13′. Conidiophores branching; conidiogenous cells short flask-shaped. . . . . 25. *Paecilomyces*
14. Conidiogenous cells cylindric with a broad apex, digitate, producing chains of conidia appressed along their length that give a prismatic appearance to mature specimens and cultures . . . . 21. *Metarhizium*
14′. Conidiogenous cells subglobose to flask-shaped with short necks . . . . . 1. *Akanthomyces*
15. Conidiogenous cells long and aculeate, produced in clusters in the capitulum of the synnema and laterally. . . . 29. *Polycephalomyces*
15′. Conidiogenous cells basally cylindrical and narrowing abruptly near the apex into a short neck . . . . . 36. *Synglíocladium*
16. Conidiogenous cells sympodially proliferating; inflated at the base and terminating in a minute zigzag rachis. . . . . 5. *Beauveria*
16′. Conidiogenous cells with multiple short denticles 17
17. Conidiophores branching in a penicillate or Paecilomyces-like fashion . . . . . 26. *Paraisaria*
17′. Conidiogenous cells produced directly from surface of synnema or host, lacking macronematous conidiophores; denticles minute. . . . . 13. *Granulomanus*
18. Conidia formed on or in a sclerotium or hard, dark macroscopic resting structure. 19
18′. No sclerotium present 20
19. Conidia hyaline or white to orange in mass, ovoid to cylindrical, formed sparsely on mononematous conidiophores on an ergot sclerotium; on grasses . . . . . 35. *Sphacelia*
19′. Conidia dark green or brown, subglobose, verruculose, resembling the teliospores of a smut fungus; on grasses . . . 39. *Ustilaginoidea*
20. Conidiomata pycnidia or acervuli. 21
20′. Conidia arising from mononematous conidiophores. 24
21. Conidia scolecosporous, three-celled, with terminal cells slightly inflated. Causing a witches'-broom disease of bamboos . . . . . 2. *Albomyces*
21′. Conidia one-celled (in *Aschersonia*, oil drops may cause the conidia to appear multicellular) 22

22. Conidiomata pycnidial, conidia fusoid, often brightly colored in mass, produced in copious slime, arising from a stroma enveloping a scale insect or whitefly. . . . . 4. *Aschersonia*
22′. Conidiomata acervular, on grasses 23
23. Conidiophores forming a hymenial layer on the surface of grass stems. Conidia hyaline, one-celled . . . . . 10. *Ephelis*
23′. Conidia produced in copious sugary slime on the inflorescences of grasses or on ergot sclerotia . . . . . 35. *Sphacelia*
24. Resting structures formed: relatively thick-walled, hyaline or dark spores or macroscopic structures with one or more cells 25
24′. No resting structures present 33
25. Resting spores microscopic, few-celled. 26
25′. Resting structures macroscopic, resembling sclerotia or bulbils. 31
26. Resting spores one-celled, variously colored 27
26′. Resting spores multicellular, usually darkly pigmented 29
27. Resting spores formed as chains of cylindrical arthroconidia . . . . . 16. *Harposporium*
27′. No arthroconidia present 28
28. Resting spores smooth, subglobose, hyaline to orange, formed in dense masses inside an insect host . . . . . 34. *Sorosporella*
28′. Resting spores verruculose, subglobose, dark, formed in and on a sclerotium-like body replacing a grass ovary. . . 39. *Ustilaginoidea*
29. Resting spores very large aleurioconidia with a lobed, dichotomous structure. Formed singly on slender stalks on the body of a dead ant host. . . . . 7. *Desmidiospora*
29′. Resting spores not as above 30
30. Resting spores flattened . . . . . 32. *Rotiferophthora*
30′. Resting spores three-dimensional dictyochlamydospores 31
31′. Conidia of phialidic synanamorph bearing an adhesive hapteron . . . . . 14. *Haptocillium*
31. Conidia of phialidic synanamorph lacking a hapteron . . . . . 28. *Pochonia*
32. Resting structures black, produced in inflorescences of a grass host 33
32′. Resting structures subglobose bulbils composed of densely packed hyphae, on the cadaver of insect hosts . . . . . 17. *Hirsutella*
33. Resting structure a true sclerotium (ergot) with a light-colored interior and a black rind, a phialidic anamorph sometimes present at the apex . . . . . 35. *Sphacelia*

33′. Resting structure loosely constructed and sclerotium-like. Dark, subglobose, verruculose spores often found intermingled and on the surface . . . . . 39. *Ustilaginoidea*

34. Conidia helically coiled 35

34′. Conidia not helically coiled 36

35. Conidia produced in small numbers from conidiogenous cells with a subglobose base and narrow neck. On nematodes, rotifers, or tardigrades. . . . . 16. *Harposporium*

35′. Conidia produced singly, laterally on the stipe of a synnema on an insect body . . . . . 17. *Hirsutella petchabunensis*

36. Conidiogenous cells polyblastic; producing conidia from more than one conidiogenous locus 56

36′. Conidiogenous cells with a single conidiogenous locus, most often an enteroblastic phialide. 37

37. Conidia produced in dry chains 38

37′. Conidia not produced in chains, or produced in slime 44

38. No complex conidiophores present; conidiogenous cells simple aculeate phialides that occur singly or in whorls 42

38′. Conidiophores more complex. 39

39. Conidia produced from a palisade-like layer of conidiogenous cells; conidial chains accumulating to form a prismatic mass, usually in shades of green . . . . . 21. *Metarhizium*

39′. Conidiophores not forming a hymenial layer, conidia green or other colors 40

40. Conidiophores penicillate or brush-like, conidiogenous cells flask-shaped, conidia in divergent chains, usually in shades of white to lilac; on insects . . . . . 25. *Paecilomyces* sect. *Isarioidea*

40′. Conidiophores not as above 41

41. Conidiophores bearing at several levels whorls of very short branches, each bearing a whorl of flask-shaped conidiogenous cells with slender necks. In shades of green or lilac. On insects or spiders . . . . . 24. *Nomuraea*

41′. Conidiophores terminating in a swollen vesicle on which many short, flask-shaped conidiogenous cells are arrayed. In nests of leaf-cutting ants. . . . . 11. *Escovopsis*

42. Conidia with a mucous hapteron, which may appear as an apical wall thickening. Conidia in short chains or slimy drops. Parasites of rotifers . . . . . 14. *Haptocillium*

42′. Conidia lacking a hapteron. 43

43. Conidiogenous cells in whorls of two or more, sometimes single . . . . . 20. *Lecanicillium*

43′. Conidiogenous cells single, at right angle to subtending hypha . . . . . 33. *Simplicillium*

44. Conidiogenous cells short flask-shaped, narrowing to a slender neck 47

44′. Conidiogenous cells other shapes 45

45. Conidiogenous cells cylindrical or aculeate, not thickened at the base 52

45′. Conidiogenous cells other shapes 46

46. Conidiogenous cells integrated in a linear conidiophore, each producing clavate conidia from a single short neck adjacent to a septum . . . . . 8. *Drechmeria*

46′. Conidiogenous cells inside the body of a nematode host. Only the short, cylindrical conidiogenous necks protrude through the host cuticle . . . . . 27. *Plesiospora*

47. Conidiogenous cells with a conspicuous collarette, conidia with a thin, filamentous appendage . . . . . 15. *Haptospora*

47′. Conidiogenous cells with subglobose base and a narrow, cylindrical neck, without a collarette 48

48. Conidiogenous cells produced singly on the mycelium, with cylindric to ellipsoid base tapering abruptly to a pronounced, slender neck. Conidia borne singly or in small groups in a drop of persistent slime. Slime sometimes appears as a roughened texture on the conidia. On insects, mites and nematodes . . . . . 17. *Hirsutella*

48′. Conidiogenous cells produced on differentiated conidiophores. . 49

49. Conidiogenous cells produced laterally and terminally on a simple conidiophore from the body of a nematode, rotifer or tardigrade; conidia often helical, crescent-, jack-, or shoe-shaped. . . . . 16. *Harposporium*

49′. Not as above 50

50. Conidiophore tree-shaped, resembling that of a *Trichoderma* or *Beauveria*, bearing terminal and lateral conidiogenous cells with a subglobose base and short, narrow, hooked neck. Colonies usually white. From soil or insects . . . . . 38. *Tolypocladium*

50′. Conidiophore less complex. 51

51. Conidiophore bearing scattered terminal and lateral conidiogenous cells with a cylindrical to ellipsoid base and short neck. From aquatic flies or rotifers . . . . . 6. *Culicinomyces*

51′. Conidiophore bearing whorls or pairs of conidiogenous cells with a cylindric base. Conidia cylindric and produced in copious slime. Synnemata often present. On insects. . . . . 36. *Synglíocladium*

52. Species occurring on grass plants, inflorescences, or seeds. Rarely isolated from soil. 53

52′. Species occurring on arthropod, nematode, or other animal hosts, sometimes isolated from soil 54
53. Conidiophores penicillate or verticillate. Occurring on the inflorescences of grasses or on ergot sclerotia. Conidia produced in copious slime . . . . . 35. *Sphacelia*
53′. Conidiophores micronematous, conidiogenous cells simple, aculeate, arising at right angles to the subtending hyphae. Occurring in grass tissues or on the surface of infested plants 23. *Neotyphodium*
54. Conidia with a small adhesive hapteron which is sometimes apparent as an apical thickening of the conidial wall. . . . . 14. *Haptocillium*
54′. Conidia lacking hapteron 55
55. Conidiogenous cells in whorls of two or more, sometimes single . . . . . 20. *Lecanicillium*
55′. Conidiogenous cells single, at right angle to subtending hypha . . . . . 33. *Simplicillium*
56. Conidiogenous cells with an ellipsoid or subglobose base and a slender neck that is prolonged into a zigzag rachis 57
56′. Rachis absent 58
57. Conidiogenous cells with subglobose base. On insects . . . . . *Beauveria* and *Microhilum*
57′. Narrow rachis emerges laterally or terminally from conidiogenous cells integrated in the conidiophore. On rotifers . 31. *Pseudomeria*
58. Conidia arising from inconspicuous denticles on the upper portion of a cylindrical conidiogenous cell. On spiders . . . 13. *Granulomanus*
58′. Conidia arising from multiple necks on an elongated conidiogenous cell. . . . . 17. *Hirsutella*

7. THE GENERA

7.1. *Akanthomyces* Lebert, *Z. Wiss. Zool.* 9:447, 1858

Type species: *Akanthomyces aculeata* Lebert.
Known teleomorphs: *Cordyceps* and *Torrubiella* species.
Diagnosis: Colonies slow-growing, typically white to cream, becoming setose with synnemata. Conidiomata synnematous; terete, usually white to cream, sometimes darkened toward the base, bearing a hymenium-like palisade of phialidic conidiogenous cells over their entire surface, or over a fertile region surmounting a short stipe. Mononematous conidiogenous cells sometimes produced sparsely in culture, and when present, longer and narrower than those found on conidiomata. Synnematous conidiogenous cells subglobose to ellipsoid to conical with a short, narrow neck or without a neck, sometimes verruculose. Conidia single-celled, hyaline, shape variable among species (ellipsoid to clavate to cylindrical), produced in dry chains.

About 10 species are known, which include pathogens of Lepidoptera, Coleoptera, and Araneida (spiders). *A. johnsonii* was reported as a saprobe or fungicolous species in leaf litter, but arthropod parasitism is unknown (Vincent et al., 1988). None of the species is well characterized in terms of its ecology, and none has been assessed as a biocontrol agent.

Early concepts of *Akanthomyces* were somewhat confused, especially with respect to its relationship with *Hymenostilbe* (Petch, 1933). Mains (1950b), Samson and Evans (1974), and Hywel-Jones (1996b) clarified its circumscription. The genus *Insecticola* Mains was segregated from *Akanthomyces* by Mains (1950b) based on the sterile stalk of the synnema, and the different origins of the conidiogenous cells. Samson and Evans (1974) felt that the continuum of variation in these characters did not support the distinction. Three species were included in *Insecticola* by Mains (1950b) (*I. clavata*, *I. fragilis*, and *I. pistillariaeformis*); a single additional species (*I. peruamazonensis* Matushima) was added by Matsushima (1993). Of these, only *I. pistillariaeformis* has a valid name as an *Akanthomyces*; the remaining three are transferred to *Akanthomyces* as follows: ***Akanthomyces clavata*** **(Mains) K. T. Hodge comb. nov.** (Basionym, *Insecticola clavata* Mains, *Mycologia* 42:577, 1950); ***Akanthomyces fragilis*** **(Petch) K. T. Hodge comb. nov.** [Basionym, *Hymenostilbe fragilis* Petch, *Trans Br Mycol Soc* 21:56, 1937; *Insecticola fragilis* (Petch) Mains]; ***Akanthomyces peruamazonensis*** **(Matsush.) K. T. Hodge comb. nov.** (Basionym, *Insecticola peruamazonensis* Matsush., *Matsushima Mycol Mem.* 7:55, 1993).

A. pistillariaeformis (Pat.) Samson & Evans is the most frequently collected species of *Akanthomyces*. It occurs on large adult sphingid moths throughout the tropics and subtropics and is the anamorph of *Cordyceps tuberculata*. The spider pathogen *A. aranearum* appears to be the anamorph of *C. thaxteri* (Mains, 1950a,b), and another spider pathogen, *A. arachnophilus* (Petch) Samson & Evans, appears to be the anamorph of *Torrubiella flava* Petch (Samson and Evans, 1974; Petch, 1923). Teleomorph connections in this genus are largely anecdotal and have yet to be confirmed through cultural study.

7.2. *Albomyces* I. Miyake in Hino, *Trans. Mycol. Soc. Japan* 3:113, 1962 (invalidly published)

Type species: *Albomyces take* Miyake.
Known teleomorph: *Aciculosporium*.
Diagnosis: Conidiomata formed in a pseudoparenchymatous stroma enclosed by and incorporating living bamboo leaf sheaths and twigs. Irregular conidiomatal locules form on the inner surfaces of bamboo leaf