

A Brief Chronicle of the Genus *Cordyceps* Fr., the Oldest Valid Genus in Cordycipitaceae (Hypocreales, Ascomycota)

Bhushan Shrestha^{1,*}, Eiji Tanaka², Jae-Gu Han¹, Junsang Oh³, Sang-Kuk Han⁴, Kang-Hyo Lee⁵ and Gi-Ho Sung^{5,*}

¹Institute of Life Science and Biotechnology, Sungkyunkwan University, Suwon 440-746, Korea

²Ishikawa Prefectural University, Nonouchi 921-8836, Japan

³College of Pharmacy, Chung-Ang University, Seoul 156-756, Korea

⁴Forest Biodiversity Division, Korea National Arboretum, Pocheon 487-820, Korea

⁵Mushroom Research Division, National Institute of Horticultural and Herbal Science, Rural Development Administration, Eumseong 369-873, Korea

Abstract The earliest pre-Linnaean fungal genera are briefly discussed here with special emphasis on the nomenclatural connection with the genus *Cordyceps* Fr. Since its valid publication under the basidiomycetous genus *Clavaria* Vaill. ex L. (*Clavaria militaris* L. Sp. Pl. 2:1182, 1753), the genus *Cordyceps* has undergone nomenclatural changes in the post-Linnaean era, but has stood firmly for approximately 200 years. Synonyms of *Cordyceps* were collected from different literature sources and analyzed based on the species they represent. True synonyms of *Cordyceps* Fr. were defined as genera that represented species of *Cordyceps* Fr. emend. G. H. Sung, J. M. Sung, Hywel-Jones & Spatafora. The most common synonyms of *Cordyceps* observed were *Clavaria* and *Sphaeria* Hall, reported in the 18th and in the first half of the 19th century, respectively. *Cordyceps*, the oldest genus in the *Cordyceps* s. s. clade of Cordycipitaceae, is the most preferred name under the “One Fungus = One Name” principle on priority bases.

Keywords *Elaphocordyceps*, Fungal taxonomy, *Metacordyceps*, One Fungus = One Name, *Ophiocordyceps*

EARLY FUNGAL GENERA

In the 16th century, *Fungus* Tourn. ex Adans. and *Tuber* P. Micheli ex F. H. Wigg. were the only two generic fungal names (Table 1) [1]. At that time, fungi were considered as nothing more than the superfluous humidity of soil, trees, rotten wood, and other decaying substances [2]; in fact,

potatoes and legume root nodules were considered to be relatives of truffles [3]. At the end of the 17th century and the beginning of the 18th century, Tournefort (1656~1708), considered the father of the modern generic concept, added five new fungal genera, including *Agaricus* L. of Bauhin (Table 1) [2, 4, 5], which were studied by successive authors of the early 18th century (Table 1) [6-8]. Subsequently, approximately 30 new fungal genera were proposed by Micheli [9], the father of mycology, which were studied by Von Haller [10, 11] who added the new genera to the list (Table 2). According to some authors [9, 12-15], *Cordyceps militaris* (L. : Fr.) Fr., the type species of *Cordyceps* Fr., was already described in the 17th and early 18th century literature under old generic names, including: *Funguli clavati*; *ex gracili caule paulatim crassiores redditi*; *ad digit minimi fere longitudinem pallid accedentes* (tentative translation: clavate, slender, gradually broadening, somewhat longitudinally similar to finger or toe, pale toward tip) [16, 17]; *Fungus parvus luteus ad ophioglossoiden nigrum accedens* (tentative translation: small, yellow, tongue-like, black toward tip) (common English name: yellow adders-tongue mushroom) [18, 19]; and *Fungoides clavatum minus* [6].

Mycobiology 2014 June, 42(2): 93-99
<http://dx.doi.org/10.5941/MYCO.2014.42.2.93>
pISSN 1229-8093 • eISSN 2092-9323
© The Korean Society of Mycology

***Corresponding author**

E-mail: bhushan.shrestha@gmail.com (B.S.),
sung97330@gmail.com (G.-H.S.)

Received February 11, 2014

Revised April 22, 2014

Accepted May 2, 2014

©This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/3.0/>) which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited.

Table 1. Early fungal genera

	De Lobel [1]	Bauhin [2]	De Tournefort* [4]	De Tournefort [5]	Dillen [6]	Buxbaum [7]	Vaillant [8]
Genera	<i>Fungus</i>	<i>Fungus</i>	<i>Fungus</i>	<i>Fungus</i>	-	<i>Fungus</i>	<i>Fungus</i>
	-	-	-	<i>Fungoides</i>	<i>Fungoides</i>	<i>Fungoides</i>	<i>Fungoides</i>
	-	-	-	-	<i>Peziza</i>	-	-
	-	-	<i>Boletus</i>	<i>Boletus</i>	<i>Boletus</i>	<i>Boletus</i>	<i>Boletus</i>
	-	<i>Agaricus</i>	<i>Agaricus</i>	<i>Agaricus</i>	<i>Agaricus</i>	<i>Agaricus</i>	<i>Agaricus</i>
	-	-	<i>Lycoperdon</i>	<i>Lycoperdon</i>	-	<i>Lycoperdon</i>	<i>Lycoperdon</i>
	-	-	<i>Coralloides</i>	<i>Coralloides</i>	-	<i>Coralloides</i>	<i>Coralloides</i>
	<i>Tubera</i>	<i>Tuber</i>	<i>Tubera</i>	<i>Tubera</i>	<i>Tuberum</i>	<i>Tubera</i>	<i>Tubera</i>
	-	-	-	-	-	-	<i>Clavaria</i>
	-	-	-	-	-	<i>Byssus</i>	-
	-	-	-	-	<i>Phallus</i>	-	-
	-	-	-	-	<i>Amanita</i>	-	-
	-	-	-	-	<i>Morchella</i>	-	-
	-	-	-	-	<i>Erinaceus</i>	-	-

*Fungal groups described under each genus are as follows (in parenthesis): *Fungus* (agaricus, boletus), *Boletus* (morels, clathrus, and phallus), *Agaricus* (polypores, bracket fungi), *Lycoperdon* (puff-balls), *Coralloides* (clavarioid forms), and *Tubera* (truffles).

OTHER GENERIC NAMES FOR CORDYCEPS FR.

Vaillant [8] reserved the name *Coralloides* Tourn. for branched forms and erected a new genus, *Clavaria* Vaill. ex L., for unbranched species that also included *Cordyceps militaris* (L. : Fr.) Fr. (as *Clavaria militaris*, *crocea* Vaill.), thus becoming the first extant generic name used for *Cordyceps s. l.* *Clavaria* became such a popular name for basidiomycetous genera that throughout the 18th century it was commonly used for several species of *Cordyceps s. l.* such as *Clavaria capitata* Holmsk. and *Clavaria pileata* Retz. for *Cordyceps capitata* (Holmsk.) Link (current name *Elaphocordyceps capitata* (Holmsk.) G. H. Sung et al.); *Clavaria lutea minima* Mich., *Clavaria militaris* L., *C. lavaria simplex oblonga pulvinata* Schmidel, *Clavaria squamosa* Lam., and *Clavaria granulosa* Bull. for *Cordyceps militaris*; and *Clavaria parasitica* Willd. and *Clavaria radicata* Bull. for *Cordyceps ophioglossoides* (Ehrh.) Link (current name *Elaphocordyceps ophioglossoides* (Ehrh.) G. H. Sung et al.); and *Clavaria sobolifera* Hill ex Watson for *Cordyceps sobolifera* (Hill ex Watson) Berk. & Broome (current name *Ophiocordyceps sobolifera* (Hill ex Watson) G. H. Sung et al.). However, Buxbaum [12] retained the genus name *Coralloides* Tourn. for *Cordyceps*, e.g., *Coralloides clavata*, *lutea*, *minor* was used for *Cordyceps militaris*.

Von Haller [11] established a new ascomycetous genus, *Sphaeria* Hall., to distinguish species with rounded, entire perithecia, furnished at the apex with a minute orifice, and asci converging and dissolving at length. Based on these characteristics, several *Cordyceps* species s. l. were transferred from *Clavaria* into *Sphaeria* thus departing from the traditional basidiomycetous classification, including: *Sphaeria agariciformis* Bolton/S. *capitata* (Holmsk.) Pers. (≠ *Cordyceps capitata*, current name *Elaphocordyceps capitata*); *S. entomorrhiza* Dicks. (≠ *Cordyceps entomorrhiza* (Dicks.) Fr., current name *Ophiocordyceps entomorrhiza* (Dicks.) G. H. Sung et al.); *S. gunnii* Berk. (≠ *Cordyceps gunnii* (Berk.)

Berk.); *S. huegelii* Corda/S. *larvarum* Westwood (≠ *Cordyceps huegelii* Corda, current name *Ophiocordyceps larvarum* (Westwood) G. H. Sung et al.); *S. innominata* R. Taylor/S. *taylorii* Berk. (≠ *Cordyceps taylorii* (Berk.) Sacc., current name *Ophiocordyceps taylorii* (Berk.) G. H. Sung et al.); *S. robertsii* Hook. (≠ *Cordyceps robertsii* (Hook.) Berk., current name *Ophiocordyceps robertsii* (Hook.) G. H. Sung et al.); *S. militaris* (L.) J. F. Gmel. (≠ *Cordyceps militaris*); *S. ophioglossoides* J. F. Gmel. and *S. radicata* De Candolle (≠ *Cordyceps ophioglossoides*, current name *Elaphocordyceps ophioglossoides*); *S. sinensis* Berk. (≠ *Cordyceps sinensis* (Berk.) Sacc., current name *Ophiocordyceps sinensis* (Berk.) G. H. Sung et al.); *S. sobolifera* (Hill ex Watson) Berk. (≠ *Cordyceps sobolifera*, current name *Ophiocordyceps sobolifera*); and *S. sphecocephala* Klotzsch ex Berk. (≠ *Cordyceps sphecocephala* (Klotzsch ex Berk.) Berk. & M. A. Curtis, current name *Ophiocordyceps sphecocephala* (Klotzsch ex Berk.) G. H. Sung et al.). By the early 19th century, *Sphaeria* had already become a large genus consisting of more than 500 species, necessitating its division into Sections, Tribes, and Series [20].

ORIGIN OF THE GENUS NAME CORDYCEPS AND ITS SYNONYMS

Cordyceps was first coined as a genus in *Pyrenomycetes* by Fries [21] from a combination of the Greek word *cordyle*, meaning a club, and the Latin word *caput*, meaning a head. However, Fries [20] himself downgraded *Cordyceps* to the tribe level of *Sphaeria* and described it as *stroma erectum, caulescens, simplex, ramosum, imarginatum, stipite sterili suffultum, perithecia peripherica, demum prominentia, ostiolis aequalibus* (tentative translation: having erect stroma with a simple or branching stem, a sterile stalk supporting the perithecia at the periphery, and projecting with openings at the apex). The treatment of Fries [20] was soon reversed by Link [22], who reaffirmed the genus-level status of

Table 2. Major fungal genera of Micheli [9] and Von Haller [10, 11]

	Micheli [9]	Von Haller [10]	Von Haller [11]
Genera	<i>Fungus</i>	<i>Fungus</i>	-
	<i>Fungoides</i>	-	-
	-	<i>Peziza</i>	<i>Peziza</i>
	<i>Boletus</i>	<i>Boletus</i>	<i>Boletus</i>
	-	<i>Agaricus</i>	-
	<i>Lycoperdon</i>	<i>Lycoperdon</i>	<i>Lycoperdon</i>
	<i>Coralloides</i>	<i>Coralloides</i>	<i>Clavaria</i>
	<i>Tuber</i>	<i>Tuber</i>	-
	<i>Clavaria</i>	<i>Clavaria</i>	<i>Clavaria</i>
	<i>Botrytis</i>	<i>Botrytis</i>	<i>Botrytis</i>
	<i>Aspergillus</i>	<i>Aspergillus</i>	<i>Aspergillus</i>
	<i>Polyporus</i>	<i>Polyporus</i>	<i>Polyporus</i>
	<i>Geaster</i>	<i>Geaster</i>	-
	<i>Lycogala</i>	<i>Lycogala</i>	<i>Lycogala</i>
	<i>Clathroidastrum</i>	<i>Clathroidastrum</i>	-
	<i>Clathroides</i>	<i>Clathroides</i>	<i>Trichia</i>
	<i>Lycoperdoides</i>	<i>Lycoperdoides</i>	-
	<i>Carpobolus</i>	<i>Carpobolus</i>	-
	<i>Lycoperdastrum</i>	<i>Lycoperdastrum</i>	-
	<i>Puccinia</i>	<i>Puccinia</i>	<i>Puccinia</i>
	<i>Cyathoides</i>	<i>Cyathoides</i>	<i>Cyathus</i>
	<i>Suillus</i>	<i>Suillus</i>	-
	<i>Fungoidaster</i>	<i>Fungoidaster</i>	<i>Agaricum</i>
	<i>Byssi</i>	<i>Byssus</i>	<i>Byssus</i>
	-	<i>Mucilago</i>	<i>Mucilago</i>
	<i>Phallus</i>	<i>Phallus</i>	<i>Phallus</i>
	<i>Clathrus</i>	-	-
	<i>Mucor</i>	<i>Mucor</i>	<i>Mucor</i>
	-	-	<i>Tremella</i>
	-	-	<i>Amanita</i>
	<i>Erinaceus</i>	<i>Erinaceus</i>	<i>Echinus</i>
	-	<i>Embolus</i>	-
	-	<i>Sphaerocephalus</i>	-
	-	<i>Buxbaumia</i>	-
	-	<i>Agarico-Polyporus</i>	-
	-	<i>Agarico-Suillus</i>	-
	-	<i>Echin-Agaricus</i>	-
	-	<i>Merulius</i>	-
	-	<i>Agarico-Merulius</i>	-
	-	<i>Agarico-Fungus</i>	-
	-	-	<i>Conferua</i>
	-	-	<i>Ulva</i>
	-	-	<i>Fuligo</i>
	-	-	<i>Embolus</i>
	<i>Lichen-Agaricus</i>	-	<i>Sphaeria</i>
	<i>Ceratospermum</i>	-	<i>Ceratospermum</i>
	-	-	<i>Merulius</i>

Cordyceps. However, the treatment of Fries [20] had such a profound effect on taxonomists that *Cordyceps* species were named under *Sphaeria* for many decades.

The genus *Cordyceps* was first conserved in the Seattle Code (1972) with citation *Cordyceps* (E. M. Fries) Link, Handb. 3: 346 (1833). However, in subsequent Botanical Codes, citations for *Cordyceps* differed from *Cordyceps* E. M. Fries, Observ. Mycol. 2: 316 (1818, cancel page) in

Sydney Code (1983) to *Cordyceps* Fr., Observ. Mycol. 2 (revis.): 316 (1824) in Tokyo Code (1994) [23]. The citation of the genus *Cordyceps* in the Sydney Code is considered to be correct, i.e., *Cordyceps* Fr., Observ. Mycol. 2(revis.): 316, 1818, nom. cons. [23-25].

Type species: *Cordyceps militaris* (L. : Fr.) Fr., Observ. Mycol. 2(revis.): 317 (1818).

The phylogenetic clade of *Cordyceps s. s.* was recently delimited [25]. Nearly 20 different genera have been reported as synonyms of *Cordyceps* Fr. in various sources (<http://www.speciesfungorum.org>, <http://www.mycobank.org>, <http://www.cybertruffle.org.uk>). We recognize only those genera that represent *Cordyceps militaris* or any other *Cordyceps* species in the clade *Cordyceps s. s.* of Sung *et al.* (for instance *C. tuberculata*) as true synonyms of *Cordyceps* Fr., [25] and they are listed below.

***Cordyceps* Fr.**

- ≡ *Clavaria* Vaill. ex L., Sp. Pl. 2: 1182 (1753).
- ≡ *Sphaeria* Hall., Hist. Stirp. Helv. 3: 120 (1768).
- ≡ *Hypoxyllum* Juss., Gen. Pl.: 6 (1789).
- ≡ *Cordylia* Fr., Observ. Mycol. 2(original): 316 (1818), nom. illegit., non Pers. (1807) [Caesalpiniaaceae].
- ≡ *Xylaria* Hill ex Grev., Scott. Crypt. Fl. (Edinburgh) 2: 2 (1823).
- ≡ *Corynesphaera* Dumort., Comment. Bot. (Tournay): 92 (1822).
- ≡ *Sphaeria* “trib.” *Cordyceps* (Fr.: Fr.) Fr., Syst. Mycol. 2: 323 (1823).
- ≡ *Kentrosporium* Wallr., Beitr. Bot. 1: 163 (1844).
- ≡ *Akrophyton* Lebert, Z. Wiss. Zool. (Leipzig) 9: 449 (1858).
- ≡ *Torrubia* Lév., in Cesati & de Notaris, Comm. Soc. crittog. Ital. 1: 192 (1863).
- ≡ *Phytocordyceps* C. H. Su & H. H. Wang, Mycotaxon 26: 338 (1986).

However, we do not recognize the following genera as true synonyms of *Cordyceps s. s.* [25]:

- Mitrasphaera* Dumort., Comment. Bot. (Tournay): 92 (1822).
- Cordyliceps* Fr., 1832.
- Campylothecium* Ces., 1846.
- Polistophthora* Lebert, Z. Wiss. Zool., (Leipzig) 9: 452 (1858).
- Racemella* Ces., Comm. Soc. crittog. Ital. 1: 65 (1861).
- Tettigorhyza* G. Bertol., Mem. R. Accad. Sci. Ist. Bologna, Ser. 3 5: 574 (1875).

Campylothecium Ces. represented *Cordyceps myrmecophila* Ces., *Polistophthora* Lebert represented *Cordyceps sphaerocephala*, and *Racemella* Ces. represented *Cordyceps robertsii*, all of which are now transferred to the new genus *Ophiocordyceps* Petch emend. G. H. Sung *et al.* (*Ophiocordycipitaceae* G. H. Sung *et al.*) [25]. Similarly, *Mitrasphaera* Dumort. represented *Cordyceps capitata* that is now transferred to a new genus, *Elaphocordyceps* G. H. Sung & Spatafora (*Ophiocordycipitaceae*) [25]. *Tettigorhyza*

G. Bertol. and *Cordylicepts* Fr. are not considered true synonyms as it is not clear which *Cordyceps* species they represent.

SUBGENERIC CLASSIFICATIONS AND AMENDMENT OF *CORDYCEPS*

As the number of species of *Cordyceps s. l.* increased, successive authors began arranging the genus on the basis of host and morphological characters. Here, the era of subgeneric classification of *Cordyceps* is tentatively divided into so-called artificial and natural classifications that correspond to the 19th and 20th century, respectively, although it is difficult to make a clear demarcation line.

Artificial classification. The insect/fungal host, shape of the stromata, and position of the perithecia were the principal characters used for the subgeneric classifications of *Cordyceps s. l.* in the 19th century (Table 3). Some of the major works under this system are mentioned here. Wallroth [26] seemingly organized entomophyte species of *Cordyceps s. l.* (under *Kentrosporium* Wallr.) into *capitata* (*stromate sphaerico*, 3 spp.) and *clavata* (*stromate clavato*, 2 spp.). Fries [27] included both entomogenous and mycogenous species in *Cordyceps* and divided them into *Entomogena* (2 spp.) and *Mycogena* (2 spp.), solely based on the nature of the host. Tulasne and Tulasne [28] classified *Cordyceps* species under a different genus, *Torrubia* Lév., into *Entomogena* (8 spp.) and *Mycogena* (2 spp.), which were further subclassified, depending on the shape of the stroma, into *Clavatae* (3 spp.) and *Capitatae* (5 spp.), and *Claviformes* (1 sp.) and *Capitatae* (1 sp.), respectively. In slight contrast to preceding authors, Saccardo [29] classified *Cordyceps* species into three main groups: *Eucordyceps* Sacc. (entomogenous with immersed perithecia, 21 spp.), *Racemella* Ces. (entomogenous with superficial perithecia, 7 spp.), and *Cordylia* Tul. (mycogenous with immersed perithecia, 2 spp.). Cooke [30] based his classification of

entomogenous species of *Cordyceps* on the stroma shape and branching pattern: capitulum globose or elliptical (18 spp.); stroma furcate, capitulum subglobose (3 spp.); stroma simple, clubs elongated (14 spp.); stroma furcate, clubs elongated (4 spp.); and clubs various, perithecia free (6 spp.).

None of the former authors designated the divisions or groups of *Cordyceps* as subgenera. It was Schroeter [31] who formally ranked the divisions of *Cordyceps* (under *Torrubia* Lév.) into the subgenera *Racemella* Ces. (species with perithecia partly embedded, 4 spp.) and *Cordylia* Tul. (both entomogenous and mycogenous species having entirely embedded perithecia, 4 spp.), and then further divided *Cordylia* into *Eucordyceps* Sacc. (entomogenous, 2 spp.) and *Cordylia* Tul. (mycogenous, 2 spp.) (Table 3). Masee [32], however, only recognized entomogenous species under *Cordyceps* and transferred any mycogenous species to *Cordylia* sensu Tul. He refrained from subgeneric classification of *Cordyceps*, but rather separated the species based on perithecial position such as *perithecia entirely or partly immersed* (40 spp.) and *perithecia superficial* (12 spp.) as well as on the septation of ascospores (Table 3). Broadly arranging *Cordyceps* species by the host type, Lindau [33] established two subgenera, *Eucordyceps* Lindau (16 spp.) for entomogenous species and *Cordylia* Tul. (2 spp.) for mycogenous species. From Table 3, it can be observed that in the 19th century there were sporadic tendencies of recognizing only entomogenous species under *Cordyceps* [26, 32, 34], although these tendencies were almost completely abandoned by the 20th century.

Natural classification. By the middle of the 19th century, microscopic details of fructifications in *Cordyceps* species had been observed, such as the number of ascospores in an ascus; the mode of arrangement of ascospores in the ascus in one or two rows or in a crowded or irregular manner; the shape and color of ascospores; septation either unicellular and simple or divided by

Table 3. Subgeneric classifications^a of *Cordyceps s. l.* in the 19th century

	Wallroth [26]	Fries [27]	Tulasne and Tulasne [28]	Saccardo [29]	Roumeguère [34]	Schroeter [31]	Masee [32]	Lindau [33]	
Groups/ Subgenera	<i>capitata</i> (3 ^b)	<i>Entomogena</i> (2)	<i>Entomogena</i> (8)	<i>Clavatae</i> (3) <i>Eucordyceps</i> Sacc. (21)	<i>Eucordyceps</i> (21)	<i>Racemella</i> Ces. (4)	<i>Perithecia</i> <i>entirely/partly</i> <i>immersed</i> (40)	<i>Spores</i> <i>septate</i> (38) <i>Spores</i> <i>continuous</i> (2)	<i>Eucordyceps</i> Lindau (16)
	<i>clavata</i> (2)		<i>Capitatae</i> (5)	<i>Racemella</i> Ces. (7)	<i>Racemellae</i> (7)	<i>Cordylia</i> Tul. (4)	<i>Eucordyceps</i> Sacc. (2)	<i>Perithecia</i> <i>superficial</i> (12)	<i>Spores</i> <i>septate</i> (11) <i>Spores</i> <i>continuous</i> (1)
		<i>Mycogena</i> (2)	<i>Mycogena</i> (2)	<i>Claviformes</i> (1)	<i>Cordylia</i> Tul. (2)		<i>Cordylia</i> Tul. (2)	<i>Cordylia</i> Tul. (2)	
			<i>Capitatae</i> (1)						

^aDelimitation of similar subgenera may differ from author to author.

^bNumber of species are shown in parentheses.

Table 4. Major subgeneric classifications^a of *Cordyceps s. l.* in the 20th century.

	Kobayasi [37]	Mains [38]	Moureau [39]	Koval [40, 41]	Kobayasi [42]
Subgenera	<i>Ophiocordyceps</i> (Petch) Kobayasi (15 ^b) <i>Eucordyceps</i> Kobayasi (116) <i>Neocordyceps</i> Kobayasi (6)	<i>Ophiocordyceps</i> (Petch) Kobayasi (1) <i>Cordyceps</i> (33) <i>Cryptocordyceps</i> Mains (1) <i>Racemella</i> (Ces.) Sacc. (6)	<i>Ophiocordyceps</i> Petch (1) <i>Eucordyceps</i> Lindau (34) <i>Torrubiella</i> Boud. (2)	<i>Ophiocordyceps</i> Petch (10) <i>Cordyceps</i> Kobayasi (43) <i>Neocordyceps</i> (Kobayasi) Koval (2) <i>Fusicordyceps</i> Koval (10)	<i>Ophiocordyceps</i> (Petch) Kobayasi (19) <i>Eucordyceps</i> Kobayasi (255) <i>Neocordyceps</i> Kobayasi (8)

^aDelimitation of similar subgenera may differ from author to author.

^bNumber of species are shown in parentheses.

transverse, transverse and longitudinal, or even oblique septa; and ascospore length [35]. Tulasne and Tulasne [28] and others also investigated the micro-characters of the *Cordyceps* species; however, such micro-characters were barely utilized in subgeneric classifications of *Cordyceps* (Table 3).

The use of micro-characters for subgeneric classification of *Cordyceps* can largely be accredited to T. Petch, E. B. Mains, and Y. Kobayasi in the 20th century (Table 4). Despite his contribution to the description of over 150 species of *Cordyceps* spanning over three decades in the first half of the 20th century, Petch [36] did not produce his own classification. The exception is the establishment of a new genus, *Ophiocordyceps* Petch, that he erected to accommodate *Cordyceps* species with non-fragmenting ascospores [36]. The genus was not recognized by later authors; however, it was recently reinstated and emended, based on the phylogenetic classification of *Cordyceps s. l.* [25]. In the history of *Cordyceps* taxonomy, the most detailed revisionary work was conducted by Kobayasi [37], who recognized three subgenera: *Ophiocordyceps* (Petch) Kobayasi (having non-fragmenting ascospores) (15 spp.), *Eucordyceps* Kobayasi (entomogenous and mycogenous species having fragmenting ascospores) (116 spp.), and *Neocordyceps* Kobayasi (having obliquely oriented perithecia) (6 spp.). He further classified these subgenera into 5 sections and 11 subsections in total, which can be considered as a workable natural classification of *Cordyceps*. Other mycologists contributed revisions to *Cordyceps* classification based on regional distributions (Table 4). For example, based on the North American species, the genus *Cordyceps* was divided into four subgenera: *Racemella* (Ces.) Sacc. (perithecia superficial and free) (6 spp.), *Cordyceps* (perithecia partly or completely immersed) (33 spp.), *Cryptocordyceps* Mains (perithecia developing in a palisade-like layer) (1 sp.), and *Ophiocordyceps* (Petch) Kobayasi (1 sp.), of which the subgenus *Cordyceps* was further divided into four sections [38]. In a somewhat similar manner [37], Moureau [39] recognized three subgenera in *Cordyceps* based on

African species: *Torrubiella* Boud. (2 spp.), *Eucordyceps* Lindau (34 spp.), and *Ophiocordyceps* Petch (1 sp.). Koval [40, 41] divided *Cordyceps* into four subgenera: *Ophiocordyceps* Petch (10 spp.), *Cordyceps* Kobayasi (43 spp.), *Fusicordyceps* Koval (10 spp.), and *Neocordyceps* (Kobayasi) Koval (2 spp.), which were further classified into nine sections. Kobayasi [42], in his second revision of *Cordyceps*, retained his previous three subgenera *Ophiocordyceps* (19 spp.), *Eucordyceps* (255 spp.), and *Neocordyceps* (8 spp.), but reduced the number of sections to seven. The subgeneric concept of his second revision [42] was not consistent with the previous revision [37]; for example, *C. sinensis* was classified in the subgenus *Ophiocordyceps* in the previous revision, but was transferred to the subgenus *Eucordyceps* in his second revision. Currently, around 400 entomopathogenic and mycoparasitic species are estimated in *Cordyceps s. l.* [25].

The revisionary work continued until the 1980s. Two new subgenera were added to *Cordyceps*; a new subgenus, *Bolacordyceps* O. E. Erikss., was proposed to include species that produce bola-ascospores, e.g., *C. bifusispora* O. E. Erikss. [43], whereas Zhang *et al.* [44] established a new subgenus, *Megalocordyceps* K. Zhang, C. Wang et M. Yan, to include species with unicellular ascospores, e.g., *C. gansuënsis* K. Zhang, C. Wang & M. Yan (current name *Ophiocordyceps gansuënsis* (K. Zhang, C. Wang & M. Yan) G. H. Sung *et al.*). However, the identification of *O. gansuënsis* is questionable and is also considered a synonym of *O. sinensis* [45].

In addition, new genera were erected to include *Cordyceps* species with abnormal characters. For example, two new genera, *Sphaerocordyceps* Kobayasi and *Wakefieldiomyces* Kobayasi, were erected to incorporate *Cordyceps* species having atypical ascospores [46]. *Cordyceps palustris* Berk. & Broome (= *C. hormospora* Möller) and *C. ussuriensis* Koval were transferred to *Sphaerocordyceps* due to their spherical secondary ascospores, whereas *C. peltata* Wakef. was transferred to *Wakefieldiomyces* based on the constriction at the middle of the filamentous ascospores and their

subsequent division into two septate fragments.

Among the subgenera of *Cordyceps s. l.*, the subgenus *Eucordyceps* Kobayasi [37, 42] is the largest (Table 4). However, Sung *et al.* [25] showed that the subgenera of *Cordyceps* (Table 4) were not only phylogenetically distant, but that their morphological characters, including those of their hosts, were also evolutionarily unrelated. Thus, the generic concept of *Cordyceps* Fr. was emended. As a result, the species of *Cordyceps s. l.* were reshuffled among four phylogenetic genera: 1) *Cordyceps* Fr. emend. G.H. Sung *et al.* (40 spp.) (Cordycipitaceae Kreisel ex G. H. Sung *et al.*); 2) *Ophiocordyceps* Petch emend. G. H. Sung *et al.* (146 spp.); 3) *Elaphocordyceps* G. H. Sung & Spatafora (21 spp.) (Ophiocordycipitaceae); and 4) *Metacordyceps* G. H. Sung *et al.* (6 spp.) (Clavicipitaceae (Lindau) Earle ex Rogerson). Among the four phylogenetic genera, *Ophiocordyceps* is the largest and is comprised of species distributed in all three morphological subgenera of Kobayasi [37, 42], indicating that the subgenera are polyphyletic. Recently, another phylogenetic genus, *Tyrannicordyceps* Kepler & Spatafora (Clavicipitaceae), was erected to accommodate six species of *Cordyceps s. l.* [47]. While nearly 175 species remain in the residual group of *Cordyceps s. l.* in *Cordycipitaceae* and many more species were missing from the phylogenetic analyses of Sung *et al.* [25], there is a high likelihood of establishing new phylogenetic genera in the future to accommodate those in the residual group as well as the missing ones. For example, *Polycephalomyces* Kobayasi was recently emended [48] to incorporate three residual *Cordyceps* species of Sung *et al.* [25] and four *Ophiocordyceps* species.

CONCLUSIONS

The present review of *Cordyceps* species *s. l.* highlights the old and deserted generic names given in the literature of the pre-Linnaean era as well as the generic synonyms associated with this genus in the post-Linnaean era. The genus *Cordyceps* has firmly stood against all its synonyms and has been used for approximately 200 years since its publication in 1818, proving itself as the oldest valid genus in Cordycipitaceae. *Cordyceps*, as a teleomorph fungus, has a clear generic concept based on characters such as perithecium, ascus, ascospore, part-spore, position of perithecia on stroma from lateral to apical, perpendicular to oblique, or superficial to immersed, and host specificity, among others [37, 38, 42]. Furthermore, *Cordyceps* is a traditionally used generic name for numerous medicinal insect fungi, especially in the eastern Asian countries [49, 50]. Recent amendment to Article 59 of the Melbourne Code has proposed protecting a single genus name for each fungal clade among the competing names on a priority basis, irrespective of the teleomorph or anamorph states of the organisms [51-55]. *Cordyceps* Fr., being the oldest valid genus name in the *Cordyceps s. s.* clade, ranks as the most preferred name over its competing names on the priority basis. Shrestha *et al.* [56] has recently discussed

the phylogenetic relationship between *Cordyceps* Fr. and *Beauveria* Vuill. in connection with the nomenclatural issue of these two genera.

ACKNOWLEDGEMENTS

This work was financially supported by the Cooperative Research Program for Agricultural and Technology Development (PJ009241) from the Rural Development Administration, Korea and the Korea National Arboretum (Project 2 No. KNA 1-1-10).

REFERENCES

- de Lobel M. Kruydtboeck oft Beschryvinghe van allerley ghewassen, kruyderen, hesteren, ende gheboomten. Antwerpen: By Chrostoffel Plantyn; 1581.
- Bauhin C. Pinax theatri botanici. Basileae Helvet: sumptibus et typis Ludovici Regis; 1623.
- Money N. The first book of mycology: Theatrum Fungorum by Franciscus van Sterbeeck (1675). *Inoculum* 2007;58:1-2.
- De Tournefort JP. Éléments de botanique: ou méthode pour connoitre les plantes. Vol. 1. Paris: De L'Imprimerie Royale; 1694.
- De Tournefort JP. Institutiones rei herbariae. Vol. 1. Paris: E Typographia Regia; 1700.
- Dillen JJ. Catalogus plantarum sponte circa Gissam Mascentium cum appendice qua plantae post editum catalogum, circa et extra Gissam observatae recensentur specierum novarum vel dubiarum descriptiones traduntur et genera plantarum nova figuris aeneis illustrata, describuntur. J.M. à Sande; 1719.
- Buxbaum JC. Enumeratio plantarum in agro Halensi crescentium. Halea Magdeburgicae (Renger); 1721.
- Vaillant S. Botanicon parisiense. Paris: Leide; 1727.
- Micheli PA. Nova plantarum genera juxta Tournefortianam methodum disposita. Florence: Typis Bernardi Paperinii; 1729.
- Von Haller A. Enumeratio methodica stirpium Helvetiae indigenarum. Vol. 1. Göttingen: Ex Officina Academica Abrami Vandenhoek; 1742.
- Von Haller A. Historia stirpium indigenarum Helvetiae inchoate. Vol. 3. Berne: Societatis Typographicae; 1768.
- Buxbaum JC. Plantarum minus cognitarum centuria. Vol. 4. St. Petersburg: Ex typographia Academiae; 1733.
- Gleditsch JG. Methodus fungorum: exhibens genera, species et varietates cum caractere, differentia specifica, synonymis, solo, loco et observationibus. Berlin: Sumtibus Scholae Realis; 1753.
- Schmidel CC. Icones plantarum et analyses partium, curante et edente Joannes Chr. Keller, Pictore Norimbergensi Typis Christiani. Pictore Norimbergensi; 1762.
- Holmskjold T. Coryphaei clavarias ramariasque complectentes cum brevi structurae interioris expositione. *Neue Annalen der Botanik* 1796;11:30-149.
- Hoffmanno M. Florae Altdorffinae deliciae hortenses, sive, catalogus plantarum horti medici. Altdorf: H. Meyer; 1660.
- Hoffmanno M. Florae Altdorffinae deliciae hortenses sive

- catalogus plantarum horti medici, quibus post felicum temporum reparationem. Altdorf: H. Meyer; 1677.
18. Ray J. Catalogus Plantarum Angliae. 2nd ed. London; 1677.
 19. Ray J. Synopsis methodica stirpium Britannicarum. London: Ray Soc.; 1690.
 20. Fries EM. Systema Mycologicum. Vol. 2(2). Lund: Gryphiswald Mauritius; 1823.
 21. Fries EM. Observationes mycologicae praecipue ad illustrandam Floram Suecicam. Pars secunda (Cancellans issue). Copenhagen: G. Bonnieri; 1818.
 22. Link JH. Handbuch zur Erkennung der Nutzbarsten und am Häufigsten Vorkommenden Gewächse. Part 3. Berlin: Haude und Spener; 1833. p. 346-9.
 23. Pennycook SR. The genus *Cordyceps* and other names published in the cancellans issue of Fries's observationes Mycologicae, Pars secunda. Mycosystema 2013;32:462-8.
 24. Rogers DP. The genus *Cordyceps* and Fries's observationes. Mycologia 1954;46:248-53.
 25. Sung GH, Hywel-Jones NL, Sung JM, Luangsa-ard JJ, Shrestha B, Spatafora JW. Phylogenetic classification of *Cordyceps* and the clavicipitaceae fungi. Stud Mycol 2007;57:5-59.
 26. Wallroth FW. Beiträge zur Botanik. Vol. 1 fasc. II. Leipzig: Hofmeister; 1844.
 27. Fries EM. Summa vegetabilium Scandinaviae. Holmiae: A. Bonnieri; 1849.
 28. Tulasne LR, Tulasne C. Selecta fungorum carpologia. Vol. 3. Paris: Paris Museum; 1865.
 29. Saccardo PA. Sylloge fungorum. Vol. 2. Padua: Typis Seminarii; 1883.
 30. Cooke MC. Vegetable wasps and plant worms: a popular history of entomogenous fungi, or fungi parasitic upon insects. London: Society for Promoting Christian Knowledge; 1892.
 31. Schroeter J. Kryptogamen-Flora von Schlesien Halfte. In: Cohn F, editor. Kryptogamen-Flora von Schlesien. Vol. 3(2). Breslau: J.U. Kern's Verlag; 1894. p. 1-597.
 32. Masee G. A revision of the genus *Cordyceps*. Ann Bot 1895;9:1-44.
 33. Lindau G. Hypocreales. In: Engler HA, Prantl KA, editors. Die Natürlichen Pflanzenfamilien. part I, section 1. Leipzig: Verlag W. Engelmann; 1897. p. 343-72
 34. Roumeguère C. Les Sphériacées entomogènes (1). Rev Mycol 1884;6:148-54.
 35. Currey F. Synopsis of the fructification of the compound Sphaeriae of the Hookerian Herbarium. Trans Linn Soc Lond 1858;22:257-88.
 36. Petch T. Notes on entomogenous fungi. Trans Br Mycol Soc 1931;16:55-75.
 37. Kobayasi Y. The genus *Cordyceps* and its allies. Sci Rep Tokyo Bunrika Daigaku Sect B 1941;84:53-260.
 38. Mains EB. North American entomogenous species of *Cordyceps*. Mycologia 1958;50:169-222.
 39. Moureau J. Nouveaux *Cordyceps* du Congo. Lejeunia Mem 1961;15:1-38.
 40. Koval EZ. Opredelitel entomofilnykh Gribov SSSR. Kiev: Naukova Dumka; 1974.
 41. Koval EZ. Klavicipitalnye griby SSSR. Kiev: Naukova Dumka; 1984.
 42. Kobayasi Y. Keys to the taxa of the genera *Cordyceps* and *Torrubiella*. Trans Mycol Soc Jpn 1982;23:329-64.
 43. Eriksson OE, Hawksworth DL. Notes on ascomycete systematics. Nos 1-224. Syst Ascomycetum 1986;5:113-74.
 44. Zhang K, Wang C, Yan M. A new species of *Cordyceps* from Gansu, China. Trans Mycol Soc Jpn 1989;30:295-9.
 45. Shrestha B, Zhang W, Zhang Y, Liu X. What is the Chinese caterpillar fungus *Ophiocordyceps sinensis* (Ophiocordycipitaceae)? Mycology 2010;1:228-36.
 46. Kobayasi Y. Revision of the genus *Cordyceps* and its allies 1. Bull Natl Sci Mus Tokyo Ser B 1981;7:1-13.
 47. Kepler RM, Sung GH, Harada Y, Tanaka K, Tanaka E, Hosoya T, Bischoff JE, Spatafora JW. Host jumping onto close relatives and across kingdoms by *Tyrannicordyceps* (Clavicipitaceae) gen. nov. and *Ustilaginoidea* (Clavicipitaceae). Am J Bot 2012; 99:552-61.
 48. Kepler R, Ban S, Nakagiri A, Bischoff J, Hywel-Jones N, Owensby CA, Spatafora JW. The phylogenetic placement of hypocrealean insect pathogens in the genus *Polycephalomycetes*: an application of One Fungus One Name. Fungal Biol 2013;117:611-22.
 49. Shrestha B, Zhang W, Zhang Y, Liu X. The medicinal fungus *Cordyceps militaris*: research and development. Mycol Prog 2012;11:599-614.
 50. Zhao J, Xie J, Wang LY, Li SP. Advanced development in chemical analysis of *Cordyceps*. J Pharm Biomed Anal 2014; 87:271-89.
 51. Norvell LL. Fungal Nomenclature. 1. Melbourne approves a new code. Mycotaxon 2011;116:481-90.
 52. Taylor JW. One Fungus = One Name: DNA and fungal nomenclature twenty years after PCR. IMA Fungus 2011; 2:113-20.
 53. Hawksworth DL. Managing and coping with names of pleomorphic fungi in a period of transition. IMA Fungus 2012;3:15-24.
 54. McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, et al. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011 (Regnum Vegetabile No. 154). Königstein: Koeltz Scientific Books; 2012.
 55. Hibbett DS, Taylor JW. Fungal systematics: is a new age of enlightenment at hand? Nature Rev Microbiol 2013;11:129-33.
 56. Shrestha B, Hyun MW, Oh J, Han JG, Lee TH, Cho JY, Kang H, Kim SH, Sung GH. Molecular evidence of a teleomorph-anamorph connection between *Cordyceps scarabaeicola* and *Beauveria sungii* and its implication for the systematics of *Cordyceps* sensu stricto. Mycoscience 2014;55:231-9.