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

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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 ophioglossoideum 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].
Table 1. Early fungal genera

| Genera         | Fungus | Fungus | Fungus | Fungus | Fungus | Fungus | Fungus |
|----------------|--------|--------|--------|--------|--------|--------|--------|
| De Lobel [1]   | Bhunin [2] | De Tournefort’ [4] | De Tournefort [5] | Dillen [6] | Buxbaum [7] | Vaillant [8] |
| Fungi          | Fungi  | Fungi  | Fungi  | Fungi  | Fungi  | Fungi  | Fungi  |
| —              | —      | —      | —      | —      | —      | —      | —      |
| —              | —      | —      | —      | —      | —      | —      | —      |
| —              | —      | —      | —      | —      | —      | —      | —      |
| —              | —      | —      | —      | —      | —      | —      | —      |
| —              | —      | —      | —      | —      | —      | —      | —      |
| —              | —      | —      | —      | —      | —      | —      | —      |
| —              | —      | —      | —      | —      | —      | —      | —      |
| —              | —      | —      | —      | —      | —      | —      | —      |
| Tubera         | Tubera | Tubera | Tubera | Tubera | Tubera | Tubera | Tubera |
| —              | —      | —      | —      | —      | —      | —      | —      |
| —              | —      | —      | —      | —      | —      | —      | —      |
| —              | —      | —      | —      | —      | —      | —      | —      |

1Fungal groups described under each genus are as follows (in parenthesis): Fungus (agaricus, boletus), Boletus (morde1, clathrus, and phalus), 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* Hall., to distinguish species with rounded, entire ascii converging and dissolving at length. Based on these perithecia, furnished at the apex with a minute orifice, and *Sphaeria* from * agariciformis* Bolton/*S. capitata* (Holmusk.) 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. huegelli* Corda/*S. larvarum* Westwood (=/* Cordyceps huegelli* 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. robertii* Hook. (= *Cordyceps robertii* (Hook.) Berk., current name *Ophiocordyceps robertii* (Hook.) G. H. Sung et al.); *S. militaris* (L.) J. F. Gmel. (= *Cordyceps militaris*); *S. ophioglossoides* J. F. Gmel. and *S. radicosa* 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*, *immarginatum*, *stipite sterilis* *suffultum*, *perithecia peripherica*, *demum prominentia*, *ostioli acualibus* (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]

| Genera            | Micheli [9] | Von Haller [10] | Von Haller [11] |
|-------------------|-------------|-----------------|-----------------|
| Fungus            | Fungus      | -               | -               |
| Fungoides         | -           | Peziza          | Peziza          |
| Boletus           | Boletus     | Boletus         | -               |
| Lycoperdon        | Lycoperdon  | Lycoperdon      | -               |
| Coralloides       | Coralloides | Clavaria        | -               |
| Tuber             | Tuber       | -               | -               |
| Clavaria          | Clavaria    | Clavaria        | -               |
| Botrytis          | Botrytis    | Botrytis        | -               |
| Aspergillus       | Aspergillus | Aspergillus     | -               |
| Polyporus         | Polyporus   | Polyporus       | -               |
| Geaster           | Geaster     | -               | -               |
| Lycogala          | Lycogala    | Lycogala        | -               |
| Clathroidiastrum  | Clathroidiastrum | -               | -               |
| Clathroides       | Clathroides | Trichia         | -               |
| Lycoperdoides     | Lycoperdoides | -               | -               |
| Carpolobus        | Carpolobus  | -               | -               |
| Lycoperdastrum    | Lycoperdastrum | -               | -               |
| Puccinia          | Puccinia    | Puccinia        | -               |
| Cyathoides        | Cyathoides  | Cyathus         | -               |
| Suillus           | Suillus     | -               | -               |
| Fungoidaster      | Fungoidaster | Agaricum      | -               |
| Byssis            | Byssus      | Byssus          | -               |
| -                 | Macilago    | Macilago        | -               |
| Phallus           | Phallus     | Phallus         | -               |
| Clathrus          | -           | -               | -               |
| Macor             | Macor       | Macor           | -               |
| -                 | Tremella    | Tremella        | -               |
| -                 | Amanita     | Amanita         | -               |
| Erinaecus         | Erinaecus   | Echinus         | -               |
| -                 | Embolus     | -               | -               |
| -                 | Sphaerocdephalus | -           | -               |
| -                 | Buxbaumia   | -               | -               |
| -                 | Agaro-Polyopus | -            | -               |
| -                 | Agaro-Suillus | -              | -               |
| -                 | Echin-Agaricus | -           | -               |
| -                 | Merulius    | -               | -               |
| -                 | Agaro-Merulius | -            | -               |
| -                 | Agaro-Fungus | -             | -               |
| -                 | -           | Conferua        | -               |
| -                 | -           | Ulva            | -               |
| -                 | -           | Fuligo          | -               |
| -                 | -           | Embolus         | -               |
| Lichen-Agaricus   | -           | Sphaerid        | -               |
| Ceratospermum     | -           | Ceratospermum   | -               |

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.speciesfungorum.org], [http://www.mycobank.org][http://www.mycobank.org]). 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).
= Hypoxylum Juss., Gen. Pl.: 6 (1789).
= Cordyli Fr., Observ. Mycol. 2(original): 316 (1818), nom. illegit., non Pers. (1807) [Caesalpiniaeceae].
= 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]:

Mitraspheera Dumort., Comment. Bot. (Tournay): 92 (1822).

Cordylices Fr., 1832.
Campylothecium Ces., 1846.
Polistophthora Lebert, Z. Wiss. Zool., (Leipzig) 9: 452 (1858).

Racemella Ces., Comm. Soc. crittog. Ital. 1: 65 (1861).

Tettigorypha 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 robertii, all of which are now transferred to the new genus Ophiocordyceps Petch emend. G. H. Sung et al. (Ophiocordycepiaceae G. H. Sung et al.) [25]. Similarly, Mitraspheera Dumort. represented Cordyceps capitata that is now transferred to a new genus, Elaphocordyceps G. H. Sung & Spatafora (Ophiocordycepiaceae) [25].
G. Bertol. and *Cordyliceps* 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 *Kentrosorium* 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 *Entomogenae* (2 spp.) and *Mycogenae* (2 spp.), solely based on the nature of the host. Tulasne and Tulasne [28] classified *Cordyceps* species under a different genus, *Torrubia* Lév., into *Entomogenae* (8 spp.) and *Mycogenae* (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 perithecium, 21 spp.), *Racemella* Ces. (entomogenous with superficial perithecium, 7 spp.), and *Cordyla* Tul. (mycogenous with immersed perithecium, 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, perithecium 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 perithecium partly embedded, 4 spp.) and *Cordyla* Tul. (both entomogenous and mycogenous species having entirely embedded perithecium, 4 spp.), and then further divided *Cordyliia* into *Eucordyceps* Sacc. (entomogenous, 2 spp.) and *Cordyla* Tul. (mycogenous, 2 spp.) (Table 3). Massee [32], however, only recognized entomogenous species under *Cordyceps* and transferred any mycogenous species to *Cordyla sensu* Tul. He refrained from subgeneric classification of *Cordyceps*, but rather separated the species based on perithecial position such as *perithecium entirely or partly immersed* (40 spp.) and *perithecium 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 *Cordyla* 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 of *Cordyceps s. l.* in the 19th century |
|---|
| **Wallroth** [26] | **Fries** [27] | **Tulasne and Tulasne** [28] | **Saccardo** [29] | **Roumeguère** [34] | **Schroeter** [31] | **Massee** [32] | **Lindau** [33] |
| **Groups/ Subgenera** | **capitata** | **Entomogenae** | **Entomogenae** | **Clavatae** | **Eucordyceps** | **Eucordyceps** | **Racemella** | **Cordyla** | **Eucordyceps** | **Spores** | **Eucordyceps** |
| **clavata** | (2) | (8) | Eucordyceps | Racemella | Ces. (4) | Perithecia | entirely/partly immersed | (40) | Sacc. (2) | Spores | Lindau (16) |
| **Capitatae** | (5) | (7) | Racemella | Ces. (7) | Cordyla | Tul. (4) | Eucordyceps | Perithecia | superficial | (12) | Spores | continuous |
| **Mycogenae** | (2) | Mycogenae | (2) | Claviformes | (1) | Cordyla | Tul. (2) | Cordyla | Tul. (2) | |
| **Capitatae** | (1) | |

*Delimitation of similar subgenera may differ from author to author.*

*Number of species are shown in parentheses.*
recognition of three subgenera in sections [38]. In a somewhat similar manner [37], Moureau the subgenus (perithecia superficial and free) (6 spp.), based on the phylogenetic classification of authors; however, it was recently reinstated and emended, ascospores [36]. The genus was not recognized by later classified into five sections and 11 subsections in total, which can be considered detailed revisionary work was conducted by Kobayasi [37], Neocordyceps species having fragmenting ascospores) (116 spp.), and Neocordyceps (Kobayasi) Koval (2). Neocordyceps Kobayasi (8)

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

| Subgenera                                      | Kobayasi [37] | Mains [38] | Moureau [39] | Koval [40, 41] | Kobayasi [42] |
|-----------------------------------------------|---------------|------------|--------------|----------------|---------------|
| **Ophiocordyceps** (Petch)                    |               |            |              | Ophiocordyceps Petch (1) Ophiocordyceps Petch (10) Ophiocordyceps (Petch) Kobayasi (19) |
| Koval (15)                                    |               |            |              |                 |               |
| Eucordyceps Kobayasi (116)                    |               |            |              | Eucordyceps Kobayasi (19) |               |
| Neocordyceps Kobayasi (6)                     |               |            |              |                 |               |
| Cryptocordyceps Mains (1)                     |               |            |              |                 |               |
| Racemella (Ces.) Sacc. (6)                    |               |            |              |                 |               |
| Torrubilla Boud. (2)                          |               |            |              |                 |               |
| **Fusicordyceps** Koval (10)                  |               |            |              |                 |               |

Delimitation of similar subgenera may differ from author to author. *Number of species are shown in parentheses.

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: *Torrubilla* 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. bifissipora* 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. gansuensis* K. Zhang, C. Wang & M. Yan (current name *Ophiocordyceps gansuensis* (K. Zhang, C. Wang & M. Yan) G. H. Sung et al.). However, the identification of *O. gansuensis* 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. usuariensis* 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 subgenus are polyphyletic. Recently, another phylogenetic genus, *Tyrranicordyceps* 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 generic 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.

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