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Circumscription of *Codonopsis* and the allied genera *Campanumoea* and *Leptocodon* (Campanulaceae: Campanuloideae). I. Palynological data

Kari E. Morris[1,2] and Thomas G. Lammers[2,3]

[1]*Department of Biological Sciences, University of Illinois at Chicago, Chicago, IL 60608, USA*

[2]*Department of Botany, Center for Evolutionary and Environmental Biology, Field Museum of Natural History, Chicago, IL 60605-2496, USA*

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Abstract. Pollen from 23 accessions of *Codonopsis* and the allied genera *Campanumoea* and *Leptocodon* was examined via light microscopy, scanning electron microscopy, and transmission electron microscopy. All grains examined were of four types. Type I grains (found in all accessions of *Campanumoea* sect. *Campanumoea*, *Codonopsis* subg. *Codonopsis*, and *Leptocodon*) were oblate sphaeroidal, circular in polar outline, 4–10-colpate, with long colpi, short spinules, and thin nexine. Type II grains (found in all accessions of *Campanumoea* sect. *Cyclocodon*) were oblate sphaeroidal, semi-angular in polar outline, 3-colporate, with long colpi, long spinules, and thick nexine. Type III grains (found in all accessions of *Codonopsis* subg. *Pseudocodonopsis*) resembled Type I grains, but had the long spinules characteristic of Type II; further, the colpi were much shorter than in Type I and II. Type IV grains (found in all accessions of *Codonopsis* subg. *Obconicicapsula*) likewise resembled Type I grains, but had colpi of a length intermediate between Type I and Type III. The uniformity of pollen morphology in *Campanumoea* sect. *Campanumoea*, *Codonopsis* subgen. *Codonopsis*, and *Leptocodon* might be interpreted as supporting their merger as a single genus, while the distinctness of Type I and Type II pollen might be interpreted as supporting the recognition of *Cyclocodon* as a genus distinct from *Codonopsis*. However, the palynological data are less clear as to the disposition of *Codonopsis* subg. *Pseudocodonopsis* and subg. *Obconicicapsula*, and a realignment of generic boundaries must await completion of studies involving additional data sets.

Keywords: Campanulaceae; Campanuloideae; *Campanumoea*; *Codonopsis*; *Cyclocodon*; Electron microscopy; *Leptocodon*; Pollen; Palynology; Ultrastructure.

Introduction

*Codonopsis** (Campanulaceae: Campanuloideae) comprises 55 species endemic to eastern Asia, from Kamchatka and Japan south to Afghanistan, Pakistan, the Himalayas, southern China, and Taiwan (Fedorov, 1957; Rechinger and Schiman-Czeika, 1965; Hong, 1983; Shimizu, 1993). The plants are perennial with tuberous roots; scandent, twining, or less commonly erect or ascending herbaceous stems; solitary or paired axillary or terminal flowers; 3–5-locular ovary with a 3–5-lobed stigma; and capsular fruits loculicidally dehiscent at apex; most have a pungent skunk-like or 'foxy' odor of uncertain chemistry. Chromosome number has been determined for eight species; all show $n = 8$ (Rosén, 1931; Gadella, 1966; Lee, 1967; Zhukova, 1967; Krasnoborov et al., 1980; Nishikawa, 1985; Sui et al., 1985; Jee et al., 1989; Yoo and Lee, 1989; Ge and Wang, 1990). The most recent classification of the genus (Hong, 1983) recognized three subgenera: *Codonopsis*, *Obconicicapsula*, and *Pseudocodonopsis*.

Some authors (Moeliono and Tuyn, 1960; Van Thuan, 1969; Lammers, 1992) have expanded the circumscription of *Codonopsis* to include *Campanumoea*. This genus of five species is likewise endemic to eastern Asia, though its distribution extends farther south than *Codonopsis*, to tropical India, Indochina, the Philippines, Malaysia, Indonesia, and New Guinea (Moeliono and Tuyn, 1960). *Campanumoea* indeed resembles *Codonopsis*, but differs in its baccate fruit; furthermore, it lacks the distinctive foxy odor found in most *Codonopsis,* and the ovary is often 6-locular with a 6-lobed stigma. The species have been divided (Clarke, 1881; Tsoong, 1935; Hong, 1983; Shimizu, 1993) between two sections: *Campanumoea* and *Cyclocodon*. According to Hong (1995), the chromosome number of the former is $n = 8$, while that of the latter is $n = 9$.

Recently, Grey-Wilson (1990) has proposed that *Codonopsis* be enlarged further through the incorporation of *Leptocodon*, a genus of two species endemic to the Himalayas, from India to Burma. *Leptocodon* resembles *Codonopsis* overall, but differs in the possession of a unique set of five glands atop the ovary, alternate with the stamens. The chromosome number of *Leptocodon* is unknown.

[3]Corresponding author. E-mail: lammers@fmppr.fmnh.org

*Authorities for all scientific names will be found in Table 1.

Simple incorporation of *Campanumoea* into *Codonopsis* is complicated by the results of a palynological analysis of the former genus. Murthy (1983) discovered that pollen of sect. *Campanumoea* was identical to that reported for *Codonopsis*: suboblate, 5–7-colpate, with spinules ca. 1 μm long. In contrast, the species of sect. *Cyclocodon* had pollen grains that were oblate sphaeroidal and 3-colporate, with spinules ca. 3 μm long. On this basis, Murthy proposed that *Campanumoea* be divided, with the species of sect. *Campanumoea* transferred into *Codonopsis* but sect. *Cyclocodon* treated as a distinct genus.** Murthy did not examine pollen of *Codonopsis* himself, but only referred to published descriptions, which represented a mere eight species, all of which belonged to subg. *Codonopsis.* Though subsequent studies have described the pollen of one or more species of that subgenus, as well as subg. *Psuedocodonopsis* (Dunbar, 1984; Lee et al., 1988; Yoo and Lee, 1989; Nowicke, 1992; Shrestha and Tarasevich, 1992), the sampling still is not comprehensive, and there has been no synthesis of palynological data in the group as a whole.

The purpose of the present study, therefore, is to re-examine Murthy's (1983) findings in *Campanumoea*, and to expand upon it by surveying pollen in a larger and more comprehensive representation of *Codonopsis* species. In particular, we wish to determine if the type of pollen seen in *Campanumoea* sect. *Cyclocodon* is truly unique to that group or whether it can also be found among the species of *Codonopsis*. Additionally, we want to examine *Leptocodon* to determine if palynological data are consistent with its inclusion in *Codonopsis*.

Materials and Methods

Herbarium specimens (Table 1) provided the pollen samples examined in this study. A total of 23 samples was examined. This included 14 samples of *Codonopsis*, representing 13 species and all three subgenera recognized by Hong (1983); eight samples drawn from all five species of *Campanumoea*; plus a single sample of *Leptocodon*.

Whole anthers were removed and acetolyzed following procedures outlined by Erdtman (1966). For light microscopy (LM), all 23 samples had pollen grains mounted in glycerin jelly and the cover slip sealed with paraffin. For scanning electron microscopy (SEM), grains from all 23 samples were sputter-coated with gold, then examined and photographed with an Amray 1810 or a Hitachi 570. For transmission electron microscopy (TEM), pollen from 20 samples was fixed in agar with osmium tetroxide, stained with uranyl acetate, and embedded in L. R. white. After sectioning, the pollen was stained in lead citrate and examined via a JEOL 100 or JEOL 1200. Characters recorded for each sample were grain shape, grain outline, polar diameter, equatorial diameter, aperture number, aperture type, colpus length, spinule length, and nexine thickness.

Results

The results of our study are presented in Table 1, together with all previously published palynological data on these genera. Despite Murthy's (1983) statement that the pollen of *Campanumoea* and *Codonopsis* fell into two shape classes, suboblate and oblate sphaeroidal, all pollen examined in our study could be assigned to a single category, oblate sphaeroidal (Punt et al., 1994). However, we did observe two classes as regards outline in polar view: circular and semi-angular. Grains with a circular outline had polar diameters (means in parentheses) of 26-(39)-56 mm and equatorial diameters of 29-(40)-66 mm. Grains with a semi-angular outline averaged a little smaller, with polar diameters of 25-(32)-39 mm and equatorial diameters of 26-(33)-40 mm. As regards aperture number and type, grains were either 3-colporate or 4–10-colpate. Colpus lengths fell into three classes: short (covering less than 1/4 the distance from pole to pole), medium (covering between 1/4 and 1/2 the distance from pole to pole), and long (covering more than 2/3 of the distance from pole to pole). Spinules fell into two length classes: short (ca. 1 mm long) and long (2–3 mm long). Nexine thickness likewise fell into two classes: thin (0.1–0.5 mm thick) and thick (0.6–1 mm thick).

On the basis of the distribution of these character states, four types of oblate sphaeroidal pollen grains could be distinguished. Judging from all available palynological literature, these four types are unique to *Codonopsis* and its allies. Type I was circular in polar outline, 4–10-colpate, with long colpi, short spinules, and thin nexine; it was found in all samples of *Codonopsis* subg. *Codonopsis* (Figures 1–3), *Leptocodon* (Figures 10–12), and *Campanumoea* sect. *Campanumoea* (Figures 13–15). Type II was semi-angular in polar outline, 3-colporate, with long colpi, long spinules, and thick nexine; it occurred in all samples of *Campanumoea* sect. *Cyclocodon* (Figures 16–18). These are the two types reported by Murthy (1983); the other two types were not. Type III was circular in polar outline, 4–6-colpate, with short colpi, long spinules, and thin nexine; it was observed in all samples of *Codonopsis* subg. *Psuedocodonopsis* (Figures 7–9). Type IV was circular in polar outline, 5–7-colpate, with medium colpi, small spinules, and thin nexine; it was present in all samples of *Codonopsis* subg. *Obconicicapsula* (Figures 4–6). Thus, Types III and IV are essentially similar to Type I grains with two exceptions: Type III has the long spinules characteristic of Type II grains and uniquely short colpi, while Type IV possesses colpi of length intermediate between Type I and Type III.

**Though Murthy retained the name *Campanumoea* for this genus, the rules of nomenclature (Greuter et al., 1994) dictate that the correct name for a genus thus constituted would be *Cyclocodon* Griff.; *Campanumoea* would become a synonym of *Codonopsis*.

Table 1. Characteristics of pollen grains of *Campanumoea*, *Codonopsis*, and *Leptocodon*.

Taxon	Voucher or reference	Origin	Shape	Outline[1]	Size (μm)[2]	Aperture condition	Colpus length[3]	Spinule length[4]	Nexine[5]
Campanumoea* Blume sect. *Campanumoea									
C. inflata C. B. Clarke	*Clark 26420* (BM)	INDIA	Oblate spheroidal	Circular	34-(36)-40 × 40	6-8 colpate	Long	Short	Thin
	Gamble 9740 (K)	INDIA	Oblate spheroidal	Circular	33-(37)-39 × 29-(36)-39	6-7 colpate	Long	Short	Thin
	Murthy (1983)	INDIA	Suboblate	—	32-(35)-40 × 40-(45)-50	6-7-colpate	Long	Short	Thin
C. javanica Blume	Dunbar (1975)[6]	CHINA	Suboblate	—	30 × 35	5-6-colpate[7]	Long	Short	—
	Hooker & Thompson 2024 (K)	INDIA	Oblate spheroidal	Circular	39-(44)-46 × 39-(44)-49	5-6-colpate	Long	Short	Thin
	Murthy (1983)	INDIA	Suboblate	—	31-(35)-36 × 36-(41)-43	5-6-colpate	—	Short	Thin
***Campanumoea* sect. *Cyclocodon* (Griff.) C. B. Clarke**									
C. celebica Blume	*Forrest 24903* (K)	INDIA	Oblate spheroidal	Semi-angular	33-(36)-39 × 29-(33)-39	3-colporate	Long	Long	Thick
	Murthy (1983)	INDIA	Oblate spheroidal	Semi-angular	28-(30)-32 × 32-(35)-37	3-colporate	Long	Long	Thick
	van Beusekom 6786 (K)	THAILAND	Oblate spheroidal	Semi-angular	29-(31)-33 × 29-(31)-33	3-colporate	Long	Long	Thick
C. lancifolia (Roxb.) Merr.	Dunbar (1975)	SUMATRA	Suboblate	—	25 × 31	3-colporate	—	Long	—
	Huang (1972)	TAIWAN	Oblate to suboblate	—	25-31 × 32-40	3-colporate	—	Long	Thick
	Steward et al. 291 (BM)	CHINA	Oblate spheroidal	Semi-angular	29-(33)-33 × 26-(31)-33	3-colporate	Long	Long	Thick
C. parviflora (A. DC.) Benth.	*Bor 6299* (K)	INDIA	Oblate spheroidal	Semi-angular	26-(31)-33 × 29-(33)-36	3-colporate	Long	Long	Thick
	Erdtman (1952)	INDIA	Suboblate	—	24 × 30	3-colporate	—	—	—
	Murthy (1983)	INDIA	Oblate spheroidal	Semi-angular	27-(30)-31 × 35-(36)-40	3-colporate	Long	Long	Thick
	Schlagintweit 208 (BM)	INDIA	Oblate spheroidal	Semi-angular	30-(31)-34 × 30-(31)-32	3-colporate	Long	Long	Thick
Codonopsis* Wall. subg. *Codonopsis									
C. affinis Hook. f. & Thompson	*Crawford et al. 64*	NEPAL	Oblate spheroidal	Circular	33-(34)-36 × 33-(34)-39	5-6 colpate	Long	Short	Thin
C. bulleyana Diels	Chapman (1967)	CHINA	Suboblate	—	38 × 45	7-colpate	—	Short	—
	Nowicke (1992)	CHINA	Oblate spheroidal	—	41-(44)-48 × 41-(46)-49	6-8-colpate	Long	Short	—
C. cardiophylla Kom.	Erdtman (1952)	—	Oblate spheroidal	—	49 × 52	7-9-colpate	Long	Short	—
C. clematidea (Schrenk) C. B. Clarke	Dunbar (1975)	CHINA	Oblate spheroidal	—	40 × 44	8-colpate	Long	Short	—
	Dunbar (1984)	CHINA	Oblate spheroidal	—	40 × 44	8-colpate	—	Short	Thin
	Erdtman (1952)	TURKESTAN	Oblate spheroidal	—	45 × 50	8-colpate	—	Short	—
	Stainton 2907 (E)	INDIA	Oblate spheroidal	Circular	46-(51)-52 × 42-(47)-49	6-8-colpate	Long	Short	Thin
C. kawakamii Hayata	Huang (1972)	TAIWAN	Oblate to prolate-spheroidal	—	28-46 × 35-47	6-7-colpate	Long	Short	Thin
C. lanceolata (Sieb. & Zucc.) Trautv.	Chapman (1967)	—	—	—	—	9-colpate	—	Short	—
	Lee et al. (1988)	KOREA	Oblate spheroidal	—	26-(27)-28 × 33-(36)-39	9-10-colpate	Long	Short	Thin
	Yao 9168 (CAS)	CHINA	Oblate spheroidal	Circular	29-(33)-36 × 33-(35)-39	9-colpate	Long	Short	Thin
	Yoo & Lee (1989)	KOREA	Oblate spheroidal	Circular	28-(32)-35 × 38-(40)-42	9-10-colpate	Long	Short	—
C. micrantha Chipp	*Maire 454* (E)	CHINA	Oblate spheroidal	Circular	42-(43)-46 × 39-(43)46	7-8-colpate	Long	Short	Thin
C. minima Nakai	Yoo & Lee (1989)	KOREA	Oblate spheroidal	Circular	27-(33)-40 × 30-(36)-47	8-10-colpate	Long	Short	Thin
C. ovata Benth.	Shrestha & Tarasevich (1992)	INDIA	—	—	50-56 × 54-66	7-8-colpate	—	—	—
C. pilosula (Franch.) Nannf.	Dunbar (1975)[8]	CHINA	Oblate spheroidal	—	38-48 × 40-46	7-colpate	Long	Short	—
	Lee et al. (1988)	KOREA	Oblate spheroidal	—	35-(39)-42 × 45-(47)-51	6-7 colpate	Long	Short	—
	Ho 1057 (CAS)	CHINA	Oblate spheroidal	Circular	39-(42)-49 × 39-(40)-46	5-6-colpate	Long	Short	—
	Yoo & Lee (1989)	KOREA	Oblate spheroidal	Circular	32-(38)-40 × 40-(44)-46	6-7 colpate	Long	Short	Thin

Table 1. (Continued)

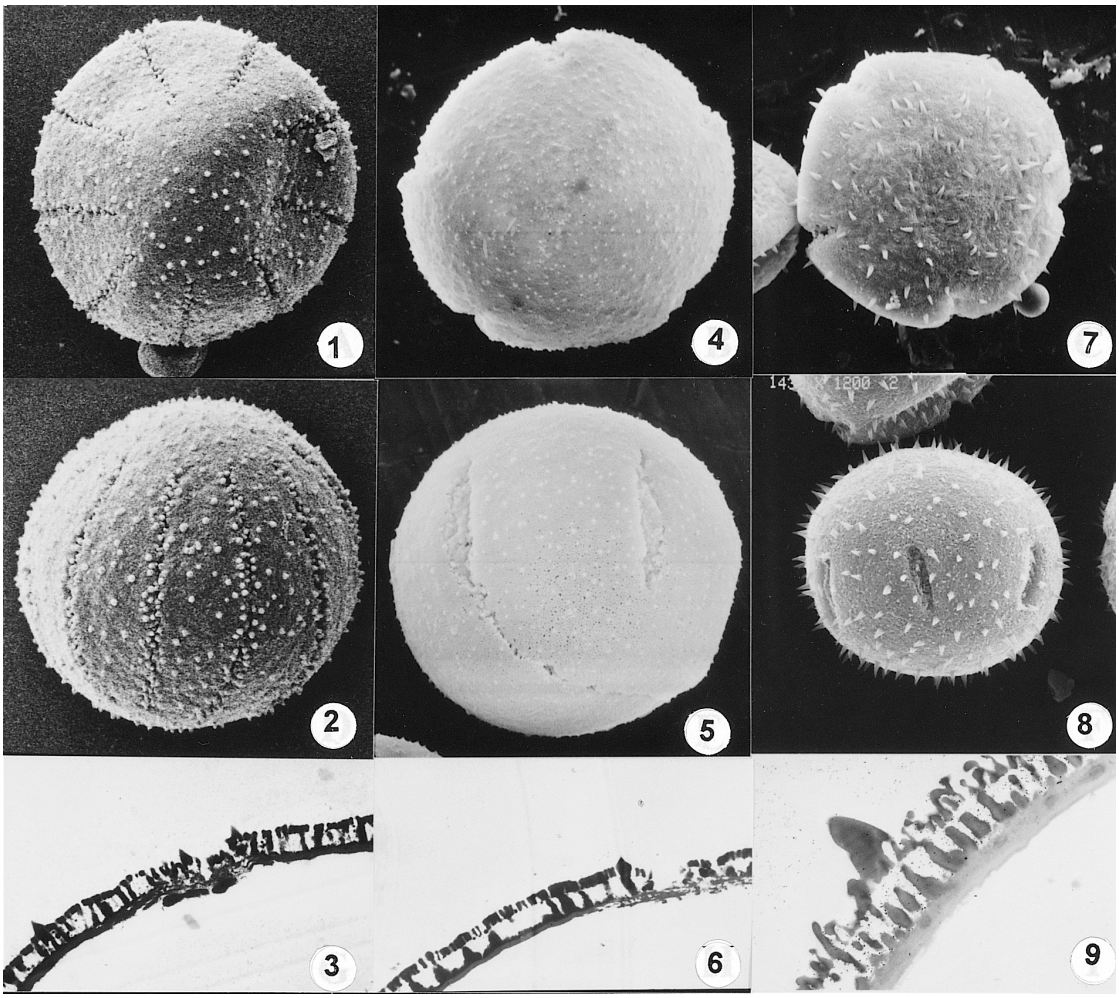
Taxon	Voucher or reference	Origin	Shape	Outline[1]	Size (μm)[2]	Aperture condition	Colpus length[3]	Spinule length[4]	Nexine[5]
C. rotundifolia Benth.	*Ludlow s.n.* (E)	TIBET	Oblate spheroidal	Circular	36-(40)-43 × 36-(39)-43	7-colpate	Long	Short	Thin
C. tangshen Oliv.	*Wilson 1023* (K)	CHINA	Oblate to prolate spheroidal	Circular	33-(36)-39 × 33-(34)-36	6-colpate	Long	Short	Thin
C. thalictrifolia Wall.	*Long 454* (E)	INDIA	Oblate spheroidal	Circular	42-(47)-52 × 42-(44)-46	7-colpate	Long	Short	Thin
C. tubulosa Kom.	*McClaren s.n.* (K)	CHINA	Oblate spheroidal	Circular	33-(36)-39 × 36-(37)-39	6-7-colpate	Long	Short	Thin
C. ussuriensis (Rupr. & Maxim.) Hemsl.	*Kobayashi 1210* (CAS)	JAPAN	Oblate spheroidal	Circular	33-(34)-36 × 33-(35)-39	8-colpate	Long	Short	Thin
	Lee et al. (1988)	KOREA	Oblate spheroidal	—	38-(40)-42 × 47-(49)-50	8-10-colpate	Long	Short	—
	Lee et al. (1988)	KOREA	Oblate spheroidal	—	31-(32)-32 × 36-(37)-38	8-10-colpate	Long	Short	—
	Yoo & Lee (1989)	KOREA	Oblate spheroidal	Circular	28-(36)-37 × 38-(31)-46	8-10-colpate	Long	Short	—
C. viridiflora Maxim.	Dunbar (1975)	—	Oblate spheroidal	—	36 × 40	8-colpate	Long	Short	—
C. volubilis Nannf.	Erdtman (1952)[8]	CHINA	Suboblate to oblate spheroidal	—	38 × 43	6-7-colporoidate	—	Short	—
***Codonopsis* subg. *Obconicicapsula* Hong**									
C. dicentrifolia (C.B. Clarke) W.W. Smith	*Crawford et al. 62* (K)	NEPAL	Oblate spheroidal	Circular	50-(54)-56 × 48-(49)-50	5-7-colpate	Medium	Short	—
	Smith s.n. (E)	INDIA	Oblate spheroidal	Circular	49-(50)-56 × 49-(50)-52	5-7-colpate	Medium	Short	Thin
***Codonopsis* subg. *Pseudocodonopsis* Kom.**									
C. convolvulacea Kurz	Nowicke (1992)	CHINA	Oblate spheroidal	Circular	38-(42)-48 × 43-(46)-51	6-colpate	Short	Long	Thin
C. forrestii Diels	*Rock 6036* (NY)	CHINA	Oblate spheroidal	Circular	40-(42)-44 × 44-(45)-46	6-colpate	Short	L ong	—
C. pinifolia (Hand.-Mazz.) Grey-Wilson	*Tén 139* (E)	CHINA	Oblate spheroidal	Circular	34-(37)-42 × 38-(39)-40	6-colpate	Short	Long	—
C. vinciflora Kom.	Erdtman (1952)	CHINA	Suboblate	—	37 × 43	4-6-colpate	Short	Long	—
***Leptocodon* Lem.**									
L. gracilis (Hook. f.) Lem.	Erdtman (1952)	INDIA	Suboblate	—	41-56 × 54-66	8-colpate	—	—	—
	Forrest 22158 (C)	CHINA	Oblate spheroidal	Circular	29-(34)-36 × 33-(35)-36	9-colpate	Long	Short	Thin
	Hong and Ma (1991)	CHINA	Oblate spheroidal	—	—	8-colpate	Long	Short	—
	Shrestha & Tarasevich (1992)	INDIA	—	—	31 × 38	9-colpate	—	—	—
L. hirsutus Hong	Hong and Ma (1991)	TIBET	Oblate spheroidal	—	—	7-colpate	Long	Short	—

[1]In polar view.
[2]Minimum-(mean)-maximum polar diameter × minimum-(mean)-maximum equatorial diameter.
[3]Short = covering less than 1/4 the distance from pole to pole; medium = covering between 1/4 and 1/2 the distance from pole to pole; long = covering more than 2/3 the distance from pole to pole.
[4]Short = ca. 1 μm long; long = 2-3 μm long.
[5]Thin = 0.12-0.59 μm thick; thick = > 0.60 μm thick.
[6]Identified as *C. maximowiczii* Honda; cf. Hong (1983).
[7]Originally as "colporate" but corrected by Dunbar (1984).
[8]Identified as *C. handeliana* Nannf.; cf. Hong (1983).

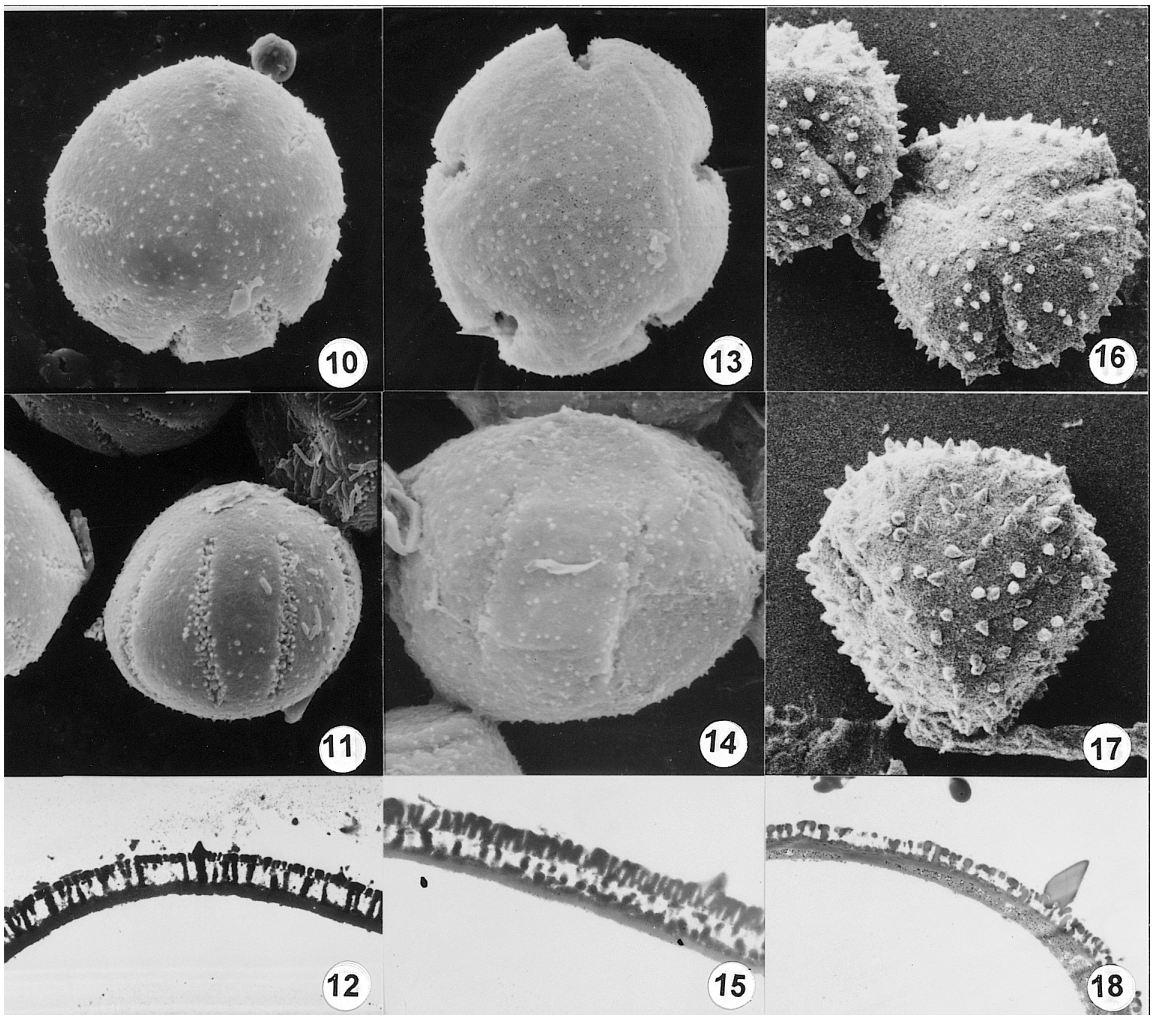
Discussion

Our results confirmed the primary finding of Murthy (1983): pollen of *Campanumoea* sect. *Campanumoea* is essentially indistinguishable from that of the species of *Codonopsis* examined previously, while pollen of sect. *Cyclocodon* is quite distinct. In fact, we detected an additional feature distinguishing the two types of pollen recognized by Murthy (1983): thickness of the nexine. Though Murthy distinguished them on the basis of shape, aperture condition, and spinule length, we found that the nexine of Type II pollen was demonstrably thicker than that of Type I (compare Figures 3 and 15 to Figure 18). This result adds additional support to Murthy's suggestion that sect. *Cyclocodon* be recognized as a distinct genus while sect. *Campanumoea* is subsumed into *Codonopsis*. Furthermore, we determined that pollen of *Leptocodon* was likewise indistinguishable from the species of *Codonopsis* examined previously. This similarly supports Grey-Wilson's (1990) proposal to merge *Leptocodon* with *Codonopsis*.

However, other results of our study suggest caution in accepting the revision of generic boundaries proposed by Murthy (1983) and Grey-Wilson (1990). Specifically, we discovered more variation among the species of *Codonopsis* than was indicated by Murthy (1983). All species known to him palynologically were members of subg. *Codonopsis* and had pollen corresponding to our Type I. While the additional samples of this subgenus examined by us likewise showed Type I pollen, the samples of subg. *Pseudocodonopsis* and subg. *Obconicicapsula* examined in our study differed. Though both resembled Type I grains in their shape, size, aperture type, aperture number, and nexine, they differed from both Type I and Type II in having shorter colpi: covering less than 1/4 the distance from pole to pole in subg. *Pseudocodonopsis* (Type III) and of intermediate length in subg. *Obconicicapsula* (Type IV). The former also differed from



Figures. 1–9. Electron micrographs of *Codonopsis* pollen. 1, *C. lanceolata*, polar view, via SEM (1215×). 2, *C. lanceolata*, equatorial view, via SEM (1333×). 3, *C. tangshen*, cross section through wall, via TEM (3960×). 4, *C. dicentrifolia*, polar view, via SEM (983×). 5, *C. dicentrifolia*, equatorial view, via SEM (1060×). 6, *C. dicentrifolia*, cross section through wall, via TEM (4800×); note thin nexine relative to sexine. 7, *C. convolulacea*, polar view, via SEM (1200×); note the long spinules and short colpi. 8, *C. convolulacea*, equatorial view, via SEM (790×). 9, *C. convolulacea*, cross section through wall, via TEM (7920×).



Figures. 10–18. Electron micrographs of *Leptocodon* and *Campanumoea* pollen. 10, *L. gracilis*, polar view, via SEM (1175×). 11, *L. gracilis*, equatorial view, via SEM (1110×). 12, *L. gracilis*, cross section through wall, via TEM (3170×). 13. *C. inflata*, polar view, via SEM (1210×). 14, *C. javanica*, equatorial view, via SEM (1200×). 15, *C. javanica*, cross section through wall, via TEM (7920×). 16, *C. celebica*, polar view, via SEM (1160×). 17, *C. lancifolia*, equatorial view, via SEM (1465×). 18, *C. lancifolia*, cross section through wall, via TEM (4750×).

Type I in having the long spinules characteristic of Type II grains. Thus, Type III grains combine features of Type I and II grains with a unique character state (the very short colpi), while Type IV is intermediate between Type I and III in that same character state.

Even if there were no potential problems with intermediacy of character states, we would be unwilling to realign generic boundaries solely on the basis of palynological data. If only for purposes of identification, genera should be distinguished by more readily discernible features than pollen type. In order to determine possible correlations between the palynological data and other taxonomic characters, the next step of our research will be detailed phylogenetic analyses of all available data, particularly morphology. Thus, we defer rendering taxonomic conclusions on the question until we have completed these analyses.

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桔梗科 *Codonopsis* 及其鄰近 *Campanumoea*, *Leptocodon* 二屬的界分 I. 花粉資料

Kari E. Morris[1, 2] and Thomas G. Lammers[2]

[1]Department of Biological Sciences, University of Illinois at Chicago
Chicago, IL 60608, USA
[2]Department of Botany, Center for Evolutionary and Environmental Biology
Field Museum of Natural History, Chicago, IL 60605-2496, USA

*Codonopsis*及其鄰近*Campanumoea*及*Leptocodon*的23個花粉樣品在本研究中以光學及電子顯微鏡（掃描式及穿透式）觀察。花粉共呈現四型。第一型出現於*Campanumoea*的*Campanumoea*組、*Codonopsis*的*Codonopsis*亞屬、以及*Leptocodon*此型的花粉扁球狀，極面圓形，4-10條溝，溝長，刺短，花粉內壁薄。第二型出現於*Campanumoea*的*Cyclocodon*組，花粉扁球狀，極面角圓形，三溝孔，溝長，刺長，內壁厚。第三型出現於*Codonopsis*的*Pseudocodonopsis*亞屬。第三型花粉近似第一型，但具有第二型的長刺，其次，花粉溝亦較第一、二型爲短。第四型花粉出現於*Codonopsis*的*Obconicicapsula*亞屬，亦近似第一型花粉，但花粉溝的長度則介於第一及第二型之間。*Campanumoea*的*Campanumoea*組、*Codonopsis*的*Codonopsis*亞屬及*Leptocodon*三者在花粉形態上的一致可視爲支持這三者合併爲一屬的一項証據；而第一、第二型花粉的明顯差異則可用以支持*Cyclocodon*獨立爲一屬。不過，花粉的結果對*Codonopsis*的*Pseudocodonopsis*及*Obconicicapsula*二亞屬的定位幫助不大，這些屬的重新界定仍有待更多的相關研究。

關鍵詞：桔梗科；桔梗亞科；*Campanumoea*；*Codonopsis*；*Cyclocodon*；電子顯微鏡；*Leptocodon*；花粉；花粉學；超微結構。