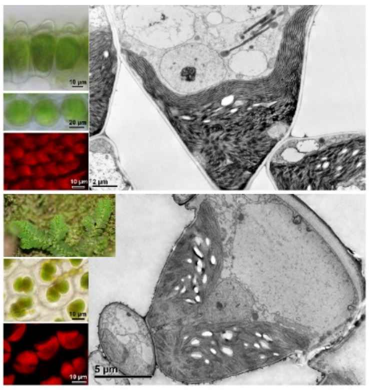
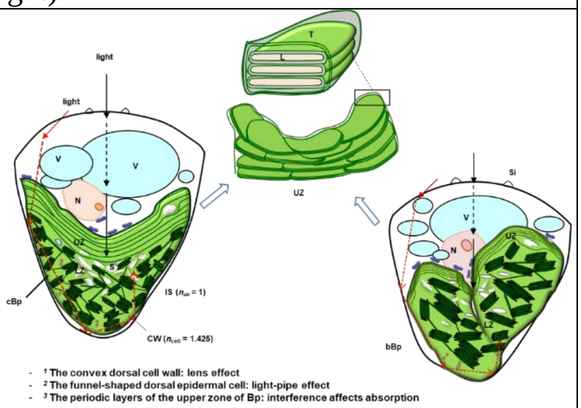
生物策略表

類別	生物策略 (Strategy)
生物策略 STRATEGY	林下耐陰的卷柏發展出巨大和特殊結構的葉綠體 (Gigantic chloroplasts, including bizonoplasts, are common in shade-adapted species of Selaginellaceae)
生物系統 LIVING SYSTEM	耐陰的卷柏植物 (Shade adapted *Selaginella*)
功能類別 FUNCTIONS	#改變大小/形狀/質量/體積 #獲取、吸收、或過濾能量 #分配能量 #Modify size/shape/mass/volume # Capture, absorb, or filter energy #Distribute energy
作用機制標題	杯狀或二裂狀巨大葉綠體和其特化的多層膜微細結構有利於吸收光線 (Gigantic cupped or bilobed chloroplasts with multilayered ultrastructure help capture light)
生物系統/作用機制示意圖	  圖 1. 卷柏巨大的二區葉綠體。上為杯狀，下為二裂狀。 圖 2. 卷柏二區葉綠體的結構和光線效應示意圖。

作用機制摘要說明 (SUMMARY OF FUNCTIONING MECHANISMS)

多數維管束植物每個光合細胞內有一群小而多數的葉綠體 (通常位於葉肉細胞內)。但有些卷柏屬植物葉背表皮細胞中有著巨大的單一葉綠體，此為維管束植物所僅有，十分奇特。這些巨大的葉綠體 (可達 40 微米) 呈杯狀、二裂狀或大盤狀。有些巨大的葉綠體在它們正常葉綠體的上方，再形成許多相互平行排列、由 3 個類囊膜堆疊組成的層狀結構群，進一步發展為具有二型微細結構的二區葉綠體 (圖 1)。

二區葉綠體 (杯狀或二裂狀) 位在漏斗狀表皮細胞的下方，並由細胞間隙圍繞。細胞內的折射係數 n_{cell} 為 1.425 遠高於空氣的值 ($n_{air} = 1$)，意即入射細胞的光線，依其角度，有相當的比例會被反射回二區葉綠體而增進吸收 (圖 2)。這樣的光學特性同樣也發生在其他不具有上區層狀結構的巨大葉綠體。而二區葉綠體上區的層狀結構與光波可有進一步的干涉，依波長和角度，具有增加光線吸收或反射光線的潛能 (Jacobs et al., 2016)。

Most vascular plants with chloroplasts have a population of small chloroplasts in each photosynthetic cell (usually mesophyll cells). Gigantic single chloroplast per dorsal epidermal cell (monoplastidy) only found in *Selaginella* truly stands out among vascular plants. These giant chloroplasts (up to 40 μm) are cup-shaped, bilobed or giant disc-like. Furthermore, some giant chloroplasts, further equipped with an upper zone with parallel layers of 3-stacked thylakoids above normal chloroplast ultrastructure, are bizonoplasts (Fig. 1).

Bizonoplasts (cupped or bilobed) are located at the bases of funnel-shaped dorsal epidermal cells surrounded by intercellular space. The refractive index inside a dorsal epidermal cell (n_{cell} = 1.425, Gausman et al., 1974) is higher than air (n_{air} = 1), which means that some portion of the light striking base of the cell, depending on its angle, will be reflected back into the bizonoplast increasing the amount of light absorbed (Fig. 2). This particular feature of a bizonoplast, however, is shared with other monoplastids that do not have a layered structure in the upper zone. The layered structure of the upper zone of a bizonoplast may additionally interfere with the light waves, with the potential to enhance absorption and reflection depending on the wavelengths and light angles (Jacobs et al., 2016).

文獻引用 (REFERENCES)

「有些卷柏屬植物在表皮細胞或葉肉細胞中有著單一巨大的葉綠體 (單一葉綠體，M)，此為維管束植物所獨有，十分特別。這些巨大的葉綠體在種間並有些許構造的差異，包含不同形式、或有著獨特兩型微細結構的二區葉綠體。」(Liu et al., 2020)

「研究全世界 76 種卷柏…我們定義出卷柏屬葉綠體的五個層級:ME (位表皮細胞的巨大葉綠體)、MM (位葉肉細胞的巨大葉綠體)、OL (少數的中型葉綠體)、Mu (多數的小型葉綠體) 和 RC (極小或殘餘的葉綠體)。表皮細胞型的巨大葉綠體在 44 種的卷柏發現，其中 11 種具有二區葉綠體，並稍具種間差異，呈杯狀 (呈凹狀的上區) 或二裂狀 (底部具一樞紐，新發現)；這些葉綠體有上區平行排列的層狀類囊膜群。巨大的葉綠體在 49 種卷柏中發現，與陰性環境強烈相關。二區葉綠體也只在生長於極陰暗的卷柏植物發現 (低於全光的 2.1%)。」(Liu et al., 2020)

「多數小型葉綠體極有可能是卷柏植物祖先型的特徵，意即巨大葉綠體和二區葉綠體是後起的特徵，此單一葉綠體至少演化出現兩次，與其適應低光的環境有關。」(Liu et al., 2020)

“Unique among vascular plants, some species of *Selaginella* have single giant chloroplasts in their epidermal or upper mesophyll cells (monoplastidy, M), varying in structure between species. Structural variants include several forms of bizonoplast with unique dimorphic ultrastructure.” (Liu et al., 2020)

“The chloroplast ultrastructure of 76 *Selaginella* species …. We delineated five chloroplast categories: ME (monoplastidy in a dorsal epidermal cell), MM (monoplastidy in a mesophyll cell), OL (oligoplastidy), Mu (multiplastidy, present in the most basal species), and RC (reduced

or vestigial chloroplasts). Of 44 ME species, 11 have bizonoplasts, cup-shaped (concave upper zone) or bilobed (basal hinge, a new discovery), with upper zones of parallel thylakoid membranes varying subtly between species. Monoplastidy, found in 49 species, is strongly shade associated. Bizonoplasts are only known in deep-shade species (< 2.1% full sunlight).” (Liu et al., 2020) “Multiplastidic chloroplasts are most likely basal, implying that monoplastidy and bizonoplasts are derived traits, with monoplastidy evolving at least twice, potentially as an adaptation to low light.” (Liu et al., 2020)
參考文獻清單與連結 (REFERENCE LIST)
Liu, J. W., S. F. Li, C. T. Wu, I. A. Valdespino, H. M. Chang, T. Y. Guu, M. F. Kao, C. Chesson, S. Das, H.Oppenheimer, A. Bakutis, P. Saenger, N. Salazar Allen, J. W. H. Yong, B. Adjie, R. Kiew, N. Nadkarni, C. L. Huang, P. Chesson and C. R. Sheue. (2020). Gigantic chloroplasts, including bizonoplasts, are common in shade-adapted species of the ancient vascular plant family Selaginellaceae. *American Journal of Botany* 107 (4): 1-15.
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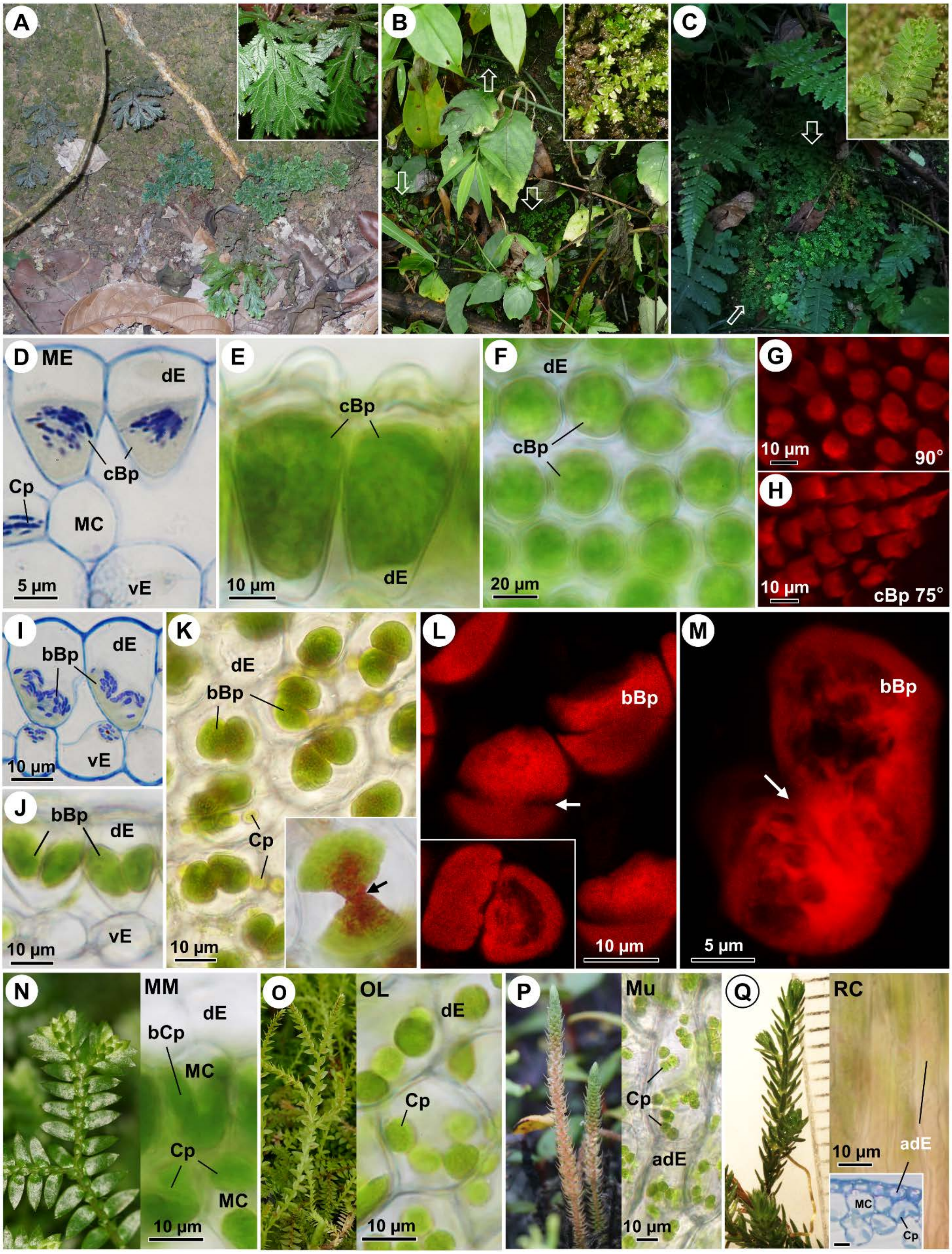

卷柏的棲地和不同的葉綠體形式。Habitats and chloroplast types of *Selaginella*. (Liu et al., 2020)