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Sieve-Element Plastids of *Caryophyllales*: Additional Investigations with Special Reference to the *Caryophyllaceae* and *Molluginaceae*

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Abstract: The subtype PIII plastids found in 16 additional species of *Caryophyllales* investigated here corroborate the homogeneity of this order with respect to the sieve-element plastids. While two new examples (*Glinus*, *Allmania*) which exhibit the rare presence of starch grains in the PIII-plastids are found, the restriction of the three forms of PIII-plastids to distinct taxa is maintained: PIIIf in *Chenopodiineae*; PIIIc'f in *Caryophyllaceae* (3 species added), *Stegnospermataceae* and *Achatocarpaceae*; PIIIcf in all other families (among the 11 species investigated 5 from *Molluginaceae*).

The dicotyledon order *Caryophyllales* as circumscribed in revised systems of classification of the angiosperms (DAHLGREN 1980, TAKHTAJAN 1980, CRONQUIST 1981) is delimited to the families strictly containing subtype PIII sieve-element plastids (BEHNKE 1976 b, 1981). Among the other important characters in this order are the blue-red betalain pigments since (1) they are not known from other flowering plant orders and (2) they are present in all families of the *Caryophyllales* with the exception of *Molluginaceae* and *Caryophyllaceae* which synthesize anthocyanins (MABRY 1976).

The two anthocyanin families, *Molluginaceae* and *Caryophyllaceae*, are also of specific interest with respect to their sieve-element plastids. All of the 21 genera of the *Caryophyllaceae* (including *Geocarpon*) so far investigated contain form PIIIc'f plastids which in addition to the order-specific peripheral ring of protein filaments are characterized by a

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polygonal protein crystal (BEHNKE 1976 a, b, 1982 b). Sieve-element plastids of the same form were also reported to occur in *Stegnospermataceae* and *Achatocarpaceae* while the majority of the families of *Caryophyllales* has form PIIIcf plastids, i.e. with a globular crystal (BEHNKE 1981). The *Molluginaceae* may be generally placed among the latter. However, the presence of cuboid protein crystals in the sieve-element plastids of its genera *Limeum* and *Macarthuria* (BEHNKE 1976 b, BEHNKE & al. 1983), besides adding new data to the putatively basic position of the *Molluginaceae* (cf. EHRENDORFER 1976), calls for the testing of additional taxa.—A few species from other families investigated here supplement the list of investigated taxa published earlier (BEHNKE 1976 b, with additions in 1978).

Materials and Methods

Longitudinal hand sections through stem pieces of the plant species listed in Table 1 were subjected to standard procedures for the investigation of sieve elements with a transmission electron microscope, including a formaldehyde-glutaraldehyde fixation followed by osmic acid fixation and a final embedment in epoxy resins (see BEHNKE 1982 a for details).—Voucher samples were prepared and deposited at the University of Calicut (India) Herbarium or at B or HEID.

Results and Discussion

Caryophyllaceae. Sieve-element plastids of the three additional genera investigated (see Table 1) are of form PIIIc'f. The frequently found 6- to 7-edged profiles of the central crystal (in addition to 3-, 4-, 5-edged, see Fig. 1, *Drymaria*) suggest that its three-dimensional structure is more complex rather than simply cubic. Therefore, the crystal is referred to as "polygonal" in thin sections. Outside *Caryophyllaceae* such crystals are reported to occur in *Stegnosperma*, *Achatocarpus*, and *Phaulothamnus* (BEHNKE 1976 b, 1981).

Molluginaceae. *Pharnaceum* and the additional species of *Mollugo* exhibit form PIIIcf sieve-element plastids which correspond with the plastids found earlier in other species of the tribe *Mollugineae* (*Hypertelis*, *Mollugo*: BEHNKE 1976 b). *Glinus* includes small starch grains (Fig. 5: s) in its sieve-element plastids (form PIIIcfs), a form not often found in the *Caryophyllales*. The central crystal is globoid (Figs. 2, 5) and sometimes partly lobed (Fig. 3, upper plastid). Occasionally, even polygonal outlines (Fig. 3, lower plastid) are encountered, but the margins of the crystal are not as sharp as in plastids of the *Caryophyllaceae* (cf. Fig. 1). However, PIII sieve-element plastids with crystals of the cubic system do occur in the tribe *Limeeae* (tribal arrangement after

Table 1. Sieve-element plastids of *Caryophyllales*
(Additions to lists published in BEHNKE 1976 b, 1978). BG = Botanical Garden

Species	Origin of material	Plastid type
Caryophyllaceae		
Drymaria cordata (L.) ROEM. et SCHULT.	Calicut/Kerala, India (SIVARAJAN 3520)	PIIIc'f
Polycarpaea aurea WIGHT et ARN.	Calicut/Kerala, India (SIVARAJAN 768)	PIIIc'f
Polycarpon prostratum (FORSK.) ASCHERS.	Calicut/Kerala, India (SIVARAJAN 242)	PIIIc'f
Molluginaceae		
Glinus oppositifolius (L.) A.DC.	Calicut/Kerala, India (SIVARAJAN 1101)	PIIIcfs
Mollugo disticha (L.) SER.	Cape Comorin, India (SIVARAJAN 9912)	PIIIcf
M. nudicaulis LAM.	Cape Comorin, India (SIVARAJAN 9914)	PIIIcf
M. pentaphylla L.	Cape Comorin, India (SIVARAJAN 9928)	PIIIcf
Pharnaceum cordifolium L.	Stellenbosch, RSA (leg. VISSER 1980-11-03)	PIIIcf
Amaranthaceae		
Allmania nodiflora R. BR. ex HOOK. f.	Calicut/Kerala, India (SIVARAJAN 1185)	PIIIfs
Cyathula prostrata (L.) BLUME	Calicut/Kerala, India (SIVARAJAN 570)	PIIIf
Aizoaceae		
Oscularia deltoides (L.) SCHWANT.	BG Berlin-Dahlem	PIIIcf
Saphesia flaccida N. E. BR.	BG Heidelberg	PIIIcf
Cactaceae		
Melocactus depressus HOOK.	BG Heidelberg	PIIIcf
Wittia amazonica K. SCHUM.	BG Heidelberg	PIIIcf
Nyctaginaceae		
Torrubia riedeliana (FISCH. ex HEIMERL in WARM.) STANDLEY	BG Berlin-Dahlem	PIIIcf
Phytolaccaceae		
Segueria aculeata JACQ.	BG Berlin-Dahlem	PIIIcf

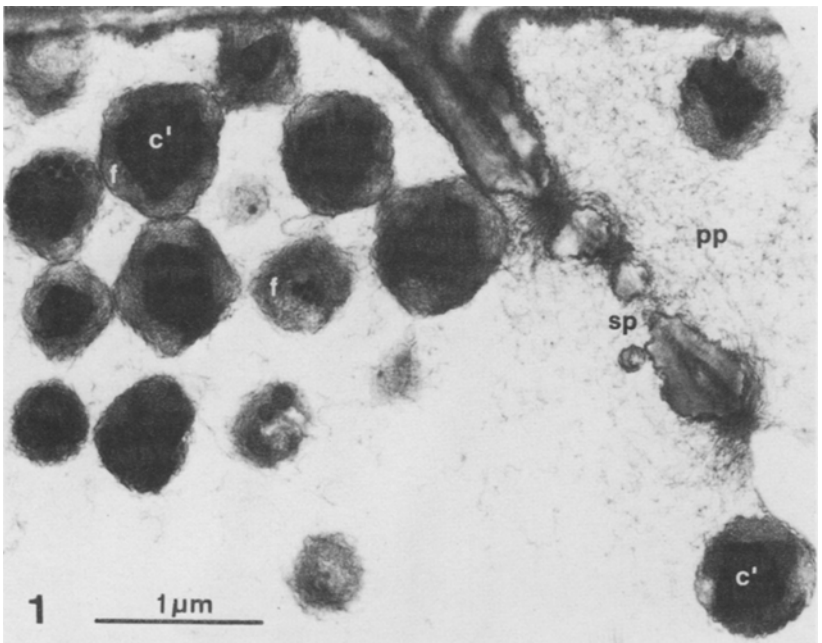
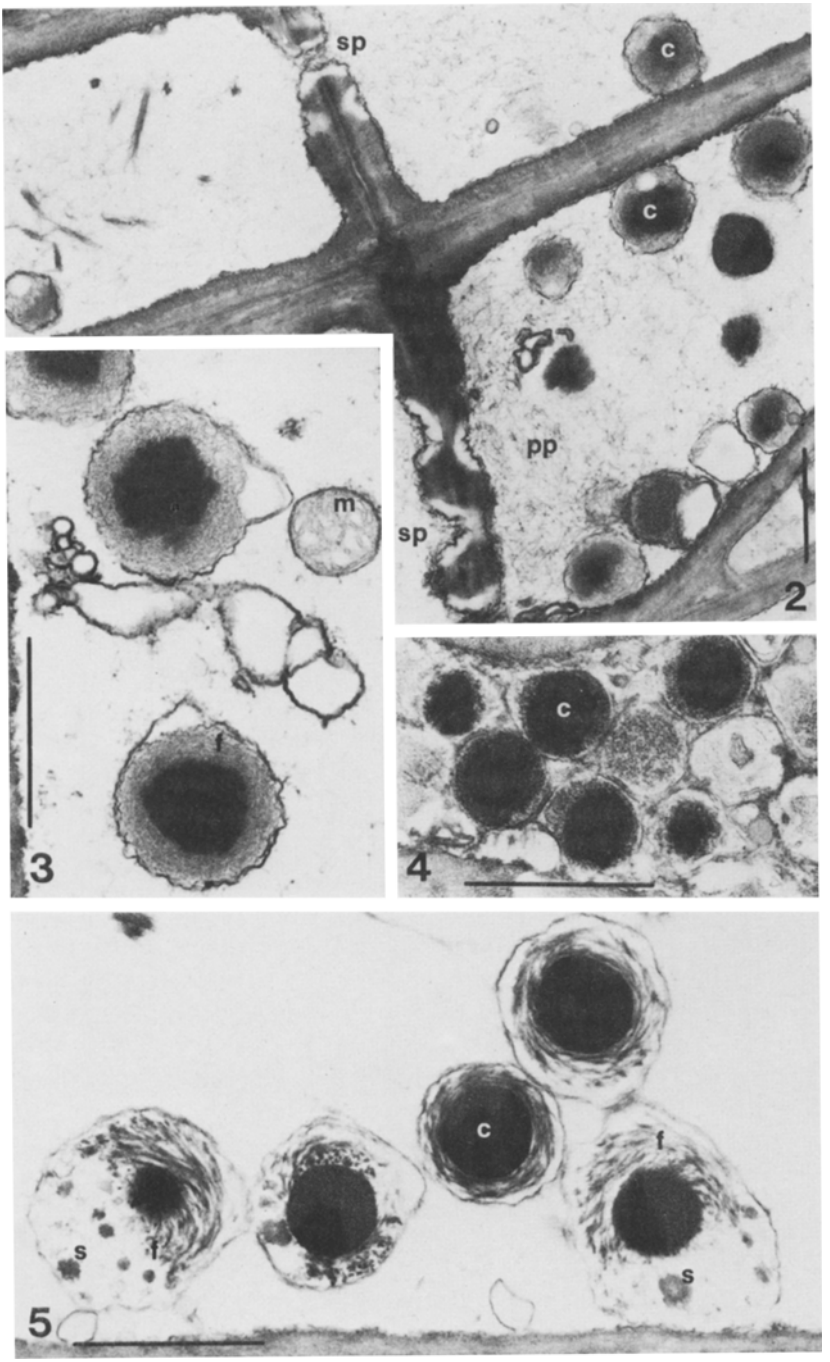


Fig. 1. *Drymaria cordata*. Longitudinal section through sieve tube with form PIIIc'f sieve-element plastids. c' = polygonal crystal, f = ring-shaped bundle of protein filaments, pp = P-protein, sp = sieve-plate pores. ×22,000

HOFMANN 1973): in *Limeum* and *Macarthuria* (BEHNKE 1976 b, BEHNKE & al. 1983). On the other hand, the genus *Gisekia* (*Gisekieae*) with form PIIIcf plastids as found in members of the tribe *Mollugineae* is now excluded from the *Molluginaceae*, since it contains betalains (MABRY & al. 1976).

Amaranthaceae. Sieve-element plastids of form PIIIf, i.e. without a central crystal as typical of suborder *Chenopodiineae* (cf. BEHNKE 1976 b), are also present in *Allmania* (Fig. 7) and *Cyathula*, with additional starch grains, found in some plastids of *Allmania* (Fig. 7: s).

Figs. 2-5. Sieve-element plastids of *Molluginaceae* (PIIIcf) with ring-shaped bundle of protein filaments (f) and a globular crystal (c) which is sometimes lobed (Figs. 2, 3) or nearly polygonal (Fig. 3, lower plastid). Rarely, small starch grains are accumulated in addition (Fig. 5: s).—Figs. 2, 3: *Mollugo pentaphylla*.—Fig. 4: *Pharnaceum cordifolium*.—Fig. 5: *Glinus oppositifolia*. m = mitochondrium, pp = P-protein, sp = sieve-plate pores, 2: ×15,000; 3-5: ×25,000. Scale bars = 1 µm



Figs. 2–5

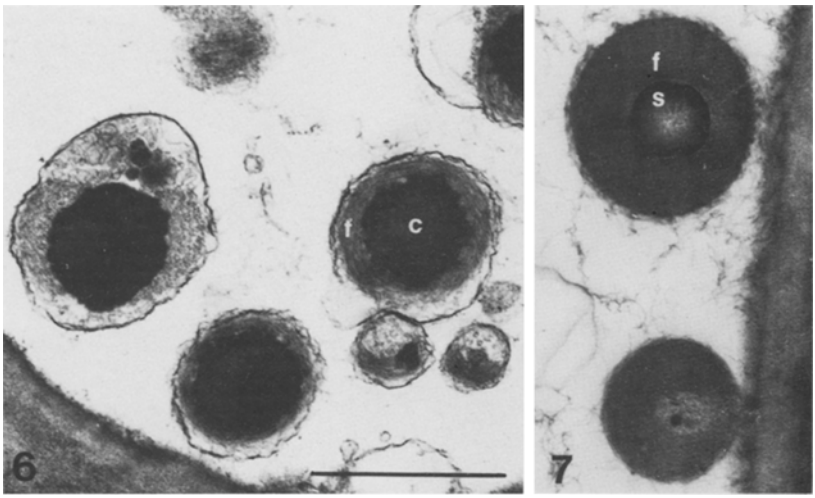


Fig. 6. Sieve-element plastids of *Wittia amazonica* (*Cactaceae*) with ring-shaped bundle of filaments (f) and globular crystal (c)

Fig. 7. Sieve-element plastids of *Allmania nodiflora* (*Amaranthaceae*): Starch grains (s; in serial sections veryfied also by enzymatic digestion) occasionally occur in the center of the plastids, surrounded by a ring-shaped bundle of filaments (f). Both; ×25,000. Scale bar = 1 μm

The remaining six species from four different families (see Table 1) all contain PIIIcf sieve-element plastids (e.g. *Wittia*, Fig. 6), the most common form in *Caryophyllales*. The sieve-element plastids of all 16 species investigated corroborate the distinction of the subtype PIII into three major forms and the affilation of different families with these forms (BEHNKE 1976 b, 1981). It is also evident that only in the more basic families *Phytolaccaceae* s.l. and *Molluginaceae* do two or more forms of PIII-plastids co-exist. Therefore, further research on sieve-element plastids of *Caryophyllales* will concentrate on these families (see BEHNKE & al. 1983).

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