Plant Syst. Evol. 126, 371—375 (1977)

Lehrstuhl für Zellenlehre der Universität Heidelberg

S-Type Sieve-Element Plastids and Anthocyanins in *Vivianiaceae*: Evidence Against its Inclusion into *Centrospermae*

By

H.-Dietmar Behnke, Heidelberg, and **Tom J. Mabry**, Austin

(Received April 10, 1976)

Key Words: *Centrospermae*, *Caryophyllales*, *Geraniales*, *Vivianiaceae*.— Sieve-element plastids, comparison of ultrastructure; anthocyanins and betalains.

Abstract: The presence of S-type sieve-element plastids and anthocyanins in the *Vivianiaceae* indicates that it is not a member of *Centrospermae* (*Caryophyllales*).

The tribe *Vivianieae* within *Geraniaceae*, comprising annual and perennial herbs, largely confined to Chile and with one species in southern Brazil and Uruguay, was separated from *Geraniaceae* and for the first time raised to the rank of a family by KLOTZSCH (1836). While most subsequent systematists treated *Vivianieae* within *Geraniaceae* (e.g. BENTHAM & HOOKER 1862–1883, REICHE 1897, KNUTH 1912 and 1931, MELCHIOR 1964, CRONQUIST 1968, THORNE 1968), several recent workers (e.g. HUTCHINSON 1959, TAKHTAJAN 1969, 1973, and DAHLGREN 1975) reestablished the separate family *Vivianiaceae*.

A comprehensive taxonomic revision of the *Vivianiaceae* comprising four genera with six species has recently been presented by LEFOR (1975).

The present investigation was prompted by TAKHTAJANS 1973 treatment of the *Vivianiaceae* as a member of his order *Caryophyllales*, thus revising his earlier (1969) view which incorporated it into *Geraniales*. TAKHTAJAN (1973) mentions probable affinities with *Caryophyllaceae* and, referring to BORTENSCHLAGER (1967), points out, in particular, similarities in the pollen structure. BORTENSCHLAGER (1967) in a "preliminary note on the pollen morphology of the family *Geraniaceae*" favored the segregation of *Vivianiaceae* and proposed its alignment with

the *Centrospermae* (*Caryophyllales*). Based primarily on palynological characters he suggested a position intermediate between *Caryophyllaceae* and *Amaranthaceae*; for example, he noted that the pollen exine of *Viviania montevidensis* (= *Caesarea*) and *V. elegans* (= *Cissarobryon*) appears similar to those reported for *Caryophyllaceae* while in other *Viviania* species the semitectate exine patterns approach those in *Amaranthaceae*. Thus, these palynological investigations provide belated support for the views of KLOTZSCH (1836) and CAVANILLES (1804) of a close relationship between *Viviania(ceae)* and the *Centrospermae*.

Since *Centrospermae* are characterized by very specific P-type sieve-element plastids (BEHNKE 1976) and by the presence of betalains in all but two families (MABRY 1976) and since our previous collaborative investigations of these characters have permitted reevaluation of the systematic position of several taxa of questionable alignment (e.g. MABRY & BEHNKE 1976), it was desirable to examine ultrastructurally and chemically members of the *Vivianiaceae* also.

For ultrastructural investigations plant specimens of *Caesarea albiflora* CAMB. [= *Viviania montevidensis* (KLOTZSCH)] REICHE were collected and sent to Heidelberg by A. R. SCHULTZ (Porto Allegre, Brazil). Fresh stem parts were fixed in a formaldehyde/glutaraldehyde mixture followed by 1% osmic acid, then embedded in epoxy resins and processed for screening with a Siemens Elmiskop 101. As a test specimen *Pelargonium tetragonum* (L. f.) L'HERIT. (*Geraniaceae*), Botan. Garten Heidelberg, was subjected to the same methods.

Reddish colored petals from herbarium specimens of *Viviania ovata* PHIL. (*V. rosea* HOOK., leg. O. ZÖLLNER No. 610 on top of Campanita, Chile, 1963-12-15, ex Herb. Mus. Bot. Berol. [B]), kindly provided by TH. ECKARDT (Berlin), were subjected to pigment analysis by standard procedures (MABRY et al. 1975).

The sieve elements of *Caesarea albiflora* contain S-type plastids (Fig. 1), a type which is widespread in dicotyledon angiosperms but entirely excluded from the *Centrospermae*. In *Caesarea* each sieve-element plastid includes in its matrix a few, often club-shaped starch grains. Bordering against the matrix and surrounding the grains are tiny starch-like particles which show the same staining properties as the large grains. Thus, *Caesarea* S-type sieve-element plastids (Fig. 1) look much like those of *Pelargonium* (Fig. 2).

The pigment in the petals of *Viviania ovata* was found to be an anthocyanin, namely a cyanidin monoglycoside (probably a glucoside based on co-chromatography kindly performed by J. B. HARBORNE).

The presence of both S-type sieve-element plastids and an anthocyanin in the *Vivianiaceae* indicates that its alignment to *Centrospermae*

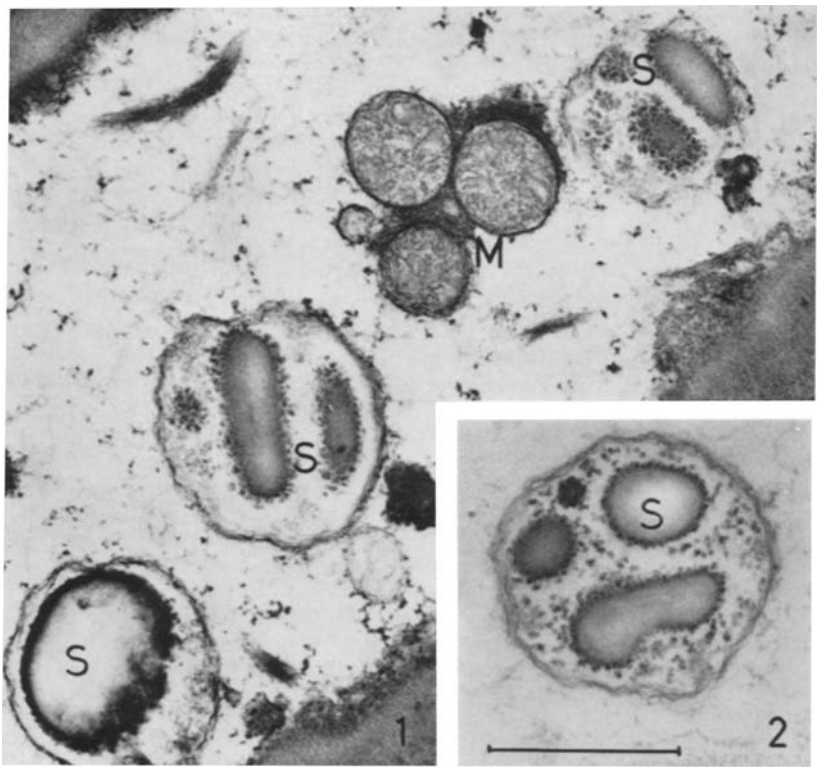

Fig. 1. *Caesarea albiflora*: Part of a sieve element with S-type sieve-element plastids (S) and mitochondria (M). ×25,000

Fig. 2. *Pelargonium tetragonum*: S-type sieve-element plastid. Marker = 1 μm. ×25,000

is unlikely. The data especially deny a close relationship to the *Caryophyllaceae* and *Amaranthaceae*: 1., although all *Centrospermae* are characterized by a very specific P-subtype of sieve-element plastids, the *Caryophyllaceae* and *Amaranthaceae* contain distinct and unique morphological forms of this subtype (BEHNKE 1976); 2., although the *Caryophyllaceae* do contain anthocyanins, *Amaranthaceae* have only betalains.

The ultrastructural and chemical data do not exclude either an alliance of *Vivianiaceae* with *Geraniales* or its placement into *Geraniaceae* as *Vivianieae*; still other treatments (e.g. placement in *Pittosporales*, HUTCHINSON 1959) are also possible.

We thank Prof. A. R. SCHULTZ (Porto Allegre, Brazil) and Prof. TH. ECKARDT (Berlin) for sending us plant specimens of *Vivianiaceae*, Dr. W. M. LEFOR (Storrs, Conn., U.S.A.) for checking the correct naming of

the specimens, Dr. J. B. Harborne (Reading, England) for co-chromatographing the cyanidin derivative with standard samples. We thank Miss B. Schmidt (Heidelberg) and Miss Carol Kidd (Austin) for technical assistance. The work was supported at the University of Heidelberg by grants from the Deutsche Forschungsgemeinschaft and, at the University of Texas, by the Robert A. Welch Foundation (Grant F-130) and the National Science Foundation (Grant BMS-79-09320).

T. J. M. was the recipient of a U.S. Senior Scientist Alexander von Humboldt Award and in residence at the University of Heidelberg during the period when this manuscript was completed.

References

Behnke, H.-D., 1976: Ultrastructure of sieve-element plastids in *Caryophyllales* (*Centrospermae*), evidence for the delimitation and classification of the order. Plant Syst. Evol. **126**, 31—54.

Bentham, G., and Hooker, J. D., 1862—1883: Genera Plantarum. London.

Bortenschlager, S., 1967: Vorläufige Mitteilungen zur Pollenmorphologie in der Familie der Geraniaceen und ihre systematische Bedeutung. Grana Palynol. **7**, 400—468.

Cavanilles, A. J., 1804: Del genero nuevo *Viviania*. Anal. Cienc. Nat. [Madrid] **7**, 211—212 (cited correctly, not after Bortenschlager).

Cronquist, A., 1968: The Evolution and Classification of Flowering Plants. London: Nelson.

Dahlgren, R., 1975: A system of classification of the angiosperms to be used to demonstrate the distribution of characters. Bot. Notiser **128**, 119—147.

Hutchinson, J., 1959: Evolution and phylogeny of flowering plants. Oxford: Univ. Press.

Klotzsch, J. F., 1836: Bemerkungen zu den Geraniaceen und deren Verwandtschaften. Linnaea **10**, 425—439.

Knuth, R., 1912: *Geraniaceae*. In Engler, A. (Ed.): Das Pflanzenreich **4**, **129**, 1—640. Bd. IV. 129, 640 S. Leipzig: Engelmann.

— 1931: *Geraniaceae*. In Engler, A., und Harms, H. (Eds.): Die natürlichen Pflanzenfamilien, 2. Aufl., **19 a**, 43—66.

Lefor, M. W., 1975: A taxonomic revision of the *Vivianiaceae*. Occasional Papers, Univ. of Conn., Biol. Sci. Ser. **2** (15), 225—255.

Mabry, T. J., 1976: Pigment dichotomy and DNA-RNA hybridization data for centrospermous families. Plant Syst. Evol. **126**, 79—94.

— and Behnke, H.-D., 1976: Betalains and P-type sieve-element plastids: The systematic position of *Dysphania* R. Br. (*Centrospermae*). Taxon **25**, 109—111.

— Eifert, I. J., Chang, C., Mabry, H., Kidd, C., and Behnke, H.-D., 1975: *Theligonaceae*: Pigment and ultrastructural evidence which excludes it from the order *Centrospermae*. Biochem. Syst. Ecol. **3**, 53—55.

Melchior, H. (Ed.), 1964: A. Engler's Syllabus der Pflanzenfamilien **II**, 12. Aufl. Berlin: Borntraeger.

Reiche, K. F., 1897: *Geraniaceae*. In Engler, A., (Ed.): Die natürlichen Pflanzenfamilien, 1. Aufl. **3** (4), 1—14. Leipzig: Engelmann.

Takhtajan, A., 1969: Flowering Plants: Origin and Dispersal. Edinburgh: Oliver & Boyd.

TAKHTAJAN, A., 1973: Evolution und Ausbreitung der Blütenpflanzen. Stuttgart: G. Fischer.

THORNE, R., 1968: Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso **6** (4), 57—66.

Addresses of the authors: Prof. Dr. H.-DIETMAR BEHNKE, Lehrstuhl für Zellenlehre der Universität Heidelberg, Im Neuenheimer Feld 230, D-6900 Heidelberg, Federal Republic of Germany. Prof. Dr. T. J. MABRY, The Cell Research Institute and Department of Botany, University of Texas at Austin, TX 78712, U.S.A.