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Pollen Morphology of the New Species *Mimulus shevockii* and a Possibly Related Species, *M. barbatus* (Scrophulariaceae)

CHARLES L. ARGUE*

ABSTRACT — The pollen grains of *Mimulus shevockii* and *M. barbatus* have three long, equally spaced, meridionally oriented apertures with transversely ruptured membranes, and the pollen walls are microreticulate with smooth muri. The pollen evidence (pollen size and shape, rupturing pattern and ornamentation of the aperture membrane, size and spacing of lumina, and ornamentation of muri) is applied to comparisons between the pollen of *M. shevockii* and that of other species in section *Paradanthus*. These data are consistent with a proposed relationship between *M. shevockii* and *M. barbatus* of the *M. rubellus/M. palmeri* group.

Introduction

In 1985 L. R. Heckard, University of California at Berkeley, sent me pollen from eight plants of a remarkable new species of *Mimulus*, *M. shevockii* Heckard and Bacig., which has a corolla unlike that of any other *Mimulus* (1 and personal communication). The present note provides the first illustrated descriptions of the pollen of this and a perhaps related species, *M. barbatus* Greene, as a supplement to previously published surveys of the pollen of *Mimulus* on a worldwide basis (2, 3, 4).

Heckard and Bacigalupi (1) place *M. shevockii* in section *Paradanthus*. Although the morphology of its corolla is unique, its calyx and vegetative morphology most closely resemble that found in several members of the *M. rubellus/M. palmeri* group (5) of this section, for example, *M. barbatus*, *M. androsaceus* Curran ex Greene, *M. gracilipes* Robinson, and *M. purpureus* A. L. Grant (1). Indeed, some early collections of *M. shevockii* that failed to show the corolla clearly were tentatively identified as *M. barbatus* (1).

Nevertheless, the infrasectional relationships of *M. shevockii* are still considered problematical (1). The possible bearing of the pollen evidence on this problem will be examined on a preliminary level for all members of the section for which SEM data are available.

Materials and Methods

Collection data and pollen measurements are summarized in Table 1. Pollen grains for scanning electron microscopy (SEM) were either not acetolyzed or acetolyzed (6) gently for one hour at room temperature and examined using a Hitachi S-450 scanning electron microscope. Brightfield and Nomarski interference contrast observations of acetolyzed and unacetolyzed whole pollen grains mounted in glycerine jelly were made using a Zeiss microscope (N.A. 1.32, apochromatic objective X100). Pollen was available from one and

eight plants of *M. barbatus* and *M. shevockii*, respectively (Table 1). Pollen diameters, including polar (P) and equatorial (E) axes, are based on a minimum of 20 fully developed unacetolyzed grains per species (Table 1) measured at X1000 under oil immersion. Measurements of pollen surface details are based on scanning electron micrographs (SEMGs) of as few as five grains, and because of this small sample size, should be treated with reserve. Terminology is defined as it is introduced and is derived from Erdtman (7), Praglowski and Punt (8), and Walker and Doyle (9).

Results and Discussion

The pollen grains of *M. shevockii* and *M. barbatus* are single, more or less spheroidal (Table 1), isopolar, and radially symmetrical with three long, equally spaced, meridionally oriented apertures (Figures 1, 4). The aperture membranes, covered by labile material in unacetolyzed pollen (Figure 1), have a rough surface (Figures 3, 6) and usually show one to three or more irregular transverse ruptures in unacetolyzed grains examined by brightfield and Nomarski interference contrast. The outer surface, or tectum, of the pollen wall consists of a mesh-like network of interconnecting rods called muri (Figures 2, 5). These surround open areas or lumina and are supported from below by radially oriented rods called columellae. The columellae, in turn, are attached internally to a third wall layer, the nexine (not illustrated), with an orientation "parallel" to that of the tectum. Important morphological features of the pollen walls in *M. shevockii* and *M. barbatus* include muri that are smooth (psilate) and subtended by a single file of columellae (simplicolumellate) and lumina that are wider than the muri but less than 1.0 μm in diameter (microreticulate). In *M. shevockii* the lumina are 0.8 (range 0.4-1.2) μm in diameter with a lumina to muri ratio of 2.3 (range 2.1-2.5). The respective values for *M. barbatus* are 0.8 (range 0.4-1.8) μm and 2.0 (range 1.8-2.3). Lumina are slightly reduced in size in both species near the apertures (Figures 3, 6).

The characters summarized above and in Table 1 place the grains of both *M. shevockii* and *M. barbatus* in a pollen group

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Table 1. Measurements and collection data for pollen of *Mimulus sbevoeckii* and *M. barbatus*

Species of <i>Mimulus</i>	Collector, collection no., and locality	N	Polar axis (P) ^{1, 2}	Equatorial axis (E) ^{1, 2}	P/E ²	
<i>M. sbevoeckii</i>	Shevock 10368 Kern Co., CA	Plant				
		1	10	36.9 (34-41)	38.4 (35-41)	0.96 (0.86-1.08)
		2	10	36.6 (33-40)	37.3 (34-40)	0.98 (0.86-1.11)
		3	10	38.2 (33-44)	38.7 (34-44)	0.99 (0.89-1.28)
		4	10	33.8 (31-35)	38.6 (34-41)	0.89 (0.75-1.00)
		5	10	36.9 (34-39)	38.2 (35-40)	0.97 (0.88-1.11)
		6	10	37.5 (31-41)	37.2 (34-40)	1.01 (0.87-1.23)
		7	10	36.2 (34-39)	40.5 (39-41)	0.90 (0.83-0.98)
		8	10	39.5 (36-42)	38.2 (34-41)	1.04 (0.95-1.11)
\bar{x}			37.0 (31-44)	38.4 (34-44)	0.97 (0.75-1.28)	
<i>M. barbatus</i>	Twisselmann 13402, Kern Co., CA		20	37.0 (31-44)	34.5 (32-39)	1.07 (0.78-1.29)

¹ Measurements are in micrometers (μm)² Mean followed by range in parentheses.

previously described as type IIb (2). This type is distinguished from other triaperturate pollen of section *Paradanthus* chiefly by the absence of supramural spinules or granules (2, 4). Among the 27 species of section *Paradanthus* with triaperturate pollen that have thus far been examined by SEM, 13 have pollen of this type. Fourteen others have pollen grains with dense supramural ornamentations and are designated type IIc (2, 4). Each of these pollen types, however, embraces a macromorphologically nonhomogeneous assemblage of species, and a further resolution of differences is needed if the pollen evidence is to be applied to an analysis of infrasectional relationships.

To this end, the pollen data for all triaperturate members of section *Paradanthus* have been reassessed based on pollen size ($\sqrt{P \times E}$), pollen shape, and the presence or absence of conspicuous transverse ruptures in the aperture membrane in unacetolyzed pollen examined by light microscopy. Also considered were the texture of the aperture membrane (psilate versus rough or granular), the size of the lumina, and the ratio of the lumina diameters to muri widths, as well as the occurrence of psilate versus ornamented muri (See 2, 4 for data). Using an equal weighting of these characters, a percentage similarity value (S) was calculated for all pairwise combinations of *M. sbevoeckii* and other taxa of section *Paradanthus* ($S = 100 \times \text{number of characters shared} / \text{number of characters compared}$). Numerical character differences were accepted as significant at the 95% level.

The limited number of independent pollen characters available for analysis and, in some cases, the restricted number of samples examined require that the results be considered preliminary. Furthermore, the taxonomic significance, if any, of the characters analyzed has not been established within this group. Such significance has, however, often been demonstrated elsewhere in the delimitation of subgenera, sections, and/or species of *Mimulus* and other taxa of tribe Mimuleae (2, 3, 4, 10, 11, 12, 13).

Clues to relationships within section *Paradanthus* based on pollen morphology are equivocal in terms of the groupings of species recognized by Grant (5). Thus, although the overall mean percentage similarity value between *M. sbevoeckii* and examined members of the *M. rubellus*/*M. palmeri* group

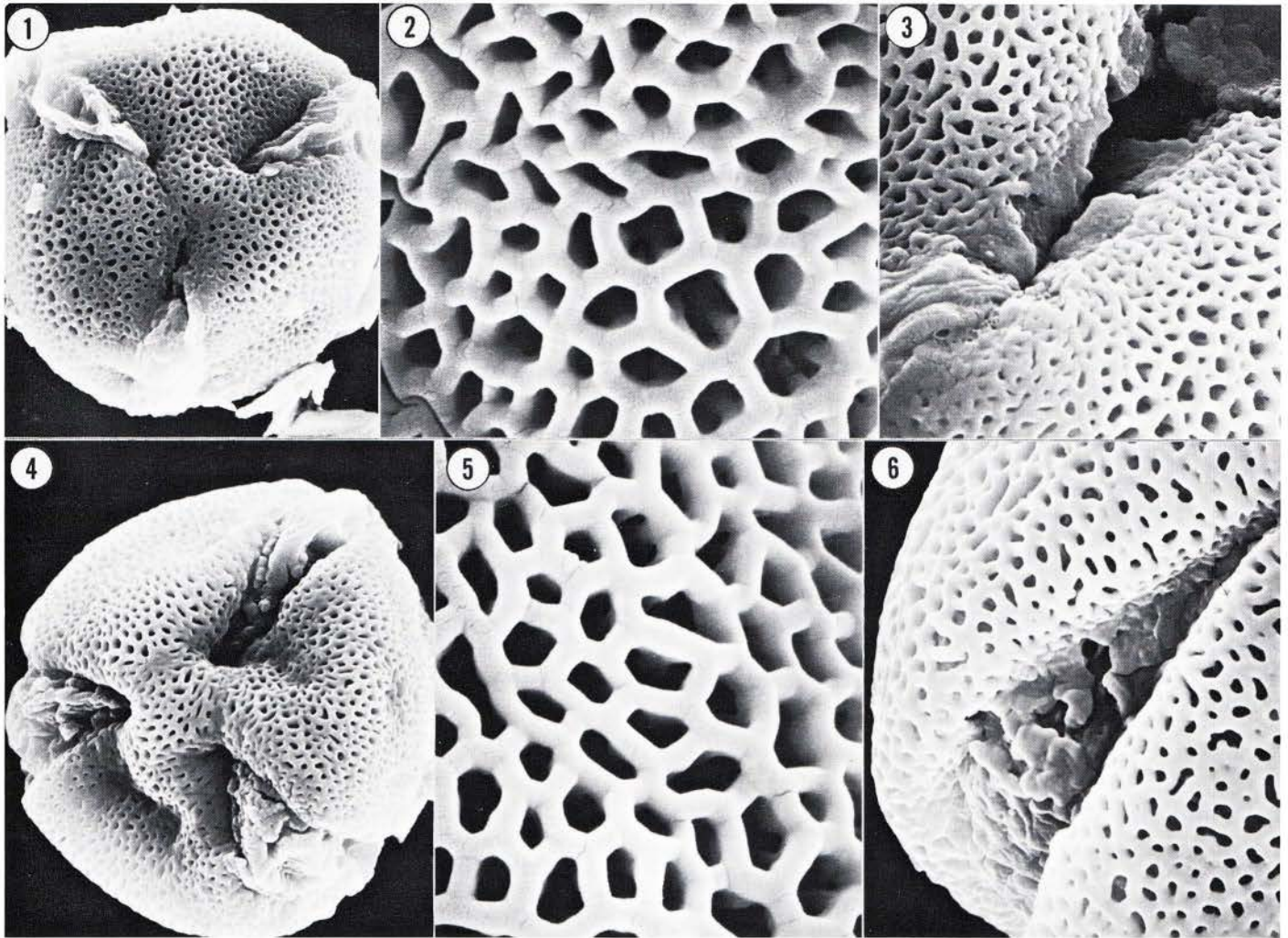
is a relatively high 87% (*M. discolor* A. L. Grant, 93%; *M. rubellus* Gray ex Torr., 86%; *M. suksdorfii* Gray, 79%; *M. barbatus*, 100%; and *M. biolettii* Eastw., 79%) and although this compares to mean values ranging from 52-72% for other species groups of section *Paradanthus*, a number of species assigned to these other groups have pollen grains that differ very little from those of *M. sbevoeckii*. For example, the grains of *M. dudleyi* A. L. Grant of the *M. moschatus* group and *M. sbevoeckii* show a percentage similarity of 86%.

On the other hand, the grains of *M. barbatus* fail to differ from those of *M. sbevoeckii* in any of the traits mentioned, and Heckard and Bacigalupi's (1) tentative association of these species based on similarities in their vegetative morphology (See Introduction) is consistent with the pollen evidence. *Mimulus discolor*, which Grant (5, Figure 1) apparently considered closely related to *M. barbatus* (as *M. deflexus* Wats.), is also very similar to *M. sbevoeckii* in pollen morphology (See above). However, the resemblance of the pollen grains of *M. androsaceus*, *M. gracilipes*, and *M. purpureus* to those of *M. sbevoeckii* remains to be explored (cf. 1).

Thus, although final assessment of the infrasectional relationships of *M. sbevoeckii* must await additional studies, the preceding preliminary analysis implies that two independent sources of provisional evidence, the data from pollen and vegetative morphology, may converge upon the same resolution. Such concordance provides a focus for further investigations within a complex where existing cytotoxic information is minimal (1) and where other lines of inquiry such as experimental biosystematic and chemotaxonomic studies have yet to be initiated.

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Figures 1-6. SEMGs of pollen of *Mimulus sbevoeckii* and *M. barbatus*. Unacetolyzed (Figure 1) or acetolyzed for one hour at room temperature (Figures 2-6). **Figures 1-3.** *Mimulus sbevoeckii*. 1. Polar view. X2000. 2. Close-up of pollen wall. X12460. 3. Close-up of aperture. X4640. **Figures 4-6.** *Mimulus barbatus*. 4. Oblique polar view. X2310. 5. Close-up of pollen wall. X12270. 6. Close-up of aperture. X4360.

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