

Axillary Meristem Development in *Mammillaria elongata* DC (Cactaceae)¹

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Abstract. Axillary meristems of *Mammillaria elongata* DC were studied with a scanning electron microscope using fresh tissue to determine their degree of development and suitability as explants in tissue culture investigations. Meristems were excised at regular intervals along the stem. The axillary meristem reached maximum size about 10 cm and maximum development about 15 cm below the stem tip. Axillary meristems closer to the base of the stem were less developed. In fully developed meristems, leaf primordia were initiated in a spiral acropetal sequence at the margins of the apical dome, resulting in a phyllotaxis of 8 + 13 contact parastichies of tubercles on the developed stem. Enlarged leaf primordia were 1- or 3-lobed and about 75 μ m in length. No flower initiation or lateral branch development was observed; however, a corky region, the result of aborted or senesced flowers, was observed in several axils. Variability in development or absence of axillary meristems in several axils make *M. elongata* axillary meristems unsuitable for critical studies on factors influencing organogenesis in tissue culture.

Mammillaria elongata, an attractive, freely branching cactus with elongated shoots and tubercles surmounted with spreading spines, is important commercially. Increased demand for plants of this type necessitates new, improved methods of propagation. During recent investigations of tissue culture propagation of several species of Cactaceae (8, 9), it was suggested that axillary meristems might make suitable explants. Among their advantages is the potential for each axil to produce and rapidly develop uniform plants from organized tissue. Therefore, this study was initiated to determine the suitability of axillary meristems as uniform explant sources with particular emphasis on variability in the degree of development of each meristem.

Boke (1, 2, 3, 4, 5, 6) investigated the developmental anatomy of the areoles, tubercles, axillary shoots, and shoot apices of several cacti. Using darkfield microscopy, he (6) produced an informative series on spine initiation in *M. lasiacantha* by combining expert dissection and skillful photographic techniques. Scanning electron microscopy (SEM) also facilitates detailed developmental studies. This is a morphogenic SEM study of *M. elongata* axillary meristems.

Materials and Methods

Axillary meristems of *M. elongata* were dissected at measured intervals along the lengths of several shoots. Fresh, uncoated specimens were examined in a JEOL JSM-U3 scanning electron microscope at accelerating voltages of 15 and 25 KV (7). Specimens were handled quickly to avoid distortion caused by desiccation.

Results and Discussion

A developmental sequence of the axillary meristems, tubercles, and leaves of *M. elongata* is presented in Fig. 1-10, il-

lustrating development from the apex to the base of a 30-cm shoot. In the initial stages of development 0.6 cm from the apex, the lateral dome of the meristem has not produced primordia and is relatively small (Fig. 1). At 1.2 cm below the apex, the size of the meristem has increased and several primordia are present on the flanks (Fig. 2). Further development, at 2.5, 5, and 7.5 cm from the apex (Fig. 3-5), involves meristem enlargement and increase in the size and number of leaf primordia. A large number of trichomes surround the meristem. In sample preparation, most trichomes were removed to expose the meristem and primordia so that only trichome bases appear surrounding the meristem (Fig. 3-5).

Maximum development occurs 10 and 15 cm from the shoot apex (Fig. 6, 8). There the meristem is 150-200 μ m wide and about 10 leaf primordia are visible. Among the well-developed lateral meristems are some less-developed similar to those nearer the shoot apex (Fig. 7).

Toward the base of the stem, meristems are smaller and have fewer and smaller leaf primordia (Fig. 9). They appear similar to the meristems near the shoot apex.

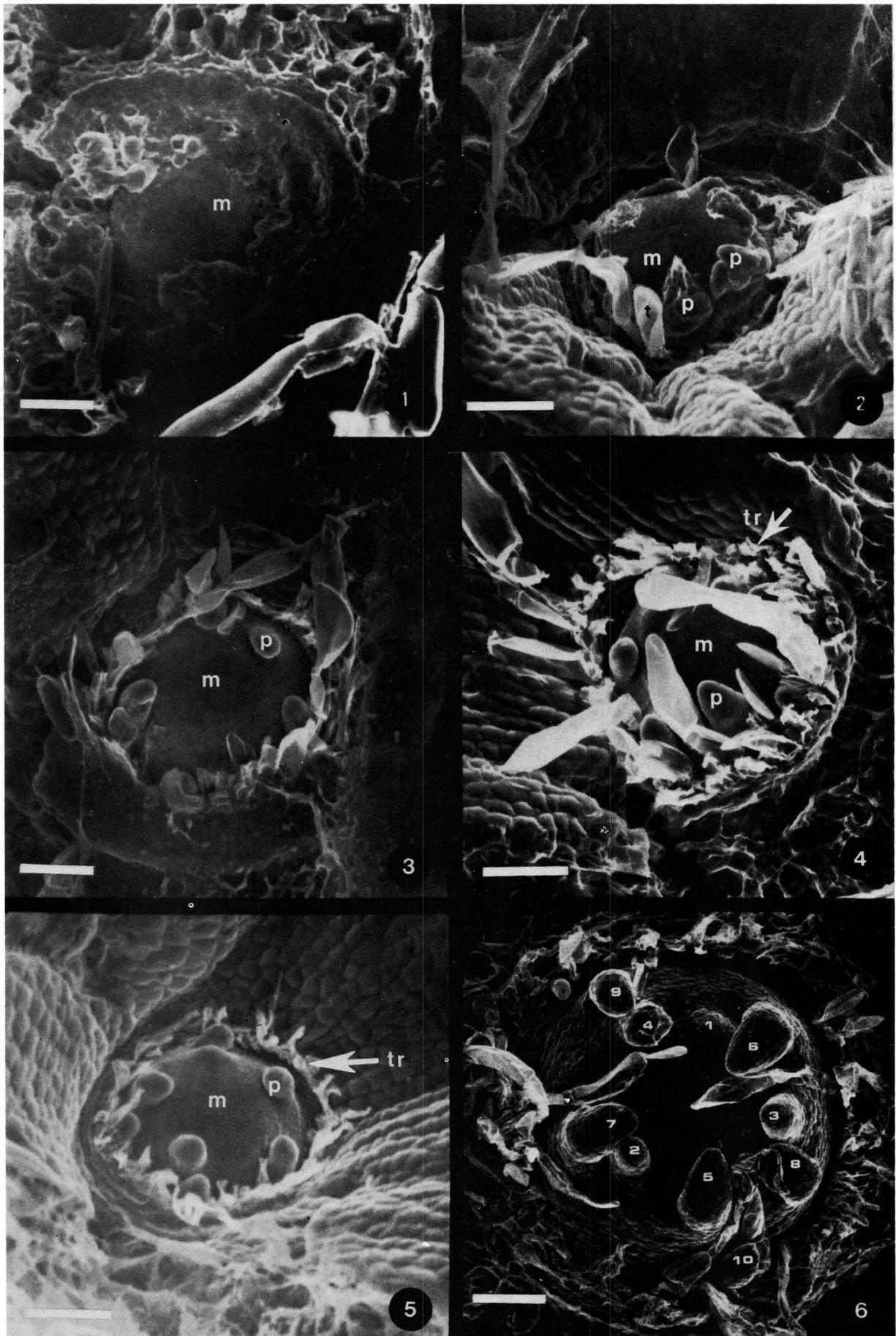
At random intervals along the stem, corky areas were observed without meristems (Fig. 10). In *M. lasiacantha*, Boke (3, 4) has reported these corky areas are the remains of aborted lateral meristems. SEM and visual observations of the growth and flowering of *M. elongata* suggest that these corky areas are bases of senesced or aborted flowers differentiated from lateral meristems. The ring of trichomes is the principal distinguishing feature. Only unorganized tissue remains where a well-defined lateral meristem might be found. Primordia on the dome of the

Fig. 1-6. (Facing page.) Axillary meristems of *Mammillaria elongata*. Fig. 1. Early development of a meristem 0.6 cm below the shoot apex. Fig. 2. Axillary meristem 1.2 cm below the shoot apex with trichome and young leaf primordia. Fig. 3. Young leaf primordia and meristem 2.5 cm below shoot tip. Fig. 4. Enlarged leaf primordia and meristem 5 cm below shoot tip. Fig. 5. Young axillary meristem and leaf primordia 7.5 cm below shoot tip. Trichomes have been removed, leaving a ring of trichome scars. Fig. 6. A well-developed meristem 10 cm below shoot tip with several well-developed leaf primordia. The initiation sequence of primordia is numbered 1 through 10. m = meristem; p = primordia; t = trichome; tr = trichome ring. Bar represents 100 μ m.

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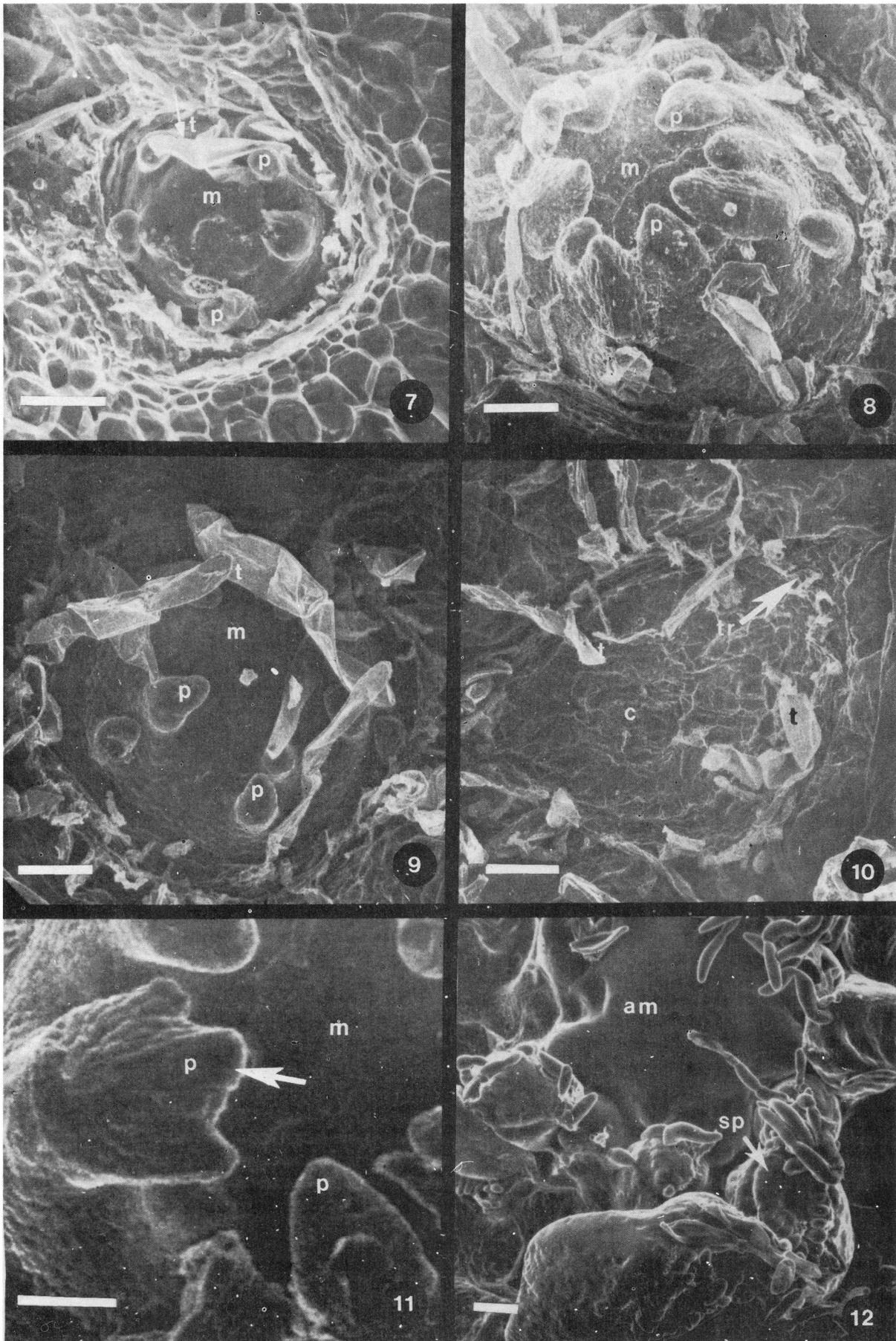


Fig. 7–10. (Facing page.) Axillary meristems of *Mammillaria elongata*. A poorly developed axillary shoot in the region of maximum development, 12.5 cm below the shoot tip. Fig. 8. A well-developed axillary meristem, 15 cm below the shoot tip. Fig. 9. A poorly developed axillary meristem, 17.5 cm below the shoot tip. Fig. 10. Corky tissue, rather than an organized meristem. Fig. 11. (Facing page.) A mature leaf, showing the lamina (arrow) at its maximum size. Fig. 12. (Facing page.) The apical meristem region of *M. elongata* with several tubercle primordia with a spiniferous meristem. c = corky tissue; m = meristem; am = apical meristem; p = primordia; t = trichome; tr = trichome ring; sp = spiniferous meristem. Bar represents 100 μ m.

lateral meristem consist of the leaf and the leaf base. In *M. elongata*, the bulk of the primordium consists of the leaf base, and the leaf blade is rudimentary. The leaf blade usually consists of a few cells on the distal, abaxial surface of the primordia and forms a small protuberance approximately 50 μ m in height (4, 6). The primordium in Fig. 11 shows a leaf of *M. elongata* at its maximum development. Following this stage, the leaf blade stops differentiating such that only the base which forms the tubercle primordium remains.

In *M. heyderi* and *M. lasiacantha*, Boke (4, 6) found an areole meristem produced on the adaxial surface near the axil of developing tubercle primordia. Continued development of the tubercle resulted in a division of the areole meristem into an axillary or lateral meristem and a spiniferous meristem which gives rise to the spines. The axillary meristem remained in the axillary position and produced either floral or vegetative shoots. The vegetative meristem developed to a predetermined stage and then became inactive. If the shoot apex is damaged, or if continued growth removes it a significant distance from lower lateral meristems, apical dominance is broken and a lateral meristem becomes active, forming a new branch. Our observations, based on gross morphology of the plant and location of the lateral and spiniferous meristem, suggest *M. elongata* may be similar. The spiniferous meristem of *M. elongata* is separated from the axil as the adaxial surface of the tubercle elongates. Eventually, the spiniferous meristem is positioned at the tip of the tubercle (Fig. 12) while the axillary meristem is positioned at the base of the tubercle.

Boke (4) stated that the shoot apex of *M. heyderi* was the largest known for any angiosperm: its usual diameter is about 1200 μ m with a maximum of 1500 μ m. The shoot apex of *M. elongata* is about 360 μ m in diameter. Fig. 12 shows a shoot

apex of *M. elongata* with several subtending primordia and developing tubercles. Several developing tubercles contain well-defined spiniferous meristems at their apices (Fig. 12, arrow). These spiniferous meristems at the stage of developing the first, outer series of spine primordia. The spine primordia are produced acropetally from the margin of the spiniferous meristem. In *M. lasiacantha*, Boke (6) noted production of three series of spine primordia and a few additional primordia before spine initiation stopped.

The phyllotaxic arrangement of the tubercle primordia can be seen in Fig. 6. Initiation follows a spiral acropetal sequence as with most cacti (6). These observations and growth pattern of the mature shoot result in a phyllotaxis of 8 + 13 contact parastichies.

This study shows that axillary meristems of *M. elongata* are variable in development. In a 30-cm branch, meristems at either end were poorly developed. Maximum development of both the axillary meristems and subtending tubercles was noted at 10 and 15 cm below the shoot apex. Lateral meristems were lacking in several axils and where a corky base formed from either aborted flowers or the base of matured fruits. Variable development and absence of many lateral shoots makes the axillary meristems unsuitable as explant material in tissue culture studies. Until some method is developed to ensure uniform selection for the presence of axillary meristems in selected explant material, reliable propagation of *M. elongata* will depend on selection of some other explant tissue (8).

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