Dissected leaves in Papaveraceae-Eschscholzioideae have an architecture frequently encountered in the basal eudicot clade Ranunculales that could represent an ancestral condition for eudicots. Developmental morphology of foliage leaves was investigated using scanning electron microscopy and focusing on primordium formation activity (primary morphogenesis) at the leaf margin. Eschscholzia californica, E. lobii, and Hunnemannia fumariaefolia had a polyternate-acropetal mode of leaf dissection. Segment formation continued around the whole leaf blade periphery. Differences in mature leaf architecture was traced to variations in regional blastozone activity and duration. Epidermal cell size measurements in E. californica indicated that the leaf tip tissue starts to differentiate already at the onset of organogenic activity and that tip cells remain larger than epidermal cells at the basal margins during further growth. It is argued that early differentiation of the tip does not set up a general basipetal differentiation gradient, but is a local effect that allows acropetal pinna initiation to occur in subapical blastozones. In Dendromecon, secondarily entire leaves have evolved through the loss of primordium formation activity. Marginal corrugations found in Dendromecon form late in development and are not reminiscent of lateral primordia.

Key words: blastozone; Dendromecon; Eschscholzia; histogenesis; Hunnemannia; leaf dissection; primary morphogenesis.

The wide variation in number and arrangement of pinnae and other leaf segments such as lobes and serrations in many dicot plants arises during an early organogenic phase of leaf development before leaves have grown to a size of 1 or 2 mm. The formation of marginal primordia during this critical period of primary morphogenesis proceeds in often distinct directions, such as acropetal or basipetal. Certain parts of the leaf blastozone (the marginal regions competent for primordium formation), such as along the developing petiole and rachis units, may become permanently inactivated at an early stage. This process may determine whether or not lateral primordia are initiated during intercalary elongation of the petiole, conditioning different architectures of the mature leaf (Gleissberg, 2002). Blastozone inactivation or loss is frequently accompanied by cell vacuolation and trichome formation, indicating that the organogenic ability of blastozones precludes histogenetic processes and requires densely cytoplasmic meristematic tissue (Hagemann and Gleissberg, 1996). Progressing histogenesis may therefore restrict blastozones and affect patterns of organogenic activity within the leaf. Beside region-specific blastozone inactivation via marginal histogenesis, a major determinant of dissection patterns may be different rates of primordium formation within the blastozone. Species with multi-dissected leaves often have periplastic blastozones, in which primordium formation activity continues around the entire growing periphery. Here, directional initiation of pinnae is soon accompanied by higher-order segmentation along the margins of pinnae initiated earlier. It was proposed that directional pinna initiation in periplastic leaves, rather than reflecting directional blastozone inactivation, is due to locally enhanced primordium formation activity resulting from differences in marginal dilation growth (Gleissberg, 1998b).

Given the high variation in leaf dissection between and within dicot lineages, it is important to characterize spatial-temporal patterns of blastozone activity in related species and genera. This can be useful in two respects. First, to provide a comparative framework for studying developmental mechanisms specifying leaf dissection, and second, to understand the evolution of these patterns. Particularly suitable for the study of leaf dissection are the periplastic leaves of Papaveraceae, in which primary morphogenesis is diverse (Gleissberg and Kadereit, 1999). While basipetal modes of pinna formation prevail in subfamily Chelidonioideae (Gleissberg, 1998a), a diversity of acropetal, basipetal, and divergent modes exists in subfamily Papaveroideae (Gleissberg, 1998b). In addition, there is evidence that leaf dissection was evolutionarily lost independently at least two times in subfamily Papaveroideae. In many genera of this family, pinnae themselves undergo further dissection. In most cases, pinna branching (higher-order dissection) was an abbreviated iteration of the pattern of leaf dissection (first-order dissection). For example, lobes on a pinna of Chelidonium majus arise in basipetal succession, as do the pinnae themselves on the leaf primordium. Conversely, in Papaver pavonimum pinna formation as well as second-order dissection of pinnae proceed acropetally. Such a repetition of patterns has been reported and discussed in other species (McLellan and Dengler, 1995).

Here, a morphological analysis of leaf development in Papaveraceae subfamily Eschscholzioideae is presented, complementing earlier studies in the two other subfamilies Papaveroideae and Chelidonioideae (Gleissberg, 1998a, b). Eschscholzioideae, the smallest subfamily of Papaveraceae, has three genera, all distributed in western North America (Kadereit, 1993), and provides interesting aspects for studies of leaf development: As sister to the two other larger subfamilies, Eschscholzioideae can be regarded as an early-diverging clade. The prevailing polyternate-acropetal leaf architecture has sim-
Fig. 1. Stages of leaf development in *Eschscholzia californica*. A–I. Scanning electron micrographs. A, B. Shoot apical meristem in side and top view, consecutive leaves are numbered. Primordia 1 and 2 are still undissected, leaves 3 and 4 have one and three lateral pinna pairs, respectively. C–I. Developing leaves viewed from the adaxial side. C. Four primary pinna pairs are present. D–F. Onset of secondary (D, E) and tertiary (F) segmentation is marked by white arrowheads. At the stage of (E), petiole elongation has commenced. H, I. Secondary morphogenesis after termination of pinna formation. J. Representative mature leaf. Scale bars = 100 μm for A–D, 200 μm for E–I, 1 cm for J.

ilarities to leaves frequently found in the outgroup family Fumariaceae. Because this type of leaf also occurs in many basal clades of other Ranunculales families such as Ranunculaceae and Berberidaceae, it might represent the ancestral condition for this basal eudicot clade (Gleissberg and Kadereit, 1999). Two genera, *Eschscholzia* with 12 species and the monospecific *Hunnemannia*, are characterized by dissected leaves, while adult plants of the third genus, the woody *Dendromecon* (two species), have undissected leaves. Hence, beside two instances in Papaveroideae, *Dendromecon* provides another example of evolutionary loss of leaf dissection in the Papaveraceae. Leaf development in *Eschscholzia californica* is described focusing on primary morphogenesis (pinna formation). Descriptions of leaf development in *Eschscholzia lobii*, *Hunnemannia fumariaefolia*, and *Dendromecon harfordii* are provided to put *Eschscholzia californica* in a comparative framework. Dissection events are mapped on mature leaf shapes to visualize spatial-temporal patterns. The study of the blastozone activity at the margin using scanning electron microscopy is related to observations indicating histogenic gradients within the growing leaf primordia.

**MATERIALS AND METHODS**

*Plant sources and cultivation*—*Eschscholzia californica* ssp. *californica* Cham. seeds were obtained from NK Lawn & Garden, Chattanooga, Tennessee, USA. *Eschscholzia lobii* and *Hunnemannia fumariaefolia* seeds were obtained from the University of Mainz Botanical Garden. Plants were grown in soil in a greenhouse at the University of Mainz. Shoots of *Dendromecon harfordii* and *D. rigida* and seedlings of *D. harfordii* were harvested from plants growing in the UC Davis Arboretum, Davis, California, USA, and fixed immediately.

*Microscopic analysis*—The first 4–6 leaves after the cotyledons, which are less complex, were excluded from the analysis. Vegetative shoot apices were mostly freshly dissected, fixed in FAA (2% formaldehyde, 5% acetic acid, 60% ethanol) or 70% ethanol, dehydrated in an ethanol series and critical-point dried. Gold sputter-coated shoot tips and leaves were viewed with a Philips XL 30 ESEM scanning electron microscope (FEI Electron Optics, Eindhoven, The Netherlands). Sequential appearance of first- and higher-order leaf segments was recorded in developing leaves of *Eschscholzia californica* and *Hunnemannia fumariaefolia* and then mapped on a representative mature leaf as described (Gleissberg, 1998b). Around 50 leaf stages were used to determine the general pattern in each species. Measurements were taken on SEM micrographs using analySIS (Soft Imaging System, Münster, Germany). For staging leaf development, lengths of growing leaves were measured from their adaxial median insertion to the tip. This method underestimates leaf sizes during acrovergent curvature. For measuring epidermal cell sizes, the longest visible diameter of the five largest epidermal cells at the leaf tip and of the margin near the leaf base was measured (see Fig. 2 for measured area) in a total of 61 individual leaves. Each value in Fig. 2 represents the mean of five cell measurements on an individual leaf.

**RESULTS**

*Eschscholzia californica* ssp. *californica*—As most herbaeous poppy species, *Eschscholzia californica* forms a rosette during the vegetative phase in which the first-formed leaves are less complex. With the onset of flowering, the primary shoot elongates forming a terminal flower. Flowering continues with lateral shoots arising from the elongated portion of the shoot and from the rosette (Günther, 1975). Leaves forming at the elongated portion of the shoot remain complex but have a reduced petiole. Rosette leaves are long-petiolate and have a finely dissected blade (Fig. 1J). The 3–5 primary pinna pairs decrease in size and complexity from the base to the tip. The proximal, most complex pinnae are dissected to the third degree. Secondary segments of the basiscopic side of lateral pinnae tend to be inserted more basally than their counterparts...
Changes in epidermal cell sizes at the leaf tip (filled triangles) and basal leaf margin (open squares) during earlier phases of leaf growth in *Eschscholzia californica*. Each dot is the mean of five measured cells on a single primordium. Vertical lines enclose the period of organogenic activity in the marginal blastozone. Values at leaf size 0 \( \mu m \) refer to cells at the shoot apical flank meristem prior to and during leaf initiation. Insets show measured areas in representative leaves from the start (left) and end (right) of the organogenic (primordium formation) growth phase, connected to corresponding values in the graph. For equivalent stages, compare to Fig. 1A, H.

on the acroscopic side, resulting in a slight pinna asymmetry. Leaf development is described for vigorous vegetative plants. After initiation from the shoot apical meristem, young leaves start to form lateral pinnae at a primordial size of 110 \( \mu m \) (Figs. 1A, B, and 2). After acropetal initiation of 3–5 primary pinna pairs from the marginal blastozone, higher-order segmentation begins at the proximal, oldest pinnae when the leaf primordium reaches a length of approximately 300 \( \mu m \) (Figs. 1C–E, 6A–D). Higher-order segmentation activity then expands acropetally (Figs. 1E–G, 6D–F). Segmentation of individual primary pinnae is also acropetal. Asymmetric development of lateral pinnae can be noticed from a slightly earlier onset of secondary segmentation at the basiscopic pinna margins (Figs. 1C, D, 6C–F). Blastozone activity persists along the entire periphery due to overlapping secondary and tertiary segmentation until all activity stops (Fig. 6G–J). This leads to a higher degree of dissection in proximal regions of the blade. At a primordial size of ca. 1300 \( \mu m \), the last higher-order segments have been initiated by the marginal blastozone.

Leaf primordia show acrovergence in early stages, an indication of preferred growth of the abaxial side (Fig. 1A–C). During higher-order segmentation and later expansion growth, the leaf axis assumes a straighter orientation (Fig. 1D–I). Dissected primary pinnae are oriented in an involute-incubous vernation during elongation growth (Fig. 1D–I).

To correlate the process of leaf dissection with marginal tissue differentiation, epidermal (protodermal) cells at the tip and base of developing leaf blades were measured (Fig. 2). Until the onset of the organogenic phase of leaf growth, mean size of leaf epidermal cells was in the range of 5.2–9.6 \( \mu m \), similar to cell sizes in the flank meristem prior to and during leaf initiation. At the onset of pinna formation (sample interval between 93 \( \mu m \) and 149 \( \mu m \) primordium length), mean cell sizes at the basal margin of the leaf were significantly smaller than at the tip (6.38 \( \mu m \), SD = 1.89, vs. 8.38 \( \mu m \), SD = 1.37; \( T = 6.25, P < 0.001, df = 103, t \) test). This difference became amplified during the subsequent exponential increase at both the tip and the base during the organogenic and early histogenetic phases. Mean epidermal cell sizes at the base vs. tip of primordia at the end of the organogenetic phase, ranging between 920 \( \mu m \) and 1536 \( \mu m \) in length, were 11.70 \( \mu m \) (SD = 1.95) and 17.13 \( \mu m \) (SD = 3.11), respectively (\( T = 10.46, df = 98, t \) test). Epidermal cell size at the tip of leaves increased approximately 2.5 times during the organogenic phase of leaf growth, indicating the slowing of cell division during epidermal differentiation. The tips of lateral pinnae similarly developed larger cells. The distal-proximal gradient in cell size that was present at the beginning of organogenic activity was maintained at least until a leaf size of 7.5 mm.

*Eschscholzia lobii*—This species is smaller than *E. californica*. Leaves are less strongly dissected and occur only in the rosette (GuÈnther, 1975). At a size of about 125 \( \mu m \), 2–4 primary pinna pairs begin to form in acropetal succession (Fig. 3A, B). Continued blastozone activity often leads to secondary segmentation on basal pinnae at a primordial size of around 400 \( \mu m \) (Fig. 3C–E), but higher-order segmentation is less pronounced compared to *E. californica*, and the organogenic
phase ends well before the primordia reach 1000 μm in length. During segmentation, young leaves are slightly acrovertely curved, later they are straighter, and vernation is involute-incubous.

_Hunnemannia fumariaefolia_—_Hunnemannia_ plants develop a few rosette leaves after which the primary shoot elongates forming more leaves before a terminal flower is made (Günther, 1975). At a size of about 145 μm, the first lateral pinna pair can be detected, followed acropetally by two more (Figs. 4A–B, 6K–N). This short acropetal sequence is accompanied by early acropetal higher-order segmentation at the marginal blastozones of the proximal pinna pairs starting at a primordial size of approximately 300 μm (Fig. 4B–E). The first-formed proximal pinnae become dissected to the tertiary degree and acquire a complexity similar to the remainder of the leaf blade (Fig. 6O–P). The basiscopic sides of the primary pinnae have accelerated development, leading to pinna asymmetry. Periplastic blastozone activity appears to be terminated at a leaf size of around 1100 μm. The degree of dissection of _Hunnemannia_ leaves is approximately half that in _Eschscholzia californica_. Leaves adopt an erect stature quite early; acroversion is evident only until the beginning of the organogenetic phase. After the organogenetic phase, pinnae adopt an involute-incubous orientation.

_Dendromecon harfordii_—In contrast to _Eschscholzia_ and _Hunnemannia_, leaves in the two species of _Dendromecon_ are simple and entire (Fig. 5H; Ernst, 1962). However, juvenile leaves on seedling plants regularly show lobing (Fig. 5L). Also, margins of leaves of adult plants are not smooth but are corrugated to various degrees. Some first-formed leaves on vigorous basal renewal shoots on adult plants sometimes had irregular toothing. Juvenile plants do not develop a distinct

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**Fig. 4.** Stages of leaf development in _Hunnemannia fumariaefolia_. A–B. Shoot apical meristems in lateral view, showing undissected primordia as well as leaves with 1–3 lateral pinna pairs. C–E. Higher-order segmentation, arrowheads in (C) mark first-formed secondary segments, in (E) first-formed tertiary segments. F–G. Secondary morphogenesis after termination of segment formation when petiole and pinna elongation occur. Scale bars = 100 μm for A–D, 200 μm for E–F, 500 μm for G, and 1 cm for H.

**Fig. 5.** Stages of leaf development in _Dendromecon harfordii_. A–B. Shoot apical meristems in apical and lateral view. C–G. Developing leaves in adaxial view. No lateral primordium formation occurs. H. Naturally macerated leaf from an adult plant showing entire margin. I–K. Details of late-occurring marginal corrugation in _D. harfordii_ (I) and _D. rigida_ (J, K). Inset in (K) gives magnified view of marginal undulation. L. Tridentate primary leaf of _D. harfordii_. Bars = 200 μm for A–E and K, 500 μm for F–G, 50 μm for I–J, 1 cm for H, and 2 mm for L.
rosette but soon develop internodes. Leaf development described here is based on vegetative shoot tips of vigorous branches of adult shrubs. Early stages of development are similar in both species and are described only for the broader-leaved *D. harfordii*.

Leaf primordia are initiated in an alternate phyllostaxy and soon curve acrovergently over the apex acquiring a scalelike shape (Fig. 5A, B). At an early stage, thickening growth of the leaf axis is distinguishable from the flatter lamina wings. No sign of lateral primordium formation is seen in stages in which these would form in the other genera (Fig. 5B–E). As primordia elongate, the median leaf axis becomes more distinct from the lamina wings also in adaxial view (Fig. 5C–G).

While leaf elongation proceeds in a fairly straight orientation, surface growth of the lamina wings progressively leads to an involute vernation. Development of the short petiole is discernible only at a late stage. Development of apical vs. basal cell size was similar to that found in *Eschscholzia californica* (data not shown).

At a size of approximately 8 mm, the smooth margins start to develop a corrugation (Fig. 5I). In the material investigated, these corrugations are more pronounced in *D. rigidida*, in which clusters of enlarged marginal cells protrude relative to intervening cells that form indentations. Marginal cells develop unicellular trichomes in some cases and further growth within the protruding and intervening sectors leads to an undulation of the leaf margin (Fig. 5J, K) that persists until maturity. At the time these structures are formed, the venation network of the lamina is already well developed.

**DISCUSSION**

*Patterns of organogenetic activity*—Dissected leaves in Papaveraceae-Eschscholzioidae are characterized by an acropetal-polyternate mode of leaf dissection (Gleissberg and Kadereit, 1999). This pattern deserves attention because it may represent the plesiomorphic condition in Papaveraceae plus Fumariaceae and possibly for the entire Ranunculales. This is also interesting because the Ranunculales are the earliest diverging clade of the eudicots. In this study, we report ontogenic details (summarized in Fig. 6) for the two genera in which dissected leaves occur, *Eschscholzia* and *Hunnemannia*. First-order pinnae always arise in a clear acropetal sequence. This is soon followed by higher-order segmentation that starts at the margins of the first-formed, proximal primary pinna pairs and extends towards the leaf tip (acropetal wave of higher-order segmentation). As in most cases reported from other Papaveraceae subfamilies, the segmentation of individual pinnae follows the same direction as first-order segmentation (acropetal here), indicating that individual pinna blastozones undergo the same developmental program as the leaf blastozone. In *E. californica* and *Hunnemannia*, several third-order segments become initiated in proximal parts of the blade. Although second-order segmentation of lateral pinna margins appears to be an abbreviated iteration of first-order segmentation of the leaf primordium, it displays asymmetry in that segmentation at basiscopic pinna margins commences slightly earlier than at the acropscopic side. This type of pinna asymmetry, promotion of the basiscopic pinna half, is more frequently observed in dicots than acroscopic pinna promotion (Troll, 1939) and might reflect a common developmental headstart of basiscopic pinna flanks. Within Papaveraceae, basiscopic pinna promotion is also more widespread than acroscopic pinna promotion, the latter occurring in species of *Papaver* (Gleissberg, 1998b).

An unknown signal leads to a nearly simultaneous cessation of blastozone activity when primordia are several 100 μm long. Discontinuation of primordium formation leads to an abbreviated pinna segmentation, particularly in upper blade portions. Therefore in mature leaves, primary pinnae are more simple in distal parts of the blade. Because no basipetal or divergent elements occur in Eschscholzioidae, it is concluded that such patterns arose after divergence of the Eschscholzioidae clade, in a clade comprising Papaveroeideae and Chelidonioideae. Although acropetal-polyternate leaves occur in some Papaveroeideae species such as *Roemeria refracta*, this type is not common in this subfamily and is absent in Chelidonioideae. An important step in the evolution of basipetal and divergent modes of dissection in Papaveraceae leaves was the retention of blastozone competence along the developing petiole margins, abolishing the strict delimitation of blade and petiole characteristic for polyternate-acropetal leaves (Gleissberg and Kadereit, 1999; Gleissberg, 2002). In Eschscholzioidae, scanning electron microscopy did not reveal noticeable indications for early histogenesis at the petiole margins, such as cell enlargement, that could account for blastozone inactivation.

Variation between species in the acropetal-polyternate developmental program reflects morphological differences. *Eschscholzia californica* ssp. *californica* develops relatively highly dissected leaves up to the third order. *Eschscholzia lobbia* is less strongly dissected but otherwise shows the same principal architecture. In *Hunnemannia fumariaefolia*, organogenetic activity in proximal pinnae is enhanced while the acropetal sequence is abbreviated. Therefore the proximal pinnae in this species have approximately the same degree of dissection as the distal rest of the blade, a characteristic of polyternate leaves. Pinna initiation in *E. californica* and *E.
lobbii and in Hunnemannia commences when primordia are between 100 and 150 μm long. For various species of subfamily Papaveroideae, onset of pinna initiation ranged between 150 and 250 μm, in Chelidonioideae between about 200 and 400 μm (Gleissberg, 1998a, b). Second-order segmentation followed quite soon, between 300 and 400 μm leaf primordium size. In comparison, second-order segments in some Papaver species became apparent later, at a size of 500–650 μm. This indicates that secondary segmentation is relatively more prominent in dissected leaves of Eschscholziioideae. Blastozone activity of the blade periphery continues until a size of 1300 μm in E. californica. In E. lobbii, where the degree of dissection is strongly reduced relative to E. californica, an earlier cessation of marginal organogenetic activity was observed. Some leaves in E. lobbii were only once-pinnate, indicating that acropetal leaves can represent simplified polyternate-acropetal leaves. Such a correlation between the degree of dissection and the duration of primary morphogenesis has also been found in species of Papaver (Gleissberg, 1998b). In general, timing and duration of segmentation in Eschscholziioideae falls within the range observed in the other Papaveraceae subfamilies.

Leaf dissection and differentiation gradients—Marginal areas with the competence for primordium formation (marginal blastozones) are characterized by the absence of histological differentiation marked by cell vacuolation or presence of idioblasts (Hagemann and Gleissberg, 1996). The onset of tissue differentiation at the margin may disable further primordium formation. Therefore the regulation of differentiation gradients between embryonic and histologically differentiating tissues during leaf development may account for blastozone activity patterns, such as that acropetal pinna initiation is associated with acropetal histogenesis, while basipetal pinna formation is associated with a basipetal wave of tissue differentiation (Kaplan, 1998). An alternative mechanism directing dissection patterns may be differential blastozone activity resulting from differential dilation of competent margins.

Trichome development is a convenient marker for regional histogenesis in other poppies, in which differential loss of marginal blastozones, e.g., at the petiole margins, was frequently correlated with appearance of trichomes (Gleissberg, 1998a, b). Because Eschscholziioideae leaves are basically glabrous, this feature cannot be used to investigate the relationship of pinna formation and histogenesis. Here, it was examined if cell size measurements can address this question.

To investigate apical-basal gradients in Eschscholzia, development of epidermal cell size at the leaf tip vs. basal leaf margin was scored and related to the period of organogenetic activity of the marginal blastozone. At the onset of pinna formation, cell sizes at the leaf tip already slightly but significantly exceeded those at the base. During and after pinna formation, this gradient was maintained while cell sizes strongly increased. This result is in line with findings for Papaver pavoninum and P. somniferum (Gleissberg, 1998b) that localized epidermal maturation at the leaf tip still allows for continued acropetal pinna initiation. Similarly, Sonntag (1887) already found that the leaf apex in certain species such as Acacia dealbata differentiates prior to acropetal pinna formation, at a primordium size of only 200 μm. In these cases, the acropetal-polyternate activity pattern of the marginal blastozone is clearly not reflected by acropetal tissue maturation. In other cases, Sonntag did find a prolonged embryonic status of the leaf tip associated with acropetal pinna formation. A particularly long duration of embryonic tip growth was found in some Apiaceae. In general, however, acropetal dissecting leaves did not necessarily have a longer maintenance of embryonic tips than basipetal leaves. This is confirmed for Papaveraceae, where leaf tip differentiation in acropetal species occurred sometimes earlier than in basipetal species (Gleissberg, 1998a, b). If cell vacuolation at the leaf tip would indicate the early acquisition of an inverted, basipetal differentiation gradient within the growing leaf, then it is difficult to imagine how pinna primordia can still be initiated acropetally below the tip. Because early cell vacuolation at tips is related to hydathode development, it may have only a local effect and therefore may not represent the onset of a general basipetal differentiation wave throughout the leaf. Isolated cell size measurements are not indicative of overall histogenic gradients within the growing leaf. Taken together, the expectation of general basipetal or acropetal gradients of tissue maturation may not adequately reflect the complexity of histogenesis during development of dissected leaves. For example, it is unknown how marginal differentiation gradients relate to the course of internal tissue differentiation, e.g., of procambium. Local histogenesis unrelated to a general gradient was observed to occur also along the petiole and leaf base margins and in developing rachis segments (Gleissberg, 1998a, b). It is proposed that in Eschscholzia, acropetal pinna initiation proceeds from subapical blastozones, mediated by differential acrotonic elongation in this region, and that histogenic events at the margin have a minor role in determining the direction of dissection.

Evolution of entire leaves—Eschscholzia and Hunnemannia are sister genera to Dendromecon, in which leaf dissection was probably secondarily lost. This is indicated by the prevalence of dissected-leaved species in Papaveraceae, in the outgroup family Fumariaceae, and in other families of the Ranunculales clade (Gleissberg and Kadereit, 1999). The process of pinna formation was shown here to be completely omitted in Dendromecon and not secondarily concealed by allometric growth during secondary morphogenesis as reported for some species with simple leaves (e.g., Coffea sp.; Bharathan et al., 2002). A fine marginal corrugation present in mature leaves develops much later when leaves are several millimeters long. Time of formation and appearance of these marginal structures is not reminiscent of marginal primordium formation.

However, primary leaves of Dendromecon are regularly lobed or dentate (Ernst, 1962), and irregular leaf toothing can also occur in basal renewal shoots (not shown). A decreased depth of sinuses between segments can result from a delayed onset of primordium formation activity of the marginal blastozone (Groot and Meicenheimer, 2000). Therefore, it is suggested that these marginal structures are equivalent to pinna in other Eschscholziioideae. This would mean that the developmental potential underlying leaf dissection is not compromised in Dendromecon, e.g., by disruption of a genetic pathway, but becomes selectively inactivated during the transition from the juvenile to the adult phase of shoot growth.

Conclusions—Of the two basic leaf types present in Eschscholziioideae, the dissected leaves of the polyternate-acropetal type in Eschscholzia and Hunnemannia are interpreted as ancestral with respect to Papaveraceae and possibly also in relation to the early diverging eucladid clade Ranunculales. Periplastic development, iteration of the acropetal dissection pro-
gram within pinnae, and the absence of any divergently or basipetally initiated segments are characteristic features. Early cell vacuolation at the leaf tip indicates compatibility of leaf tip differentiation with acropetal pinna formation. The development of entire leaves in *Dendromecon* is derived within Papaveraceae and is probably due to selective suppression of blastozone activity after the seedling stage rather than by mutational disruption of a genetic pathway. Marginal corrugation found in *Dendromecon* does not correspond to a dissection activity of the marginal blastozone.

In the future, investigations using molecular markers for blastozone competence (Gourlay et al., 2000; Dengler and Tsukaya, 2001; Bharathan et al., 2002; Gleissberg, 2002), cell division (Brandstätter et al., 1994; Kang and Dengler, 2002) and levels of plant growth regulators such as auxin (Ljung et al., 2001; Tsiantis et al., 2002; Aloni et al., 2003) should help to clarify relationships between the directionality of dissection, histogenesis, and of growth distribution.

**LITERATURE CITED**


