1989

The Status of *Erythronium albidum* and *E. mesochoreum* (Liliaceae) in Nebraska

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1989: Transactions of the Nebraska Academy of Sciences XVII: 71–79

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Two species of *Erythronium* grow in the eastern quarter of Nebraska, but there are none elsewhere in the State. *Erythronium albidum* is locally abundant, mostly in upland bur oak forests, and has been collected in 18 counties since 1864. *Erythronium mesochoreum* is becoming rare because its habitat—virgin tall-grass prairie—is disappearing. It is known to grow now in six east-central counties, but it probably could be found in some remnant prairies in all counties south and east of the Platte and Big Blue rivers, respectively. Distributional data about these species is herein brought up to date relative to earlier published reports. Although the literature suggests that the two species are not always clearly distinct, observations of living specimens in Nebraska mostly support their status as separate species.

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Two species of *Erythronium* are the only members of the genus native to Nebraska. They are bulbous perennials of the eastern quarter of the State. One, *E. albidum* Nuttall, is a woodland species; the other, *E. mesochoreum* Knerr, is usually in virgin tall-grass prairies and occasionally in woodlands. Both species flower and fruit in spring and wither by early summer, and so the plants are visible above ground only about two months of the year.

Various common names are used: the mottling of the leaves of *E. albidum* (and of some other species) has resulted in the names trout-lily and fawn-lily, and that and some other species are known as adder's tongue or dog-tooth violet, the latter after *E. dens-canis* of Europe, but they are not at all closely related to the true violets (Violaceae: *Viola*). The prairie erythronium, *E. mesochoreum*, takes that common name from its typical habitat. Species of montane western North America are sometimes called avalanche lilies or glacier lilies as well; they do not reach Nebraska.

TAXONOMY AND NOMENCLATURE

Erythronium L. is placed in the Liliaceae even when that family is defined in its narrowest sense (e.g., Dahlgren, Clifford, and Yeo, 1985). Its species are mostly North American and are closely related to the tulips (*Tulipa* L.), all of which are Eurasian.

Erythronium albidum was formally named by Nuttall in 1818, and *E. mesochoreum* was described as a species distinct from *E. albidum* by Knerr (1891), who did not designate a type specimen (a specimen with which the name is permanently associated). Robertson (1966) designated a neotype (*sic*) specimen (*Knerr s.n., 24 April 1891*, in the herbarium of the Missouri Botanical Garden) collected by Knerr in the same year and locality (1891; Atchison County, Kansas) as the original specimen from which the description was made. Although Knerr was the first person formally to describe the species, its distinctiveness had been noted by Burgess (1877) and Panton (1877) in Iowa and Kansas, respectively.

Erythronium albidum in its broad sense includes several entities that at various times have been given varietal, subspecific, or specific status. *Erythronium albidum* var. *coloratum* Sterns was described by Sterns (1888) for pink-to-red flowered plants with very strongly mottled leaves (such plants have never been reported from Nebraska); Steyermark (1963: *434*) believed those to be color variations of *E. albidum* var. *albidum*. Rickett (1937) found overlapping characteristics of *E. albidum* and *E. mesochoreum* in central Missouri and proposed the name *E. albidum* Nutt. var. *mesochoreum* (Knerr) Rickett. Steyermark (1963) used that combination, but some floristic works accord *mesochoreum* specific status (e.g., Great Plains Flora Association, 1986), others do not recognize it, and some reject it (e.g., Smith, 1988). However, Steyermark found the two entities to be readily distinguishable in the field in Missouri, and he questioned the varietal status of *mesochoreum*, suggesting that it is perhaps an "incipient species." Ireland (1957) showed that *E. albidum* and *E. mesochoreum* retained their distinctiveness when grown in a common garden, and he concluded that the latter should be placed in subspecific status to the former. Churchill (1986: *1250*), citing unpublished data of Churchill and Bloom, noted that "nearly every aspect of the life history and morphology of *E. mesochoreum* differs from *E. albidum*. The distinctive features of both species that are evident in the field are often not apparent in mounted herbarium specimens." That statement presumably applies at least to Kansas and Nebraska, where their observations were made. Perhaps there, at the very western limits of the ranges, they are fully differentiated as species but are possibly less so farther east.

My colleagues and I have little trouble distinguishing these entities in the field in Nebraska and Kansas, but the plants lose some diagnostic characteristics when pressed and dried and so present problems of identification as herbarium specimens. Robertson (1966) summarized the distinctions between *E. albidum* and *E. mesochoreum*, respectively, as follows: leaves abruptly vs. gradually attenuate, mottled vs. not mottled, flat vs. conduplicate; perianth reflexed vs. spreading; mature fruits held erect vs. resting on the ground; sterile individuals forming stolons and offsets vs. droppers and offsets; chromosome numbers 2 n = 44 vs. 22; habitat moist woods vs. prairies and dry woods. My observations in the field

generally support these distinctions, with modifications. I have found an occasional barely-mottled leaf in living *E. mesochoreum*. In *E. albidum*, it is common that older, senescing leaves lose their mottling, and leaves in sunny exposures often show reduced or even no mottling. While the leaves of *E. mesochoreum* are usually conduplicate at flowering time, they usually open with age, becoming flat and losing their glaucousness and appearing more lustrous. The position of the perianth—reflexed or spreading—is not always reliable because the perianth opens and closes daily. Thus, the reflexed perianth of *E. albidum* is merely spreading when the flower is only partially open, as is evident from Figure 5, in which some tepals are fully reflexed but others are not yet spreading. Figures 7 and 8, however, show the typical spreading condition of the perianth in *E. mesochoreum*. Furthermore, I have not seen the mature fruits of that species in anything but the prostrate position, but those of *E. albidum* may take either position, both conditions occurring in the same colony. The very largest fruits (ca 15mm long) are prostrate, probably because of their greater weight, but some smaller mature fruits are also prostrate.

In both species, the inner face of the perianth is white, but the outer face usually becomes pale blue with age, especially on the lower three petals.

Morphometric data on leaves and flowers suggest differences between the species. According to the literature, *E. mesochoreum* generally has larger flowers and fruits and narrower leaves than does *E. albidum* (e.g., Rickett, 1937; Robertson, 1966).

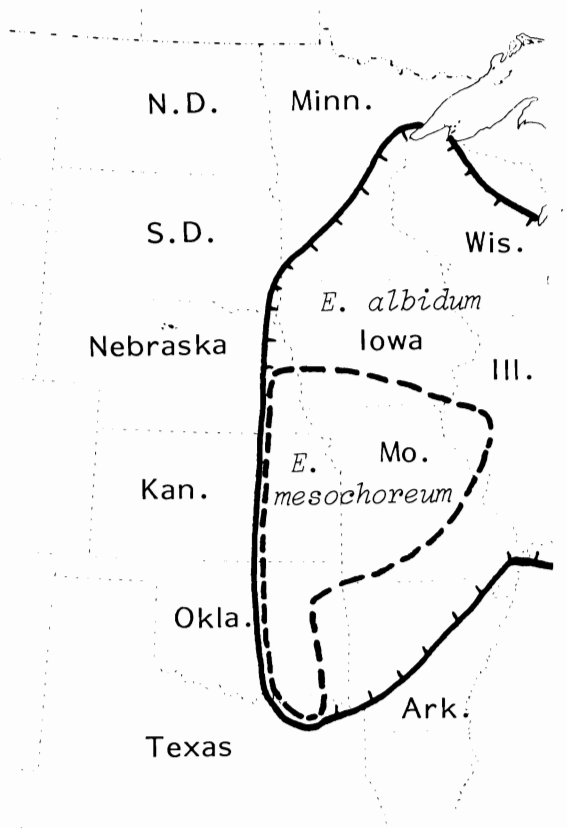


FIGURE 1. The ranges of Nebraska's two species of *Erythronium*.

GEOGRAPHIC DISTRIBUTION

Erythronium has 12–18+ species (the number depending upon taxonomic interpretation) of the middle latitudes in North America, and 1–4 extending across Europe and Asia. The North American species occur in two geographically-separate groups that share no species. The western group, variously interpreted to have 6–12 species, occurs from California north to British Columbia and east to the mountains of Montana and Colorado but does not reach Nebraska. The eastern group ranges from northwestern Minnesota south to northeastern Texas, east to New Brunswick and Florida. It has about six species, two reaching their western limits in eastern Nebraska (Fig. 1). According to Applegate (1935), the eastern species (including both species in Nebraska) are more closely related to the Eurasian species than to the geographically-closer species of western North America.

Erythronium albidum is among the widest-ranging of the eastern North American species: northwestern Minnesota to northeastern Texas eastward at least to Pennsylvania. In Nebraska it is locally common in upland forests in counties bordering the Missouri River from Dakota to Richardson counties and in upland bur-oak forests west to Cuming, Dodge, Butler, and Seward counties (Fig. 2). It does not occur in oak forests of Ponca State Park, Dixon County (Rolfsmeier, pers. comm.), and is not recorded in oak forests of Brown, Cherry, and Keya Paha counties in the Niobrara River Valley (Churchill, Freeman, and Kantak, 1988; Kaul, Churchill, and Kantak, 1988). Although there are no voucher specimens from Gage, Jefferson, or Saline counties, careful searching is likely to show the species to be there because suitable habitats exist and it has been found in nearby counties. The indication of this species occurring in Franklin County in the *Atlas of the Flora of the Great Plains* (Great Plains Flora Association, 1977) probably refers to a specimen now in the University of Nebraska–Lincoln herbarium that was collected by Hussong in 1896; it is labelled "*E. americanum*" from "Franklin County," but certainly is not from Franklin County, Nebraska. In fact, there are no records of *E. albidum* from the Republican River Valley, although suitable habitat, i.e., bur-oak forest, exists there in Franklin County and elsewhere (Kaul, 1975), on north-facing slopes of the south wall of the valley. (There are many of Hussong's specimens in that herbarium labelled to be from Franklin County, Nebraska, but the species represented are very unlikely to be from there because suitable habitats are absent and their ranges mostly don't come close to that county. Probably they are from a Franklin County in an eastern state, and their attribution to Nebraska appears to be the result of incorrect labelling of specimens received as a gift or by exchange.)

The distribution of *E. mesochoreum* is much smaller than that of *E. albidum* but is essentially included within the latter's range (Fig. 1). The prairie erythronium is a plant of the western tall-grass prairies and its western limits are rather well-defined: the southeastern quarter of Nebraska, the eastern third of Kansas and Oklahoma, and northeastern Texas (Great Plains Flora Association, 1977). Steyermark (1963: *435*) showed it for most of Missouri except the southeast. It occurs in southern Iowa (Great Plains Flora Association, 1977; Pleasants and Wendel, 1989). Robertson, McClain, and Koelling (1983) reported it from Macoupin County, Illinois, and Koelling et al. (*in litt.*) found it in Morgan and Pike counties in that state. Braun (1967) suggested introgression of *E. mesochoreum* (as a variety of *E. albidum*) into *E. albidum* in southwestern Ohio, where she noted that some plants are smaller, flower earlier, grow on drier sites than typical *E. albidum* there, and do not produce the offshoots so characteristic of typical *E. albidum*.

In Nebraska, *E. mesochoreum* is known to grow now in Butler, Douglas, Lancaster, Sarpy, Saunders, and Seward counties (Fig. 3). It probably occurs in other southeastern counties; its presence in nearly all northern Kansas counties west to Riley County (Great Plains Flora Association, 1977) suggests that it could be found in all Nebraska counties south and east of the Platte and Big Blue rivers, respectively. It is a plant mostly of undisturbed prairies and is disappearing with them.

HABITAT

The two species do not usually share the same habitat in Nebraska, but sometimes their populations abut at the border of prairie with forest.

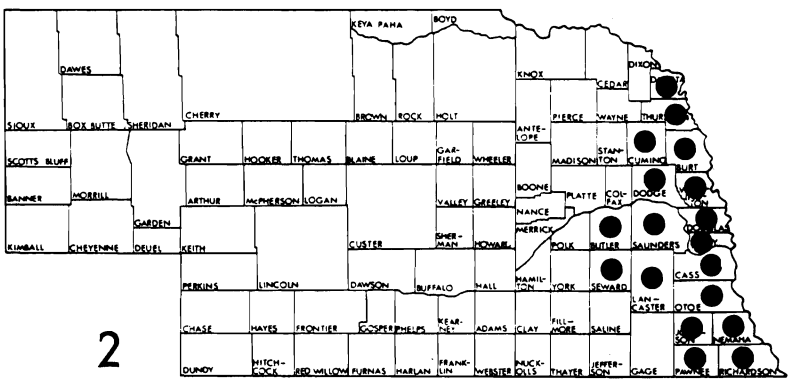
Erythronium albidum—In Nebraska, this species occurs in upland forests usually dominated by bur oak (*Quercus macrocarpa*), where it sometimes forms large colonies; the ground in places is white with the flowers in spring, before the leaves of the trees are fully formed. It is locally abundant in suitable habitats in every county bordering the Missouri River from Dakota County southward. For example, it is common in upland oak-hickory woods in Fontenelle Forest, Sarpy County, but uncommon in ravines at Neale Woods, Washington County (Garabrandt, 1988); it is locally abundant in Hummel Park, Douglas County. The labels on a few herbarium specimens note a floodplain habitat for the species in Richardson County, where presumably it occurs in the forests of sycamore, cottonwood, and soft maple.

It occurs in counties west of those bordering the Missouri River too. In Lancaster County it is now known only from Wilderness Park, where it is very local on the flat, moist land above deeply-entrenched Salt Creek, in the forest of bur oak, hackberry, American elm, honey locust, green ash and bitternut hickory; commercial development adjacent to the park destroyed large numbers of the plants in the 1970s. Rolfsmeier (1988) found it to be abundant in a few bur oak forests on slopes in eastern Seward County, and he reports it (pers. comm.) for Butler County, the apparent western limits for the species in the State.

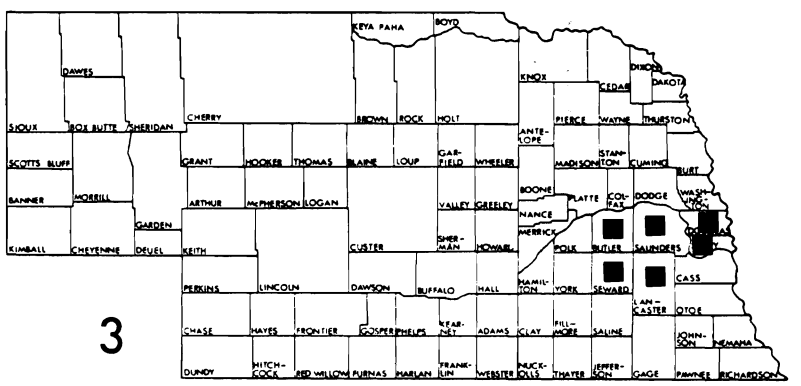
Erythronium mesochoreum—The prairie erythronium is a plant mostly of virgin tall-grass prairies and, like them, has largely disappeared from Nebraska. It is present in some of the dozens of small remnant virgin prairies in southeastern Nebraska where it is sometimes abundant. For example, at a site just west of Omaha, Douglas County, it is rather common in a moderately-sloping remnant tall-grass prairie in the lower part of the slope. Although that site is leased by the Omaha Audubon Society, new housing construction is underway adjacent to the prairie and it will probably be lost to urbanization. That fate is likely to befall a population just west of Bellevue, Sarpy County. In Saunders County, the species is abundant in a small, gently- sloping prairie remnant dense with needle-and-thread grass (*Stipa spartea*), and it is known from three other sites as well.

There are dozens of small prairie remnants in Lancaster County (Jensen, Rousek, Hutchinson, and Bohaty, 1985), but few have *E. mesochoreum*. A small, privately-held piece of virgin prairie has a few individuals. Near that site, by contrast, the largest well-preserved virgin tall-grass prairie in eastern Nebraska—Nine-Mile Prairie (240ac, 97ha)—lacks the species now (Kaul and Rolfsmeier, 1987) and didn't have it sixty years ago (Steiger, 1930), although suitable habitat apparently exists.

The records of *Erythronium mesochoreum* are perhaps incomplete, for four reasons: 1) the plants flower before other prairie species and before the grasses begin to grow, and therefore botanists are unattracted to the prairies when it is most visible; 2) even when flowering, the plants are easily overlooked because they are often hidden among dry grasses—their folded, rather glaucous leaves and large but dull flowers are not prominent (Figs. 6, 8); 3) the plants are soon hidden in the luxuriant foliage of rapidly-growing associated



ERYTHRONIUM ALBIDUM



ERYTHRONIUM MESOCHOREUM

FIGURES 2, 3. Distribution of *Erythronium* in Nebraska as represented by herbarium specimens.

plants; and 4) the leaves wither and fruits disintegrate in late spring or early summer.

Figure 6 is a photograph taken, according to the inscription on its reverse side, "near Havelock Nebr" (now incorporated into the City of Lincoln, Lancaster County) probably in the 1920's, showing a level prairie with abundant *E. mesochoreum*. I know of only one place—the Saunders County site mentioned above—where a photograph showing so many of the plants could be taken now in Nebraska.

Erythronium mesochoreum is also known today in upland forests in Sarpy and Saunders counties, where it grows in adjacent prairie too; perhaps the forests have invaded the prairies but the species has persisted. In the Sarpy County forest, *E. albidum* is also present, but the two species are distinct there and the populations are not mixed (Sutherland, *in litt.*). However, at the forest border some individuals are difficult to assign to a species.

The role of mowing, grazing, and prairie fires in maintaining this species is unknown, but presumably they are as important for the prairie erythronium as for other prairie plants. The species is abundant in one Douglas County prairie that is regularly burned and in a Saunders County prairie that is mowed every August. It is common in a bur oak forest in Saunders County that has not been burned for more than twenty years but was grazed by cattle until about 8 years ago. It is uncommon in a Sarpy County prairie that has not been burned, mowed, or grazed in recent years. However, there are no records of its abundance in any of these places before these treatments began and thus the effects of those treatments cannot be assessed.

REPRODUCTION

Sexual reproduction—Evidence from specimens in the University of Nebraska herbaria in Lincoln (*NEB*) and Omaha (*OMA*) and in my personal collections shows that *Erythronium albidum* has been collected in flower in Nebraska as early as April 4 (in Nemaha County in 1904) and as late as May 5 (in Sarpy County, 1951), but it is most often found in bloom in the second half of April (Fig. 9). *Erythronium mesochoreum* has a shorter flowering span, having been collected in flower as early as April 7 (in Saunders County in 1934) and as late as April 23 (in Sarpy County, 1989). In 1988 and 1989—years with a warm spring season—it was in full flower on April 8 in Saunders and Sarpy counties.

Fruiting specimens of these species are seldom collected in Nebraska, although in many years the fruits are abundant. *Erythronium albidum* has been found with full-sized (but not necessarily mature) fruits on

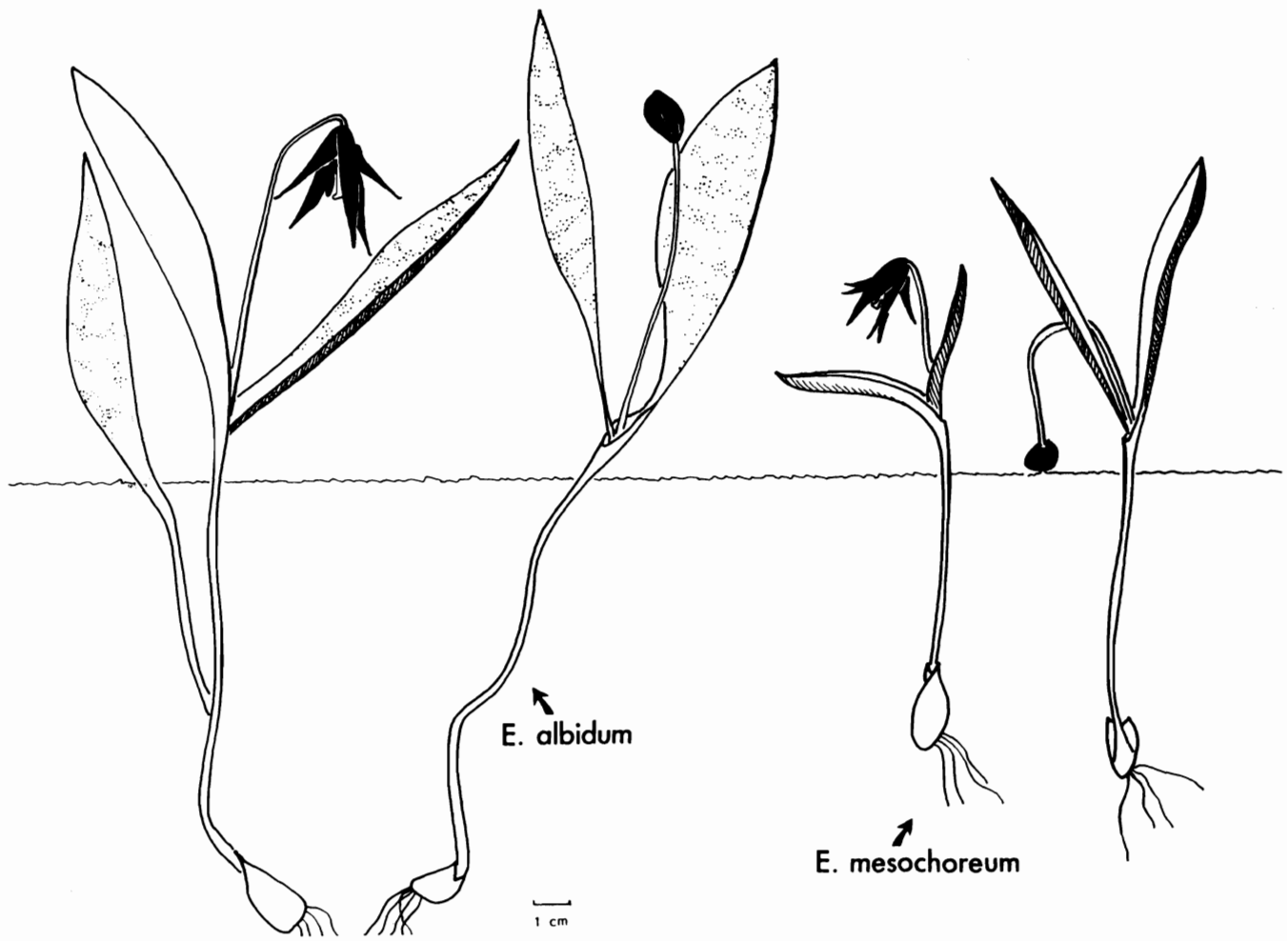


FIGURE 4. Flowering and fruiting habits of *Erythronium albidum* and *E. mesochoreum*. The flowering specimen of *E. albidum* is shown with three leaves, but two leaves are typical of the species.

FIGURE 5. *Erythronium albidum* in a forest near Lincoln, as photographed by Dr. Elda Walker sometime in the 1920's.

FIGURE 6. *Erythronium mesochoreum* "near Havelock Nebr" according to the inscription on the reverse side of the original photograph, which was taken by Dr. Elda Walker sometime in the 1920's.

May 7, 1864 and 1942, on May 9, 1989, and on May 12, 1975. (The specimen of 1864 is probably the oldest Nebraska specimen of this genus in any Nebraska herbarium.) *Erythronium mesochoreum* has been collected with full- sized fruits on April 30, May 8 and 17 (all in 1942), May 6 and 9, 1989, and May 19, 1982.

Erythronium albidum produces flowers every April in the Nebraska colonies that I have observed annually from 1967 to 1989, but only a few of the thousands of plants bear flowers each year. The many sterile, mostly one-leaved individuals are perhaps too young or too starved from crowding to produce flowers. The two-leaved individuals are most likely to produce flowers, but a few do not. Very occasionally a plant has three leaves (Fig. 4), and all such individuals that I have seen in the field and in herbaria are fertile. Some colonies are more floriferous than others, and there is year-to-year variation within colonies as well. In Hummel Park, Douglas County, the species is locally abundant, but only the colonies on steeper, south-facing (but moist and shaded) slopes were floriferous in 1989, while the abundant individuals elsewhere were mostly one-leaved and sterile. In 1989 (a dry spring following the dry summer and winter of 1988), the large, dense, luxuriant colonies in the Seward County forest bore very few flowers, but colonies at the forest edge along a road were floriferous. The sparser, less robust colonies in Lancaster County had far fewer flowers than they did in 1988.

It is known that flowering in *Erythronium* is determined by conditions of the preceding growing season, as it is for many woodland perennial herbs (Foerste, 1891). However, Muller (1979) found no evidence that vegetative reproduction is determined prior to the current season's growth. The reproductive ecology of *E. albidum* has been studied in Kentucky by Baskin and Baskin (1985). There the seeds are dispersed in late May, when the embryos are little-developed and physiologically dormant. Seeds outdoors in moist litter become active from September to November; in culture, a stratification regime of four weeks of warm and eight weeks of cold temperatures produced 100% germination. Such a regime occurs in nature: the seeds are naturally warm-stratified in summer and then cold- stratified in early autumn and winter. The embryos are fully elongated by January, and actual germination occurs in late winter and earliest spring. In Illinois, Muller (1979) found first-year seedlings to be infrequent in the population he studied. He found that allocation of biomass per successfully established propagule was much higher for seeds than for vegetatively-produced corms, but absolute biomass allocation was greater in vegetatively-reproducing plants, the difference being due to the much lower rate of successful establishment of seeds than of new corms.

Banks (1980) found that *E. albidum* in Minnesota showed a mean pollen-ovule ratio of 966:1 and she suggested that it is self-compatible but adapted for outcrossing too. She showed that the single stamen opposite each of the three outer perianth members is not only shorter but also dehisces earlier than the single stamen opposite each of the three inner members; the flowers are protandrous as well. As the temperature rises each day, the petals reflex and remain so until evening cooling, the flowers thus being available to the pollinators (mostly a miner bee, *Andrena carlini*) 6–7 hours each day of anthesis. She showed that the flowers are self-fertile, but the pollen must be applied to the stigma by an insect or by diurnal movements of the floral appendages, causing contact of anthers and stigma. She found the mean of stainable (viable) pollen was 57%, using 1% aniline blue in lactophenol. She did not detect apomixis. Her study plants had an average of about 40 ovules per flower, of which an average of only 4 matured into a seed; she cited work done in Wisconsin that showed an average of only two seeds per flower in *E. albidum*.

Morley (1982) found that an average of only 3.8% (1.1–9.9%) of the plants bore flowers in 53 Minnesota colonies of *E. albidum* that he studied in 1980 and 1981. However, he cautioned that the figure is an overcalculation because he did not include data from numerous large, non-flowering colonies. He cited the comparable figures from other authors of <1% from Illinois populations, 0.156% from Wisconsin, and 0.1% from Kansas. My observations in Nebraska are consistent with such findings.

Banks (1980) successfully hybridized *Erythronium albidum* with *E. propullans* Gray, a rare species endemic in two counties in southeastern Minnesota, where they are sympatric. She found a few putative hybrids in the wild, but she suggested that the species are essentially reproductively isolated by asynchronous flowering due to differences in micro-habitats. She noted that the two are also somewhat isolated by the preference of their common pollinator—the bee *Andrena carlini*—for the more conspicuous flowers of *E. albidum*. In fact, she found that *E. propullans* is successfully pollinated in the wild only when it greatly outnumbers *E. albidum* at a site, an uncommon situation. Because sexual reproduction is so rare in *E. propullans*, if it occurs at all, she postulated that the entire species is perhaps a single, asexual clone. Pleasants and Wendel (1989) believed that *E. propullans* is a recent (within the last 9,000 years) and local derivative of *E. albidum*.

Erythronium mesochoreum is not as strongly colonial as *E. albidum*, and its reproductive ecology is less well known. Many individuals produce flowers annually, and apparently there are relatively fewer sterile plants than has the latter species. In the large population in Saunders County, most plants produce flowers yearly (for example, 67 of 74 plants I observed in 1989), including years such as 1989 (following the severe drought of 1988-9) when *E. albidum* is sparsely floriferous nearby.

Michener and Rittenmeyer (1956) found *Erythronium mesochoreum* to be pollinated in Kansas by the solitary, presumably oligolectic bee *Andrena erythronii*; they suggested that "it seems likely that *Erythronium* [*mesochoreum*] is actually necessary for the survival of this bee." The plant is the first prairie wildflower to bloom there in the spring and is the only source of food for the bee at that time. Male and female bees visit the flowers, but the males, being shorter-lived, visit fewer times. The female bees dig 1–3 burrows, each with a few chambers. They pack each chamber with a firm mass of pollen and nectar from *E. mesochoreum*, then lay a single egg on each mass and die by late April or early May. Michener and Rittenmeyer (1956) noted that *Andrena erythronii* also took oak pollen after *E. mesochoreum* went out of bloom, and that oak pollen is unused by other bees. Thus, they suggested that *Andrena erythronii* gathers pollen from two sources for which it has almost no competition: *E. mesochoreum*—not ordinarily visited by other bees (although they did note a few visits by *Apis*); and oak, whose wind-pollinated, inconspicuous, odorless flowers are not much visited by insects of any kind. However, they noted that in a year when early hot weather killed the flowers of *E. mesochoreum*, *Andrena erythronii* visited dandelion, plum, and apple flowers, but that in most years they avoid those flowers, which are readily visited by other insects. Presumably the bee is much less abundant now that its primary food source is much rarer than formerly, and it could be approaching extinction.

FIGURE 7. Excavated specimens of *Erythronium mesochoreum*. Photograph taken at the same time and place as Figure 6.

FIGURE 8. *Erythronium mesochoreum* in Saunders County. 8 April 1989. The coin is a quarter-dollar. The photograph was taken by the author on an unusually cold and windy day, which perhaps explains why the flowers are not open.

Vegetative reproduction—Like other species of the genus, *Erythronium albidum* and *E. mesochoreum* reproduce asexually by vegetative means, but by somewhat unlike methods that are taxonomically useful. (Details of vegetative reproduction in the genus are given by Blodgett [1894, 1900, 1910], Rickett [1937], Muller [1979], and Morley [1982, 1988].)

Erythronium albidum reproduces vigorously by producing "runners": 2 (1–3) scaless, starchy, more-or-less horizontal shoots up to perhaps 10 cm long that arise from the base of the bulb. These terminate in an apical meristem that eventually produces a new bulb some distance from the parent bulb. The runners and parent bulbs shrivel when the new bulbs form. Huge, dense colonies are thus often formed in the forests, and some are likely to be single clones of considerable age. According to Rickett (1937), a bulb that produces flowers does not simultaneously produce runners, but instead produces a renewal bulb *in situ*. However, Morley (1982) found that perhaps 25% of the flowering bulbs produced runners in the Minnesota colonies he studied.

E. mesochoreum, by contrast, does not produce runners but forms "offshoots"—daughter bulbs formed adjacent to the mother bulb (Fig. 7). Thus, the species does not form large, dense colonies, but instead exists as scattered individuals or small groups in the prairie. Even in the bur oak forest in Saunders County in which this species persists, the plants are scattered.

DISCUSSION

Erythronium albidum is probably somewhat less common today than before agrarian settlement in Nebraska because of grazing and logging in the forests of the eastern part of the State. However, it can withstand light grazing but not heavy trampling. Because some of the forests have actually expanded following successful control of the prairie fires that limit expansion of forests into the grassland, the species has possibly expanded here and there as well. However, there are no records that give even an approximation of its abundance during early agrarian times. Substantial populations are protected in Neale Woods, Hummel Park, Fontenelle Forest, Indian Cave State Park, Wilderness Park, and Bur Oak Wildlife Management Area.

The fate of *E. mesochoreum* is less certain. Like so many other prairie species, it no doubt was once a common plant in southeastern Nebraska, but now that perhaps 99% of the virgin prairie is gone it is uncommon, yet where it occurs it is thriving and producing flowers and seed-filled fruits. Now it is protected in only four sanctuaries—one each in Douglas and Sarpy counties and two in Saunders County—but only the Saunders County sites, one of which is owned by the University of Nebraska Foundation, are secure. The Douglas County site is leased to the Omaha Audubon Society and the Sarpy County site is leased to the University of Nebraska at Omaha; the pressures of urbanization are evident adjacent to them.

Further work is needed to clarify the relationship of the two species, which clearly is a close one. *Erythronium mesochoreum* is probably a derivative of *E. albidum*, perhaps by mechanisms like those that produced *E. propullans* from *E. albidum* as outlined by Banks (1980) and Pleasants and Wendel (1989).

ACKNOWLEDGMENTS

Martha Kaul, David Sutherland, and Steven Rolfsmeier have kindly provided assistance and some of the data. R. L. McGregor (University of Kansas), T. Morley (University of Minnesota), and D. Suther-

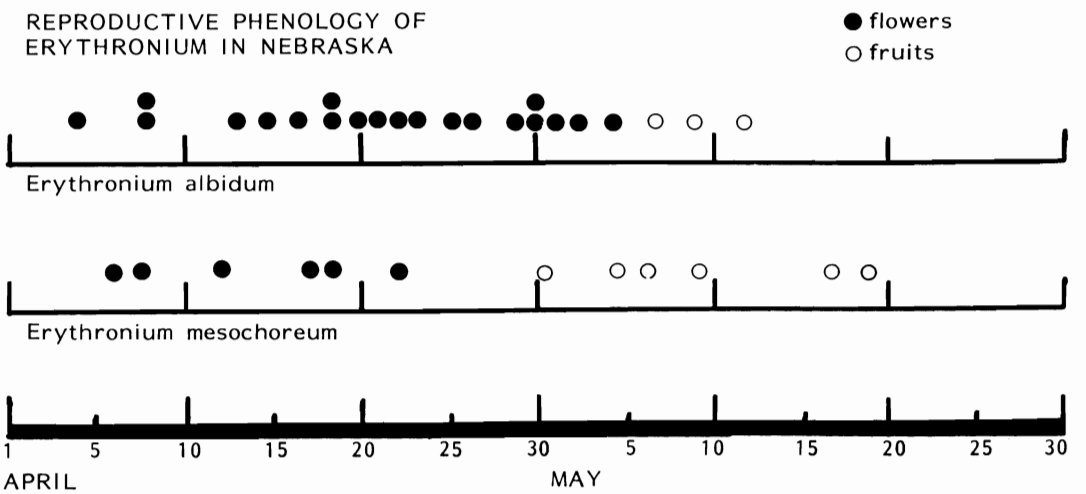


FIGURE 9. Flowering and fruiting phenology as taken from herbarium specimens and personal observations.

land (University of Nebraska at Omaha) reviewed the manuscript and made helpful suggestions. A. C. Koelling (Illinois State Museum, Springfield) has kindly contributed information about *E. mesochoreum* in Illinois. The photographs (Figs. 5–7) taken by the late Dr. Elda R. Walker, professor of botany at the University of Nebraska–Lincoln from 1906 to 1947, stimulated this effort.

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