and the Cumberlands, the hot Mississippi Embayment and the Gulf and Atlantic dunes and coastal plains, the cool and moist Appalachian deciduous forest, and even arctic and subarctic Alaska.

Revegetation of soilless, sterile glaciated areas took time. The migration of propagules and ensuing invasion of rich flora had to necessarily follow the development of soil, mycorrhizae incursion, and shade for mesophytes. These building stages were followed by an incongruous, helter-skelter floristic mixture of periglacial conifers and tundra plants, deciduous trees and shrubs, and heliophytic prairie plants. These soon sorted themselves out under the dictates of competition and succession into plant communities reflecting the regional climate. Eventually, in the climatic wedge of the Prairie Peninsula, those species that liked a prairie climate flourished—no matter what their region of origin. Many other species became extinct, while a vast number survived elsewhere, for example in the forests to the north or in specialized habitats in the Driftless Area. It is thus not surprising that our prairie flora is now composed of a large number of broadly adapted, widespread species that had their roots in diverse habitats.

The story is, of course, much more complex. There must have been tallgrass prairie communities in favorable places south of the Prairie Peninsula during the Wisconsin Ice Age, and in the Prairie Peninsula periodically during the past million years. Natural selection for plants favoring a tallgrass climate in the same general geographic region as today must have occurred at least three separate times during the substages of the Wisconsin glaciation (and probably more frequently, in view of the evidence today of eight or so substages during the Late Wisconsin, and at least 20 glacial-interglacial cycles during the late Quaternary). During this epoch of more than a million years, the speciation that resulted in some 300 or more regional prairie endemics must have occurred, a winnowing and sifting of floristic candidates preadapted to such a climate, all contributed (then as now) by surrounding ecosystems to the ecological melting pot.

An interesting aspect of the hypothesis of glacial survivia, one that indirectly supports the whole concept, is the evolutionary divergence of many phylads into species pairs, one eastern and mesophytic, one more western and either xerophytic or cordilleran (montane/subalpine meadow examples include *Dodecatheon, Polemonium,* and *Camassia).* The two ranges, once separated by huge distances plus climate, glaciers, dry grasslands, and other factors for tens of millenia, reexpanded west and east, as the case may be, and in some cases overlapped in the deglaciated regions. Where sympatric in similar habitats, the species hybridized.

This east-west pairing includes forest species as well as prairie species, and is of great evolutionary interest. Among the most striking examples are our two species of fringed gentian, in the segregate genus *Gentianopsis:* the mesophytic, acidophilic, Appalachian *G. crinita,* and the relatively xerophytic, calciphilic *G. procera* of the High Plains. Although separated by different ecologies and flowering periods *(G. procera* blooms earlier, as befits a species coming from a shorter growing season), the two do hybridize in the calcareous fen-like Chiwaukee Prairie and in northern Indiana (Iltis 1965, Mason & Iltis, 1966). A similar, but even more remarkable case involves the highly distinct, sand-loving species of *Cyperus* sect. *Laxiglumi,* the western Schweinitz's Cyperus *(C. schweinitzii),* native to the Great Plains sand prairies and the Nebraska Sand Hills and beyond, with openly branched inflorescences, and the more specialized, tight-headed Sand Cyperus *(C. lupulinus* ssp. *macilentus)* of rocky or sandy, sunny "islands" within the Appalachian forests (Marcks & Iltis 1967, Marcks 1974). When they eventually flowed together in the Upper Middle West early on after the final glacial retreat (± 6,000 yr B.P.), they hybridized to produce a widespread introgressed population (basically *C. schweinitzii* introgressed with *C. lupulinus* ssp. *macilentus),* one that because of its morphological stability has earned recognition as a full-fledged species, Houghton's Flat Sedge, *C. houghtonii.* But within the last 150 years, with the drastic increase in disturbance due to agriculture, lumbering, and other human activities, the extensive sympatric populations of the parental species have undergone a second cycle of hybridization, producing especially on the sand terraces along the lower Wisconsin River Valley extensive hybrid swarms of enormous variability, a variability that confounds the taxonomic amateur and delights the evolutionary-oriented systematist.

Many other such east-west pairs could be mentioned (e.g., the white and red baneberries, *Actaea* spp.), all of which overlap their ranges and hybridize only in once-glaciated regions, but the two cited cases of prairie plants exemplify the dynamic interaction of biogeography, ecology, systematics, and history that make even our rather depauperate flora a fascinating subject for study.

It should be emphasized that assignment to this or that glacial survival region is not always clear or easy, certainly

not in the many widespread forest species of the southern states that may occur from North Carolina clear to Arkansas and the prairie border. But even in these cases, new molecular techniques, cytotaxonomic insights (polyploidy), and center(s) of a species' variability can usually identify the general area of survival (i.e., origin). Norman Fassett (1944a; see Iltis & Shaughnessy 1960), Wisconsin's great taxonomist, made an intensive study of Eastern Shooting-star, *Dodecatheon meadia*, and was able to show that its center was in the Ozarks and west-central southern states. There, the plants within any population were much alike, either all white or all pink or purple, this due presumably to inbreeding, whereas in Wisconsin such as along the railroad west of Madison or on the Chiwaukee Prairie, they were a riotous mixture of all shades of purple to white, suggesting a post-glacial mass immigration and intermingling of the various southern types.

A splendid example of tracing migration from the southern Appalachians involves the Rock Spike-moss *(Selaginella rupestris)*, a species sufficiently widespread—from the eastern mountains north to Wisconsin and also in the Ozarks—that its area of survival was an open question. Tryon (1955) was able to show that the Appalachian plants regularly produced spores by sexual means, the original and therefore primitive condition. On the other hand, plants in populations to the north, then west to Wisconsin and again south to the Ozarks, were increasingly apomictic (i.e., producing spores asexually without benefit of fertilization), a highly specialized condition. Ozarkian plants were 100% apomictic, establishing the direction of migration. Other cytotaxonomic examples show similar patterns, with the primitive diploids restricted to the southern states and the polyploids widespread in the glaciated northern areas.

Affinities of the Flora

The contemporary flora of Wisconsin's Prairie-Southern Forest Province may be young, but it is diverse. This territory includes both the unglaciated Driftless Area, with its great variety of habitats including cool moist gorges, dry sunny hilltops, and exposed bedrock, and glaciated topography, with its monotonous cover of undulating drift left by the melting ice sheets. All this constituted available surfaces for immediate or eventual occupation by plant life. Afull range of floristic elements expanded into Wisconsin's developing landscape, albeit within limits exerted by local environmental conditions. At the present time, the southern region of Wisconsin has favorable environmental conditions for both prairies and eastern forests, because it contains practically the full complement of our Prairie and Alleghenian elements.

Existing stands of a particular community type probably do not exactly or even closely resemble those that once existed either here or elsewhere in North America prior to the Pleistocene. Each community in general, and any given stand in particular, is the result of diverse historical happenings and environmental factors that were in operation while species naturally organized themselves into different assemblages or communities. "The expansion of prairies in Wisconsin was not a single, unified movement of a homogeneous plant formation" (Curtis 1959, p. 290). Instead, species of each floristic element, whether Alleghenian and entering directly from the east, Coastal Plain from the east and south, Ozarkian and Prairie from the south and west, or Arctic and Cordilleran elements from the west and north, migrated or dispersed by various routes and at different times, in different ways, to different habitats. New England Aster *(Aster novae-angliae)*, Canadian Tick-trefoil, Early Buttercup *(Ranunculus fascicularis)*, and Eastern Figwort *(Scrophularia marilandica)*, deciduous forest elements that spread westward to the grasslands, must have entered Wisconsin from the east; species of the interior like Heath Aster, Illinois Tick-trefoil, and Prairie Buttercup *(R. rhomboideus)* could have dispersed from the south; and western elements like American Figwort *(S. lanceolata)*, directly from the west. The southwestern or Mexican element Plains Prickly-pear *(Opuntia macrorhiza)*, adapted to the hot, dry climate of the arid Southwest, occurs today on open sandy blufftops in southwestern Wisconsin alongside Paper Birch *(Betula papyrifera)*, a species characteristic of the Boreal Forest Region and adapted to long cold winters and cool moist summers. However, many blufftops in the area have only one species or the other, or neither, illustrating that while the flora of a particular place consists of species of diverse origins and histories, each differs from that of other places because of the way species react to local microclimates.

Basic Patterns of Distribution

The Wisconsin flora is made up of numerous temperate American species and smaller numbers of Eurasian, Mexican, and South American immigrants. Most of these species were members either of the world-wide Arcto-Tertiary and Boreo-tropical geofloras or the southwestern Madro-Ter-

tiary geoflora. There are rare cases of plants that seem clearly to have originated on other continents. Besides these elements, there are disjunct populations and endemic taxa of more limited occurrence, the distributions of which are difficult or seemingly impossible to interpret.

In general, the majority of prairie and savanna species are wide-ranging plants of north-temperate to subarctic regions, including not only those endemic to North America, but also circumboreal and Arctic-alpine species. A large number have an essentially transcontinental or least a very wide range, e.g., Nodding Wild Onion, Meadow Anemone, Smooth Aster *(Aster laevis),* Canada Wild-rye, Tall Sunflower (*Helianthus giganteus),* False Dandelion *(Krigia biflora),* Wild Lettuce (*Lactuca canadensis),* Fringed Loosestrife *(Lysimachia ciliata),* Purple Meadow-rue, Blue Vervain *(Verbena hastata),* etc. Other taxa are restricted to the eastern half of the continent, but often with sister species in the West, e.g., Marsh Fern (*Thelypteris palustris* var. *pubescens),* Wild Columbine, Calico Aster (*Aster lateriflorus),* Pasture Thistle, Bottle Gentian, Wood-betony *(Pedicularis canadensis),* Prairie Phlox, Culver's-root, (*Veronicastrum virginicum),* or the western half, e.g., White Sage (*Artemisia ludoviciana),* Wild Licorice *(Glycyrrhiza lepidota),* and American Figwort. Other temperate endemics are interior Midwest species with diverse relationships like Wild-hyacinth, *Camassia scilloides* (to the Pacific Northwest); White Prairie-clover, *Dalea candida* (to Mexico); Mullein-foxglove, *Dasistoma macrophylla* (to the eastern United States); Carolina Larkspur, *Delphinium carolinianum* (to the southwestern mountains); and Common Ironweed, *Vernonia fasciculata* (to tropical America). Finally, there is a rather heterogeneous group comprising disjunct populations and regional endemics. These taxa generally are confined to the Driftless Area or the Great Lakes.

Outline of Floristic Elements

Each floristic element is comprised of species that share the same pattern of geographical distribution and by implication a common historical background. Of the several major elements, the Alleghenian, Ozarkian, and Prairie and Great Plains are the ones contributing the greatest number of species to the prairies and savannas of Wisconsin (see Figures 19–22). Two other elements well represented in the state, the Boreal Forest and Coastal Plain, are less significant contributors. Members of the former group occur primarily in the Mixed Conifer-Northern Hardwoods Province but are nonetheless represented in prairies (e.g., Slender Wheat Grass *[Elymus trachycaulus])* and savannas (e.g., Starry False Solomon's-seal *[Smilacina stellata]),* whereas on the whole, those of the Coastal Plain, although substantial in number, are often of local occurrence or are associated with sandy shores, swales, and fens. However, several species of this element occur in grassland habitats, usually in oak and sand barrens: Dune Three-awn Grass *(Aristida tuberculosa),* Hoary Frostweed *(Helianthemum bicknellii),* Common Rock-rose *(H. canadense),* Greene's Rush *(Juncus greenei),* Wild Lupine *(Lupinus perennis),* Joint-weed, Steeplebush *(Spiraea tomentosa),* and Grass-leaved Goldenrod *(Euthamia graminifolia).* Comparatively few species of Mexican or South American affinity and of Cordilleran (western mountain) or Arctic-alpine relationships have reached Wisconsin.

The Alleghenian-Ozarkian Element (that group of species centering on the southern Appalachians, ranging from Alabama to southeastern Quebec, and often throughout the Eastern Deciduous Forest Region all the way to the Ozarks) is composed of a large group of temperate forest species, many common and widely distributed. American groups with this relationship are represented in prairies by Bush-clover *(Lespedeza capitata)* (most *Lespedeza* species are southeastern, but some occur in Asia and Australia), Lance-leaved Loosestrife *(Lysimachia lanceolata;* Figure 19A) *(Lysimachia* section *Steironema* is a small group endemic to the Southeast), Clasping Milkweed *(Asclepias amplexicaulis;* Figure 19B) (many *Asclepias* species are southeastern, many also southwestern and Mexican, a few South American and African), and New England Aster *(Aster* section *Aster,* like the genus *Solidago,* the goldenrods, is a very large, actively evolving, taxonomically difficult group with its center of diversity in the East). This element is well represented in Wisconsin's woods, savannas, and barrens: Hog-peanut, Prairie Red-root *(Ceanothus herbaceus),* Upland Boneset *(Eupatorium sessilifolium),* Hairy Puccoon *(Lithospermum caroliniense),* Wood-betony, Hairy Beard-tongue *(Penstemon hirsutus),* Lopseed *(Phyrma leptostachya),* Red-stalked Plantain *(Plantago rugelii),* Black Cherry, and Yellow Pimpernel *(Taenidia integerrima).* Many savanna species have as their immediate region of origin the lower Midwest and Southeast. Forest-border species having this basic pattern include Purple Milkweed (Figure 20A), Pale Indian-plantain, Bottlebrush Grass, Cream Gentian (Figure 20B), Veiny Pea, Violet Bush-clover *(Lespedeza violacea;* Figure 20C), Broad-leaved Panic Grass *(Panicum latifolium),* Starry Campion *(Silene stella-*

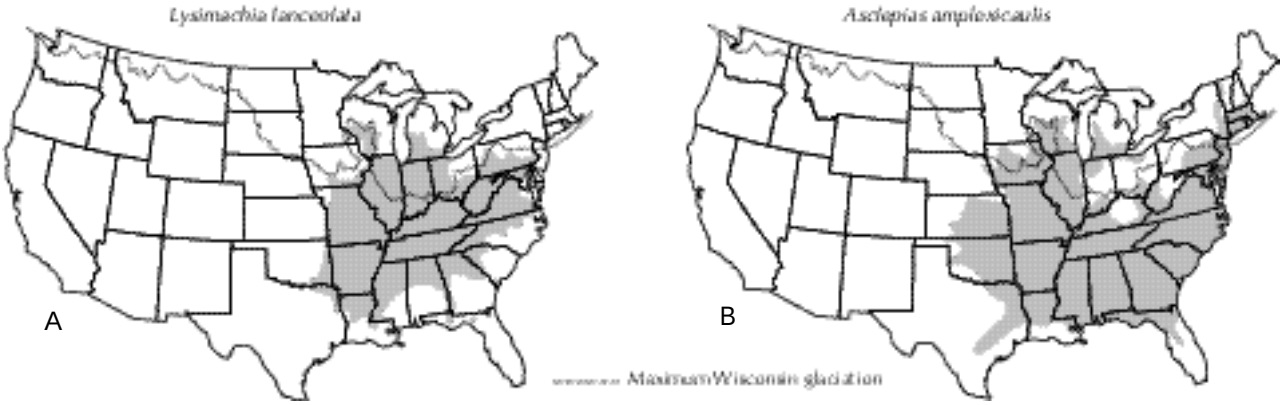

Figure 19. Distribution of Alleghenian-Ozarkian elements of the Wisconsin grasslands. **A.** *Lysimachia lanceolata,* Lance-leaved Loosestrife. Redrawn in part after Ray (1944). **B.** *Asclepias amplexicaulis,* Clasping Milkweed. Modified after Woodson (1954).

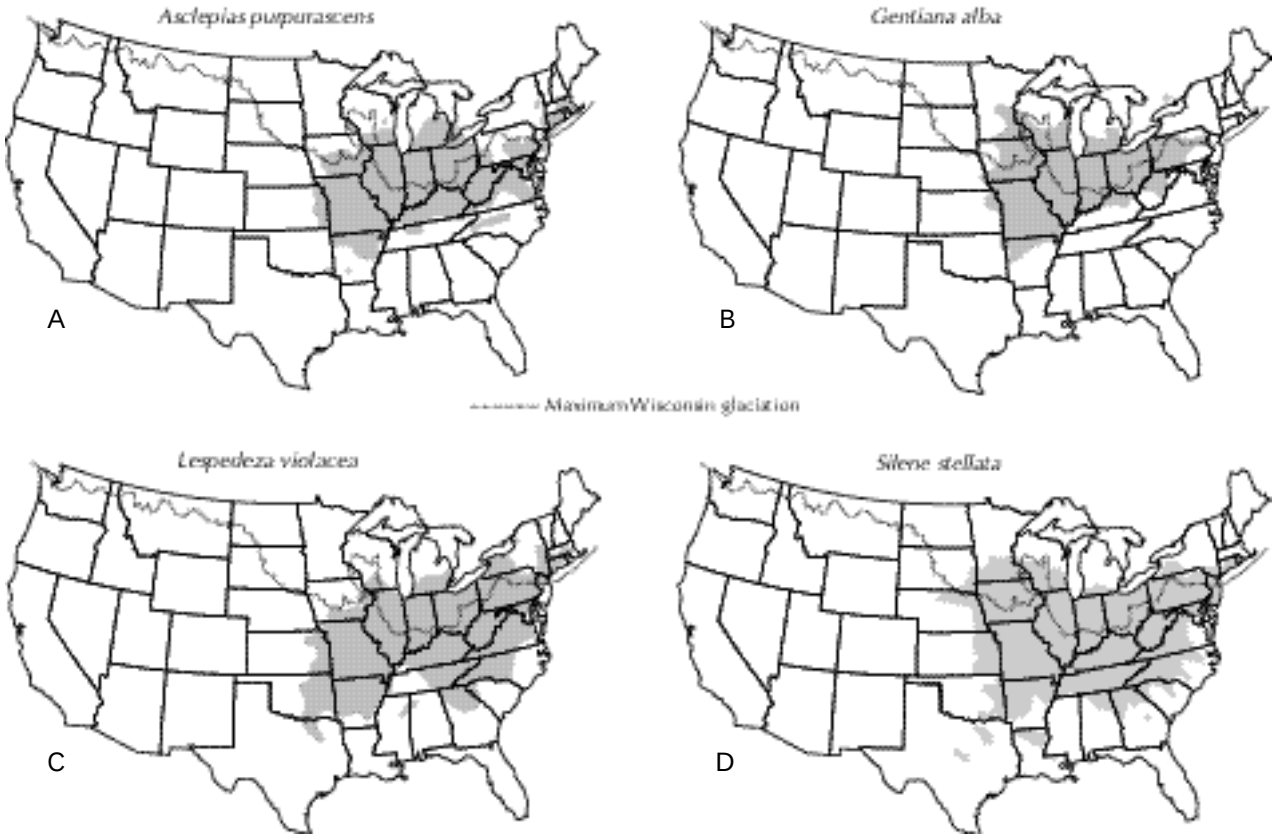

Figure 20. Distribution of Alleghenian (and/or Ozarkian) elements of Wisconsin savannas and prairies. **A.** *Asclepias purpurascens,* Purple Milkweed. Redrawn after class term paper by S. Kroken (1989). **B.** *Gentiana alba,* Cream Gentian. Modified slightly after Pringle (1967). **C.** *Lespedeza violacea,* Violet Bush-clover. Modified slightly after Clewell (1966). **D.** *Silene stellata,* Starry Campion. Compiled from various sources, including Hitchcock and Maguire (1947).

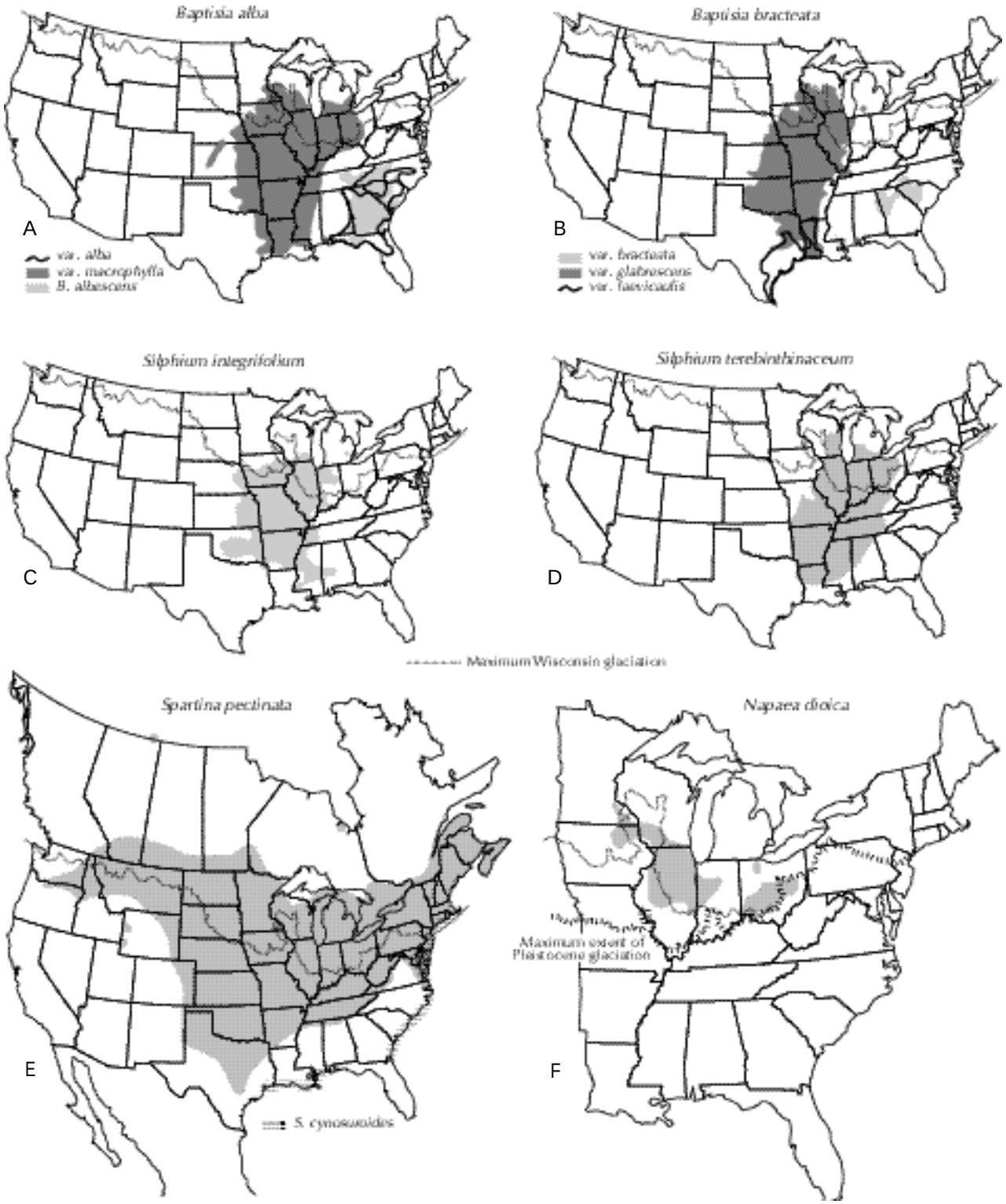

Figure 21. Distribution of Prairie elements of the Wisconsin grasslands. **A.** The two varieties of *Baptisia alba,* Milky Wild Indigo, and a related species. Compiled from various sources. **B.** The three varieties of *Baptisia bracteata,* Cream Wild Indigo. Compiled from various sources. **C.** *Silphium integrifolium,* Prairie Rosinweed. Modified after Settle and Fisher (1970). **D.** *Silphium terebinthinaceum,* Prairie-dock (generalized). Most species of *Silphium* are southeastern. **E.** *Spartina pectinata,* Prairie Cordgrass, probably derived from *S. cynosuroides.* Redrawn after Mobberley (1956). **F.** *Napaea dioica,* Glade Mallow, a monotypic genus and our only Midwestern endemic genus. Redrawn after Iltis (1963).

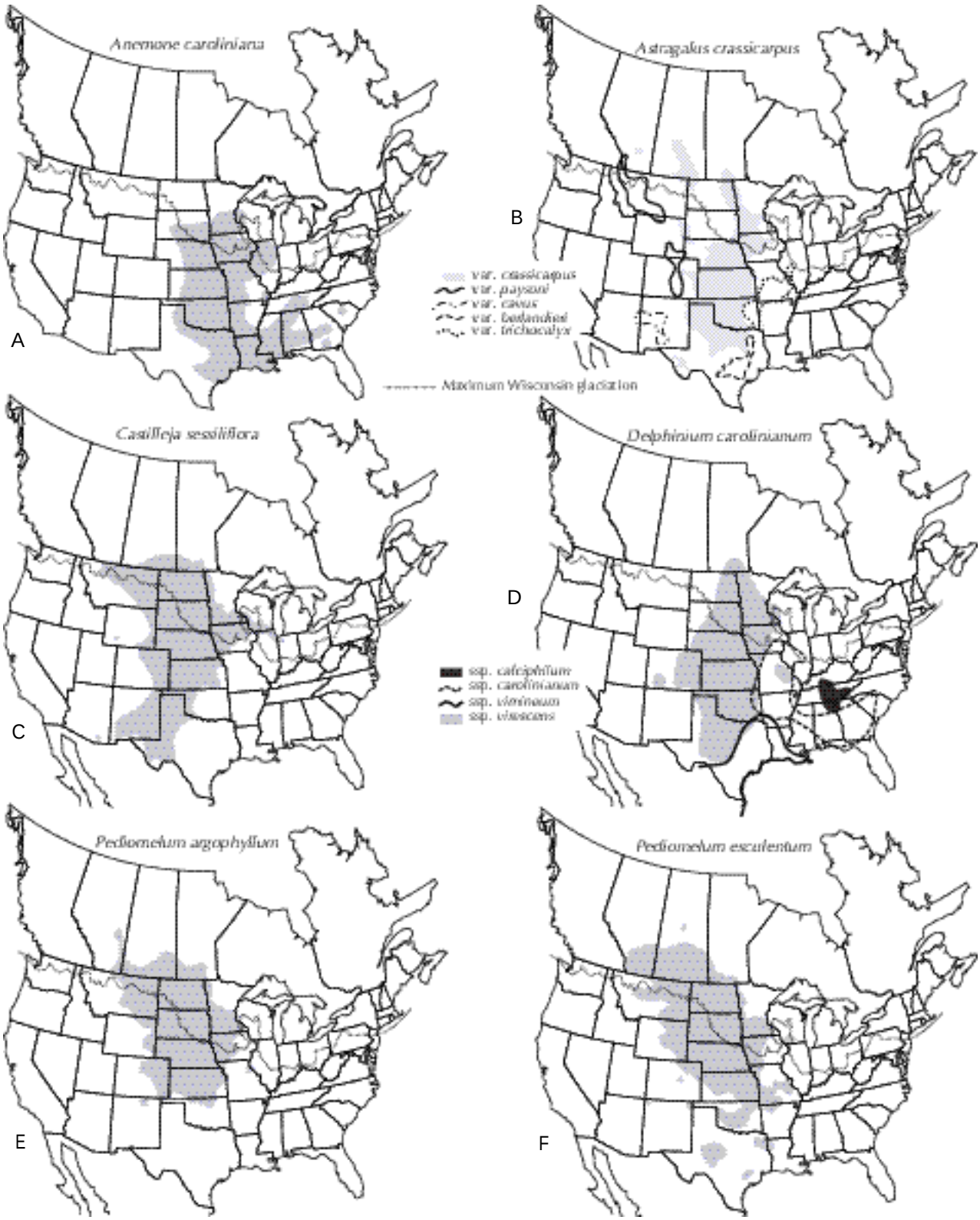

Figure 22. Distribution of Prairie-Great Plains elements reaching their eastern range limit in Wisconsin. **A.** *Anemone caroliniana*, Carolina Anemone. Redrawn after Dutton et al. (1997). **B.** The five varieties of *Astragalus crassicarpus*, Ground-plum. Redrawn after Barneby (1964). **C.** *Castilleja sessiliflora*, Downy Painted-cup. Modified after Pennell (1935). Its closest relatives (four species) are in the western United States and Mexico. **D.** The four subspecies of *Delphinium carolinianum*, Plains Larkspur. Redrawn after Warnock (1997). **E.** *Pediomelum argophyllum*, Silvery Scurf-pea. Modified after Fassett (1939). **F.** *Pediomelum esculentum*, Breadroot Scurf-pea. Modified after Fassett (1939).

ta; Figure 20D), and Late Horse-gentian *(Triosteum perfoliatum),* most of which are listed by Packard (1988b, 1993) in his summaries of restoration work on savannas in Illinois.

The prairie flora, that group of species having an overall range that covers part or all of the existing prairies, may be classified among several elements. One element involves plants of the true prairie, which generally range from the southern Great Plains northward toward or into the Prairie Provinces of Canada and eastward into the Prairie Peninsula. A large percentage of species belonging to the Prairie element are derived from the southeastern deciduous forest region and have geographical distributions that center on the Ozark Mountains, from which they radiate in all directions—east to the deciduous forest, west to the plains, and north into the Prairie Peninsula. Plants of the true prairie in Wisconsin include two *Baptisia* (Figures 21A& B) and four *Silphium* species (the geographical distributions of Rosinweed, *S. integrifolium,* and Prairie-dock are shown in Figures 21C & D, respectively), Prairie Indian-plantain *(Cacalia [Arnoglossum] plantaginea),* Purple Prairie-clover, Missouri Goldenrod *(Solidago missouriensis),* Stiff Goldenrod *(S. rigida),* Prairie Cordgrass (Figure 21E), and Porcupine Grass *(Stipa spartea),* as well as Glade Mallow (Figure 21F).

Asecond natural subdivision of the prairie flora in Wisconsin includes the Great Plains elements that reach their eastern limits in Wisconsin. Presumably, climatic conditions explain why some species of Great Plains affinity have only barely reached Wisconsin, because many others extend southward and eastward into the Prairie Peninsula or beyond. Most of these genera are Arcto-Tertiary in origin. *Anemone, Astragalus,* and *Stipa* are large genera of northern grasslands; *Besseya, Castilleja,* and *Penstemon* are endemic, mainly Cordilleran genera with Eurasian relatives; only *Pediomelum* has Southern Hemisphere relationships. The total ranges of Carolina Anemone *(Anemone carolinia),* Ground-plum, Downy Yellow Painted-cup *(C. sessiliflora),* Carolina Larkspur, Silvery Scurf-pea, and Prairie-turnip *(Pediomelum esculentum),* are shown in Figure 22. The following species all have the same basic distribution pattern: Autumn Onion *(Allium stellatum),* Short Green Milkweed, Prairie Sand-reed, Alum-root, Northern Plains Blazing-star *(Liatris ligulistylis),* Dotted Blazing-star, Prairie Dandelion *(Microseris cuspidata),* Slender Beard-tongue *(Penstemon gracilis),* Early Buttercup, and Prairie Dropseed. Kitten's-tail, *Besseya bullii,* is much more restricted, being limited to seven Midwestern states.

In the third element belong those plants occurring throughout a much larger region of the West and, in the northern Great Plains, reaching their eastern and southern limits in America. These Arcto-Tertiary elements often have their generic relationships to arid, cool-temperate Eurasia and often have centers of diversity in the West. They include Prairie Sagewort (Figure 23A), Louisiana Sagewort (Figure 23B), Fleabane *(Erigeron glabellus),* June Grass, Clustered Broom-rape *(Orobanche fasciculata,* Figure 23C), Tall Cinquefoil *(Potentilla arguta,* Figure 23D), and Pasqueflower *(Pulsatilla [Anemone] patens,* Figure 23E).

The Western or Cordilleran element constitutes a large group of alpine, plateau, and foothill species that on the whole has a range centering in the western mountains of Canada and the United States, but has a surprisingly large contingent that migrated east once the ice melted. Some of these species are disjunct from the Arctic and are considered part of the Arctic or Arctic-Alpine Element. In Wisconsin, this is a significant group, members of which often reach their eastern limits in the western Great Lakes region. Typical species include Richardson's Sedge *(Carex richardsonii),* Prairie-smoke *(Geum triflorum),* Edible Valerian *(Valeriana edulis),* and White Camass *(Zigadenus elegans),* and such shrubs as Red Osier Dogwood *(Cornus stolonifera)* and Wolfberry *(Symphoricarpos occidentalis).*

The Arctic Element, sometimes called the Arctic-alpine Element, comprises a rather small group in the flora of Wisconsin; its representatives often have no close affinity to other species or groups in our flora. We even have one tundra species, the exceedingly rare Lapland Azalea *(Rhododendron lapponicum),* but a number of subarctic plants endemic to North America such as Spreading Dogbane *(Apocynum androsaemifolium),* Fringed Brome *(Bromus ciliatus),* Blue-joint, Common Water-hemlock *(Cicuta maculata),* Bog Lobelia *(Lobelia kalmii),* and Golden Ragwort *(Senecio [Packera] aureus)* are common in our prairies, fens, and sedge meadows. The group is usually defined broadly enough to contain the Arctic-circumpolar species, those occurring in Europe and/or Asia as well as North America: Common Horsetail *(Equisetum arvense),* Cut-leaved Anemone *(Anemone multifida)* (also bipolar; very rare in Wisconsin), Lyrate Rock Cress, Grove Sandwort *(Arenaria lateriflora),* Rock Sandwort *(Arenaria stricta* ssp. *dawsonensis,* a Wisconsin rarity), Harebell, Northern Bedstraw *(Galium boreale),* Sweet Grass *(Hierochloe hirta),* Marsh Pea, and Shrubby Cinquefoil *(Pentaphylloides [Potentilla] floribunda).*