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images, however, favor models with higher viscosities and thicker weak zones. The predicted deformation pattern (Fig. 1C) can match the observations (Fig. 1A) better if a weak zone of 13 km and a viscosity of  $1.6 \times 10^{18}$  Pa s are used. Moreover, we find that the match between the InSAR images and model calculations can be improved if a nonuniform weak layer, (24), is used. The weak layer thickness at depth is determined from the geographical variations of the Moho depth (23). The calculated amplitude of uplift to the west of the Johnson Valley fault is closer to what is shown on the interferogram (25).

A viscosity on the order of  $10^{18}$  Pa s in the lower crust is consistent with a maximum viscosity of the lower crust of  $10^{19}$  Pa s that is inferred from the uplift and tilting of Quaternary lake sediments on the Halloran Hills in the eastern Mojave desert (26). The weakness of the lower crust could be related to the thermal structure of the Basin and Range province, so it can help understand the physical mechanism responsible for the extension of the general area.

Our study on postseismic rebound does not resolve the mechanism responsible for interseismic deformation associated with major strike-slip faults (27). The postseismic deformation involves a sudden coseismic stress concentration close to the rupture zone, while the interseismic deformation only involves gradual strain concentration. So it is possible that a mechanism other than viscoelastic flow, such as stable sliding, is also related to the interseismic process (27).

Because viscosity governs the evolution of the stress field and thus the loading and unloading processes of major earthquake-generating faults, our estimate of the viscosity beneath the Landers earthquake region will help to assess earthquake hazards in southern California and further characterize the behavior of earthquake-related processes.

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18. We note that the first-motion mechanism presented by Hauksson *et al.* (20) has a rake angle of  $170^\circ$  on a fault striking in  $N10^\circ W$ . The mechanism solution of the second point source obtained by Qu *et al.* (28) (shown in Fig. 1), which is located near the southern end of the Emerson fault, has a rake angle of  $153^\circ$ , which involves even a larger dip-slip component than Hauksson *et al.*'s (20). Also several aftershocks near the Emerson fault show a significant thrust component (20). The aftershock distribution along the Emerson fault shown by figures 10a and 10b of (20) suggests a northeast dipping fault, which is qualitatively consistent with the solution of Qu *et al.* (28). F. Cotton and M. Campillo [*Geophys. Res. Lett.* **22**, 1921 (1995)] showed that the Landers earthquake is almost pure strike-slip, but the rake angle varies considerably around  $180^\circ$  on the Emerson and Camp Rock faults. Their average rake angle is about  $176^\circ$ . Surface rupture measurements [For example, J. R. Arrowsmith and D. D. Rhodes, *Bull. Seism. Soc. Am.* **84**, 511 (1994)] also showed some direct evidence of up to 2.5 m of vertical motion along a short segment of the Emerson fault. The various rake angles suggest that 7 to 45% of the seismic moment is released through dip-slip motion along the Emerson Fault segment, corresponding to 0.3 to 1.8 m of dip-slip displacement. In our calculations, we assume 0.7 m of dip-slip motion.
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25. We fixed the upper boundary of the weak zone to be 15 km deep, and assume that the lower boundary of the weak layer is the Moho surface, constrained from the Moho-reflected PmP arrivals (23). A thicker weak zone to the west of the Johnson Valley fault (Moho is about 32 km deep) (23) leads to a larger uplift rate in that region, compared to models with uniform Moho depth (28 km).
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# In Search of the First Flower: A Jurassic Angiosperm, *Archaeofructus*, from Northeast China

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Angiosperm fruiting axes were discovered from the Upper Jurassic of China. Angiosperms are defined by carpels enclosing ovules, a character demonstrated in this fossil. This feature is lacking in other fossils reported to be earliest angiosperms. The fruits are small follicles formed from conduplicate carpels helically arranged. Adaxial elongate stigmatic crests are conspicuous on each carpel. The basal one-third of the axes bore deciduous organs of uncertain affinities. No scars of subtending floral organs are present to define the individual fertile parts as floral units, but the leaf-like structures subtending each axis define them as flowers. These fruiting axes have primitive characters and characters not considered primitive.

It has been thought that angiosperms first appeared about 130 million years ago in the Lower Cretaceous (1, 2). There are several

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recent reports of Triassic, Jurassic, and low-ermost Cretaceous-aged fossils identified as angiosperms (3–7), but none of these reports can be accepted as conclusive evidence for the presence of angiosperms. Many reports of early angiosperms are based on pollen, leaves, and wood with vessels, none of which are definitive characters of angiosperms. Some are based on flowers and fruits that are too poorly preserved to demonstrate ovules or seeds enclosed in the carpels. The unique character of angiosperms is that the ovules

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are completely enclosed in a carpel. Here, we describe such early angiosperm fruits collected from the Upper Jurassic “Jianshangou Bed” in the lower part of the Yixian Formation of Huangbanjiegou village near Shangyuan Town of Beipiao City, western Liaoning Province, northeast China (Fig. 1).

The Yixian Formation (8–12) consists of layers of volcanic rocks sandwiched between sedimentary rocks. The sedimentary rocks contain abundant freshwater and terrestrial fossils, including plants, bivalves, fish, conchostracans, ostracods, gastropods, insects, turtles, lizards, shrimps, dinosaurs, birds, and mammals that constitute the Jehol biota (13, 14). The Yixian Formation is about 2000 to 2500 m thick and is considered to be latest Jurassic in age (8–15). We classify our discovery as follows:

Division Magnoliophyta  
 Class Magnoliopsida  
 Subclass Archaeagnoliidae  
 Genus *Archaeofructus* Sun, Dilcher, Zheng et Zhou, gen. nov.

Type-species: *Archaeofructus liaoningensis* Sun, Dilcher, Zheng et Zhou, sp. nov.

Generic diagnosis: Reproductive axes branched or unbranched, bearing helically arranged fruits (follicles) on short pedicels. Fruits mature distally, occupying the distal two-thirds of an axis; carpels or stamens deciduous, leaving short peg-like pedicel bases on the proximal one-third of an axis. Fruits derived from conduplicate carpels commonly bearing three (two to four) ovules. Fertile axes are subtended by leaf-like structures (16). Details of the diagnosis of *Archaeofructus liaoningensis* are presented in (17).

The fruits presented here are recognized as angiosperms on the basis of the ability to remove seeds completely enclosed within them. The occurrence of this angiosperm-defining character in *Archaeofructus* is important because it demonstrates that *Archaeofructus* has angiosperm affinities, and it establishes a benchmark in time for when the closed carpel is first found. This character occurs in combination with other reproductive characters, resulting in a new mixture of characters. This unique set of characters should change our understanding of the nature of the early angiosperm flower.

The pollen-bearing organs of *Archaeofructus* are unknown. They were not present with carpels in the fossil material examined. The proximal one-third of each fertile axis has what appears to be pedicel bases that may have borne deciduous fruits or other organs such as stamens. *Archaeofructus* may have been either unisexual (monoecious or dioecious) or bisexual. No pollen was found attached to any surface of the fruits or axes, and no angiosperm pollen has been isolated from the matrix. The only sterile organs associated with *Archaeofructus* are two poorly preserved leaf-like structures (Fig. 2A).

The lateral axis is borne in the axil of a leaf-like structure occurring on the main axis. Examination by epi-illumination and fluorescence epi-illumination of the surfaces of this fertile complex revealed some cellular detail of the epidermal cells covering the fruits and axes, but no pollen or evidence of scars of any deciduous organs were found except for the peg-like pedicels basal in each fertile axis. Therefore, there may have been deciduous floral organs of an unknown nature associated with these fruiting axes when they were young. These fossils are fruiting axes bearing individual conduplicate carpels (Fig. 2, A and B), and each axis should be regarded as originating from a floral unit (Fig. 2A). The elongate nature of the axes may have been more extended in the fruiting stage than at pollination. The crowded carpels at the apices suggest this (Fig. 2B). Also, in the young carpels the stigmatic tissue occupies proportionately more area, and the apical prominence appears to continue to enlarge as the carpel matures.

The carpels of *Archaeofructus* are closed in a conduplicate fashion, contain more than one ovule, and are clustered together. Subtending each “flower” is a leaf-like structure consisting of a petiole that terminates in a branched pattern of possibly three major veins extending into a crumpled leaf lamina (Fig. 2A). A few of the basal reproductive organs were deciduous at maturity while the subtending leaves and distal carpels remained attached. It is possible that the crumpled leaf-like organs subtending each fertile axis were colored or patterned in some way to attract the attention of insect pollinators. The stigmatic surface may have produced an exudate on which the dipterians, known from the same sediments, may have fed (12). It is also possible that the extended tips on the stigmatic crests of each carpel functioned similarly to those of *Ascarina* of the Chloranthaceae, which is wind pollinated (18). Thus, there is no single

pattern of pollination biology present, as is found for specific fossil angiosperm taxa occurring during the latter Cretaceous (19), but both insects and wind may have been involved. Insect pollination offers a biological environment that would have contributed to an early and rapid diversification of the angiosperms.

*Archaeofructus* has helically arranged carpels, and the placement of the two leaf-like organs suggests this pattern continued in the foliage. In contrast, many members of Gnetales (20), found in the Mesozoic, are characterized by oppositely placed leaves, branches, and reproductive organs. Probable fossils of Gnetales that co-occur with *Archaeofructus* in the Yixian Formation include *Chaoyangia liangii* (21) and *Eragrosites changii* (22). These were both described recently as the earliest record of angiosperms. *Chaoyangia liangii* has ribbed stems with conspicuous nodes, each bearing two oppositely arranged leaves. The stems branch oppositely to produce a cyme-like pattern on which winged fruits or seeds are borne. These winged fruits or seeds are similar to those previously described as *Gurvanella* (23, 24)

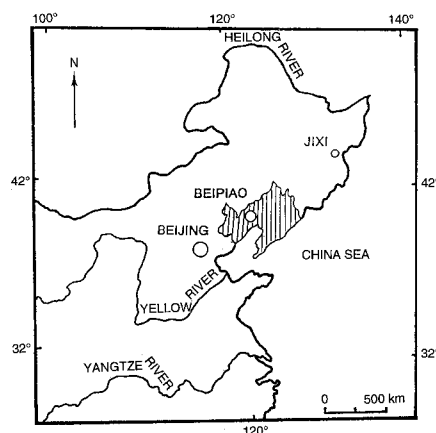


Fig. 1. Map showing the geographic location of the angiosperm fruiting axes *Archaeofructus liaoningensis* gen. et sp. nov. Vertical lines represent Liaoning Province. Fossil localities are southwest of Beipiao.

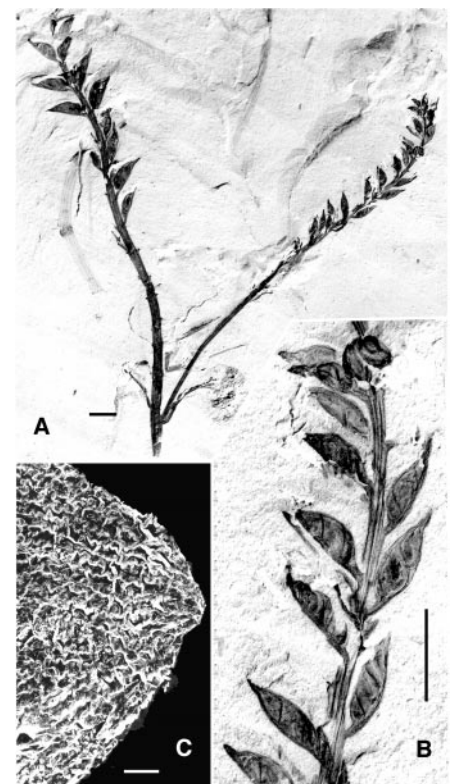


Fig. 2. *Archaeofructus liaoningensis* Sun, Dilcher, Zheng et Zhou gen. et sp. nov. (A) Holotype, SZ0916; fruiting axes and remains of two subtending leaves. Scale bar, 5 mm. (B) Enlarged view of the carpels showing remains of the adaxial crest, abaxial venation, seeds in each carpel, and finger-like prominences. Scale bar, 5 mm. (C) Portion of a seed removed from a carpel, as viewed by scanning electron microscopy. Scale bar, 25  $\mu$ m.



and have a distinct resemblance to the winged seeds of *Welwitschia mirabilis*. *Chaoyangia liangii* is an interesting fossil plant, but the ribbed stems, opposite branching, and winged fruits or seeds suggest that it has affinities with Gnetales rather than the angiosperms. It is unlike any living Gnetales, and careful analysis of the described specimen and additional material needs to be carried out. Before it can be accepted unequivocally as an angiosperm, the nature of the winged fruits or seeds must be clearly understood, and we conclude at this time that it most probably is an extinct genus of Gnetales.

*Eragrosites changii* is a name given to fossils interpreted as grass-like remains (22). These fossils also have reproductive organs borne on ribbed axes with distinct nodes that are oppositely branched, characters typical of Gnetales. In addition, the tightly crowded grass-like seed heads have oppositely arranged bracts that are reminiscent of the seed-bearing organs of *Ephedra* and *Welwitschia*. We consider this fossil grass to represent fossil remains of an extinct Gnetales, and it definitely is not an angiosperm.

*Archaeofructus* presents a new set of characters not previously known in angiosperms. Typically the division Magnoliophyta (25) is used for angiosperms or flowering plants, and the class Magnoliopsida is used for the dicotyledons and Liliopsida for the monocotyledons. We suggest that a new subclass, Archaeomagnoliidae, be constructed for angiosperms that do not conform to the character sets of any of the existing subclasses of the Magnoliophyta. This new subclass is characterized by flowers subtended by only a single leaf or leaf-like organ. Flowers consist of elongate receptacles bearing conduplicate carpels helically. The nature of the male floral organs is unknown at this time. Flowers appear to terminate axes and predate the evolution of any floral patterns. The subclass does not fit the concepts of "paleoherb" or of "eoangiosperm," as both represent collections of angiosperm taxa already more specialized and modified (26) than *Archaeofructus* of the subclass Archaeomagnoliidae.

Although *Archaeofructus* fits the general plan of the "fundamental axis" for the primitive angiosperm (26), there are no subtending bracts present; the carpels, leaves, and branching are helical; and the development of carpels is conduplicate (plicate) (27) rather than ascidiate (27, 28). Some cladograms (28, 29) suggest that ascidiate carpels with one or two ovules are most primitive, on the basis of the occurrence of these characters in extant angiosperms such as Chloranthaceae. This family is schematically derived through a gnetalian ancestry based on these characters (28). *Archaeofructus* does not support this proposed evolutionary scheme.

In extant angiosperms, ovules are formed on

the inner surface of the carpel, which histologically is different from the outer surface. After fusion of the carpel, the ovules are enclosed and isolated from external environmental factors. Endress (27) has maintained that the so-called "open carpels" of some angiosperms are a myth because secretions produced by the inner lining of the carpels fill any gap. The pollen grain and the pollen tube are required to interact with the biochemical barrier as well as, in most carpels, the physical barrier to the male gametophyte presented by the closed carpel (30, 31). This important step in angiosperm reproduction is clearly well developed in the Upper Jurassic in *Archaeofructus*. It allowed for incompatibility to develop between the male gametophyte and the carpel very early in angiosperm evolution.

Overall, *Archaeofructus* looks more like a seed fern-type plant than like bennettitid or gnetalian plants, which have received support as ancestral groups (26, 32, 33). The leaf-like nature of the fertile shoots, the helical disposition of the carpels, the conduplicate nature of the carpels with multiple ovules, and the subtending leafy structures are characters that would support the possible seed fern ancestry of *Archaeofructus*. Gnetales are considered a sister group of the angiosperms, just as they might be thought of as a sister group of some of the Mesozoic seed ferns. The Mesozoic seed ferns are poorly understood and probably do not represent a natural group of plants. Many seed ferns became extinct during the Triassic or the Jurassic, and all became extinct by the mid-Cretaceous (34). Perhaps some lineages of Mesozoic seed ferns are the ancestors of the Mesozoic radiation of the angiosperms, explaining why Gnetales and angiosperms are often found to be sister clades.

*Archaeofructus* is more than 85 mm long and consists of two fertile axes, which give rise to nearly 60 carpels and two leaves (Fig. 2, A and B). This compression-impression plant material was recovered by cleaving apart sedimentary layers of rock. The fossil is unlike the charcoalified remains, recovered by sieving, that have added much to our knowledge of early angiosperm reproduction (35, 36). Those flowers and fruits are minute relative to the material of *Archaeofructus*. Thus, *Archaeofructus* is a clear indicator that large reproductive axes of angiosperms existed early in angiosperm evolution, even if only a few have been recovered. This may suggest that the small angiosperm flowers and fruits of early angiosperms are derived and reduced to small sizes from an ancestor with large flowers.

By the mid-Cretaceous and into the lower Upper Cretaceous, a tremendous increase in angiosperm diversity appears in the fossil record (37–41). Nearly all of these fossils represent lines of evolution progressing toward extant taxonomic clades of angiosperms at the family or generic level (24). The evolution of modern angiosperm taxonomic

groups thus seems to have transpired relatively quickly during the Lower Cretaceous.

For nearly a century, many paleobotanists and botanists have considered the angiosperms to have originated in the tropical regions of the world (42–45). The presence of *Archaeofructus* and early angiosperms from the Lower Cretaceous of Jixi, in northeast China (46, 47), suggest that there were early angiosperms in China and that this was one of the areas where early diversification of the angiosperms was taking place. Angiosperms and angiosperm-like plants have also been reported from the early Cretaceous of Mongolia and Lake Baikal in eastern Russia (23, 24, 48). These fossils are similar to the Yixian flora and are associated with similar fossil fauna (that is, the Jehol fauna characterized by the *Lycoptera-Eoestheria-Ephemeropsis* assemblage). Therefore, angiosperms may have originated in Asia (42).

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- P. E. Smith et al. [*Can. J. Earth Sci.* **32**, 1426 (1995)] suggested that the age of these rocks is Lower Cretaceous (122 million years). However, Chen et al. (13) maintain that the samples analyzed came from intrusive volcanic rocks many millions of years younger, rather than from the fossil-bearing sediments (which they presume to be about 145 million years ago) deposited in the Upper Jurassic. Associated with the angiosperm fruiting axes reported here are abundant remains of non-angiospermous plants, which indicate a Late Jurassic to Early Cretaceous age. We have identified these plants as *Thalites* sp., *Equisetites* spp., *Onychiopsis elongata* (Geyl.) Yok., *Coniopsis* spp., *Ruffordia goeppertii* (Dunk.) Sew., *Cladophlebis* spp., *Pterophyllum* sp., *Nilssonina* sp., *Otozamites* sp., *Neozamites* sp., *Baiera hastata* Krassilov, *Sphenobaiera* sp., *Czekanowskia rigida* Heer, *Solenites murrayana* L. et H., *Phoenicopsis* sp., *Schizolepis jeholensis* Yabe et Endo, *Pityophyllum* sp., *Pityocladus yabei* (Toyama et Oishi) Chang, *Elatocladus manchurica* (Yok.) Yabe, *Brachyphyllum* sp., *Sphenolepis* sp., *Gurvanella* sp. Krassilov, and *Potamageton? jeholensis* Yabe et Endo. The theropod dinosaur, *Sinosauropteryx*, from the lower part of this formation (13) is comparable to *Compsognathus* from the Upper Jurassic (Tithonian) Solnhofen Beds in Germany [P. Wellnhofer, *Archaeopteryx* **11**, 1 (1993)]. In addition, the mouth parts of flies from the Yixian Formation (12) are similar to those known from the Upper Jurassic of Kazakhstan (11). Therefore, we consider the lower Yixian Formation to be Late Jurassic in age.
- Etymology: *Archae-* for ancient; *fructus* for fruiting. The species *liaoningensis* is named for the province in China from which the specimens were collected. Specific diagnosis: Same as for the genus. Holotype: Deposited in the Nanjing Institute of Geology and Palaeontology, Academia Sinica, number SZ0916

(Fig. 2). Age and stratigraphy: Upper Jurassic, Yixian Formation.

17. Description: Fertile axes vary in size (Fig. 2A). Main axis is 85 mm long from leaf axis and 3 mm wide basally, tapering to 1 mm wide distally. The lateral fertile axis originates from a leaf axil, 86 mm long and 1 mm wide basally, tapering to 0.3 mm wide distally. Fruits are attached by pedicels that are 0.75 to 1.5 mm long by 0.25 to 0.6 mm wide. Fruits are larger basally, 7 to 9 mm long by 2 to 3 mm wide, each containing three (two to four) seeds. Finger-like prominences extend about 1 mm from apex of fruits (Fig. 2B). The fruits are positioned at acute angles to the axis. The main axis has 18 fruits and 11 peg-like bases of pedicels (that bore deciduous reproductive organs) about 0.5 mm long. The lateral axis has 30 fruits and four peg-like remnants of the pedicels that bore deciduous reproductive organs, and smaller fruits, 5 to 6 mm long by 1.5 to 2 mm wide. The fruits are crowded at the axis apex where fruit size decreases. Fruits near the apex are 3 mm long by 2 mm wide, each with two seeds. One other fruiting axis (SZ0917, not figured) contains 17 fruits crowded into 35 mm of the fragmentary axis. Seeds fill fruits and have an oblique orientation. They appear to be attached to the adaxial side of the fruit. Seeds may overlap within fruits or may be distinctly separated by oblique bands of tissue. Cuticles of the seed coats are thin. Epidermal cells are rectangular-polygonal, about 25 to 45  $\mu\text{m}$  by 12 to 20  $\mu\text{m}$ . Anticlinal cell walls are sinuous and cutinized, about 2.5 to 3.5  $\mu\text{m}$  thick (Fig. 2C). Periclinal cell walls are somewhat unevenly cutinized.

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## Tracking the Long-Term Decline and Recovery of an Isolated Population

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Effects of small population size and reduced genetic variation on the viability of wild animal populations remain controversial. During a 35-year study of a remnant population of greater prairie chickens, population size decreased from 2000 individuals in 1962 to fewer than 50 by 1994. Concurrently, both fitness, as measured by fertility and hatching rates of eggs, and genetic diversity declined significantly. Conservation measures initiated in 1992 with translocations of birds from large, genetically diverse populations restored egg viability. Thus, sufficient genetic resources appear to be critical for maintaining populations of greater prairie chickens.

The conservation implications of small population size are controversial (1–4). A significant loss in genetic variation may decrease fitness or limit the long-term capacity of a population to respond to environmental challenges (5). Alternatively, chance environmental and demographic events may pose a more immediate threat to small populations (1, 2). Conservation strategies can be different depending on the relative importance of these factors (1, 3, 6), but fundamental questions persist because there are few data on long-term changes in the demography and genetics of wild populations.

Here we report the results of a long-term study on a remnant population of greater prairie chickens (*Tympanuchus cupido pinnatus*) in southeastern Illinois (7). Over the 35-year peri-

od of this study, we documented concurrent declines in population size and fitness as well as an overall reduction in genetic diversity. In addition, we report on a conservation strategy initiated in 1992, whereby translocations of individuals from large, genetically diverse populations increased fitness.

Greater prairie chickens are grassland-dependent birds still found in areas of suitable habitat ranging from northwestern Minnesota south to northeastern Oklahoma, and from southeastern Illinois west to northeastern Colorado (8). Leks (or booming grounds) are used as arenas for territorial display and breeding by two or more males (9). Loss of habitat suitable for successful nesting and brood rearing is the single most important factor leading to declines, isolation, and extirpations throughout the species' range in the midwestern United States (10). The eastern subspecies *Tympanuchus cupido cupido*, also known as the heath hen, has been extinct since 1931 (11) and Attwater's prairie chicken *Tympanuchus cupido attwateri*, which is restricted to Texas, is near extinction (12, 13).

In Illinois, native prairie habitat for prairie chickens originally covered >60% of the state (Fig. 1), but fewer than 931 ha (<0.01%) of the original  $8.5 \times 10^6$  ha of high-grade prairie remain (14). There were possibly several million prairie chickens statewide in the mid-19th century (15); by 1962 an estimated 2000 birds

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