

Proceedings of the Iowa Academy of Science

Volume 91 | Number

Article 10

1984

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Howe, Robert W. (1984) "Zoogeography of Iowa's Paleozoic Plateau," *Proceedings of the Iowa Academy of Science*: Vol. 91: No. 1 , Article 10.

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Zoogeography of Iowa's Paleozoic Plateau

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The Paleozoic Plateau and adjacent rocky outcrop areas of northeastern Iowa harbor many of the state's most unique animal species. Nearly 40% of the state's endangered or threatened vertebrates and all of Iowa's animals on the national list are known from this region. Quantitative comparisons with other parts of the state confirm the existence of a rich vertebrate fauna in the Paleozoic Plateau region. Its peripheral location within Iowa, extensive forest cover, and relatively undisturbed river systems account largely for the occurrence of species found rarely or not at all elsewhere in the state.

Less mobile organisms such as land snails and other invertebrates have been influenced more directly by northeast Iowa's peculiar geological history. The Paleozoic Plateau probably has served as both a glacial and post-glacial refugium for relict species. Recent studies suggest that the biological uniqueness of the region might not be fully realized.

INDEX DESCRIPTORS: Iowa fauna, Paleozoic Plateau, Driftless Area, biogeography

Information about animal distributions in the Paleozoic Plateau of northeastern Iowa (Prior *et al.* 1982) is scattered among general publications (e.g., Cleary 1956, Bowles 1975, Roosa 1977), local inventories (e.g., Roslien 1979, Hinman *et al.* 1980) and reports of personal observations (e.g., Polder 1958, Schaufenbuel 1979). No previous work has focused on animal distributions of the region as a whole, although Hoslett's (1954) analysis of mammals in Allamakee and Winneshiek Counties and results from the 1978 State Preserves Board "foray" (Koenig 1979) provide useful references for much of the area. Publications about land snails (Shimek 1888, Frest and Fay 1982), freshwater mussels (Geiser 1901, Reis 1980, Havlik and Stansbery 1977), stream invertebrates (Meierhoff and Prill 1982, Eckblad 1979), collembolids (Christiansen and Bellinger 1980), and cave invertebrates (S. Peck, *in prep.*), in addition to work by Eckblad and associates (see article in this issue), add significantly to our understanding of the region's fauna.

The purpose of this paper is to examine general zoogeographic patterns in Iowa's portion of the Paleozoic Plateau. I will attempt to answer a fundamental question about the fauna of this area: Is the fauna unique when compared with other parts of Iowa? If the answer to this question is affirmative, I will discuss how the fauna is unique, and why it is unique.

METHODS

A quantitative comparison of species richness among different parts of Iowa is possible for vertebrates because distributional maps and numerous locality records are available. I chose five sites of roughly equivalent area: 1) Allamakee County in the extreme northeastern corner of the state — in the heart of the Paleozoic Plateau, 2) Lee County in the state's extreme southeastern corner, 3) Fremont and Mills Counties in the southwest, 4) Dickinson and Clay Counties in the northwest, and 5) Polk and Story Counties near the center of the state. Each area has been surveyed relatively intensively during recent State Preserves Board "forays" (areas 1-3) or through nearby academic institutions (areas 4 and 5). Iowa Lakeside Laboratory is located in Table 1. Numbers of vertebrate species known or likely to breed in selected Iowa counties during the past 50 years.

Dickinson County; Iowa State University and Drake University are located in Story and Polk Counties, respectively. Lists of vertebrate species observed during approximately the past 50 years were compiled for each area. Species known from nearby areas but not documented recently in these counties were included, given little or no indication that the species range has contracted. Major references include Cleary (1956), Rasmussen (1979) and Lee *et al.* (1981) for fishes; Conant (1975) for reptiles and amphibians; Brown (1971), Johnsgard (1979) and Peterson (1980) for birds; and Bowles (1975) for mammals. Results from natural history forays (Roosa 1977, Silcock 1977 and 1979, Peterson 1979, Koenig 1979) and personal observations (especially those in *Iowa Bird Life* and those of Dr. James Christiansen of Drake University) also were used. Species checklists provided by Menzel (1981), Christiansen (1981), Dinsmore (1981) and Bowles (1981) were used as references, with several minor modifications. Lists of species from each area are available from the author upon request.

Information about invertebrates is far less complete than that for vertebrates. My analysis of Paleozoic Plateau invertebrates focuses on species that are limited in distribution or rare across their range. Iowa is traversed by no major geographic barriers and most of its habitat types are well represented elsewhere. Very few, if any, endemic species occur within the state's borders. Hence, presence of regional endemics or complexes of rare species renders any area in Iowa containing such species unique.

RESULTS

Vertebrate Species Richness

Approximately 73% of Iowa's vertebrate species occur in Allamakee County, more than in any of the other four areas chosen (Table 1). Lee County also supports many species, while Dickinson and Clay Counties are most depauperate. These numbers can be better understood if each taxonomic group is treated separately. Mammal species richness is fairly evenly distributed across the areas chosen, the highest number occurring in Polk and Story Counties. Reptiles and amphi-

	Allamakee	Lee	Fremont/Mills	Dickinson/Clay	Polk/Story	State Total
Fishes	101	82	54	68	69	137
Amphibians & Reptiles	35	54	42	21	36	66
Birds	125	120	118	107	109	156
Mammals	42	43	43	40	46	57
Total	303	299	257	236	260	416

bians are more diverse in southern Iowa than farther north, with Lee County far and away the richest in species.

The relatively rich diversity of vertebrates in northeastern Iowa is due primarily to its large numbers of fishes and, secondarily, to its numerous bird species. The number of fishes known to occur in Allamakee County is nearly 20 greater than in Lee County, the next richest area. The bird fauna of the Paleozoic Plateau is perhaps richer than a simple comparison of numbers indicates. For example, recent Iowa breeding records of the nationally endangered bald eagle (*Haliaeetus leucocephalus*) have been documented only in Allamakee County. Last reported nesting of the endangered peregrine falcon (*Falco peregrinus*) came from the same area. Species such as Cooper's hawk (*Accipiter cooperii*), red-shouldered hawk (*Buteo lineatus*), great blue heron (*Ardea herodias*), great egret (*Casmerodius albus*), pileated woodpecker (*Dryocopus pileatus*), least flycatcher (*Empidonax minimus*), hooded warbler (*Wilsonia citrina*), and cerulean warbler (*Dendroica cerulea*) occur elsewhere in Iowa, but achieve their greatest abundance in the Paleozoic Plateau. In summary, the Paleozoic Plateau (as represented by Allamakee County) compares poorly with other parts of the state only in number of reptile and amphibian species. Overall, its vertebrate fauna is probably Iowa's most diverse.

Species with limited or relict distributions

Presence of species found nowhere else in Iowa and, in a few cases, few or no other places in the world, also suggests that the Paleozoic Plateau is biologically unique. At least 21 species of Iowa vertebrates (Table 2) are found primarily or exclusively in this region, more than in any equivalent-sized area within the state.

Recent work suggests that invertebrates of Iowa's Paleozoic Plateau are particularly interesting. The region's significance is best illustrated by its unique land snail fauna, which has been the subject of national attention. In 1928, a small snail, *Discus macclintocki*, was described by F. C. Baker from fossil deposits in Illinois. At about the same time, the noted Iowa naturalist Bohumil Shimek collected live specimens on a cool, rocky slope in northeastern Iowa. Shimek did not recognize the significance of his find. His collections eventually were deposited at the U.S. National Museum, and it was not until the material was reviewed by J.P.E. Morrison that Shimek's *Discus* was rescued from obscurity. Morrison (1948) reported his discovery in an article entitled "Another Pleistocene snail is not extinct." Fifteen years passed before Leslie Hubricht, one of North America's prominent malacologists, finally rediscovered a living population of *D. macclintocki* in southern Clayton County, Iowa. This remained the only known population until 1980, when the Iowa State Preserves Advisory Board commissioned a study by Terry Frest. Frest, a geologist from the University of Iowa, succeeded beyond all expectations. He located fifteen additional populations, all on specialized, cold-producing (algific) talus slopes in two northeastern Iowa counties. Recently, he has found another small population in Illinois, but searches in Minnesota and Wisconsin so far have yielded no *D. macclintocki* specimens (Frest pers. comm. 1983).

Algific talus slopes — home of Iowa's relict snails — are the result of a unique combination of substrate, aspect, and geological processes (Frest 1982). A more or less continuous flow of cool, moist air through loose rocks provides a favorable microclimate for mosses and relict plants, which in turn provides suitable conditions for the unusual snails. Frest (1982) believes that the microclimatic conditions characterizing algific slopes are themselves "relict," once having enjoyed a wide distribution during the Pleistocene.

Discus macclintocki is not the only relict snail found on Iowa's algific talus slopes. Three species first described as fossils, *Vertigo gouldi hubrichtii* (Pilsbry 1948), *Vertigo occulta* (Leonard 1972), and *Hendersonia occulta* (Say 1831), were found by Frest in northeastern Iowa; the latter species, which also had been collected by Shimek (1904), was found to be quite common on the Paleozoic Plateau. Other rare or

Table 2. Vertebrate species known primarily or exclusively in Iowa from the Paleozoic Plateau and nearby counties.

Mammals	
River otter	(<i>Lutra canadensis</i>)
Bobcat	(<i>Lynx rufus</i>)
Black bear	(<i>Ursus americanus</i>)
Birds	
Bald eagle	(<i>Haliaeetus leucocephalus</i>)
Red-shouldered hawk	(<i>Buteo lineatus</i>)
Yellow-bellied sapsucker	(<i>Sphyrapicus varius</i>)
Brown creeper	(<i>Certhia familiaris</i>)
Winter wren	(<i>Troglodytes troglodytes</i>)
Chestnut-sided warbler	(<i>Dendroica pensylvanica</i>)
Reptiles	
Five-lined skink	(<i>Eumeces fasciatus</i>)
Fishes	
Chestnut lamprey	(<i>Ichthyomyzon castaneus</i>)
Brook trout	(<i>Salvelinus fontinalis</i>)
*Pallid shiner	(<i>Notropis amnis</i>)
*Ghost shiner	(<i>Notropis buchmanii</i>)
*Mimic shiner	(<i>Notropis volucellus</i>)
*Pugnose minnow	(<i>Notropis emilae</i>)
Longnose dace	(<i>Rhinichthys cataractae</i>)
*Mud darter	(<i>Etheostoma asprigene</i>)
*Bluntnose darter	(<i>Etheostoma chlorosomum</i>)
Mottled sculpin	(<i>Cottus bairdi</i>)
Slimy sculpin	(<i>Cottus cognatus</i>)

*restricted to Mississippi River

relict species also were documented by Frest in northeastern Iowa, including *Striatura exigua*, *Vallonia costata*, *Discus cronkhitei catskillensis*, *Vertigo bollesiana*, *V. elatior*, *V. pygmaea*, *V. meramecensis*, and *Zonitoides limatulus*. *V. meramecensis* was first described in 1979 by Van Devender (1979) from a single locality in Missouri. During the past several years, Frest and co-workers (Frest and Fay 1981, Frest 1982) discovered approximately ten new populations, all in northeastern Iowa.

Presence of other endemic or relict invertebrates provides additional evidence for the Paleozoic Plateau's unique character. *Stygobromus iowae*, an aquatic amphipod, is known from only a few caves and seeps in Iowa (Holsinger 1972). Two species of cave-dwelling collembolids, *Onychiurus gelus* and *O. eous*, have been collected from few localities outside Iowa. *O. gelus*, for example, has been collected only from Wisconsin (Richland County), Iowa (Winneshiek County) and lava-formed caves in Skamania County, Washington (Christiansen and Bellinger 1980).

A soil nematode, *Geocenamus* sp., recently has been discovered by Dr. Donald Norton of Iowa State University at a state preserve in Allamakee County (Norton, pers. comm. 1983). The taxonomic relationship of Iowa's population is not clearly understood, but similar specimens are known only from a few sites in Canada and Poland. This species appears to be a boreal relict associated with firs (*Abies* spp.).

Fitzpatrick (1968) described a new species of crayfish, *Orconectes iowaensis*, believed to be endemic to coldwater streams in northeastern Iowa. Phillips (1982 and pers. comm. 1983), however, has shown that the Iowa specimens are merely variants of a common eastern species, *Orconectes propinquus*, at the periphery of its range. In Iowa, *O. propinquus* does not occur outside the Paleozoic Plateau and nearby Mississippi River.

The Paleozoic Plateau is inhabited by no endemic freshwater mussels, but several rare species are known from the adjacent Mississippi River. Four of seven Recommended Essential Habitat sites for the federally endangered *Lampsilis higginsii* are located in the river next to Iowa's Paleozoic Plateau (Stern et al. 1982). Collections in the vicinity of McGregor, Iowa, and Prairie du Chien, Wisconsin — directly across from Iowa's Paleozoic Plateau — reveal one of the most diverse mollusk faunas in the Mississippi River (Havlik and Stansbery, 1977).

Future studies are likely to find more unique invertebrates in northeastern Iowa. Stewart Peck of Carleton University in Ottawa, Canada (pers. comm. 1983) suggests that certain invertebrates might be restricted to subterranean waters of the Paleozoic Plateau. Isopods in the aquatic genus *Asellus*, in particular, tend to show high levels of endemism. Another curious organism, a white flatworm of uncertain identity, was collected by Dr. Jerry Carpenter of Northern Kentucky University at Maquoketa Caves in Jackson County — near the periphery of Iowa's Paleozoic Plateau. Carpenter (pers. comm. 1983) suggests that the organism could be related to *Macrocotyla glandulosa*, a species known only from a river cave system in eastern Missouri.

Comparison with other regions

Although Iowa's Paleozoic Plateau is biologically rich on a regional scale, localities immediately south of the maximum Pleistocene glaciation appear to be even richer. An area in south-central Missouri roughly equivalent in size to Allamakee County supports approximately 125 fish species (Lee et al. 1980), compared with only 101 in northeastern Iowa. According to Johnson (1980), many (21) species of freshwater mussels occur in the Ozark Region of Missouri, Kansas, Arkansas, and Oklahoma (south of the maximum Pleistocene glaciation) but not in the Upper Mississippi/Missouri Valley. The reverse is true for few or no species.

DISCUSSION

Richness of its vertebrate fauna and presence of relict or endemic invertebrate species imply that the Paleozoic Plateau is biologically unique — at least relative to other parts of Iowa, and perhaps to the entire Upper Mississippi Valley. Below, I outline several interrelated explanations for the region's unusual biological diversity.

1. *Geographic location.* The Paleozoic Plateau lies at Iowa's extreme northeastern corner, where a number of peripheral species, particularly birds, reach the limits of their range. Boreal birds occurring in the Paleozoic Plateau include the yellow-bellied sapsucker (*Sphyrapicus varius*), winter wren (*Troglodytes troglodytes*), brown creeper (*Certhia familiaris*), chestnut-sided warbler (*Dendroica pensylvanica*), and perhaps the alder flycatcher (*Empidonax alnorum*), mourning warbler (*Oporornis philadelphia*), Canada warbler (*Wilsonia canadensis*), and others (Koenig, pers. comm. 1982 and H. Hadow in Hinman et al. 1980). Ranges of several fish species such as *Rhinichthys cataractae* also extend only into Iowa's northeastern corner.

Of course, these peripheral species would not be present were it not for the availability of suitable habitat. Also, four of the five areas chosen for my analysis of vertebrate species richness are located at or near a corner of the state; peripheral species are present in each of these four areas.

2. *Habitat availability.* Presence of many uncommon Iowa species in the northeastern corner can be attributed to the abundance of habitats that are absent or rare elsewhere in the state. Before European settlement, Iowa was primarily covered by prairie, with major forest areas near the eastern border and along river margins (Thompson and Hertel 1981). Today, Iowa's largest forest remnants can be found on the Paleozoic Plateau (Anderson et al. 1976). Numerous forest species whose ranges once included much of the state now reach their greatest abundance or are restricted to the northeastern corner. This is

especially true of animals with large home ranges (Table 3) such as the bobcat (*Lynx rufus*), Cooper's hawk, broad-winged hawk (*Buteo platyterus*), and pileated woodpecker. Nearly all recent Iowa sightings of black bear (*Ursus americanus*), a species once widespread in the state, have come from the Paleozoic Plateau or nearby counties (Bowles 1975, D. Roslien pers. comm. 1983). The same is true of river otters (*Lutra canadensis*) (Milligan and Wilson 1983) and red-shouldered hawks (Bednarz 1979, J. Stravers, pers. comm. 1983). Data from eastern North America (Robbins 1979, Whitcomb et al. 1981) warn of declines in forest interior bird species (e.g., ovenbird, *Seiurus aurocapillus*; hooded warbler; scarlet tanager, *Piranga olivacea*) as forest fragmentation continues. Large, contiguous forests of the Paleozoic Plateau could become critical for the long-term persistence of these species in Iowa.

Rugged topography has prevented the clearing of extensive forest tracts in northeastern Iowa. These forest remnants, together with sheltered rocky substrates, have helped maintain clear, coldwater streams, home for a rich diversity of fishes. Iowa's only native trout, the brook trout (*Salvelinus fontinalis*), is restricted to northeastern Iowa, as are the longnose dace (*Rhinichthys cataractae*), ozark minnow (*Notropis nubilis*) and two species of sculpins (*Cottus bairdi* and *C. cognatus*). Other fishes (e.g., *Notropis umbratilis*, *Etheostoma zonale*) seem to reach their greatest abundance in streams of the Paleozoic Plateau (Cleary 1956).

Rocky outcrops of the Paleozoic Plateau and nearby areas provide habitats for timber rattlesnakes (*Crotalus horridus*) and other reptiles, including the locally distributed five-lined skink (*Eumeces fasciatus*). Caves and fissures provide roosting habitats for bats such as the eastern pipistrelle (*Pipistrellus subflavus*). Iowa's only records of overwintering by the federally endangered Indiana bat (*Myotis sodalis*) are from Dubuque County (Muir and Polder 1960, Bowles 1981). These reptiles and bats are known to occur elsewhere in the state, but rocky landscapes of the Paleozoic Plateau offer exceptionally good conditions.

3. *Presence of the Upper Mississippi River.* Species associated with the Mississippi River add significantly to the diversity of vertebrate species in northeastern Iowa. Chestnut lamprey (*Ichthyomyzon castaneus*), pallid shiner (*Notropis amnis*), ghost shiner (*Notropis buchmanii*), pugnose minnow (*Notropis emilae*), mimic shiner (*Notropis volucellus*), mud darter (*Etheostoma asprigene*), and bluntnose darter (*Etheostoma chlorosomum*) are known primarily or exclusively in Iowa from the Mississippi River adjacent to the Paleozoic Plateau. Several other fishes (e.g., *Aphredoderus sayanus*) are restricted to the Mississippi River, but occur in both northern and southern parts of the state (Cleary 1956, Rasmussen 1979).

Extensive floodplain forests along the Mississippi River also provide key animal habitats in northeastern Iowa. Nearly all of Iowa's nesting localities for the state-endangered red-shouldered hawk are located in this part of the state (Bednarz 1979, Jon Stravers pers. comm. 1983). Other rare Iowa species associated with the river include the bald eagle, river otter, and great egret.

Table 3. Approximate home range or territory size for selected animal species.

Species	Area (acres)	Source
Cooper's hawk	557	Craighead and Craighead 1956
Red-shouldered hawk	540	Bednarz and Dinsmore 1979
Pileated woodpecker	247	Whitcomb et al 1981
Black bear	5000 +	Chapman and Feldhamer 1982
Bobcat	1300 +	Chapman and Feldhamer 1982

Three of the four areas with which the Paleozoic Plateau has been compared also are traversed or bordered by a major river. The exception (Clay and Dickinson Counties) lies in the heart of Iowa's lake region. Hence, the Mississippi River, with its significant contribution to the fauna of Iowa's Paleozoic Plateau, appears to be special among Iowa's major waters.

4. *Geological History.* The role of the Paleozoic Plateau as a biological refugium is open to several interpretations. Glacial ice is believed to have covered all or most of the region during the oldest (Nebraskan) Pleistocene glacial advance, about 2.5 million years B.P. (Anderson 1983). Today's fauna is probably derived exclusively from species which survived in southern refugia during maximum glaciation. For example, Johnson (1980) presents evidence that Unionacean clams have repopulated the Upper Mississippi Valley from refugia in southern rivers, particularly those of the Cumberland and Ozark Plateaus. Because the Upper Mississippi River mollusks are not autochthonous, their diversity is significantly lower than in rivers of the southern and central United States. The next glacial advance (Kansan) covered all of Iowa except the extreme northeastern corner (Anderson 1983), where conditions must have been exceedingly harsh. If any organisms were able to persist in the Paleozoic Plateau during early Pleistocene advances, they must have survived in highly sheltered habitats. Stewart Peck (pers. comm. 1983) suggests that subterranean streams or pools might constitute one such habitat; perhaps the ranges of a few aquatic invertebrates like *Styobromus iowae* and *Asellus* isopods predate the Kansan glaciation.

Other species of the Paleozoic Plateau almost certainly arrived later during the Pleistocene. The Paleozoic Plateau and other parts of Iowa may have served as refugia for boreal animals during Illinoian and Wisconsin glacial stages. Evidence from deposits in northeastern Iowa document the presence during the late Wisconsin period of boreal or tundra species, including the arctic ground squirrel (*Spermophilus parryi*), collared lemming (*Disicrostonyx torquatus*), and yellow-cheeked vole (*Microtus xanthognathus*). *Discus macclintocki* is known to have lived in the Paleozoic Plateau at the same time, approximately 20,530 years B.P. (Woodman 1982).

Most of the species that occupied the Paleozoic Plateau during the Ice Age have since become extinct or have migrated north as climatic conditions have changed (Prior *et al.* 1982). However, the rugged topography of northeastern Iowa provides moist north-exposed ravines, rocky cliffs, cool streams, and other features that serve as relict or refugial habitats for species more typical of colder climates. Hence, not only was the Paleozoic Plateau a periodic refuge from glacial ice, but the area also has become a refuge from warmer, drier postglacial conditions that characterize the rest of Iowa and nearby states. Such a "postglacial refugium" is illustrated by distribution of the sculpin, *Cottus cognatus*. This small fish occurs in spring-fed streams of Allamakee, Clayton, Winneshiek, Jackson, and Delaware Counties. Iowa's populations represent a southern extension of a distribution that lies primarily in Canada, the Great Lakes, and mountainous regions of the northern United States. Frest (1982) also suggests that the Paleozoic Plateau is a postglacial refugium for relict land snails. *Discus macclintocki*, for example, is represented by Pleistocene fossils in Iowa, Nebraska, Missouri, Illinois, and Indiana. Fossils of this species from the Paleozoic Plateau are rare and fairly recent; apparently populations moved into the Paleozoic Plateau as cool, moist conditions moved northward behind late Pleistocene glacial retreats. Unlike most postglacial relicts, *Discus macclintocki* and several other ecologically related species do not occur farther north.

CONCLUSION

The Paleozoic Plateau probably is Iowa's most zoologically diverse region. Reasons for its comparative richness include presence of a relatively undisturbed stretch of the Mississippi River, geographic location at a corner of the state, and a rugged, largely forested

landscape. The latter provides favorable habitats for northern or relict species. The region's rocky terrain also is responsible for less intensive land use than occurs in other parts of Iowa.

Although regionally significant, the numbers of vertebrate and invertebrate species from Iowa's Paleozoic Plateau are apparently less than in similar regions to the south (e.g., Ozark Plateau), presumably because glaciation early in the Pleistocene eliminated most or all of Iowa's autochthonous fauna.

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