First accelerator mass spectrometry ^{14}C dates documenting contemporaneity of nonanalog species in late Pleistocene mammal communities

Thomas W. Stafford, Jr.*   Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado 80309, USA
Holmes A. Semken, Jr.   Department of Geology, University of Iowa, Iowa City, Iowa 52242, USA
Russell W. Graham   Department of Earth Sciences, Denver Museum of Natural History, Denver, Colorado 80205, USA
Walter F. Klippel   Department of Anthropology, University of Tennessee, Knoxville, Tennessee 37916, USA
Anastasia Markova   Institute of Geography, Russian Academy of Sciences, Staromonetny per. 29, Moscow 109017, Russia
Nikolai G. Smirnov   Institute of Plant and Animal Ecology, Russian Academy of Sciences, 8 Marta 202, Ekaterinburg 620008, Russia
John Southon   Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Livermore, California 94451, USA

ABSTRACT

Worldwide late Pleistocene terrestrial mammal faunas are characterized by stratigraphic associations of species that now have exclusive geographic ranges. These have been interpreted as either taphonomically mixed or representative of communities that no longer exist. Accelerator mass spectrometry ^{14}C dates (n = 60) on single bones of stratigraphically associated fossil micromammals from two American and two Russian sites document for the first time that currently allopatric mammals occurred together between 12,000 and 22,000 yr B.P. on two continents. The existence of mammal communities without modern analogs demonstrates that Northern Hemisphere biological communities are ephemeral and that many modern biomes are younger than 12 ka. Future climate change may result in new nonanalog communities.

INTRODUCTION

Late Pleistocene terrestrial mammal faunas are characterized by the stratigraphic association of extant species that do not currently live together (Figs. 1 and 2). Because there are no modern counterparts, these faunas have been described as nonanalog (Graham and Mead, 1987), disharmonious (Semken, 1988; Lundelius, 1989), intermingled (Graham, 1985), mixed (Markova, 1992), or extraprovincial (Roy et al., 1995). If these fossil associations are not taphonomic artifacts, they represent ecological conditions fundamentally different from those of today and raise intriguing questions about the response of biotas to climate change.

Nonanalog Pleistocene fossil mammal faunas are recorded worldwide, including Russia (Markova, 1992), Poland (Nadachowski, 1989), Australia (Lundelius, 1989), Siberia (Borodin, 1996), and South Africa (Klein, 1994). Holocene faunas, except some from South America (Simonetti, 1994), characteristically are analog, or nearly so. Although nonanalog associations are most commonly cited in the mammal literature, they are also reported for fossil birds (Emslie, 1985), reptiles and amphibians (Holman, 1985), pollen (Overpeck et al., 1992), plant macrofossils (Baker et al., 1993), insects (Ashworth, 1996), and molluscs (Miller et al., 1994).

ACCELERATOR MASS SPECTROMETRY ^{14}C DATES APPLIED TO PLEISTOCENE MICROMAMMALS

Absolute ^{14}C dating of individual fossil specimens is the best method to test whether nonanalog species associations are taphonomic artifacts without biological implications or if they are evidence of communities dramatically different from those of today. Taphonomically mixed specimens would differ significantly in geologic age (~500–1000 yr); conversely, overlapping radiocarbon dates at 2 σ or less on individual specimens, even with taphonomic disturbance, would document contemporaneity. Taxa chosen for ^{14}C dating (Table 1) are typical of late Pleisto-
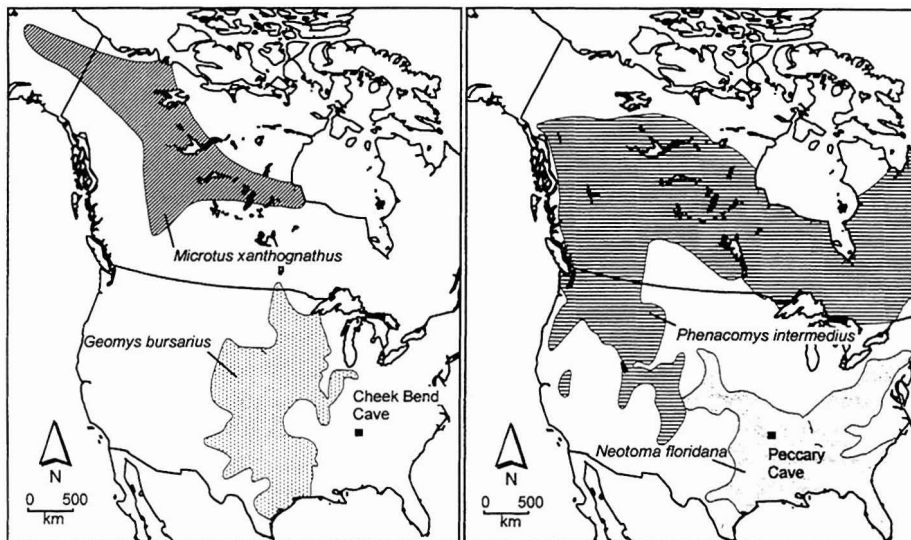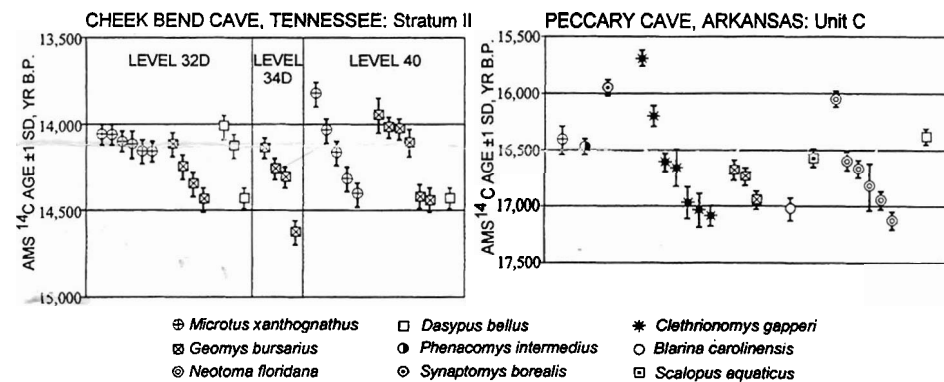

Figure 1. Modern geographic ranges, site locations, and accelerator mass spectrometry (AMS) ^{14}C dates for stratigraphically associated nonanalog species from America.

Geology; October 1999; v. 27; no. 10; p. 903–906; 2 figures; 1 table.
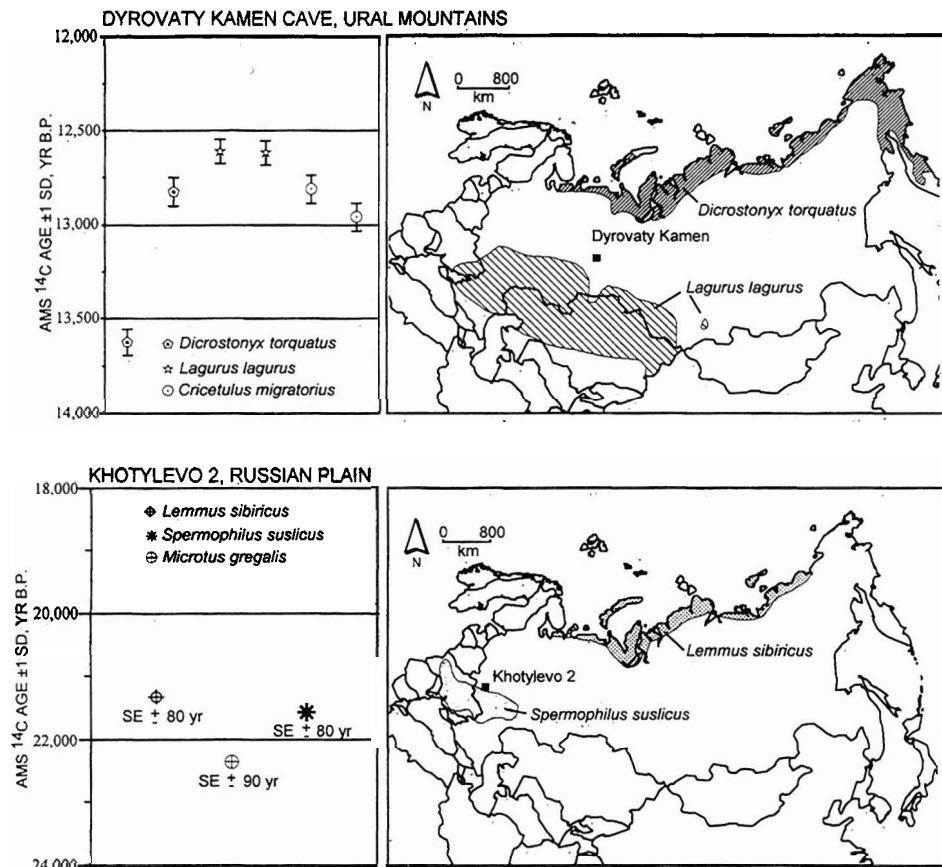
903

Figure 2. Modern geographic ranges, site locations, and accelerator mass spectrometry (AMS) ^{14}C dates for stratigraphically associated nonanalog species from Russia. *Microtus gregalis*, not discussed, is included for completeness.

cene nonanalog faunas. The beautiful armadillo (*Dasypus bellus*) is the only extinct taxon; however, it is considered subspecific with, and physiologically similar to, the living subtropical nine-banded armadillo (*D. novemcinctus*; Klippel and Parmalee, 1984). The tundra-boreal forest-edge yellow-cheeked vole (*Microtus xanthognathus*) is the most northern species dated from America. Today, this vole is separated (Fig. 1) by 1400 km from the eastern woodrat (*Neotoma floridana* complex) and by 2400 km from the nine-banded armadillo. The only dated species discussed that are sympatric with each other today (Fig. 1) are the plains pocket gopher (*Geomys bursarius*) and the eastern woodrat, both of which co-occur only in the prairie-forest ecotone. In the Russian local faunas (Fig. 2), two tundra species, the Siberian lemming (*Lemmus sibiricus*) and the pied lemming (*Dicrostonyx gulielmi* near *D. torquatus*), are separated at present from steppe taxa, the gray hamster (*Cricetulus migratorius*), steppe lemming (*Lagurus lagurus*), and spotted suslik (*Spermophilus suslicus*) by at least 1000 km. Requirements for fossil mammal specimens selected for dating were that: (1) taxa have distinctly different modern biogeographical and ecological parameters; (2) fossils are readily identifiable to species or species complex; and (3) specimens could be attributed to different individuals. At Cheek Bend Cave, the armadillo osteo-

derms (armor) and some pocket gopher remains may represent single individuals, but this is unlikely because of recovery from separate levels.

Dating single osteological elements eliminates the need to combine specimens of potentially dissimilar age to achieve an adequate sample. All ^{14}C ages here are on collagen hydrolyzates highly purified with XAD® (Stafford et al., 1991). Samples were combusted and converted catalytically into graphite and then analyzed at the Lawrence Livermore National Laboratory Center for Accelerator Mass Spectrometry. Advances in chemical pretreatment and accelerator physics now yield accurate radiocarbon measurements with precisions of 0.6%–0.8 % over the past 30 k.y. on specimens as small as a mouse tooth.

The two American (Fig. 1) and two Russian (Fig. 2) sites selected for ^{14}C dating are well-documented localities with characteristic nonanalog species. Both American sites are now in the eastern deciduous forest (Bailey, 1981). Peccary Cave, in the Ozark Mountains of Arkansas, was excavated in 30 cm arbitrary levels within 1 m squares. Specimens were selected from stratigraphic unit C, trench 15, squares 9 and 10, because this sample produced the greatest number of micromammal species (33) within the deposits (Semken, 1984). At Cheek Bend Cave, on the Highland Rim of central Tennessee, three contiguous 1 × 2 m test squares were exca-

vated in 10-cm-thick levels within natural stratigraphic units (Klippel and Parmalee, 1984). Stratum II, the second lowest, yielded 23 micromammal species. The three most ecologically distinct species (yellow-cheeked vole, plains pocket gopher, and beautiful armadillo) from both Peccary and Cheek Bend caves represent boreal forest, temperate steppe, and subtropical parkland environments, respectively.

The Russian cave, Dyrovaty Kamen, in the coniferous forest of the south taiga on the western slopes of the middle Urals (Fig. 2), was sampled by a 1 m[2] test excavation (Smirnov, 1995). A 10 cm increment within the brown loam horizon produced 10 micromammal species, including the tundra-dwelling pied lemming with temperate steppe-dwelling gray hamster and steppe lemming. The second Russian site, Khototylevo 2, on the Russian plain, contains mammoth remains with Paleolithic artifacts buried in Desna River alluvium. This bone bed, level 7, yielded five micromammal taxa including two tundra species (Siberian and pied lemmings) and the temperate steppe-living spotted suslik (Markova, 1982).

CONTEMPORANEITY OF NONANALOG PLEISTOCENE MICROMAMMALS

At Cheek Bend Cave, taxa from steppe, deciduous forest, and tundra-boreal forest environments were contemporaneous at 1 σ for three specific times: 14,050, 14,120 and 14,420 yr B.P. (Fig. 1). In the youngest series, dates on the yellow-cheeked vole (14,060 ± 70, 14,060 ± 70, 14,040 ± 70 yr B.P.) overlap those of the plains pocket gopher (14,020 ± 60, 14,030 ± 60 yr B.P.) and beautiful armadillo (14,020 ± 80 yr B.P.). In the second series, these three taxa are documented together at 14,120 yr B.P. The third and oldest set confirms the contemporaneity of the yellow-cheeked vole (14,410 ± 70 yr B.P.), plains pocket gopher (14,440 ± 70, 14,420 ± 70, 14,440 ± 70 yr B.P.), and beautiful armadillo (14,430 ± 60, 14,430 ± 60 yr B.P.).

Of the 22 Peccary Cave dates (Fig. 1), 20 are evidence that contemporaneous nonanalog faunas existed between 16,000 and 17,250 yr B.P. Dates on mammals with the greatest modern ecological dissimilarity juxtapose the boreal forest-tundra-dwelling yellow-cheeked vole (16,415 ± 125 yr B.P.) and the boreal-dwelling heather vole (*Phenacomys intermedius*; 16,470 ± 70 yr B.P.) with the subtropical beautiful armadillo (16,380 ± 70 yr B.P.), eastern woodrat (*Neotoma floridana*; 16,600 ± 80 yr B.P.), and eastern mole (*Scalopus aquaticus*; 16,570 ± 80 yr B.P.). Moreover, the beautiful armadillo (16,380 ± 70 yr B.P.) co-existed with the boreal-dwelling red-backed vole (*Clethrionomys gapperi*) at 16,200 ± 90 yr B.P. The boreal northern bog lemming (*Synaptomys borealis*) was contemporaneous with the eastern woodrat at the 1 σ level at 16,000 yr B.P.

The accelerator mass spectrometry dates (Fig. 2), on two nonanalog species from Dyrovaty Kamen Cave document overlapping ages at 2 σ

TABLE 1. AMS ¹⁴C AGE MEASUREMENTS ON STRATIGRAPHICALLY ASSOCIATED SPECIES FROM TWO NORTH AMERICAN AND TWO RUSSIAN LATE PLEISTOCENE LOCAL FAUNAS

Taxon	Common name	Habitat*	Catalog no.†	Element	¹⁴C date Yr B.P. ±1 std.dev.	Lab no.§
Peccary Cave, Arkansas, Unit C						
Microtus xanthognathus	Yellow-cheeked vole	TB	SUI-37387a	Mandible	16,415 ± 125	AA 6695
Phenacomys intermedius	Heather vole	B	SUI-80146	Left mandible	16,470 ± 70	CAMS 19913
Clethrionomys gapperi	Red-backed vole	B	SUI-38250a	Left mandible	15,690 ± 70	CAMS 20859
			SUI-38250b	Left mandible	16,200 ± 80	CAMS 20861
			SUI-38250c	Left mandible	16,610 ± 80	CAMS 20860
			SUI-38250d	Left mandible	16,660 ± 165	AA 4941
			SUI-38250e	Left mandible	16,970 ± 140	CAMS 20863
			SUI-38250f L	Left mandible	17,040 ± 150	CAMS 20862
			SUI-38250g	Left mandible	17,090 ± 90	CAMS 20864
Synaptomys borealis	Northern bog lemming	B	SUI-38267	Right mandible	15,950 ± 70	CAMS 19914
Scalopus aquaticus	Eastern mole	D	SUI-38297	Right mandible	16,570 ± 80	CAMS 19915
Neotoma floridana	Eastern wood rat	D	SUI 38276f	Right molar	16,600 ± 80	CAMS 20852
			SUI-38276e	Right mandible	16,670 ± 80	CAMS 20851
			SUI-38276t	Right mandible	16,830 ± 210	AA 4942
			SUI-38276a	Right mandible	16,950 ± 80	CAMS 20856
			SUI-38276d	Right mandible	17,130 ± 80	CAMS 20850
			SUI-38276k	Right mandible	16,050 ± 70	CAMS 13028
Blarina carolinensis	Southern short-tailed shrew	D	SUI-38339	Left mandible	17,030 ± 100	CAMS 20847
Geomys bursarius	Plains pocket gopher	S	SUI-38294a	Right mandible	16,680 ± 90	CAMS 20853
			SUI-38294b	Right mandible	16,740 ± 80	CAMS 20854
			SUI-38294c	Right mandible	16,950 ± 80	CAMS 20858
Dasypus bellus	Beautiful armadillo	ST	SUI-38329	Osteoderm	16,380 ± 70	CAMS 19917
Cheek Bend Cave, Tennessee: Level 32 D						
Microtus xanthognathus	Yellow-cheeked vole	TB	UT 1-79	Mandible	14,060 ± 70	CAMS 19907
			UT 1-79	Mandible	14,060 ± 70	CAMS 19908
			UT 1-79	Mandible	14,100 ± 70	CAMS 19909
			UT 1-79	Mandible	14,120 ± 70	CAMS 19910
			UT 1-79	Mandible	14,160 ± 70	CAMS 19911
			UT 1-79	Mandible	14,160 ± 60	CAMS 19912
Geomys bursarius	Plains pocket gopher	S	UT 1-79	Femur	14,120 ± 80	CAMS 20010
			UT 1-79	Femur	14,250 ± 60	CAMS 20011
			UT 1-79	Femur	14,350 ± 60	CAMS 20009
			UT 1-79	Femur	14,440 ± 70	CAMS 20008
Dasypus bellus	Beautiful armadillo	ST	UT 1-79	Osteoderm	14,020 ± 60	CAMS 19905
			UT 1-79	Osteoderm	14,130 ± 60	CAMS 19906
			UT 1-79	Osteoderm	14,430 ± 60	CAMS 19920
Level 34 D						
Geomys bursarius	Plains pocket gopher	S	UT 112-79d	Prox. scapula	14,140 ± 60	CAMS 20020
			UT 112-79b	Ilium	14,260 ± 60	CAMS 20021
			UT 112-79a	Prox. tibia	14,310 ± 60	CAMS 20018
			UT 112-79c	Maxilla	14,630 ± 70	CAMS 20019
Level 40						
Microtus xanthognathus	Yellow-cheeked vole	TB	UT 6-78d	Maxilla	13,830 ± 70	CAMS 19903
			UT 6-78b	Mandible	14,040 ± 70	CAMS 19901
			UT 6-78a	Mandible	14,170 ± 70	CAMS 19900
			UT 6-78e	Maxilla	14,320 ± 70	CAMS 19904
			UT 6-78c	Mandible	14,410 ± 70	CAMS 19902
Geomys bursarius	Plains pocket gopher	S	UT 6-78e	Prox. humerus	13,950 ± 100	CAMS 20016
			UT 6-78d	Humerus	14,020 ± 60	CAMS 20015
			UT 6-78c	Ilium	14,030 ± 60	CAMS 20014
			UT 6-78b	Prox. ulna	14,110 ± 80	CAMS 20013
			UT 6-78a	Dist. humerus	14,420 ± 70	CAMS 20012
			UT 6-78d	Ulna	14,440 ± 70	CAMS 20017
Dasypus bellus	Beautiful armadillo	ST	UT 6-78a	Osteoderm	14,430 ± 60	CAMS 19899
Khototylevo 2, Briansk: Level 7						
Lemmus sibiricus	Siberian lemming	T	Kh2	Left mandible	21,300 ± 80	CAMS 35903
Spermophilus suslicus	Spotted suslik(grd. Squirrel)	S	Kh2	Right m1-3	21,610 ± 80	CAMS 35888
Microtus gregalis	Narrow-headed vole	S	Kh2	Left mandible	22,340 ± 90	CAMS 35902
Dyrovaty Kamen, Ekaterinburg: 10 cm test						
Dicrostonyx guilielmi	Pied lemming (var.)	T	EI-728	Right mandible	12,820 ± 60	CAMS 35894
			EI-728	Left mandible	13,620 ± 60	CAMS 35895
Lagurus lagurus	Steppe lemming	S	EI-728	Left mandible	12,610 ± 60	CAMS 35896
			EI-728	Right mandible	12,620 ± 60	CAMS 35897
Cricetulus migratorius	Gray hamster	S	EI-728	Right mandible	12,810 ± 60	CAMS 35898
			EI-728	Left mandible	12,960 ± 60	CAMS 35899

*D—deciduous forest, S—steppe, FS—forest steppe, B—boreal, ST—subtropical, T—tundra, and TB—tundra-boreal forest.

†Repositories for specimens: SIU—University of Iowa Geological Repository, Peccary Cave; UT—University of Tennessee Archaeological Laboratory, Cheek Bend Cave; EI—Institute of Plant and Animal Ecology, Ekaterinburg, Dyrovaty Kamen Cave; IGM—Institute of Geography and RAS Collection, Moscow, Khototylevo 2.

§Sample numbers refer to University of Arizona NSF Facility for Radioisotope Analysis (AA) and to Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory (CAMS).

for the pied lemming (12,820 ± 60 yr B.P.) and the steppe lemming (12,610 ± 60 and 12,620 ± 60 yr B.P.). At Khototylevo 2, a 2 σ overlap exists for the Siberian brown lemming (21,300 ± 80 yr B.P.) and the spotted suslik (21,610 ± 80 yr B.P.). Clearly, these dates are not contemporaneous with the same precision as those from Cheek Bend and Peccary caves. However, the 2 σ level (<200 yr) reported here is smaller than many 1 σ levels (>200 yr) for conventional ^{14}C dates. In addition, contemporaneity can be defined at many scales (e.g., seasonal, annual, millennial). Resolution of contemporaneity below 50 yr for late Pleistocene specimens is beyond current ^{14}C dating technology.

The Russian dates would be accepted as geologically contemporaneous. Furthermore, in these types of deposits, the chances of obtaining overlapping ^{14}C dates with low sigma levels on nonanalog taxa may be a function of the number of specimens dated. For example, at Peccary Cave, only seven out of 22 nonanalog species dates (32%) overlap at 1 σ. Therefore, the limited number of specimens dated from the Russian sites reduces the odds for a 1 σ overlap if the deposits are time averaged for 500 yr. With saturation dating as in the American sites, dates on additional Russian specimens would likely reveal overlaps at 1 σ.

The final consideration for interpreting our data as direct evidence for contemporaneity is the existence of radiocarbon plateaus. The ^{14}C calibration curve is affected by periods of differing atmospheric ^{14}C/^{12}C ratios. During the Pleistocene-Holocene transition, these ^{14}C/^{12}C ratios fluctuated sharply at times. The resulting radiocarbon plateaus are intervals where samples with identical ^{14}C dates could differ in calendar ages by as much as 600 yr. Although the detailed calibration curve for ages older than 10,000 yr B.P. is still being determined (Goslar et al., 1995; Hughen et al., 1998), the only plateau of concern here is the one between 12,100 and 12,600 ^{14}C yr. B.P. (13.8–15 ka). At least three and possibly all Dyrovaty Kamen specimens could be anywhere within this 12,100–12,600 yr B.P. plateau. They are contemporaneous within these limits. No other date reported here is within any known plateau (Kitagawa and van der Plicht, 1998).

CONCLUSIONS

Our data confirm that some nonanalog mammal faunas represent unique late Pleistocene communities in North America and Europe. While taphonomic agents undoubtedly can create nonanalog associations, biological explanations must be considered whenever and wherever nonanalog faunal associations are encountered (Faunmap Working Group, 1996). Nonanalog mammal communities vary geographically and do not imply uniform late Pleistocene conditions. Climates, environments, and faunas varied regionally then as now (Graham and Mead, 1987). However, nonanalog faunas document individ-

ualistic species response to fluctuating climates (Faunmap Working Group, 1996) and reinforce the ephemeral nature of communities. Ongoing climate change may result in new biotic communities; conservation plans must consider future biotas with currently unknown species associations (Graham and Grimm, 1990).

REFERENCES CITED

Ashworth, A. C., 1996, The response of beetles to Quaternary climatic changes, in Huntley, B., et al., eds., Past and future rapid climatic change: The spatial and evolutionary response of terrestrial biota: NATO Advanced Studies Institute Series 1, Global Environmental Change, v. 47, p. 119–127.

Bailey, R. G., 1981, Ecoregions of North America: Reston, Virginia, U.S. Geological Survey, U.S. Department of the Interior Fish and Wildlife Service map, scale 1:12 000 000.

Baker, R. G., Bettis, E. A., and Horton, D. G., 1993, Late Wisconsinan–early Holocene riparian paleoenvironments in southeastern Iowa: Geological Society of America Bulletin, v. 105, p. 206–212.

Borodin, A. V., 1996, Quaternary small mammal faunas from the west Siberian plain: Acta Zoologica Cracoviensia, v. 39, p. 75–81.

Emslie, S. S., 1985, The late Pleistocene (Rancholabrean) avifauna of Little Box Elder Cave, Wyoming: Wyoming Contributions to Geology, v. 23, p. 63–82.

Faunmap Working Group, 1996, Spatial response of mammals to late Quaternary environmental fluctuations: Science, v. 272, p. 1601–1606.

Goslar, T., Arnold, M., Bard, E., Kuc, T., Pazdur, M. F., Rozanski, K., Tisnerat, N., Walanus, A., Wicik, B., and Wieckowski, K., 1995, High concentrations of ^{14}C during the younger Dryas cold episode: Nature, v. 37, p. 414–417.

Graham, R. W., 1985, Diversity and community structure of the late Pleistocene mammal fauna of North America: Acta Zologica Fennica, v. 170, p. 181–192.

Graham, R. W., and Grimm, E. C., 1990, Effects of global climatic change on the patterns of terrestrial biological communities: Trends in Ecology and Evolution, v. 5, p. 289–292.

Graham, R. W., and Mead, J. I., 1987, Environmental fluctuations and evolution of mammalian faunas during the last deglaciation in North America, in Ruddiman, W. F., and Wright, E., Jr., eds., North America and adjacent oceans during the last deglaciation: Boulder, Colorado, Geological Society of America, Geology of North America, v. K-3, p. 371–402.

Holman, J. A., 1985, Herpetofauna of Ladds Quarry: National Geographic Research, v. 1, p. 423–426.

Hughen, K. A., Overpeck, J. T., Lehman, S. J., Kaskgarian, M., Southon, J., Peterson, L. C., Alley, R., and Sigman, D. M., 1998, Deglacial changes in ocean circulation from an extended radiocarbon calibration: Nature, v. 391, p. 65–68.

Kitagawa, H., and van der Plicht, J., 1998, Atmospheric radiocarbon calibration to 45,000 yr B.P.: Late glacial fluctuations and cosmogenic isotope production: Science, v. 279, p. 1187–1190.

Klein, R. G., 1994, Southern Africa before the iron age, in Corruccini, R. S., and Ciochon, R. L., eds., Integrative paths to the past: Advances in Human Evolution Series, Volume 2: Seattle, University of Washington, p. 471–519.

Klippel, W. E., and Parmalee, P. W., 1984, Armadillos in North American late Pleistocene contexts, in Genoways, H. H., and Dawson, M. B., eds., Contributions in Quaternary vertebrate paleontology: Carnegie Museum of Natural History Special Publication 8, p. 149–160.

Lundelius, E. L., Jr., 1989, The implications of disharmonious assemblages for Pleistocene extinctions: Journal of Archaeological Science, v. 16, p. 407–417.

Markova, A. K., 1982, Pleistocene rodents of the Russian Plain: Moscow, Nauka, 184 p. (in Russian).

Markova, A. K., 1992, Influence of paleoclimatic changes in the composition of small mammal faunas: Data from eastern Europe: Courier-Forschungsinstitut Senckenberg, v. 153, p. 93–100.

Miller, B. B., Mirecki, J. E., and Follmer, L. R., 1994, Pleistocene molluscan faunas from central Mississippi valley loess sites in Arkansas, Tennessee, and southern Illinois: Southeastern Geology, v. 34, p. 89–97.

Nadachowski, A., 1989, Origin and history of the present rodent fauna in Poland based on fossil evidence: Acta Theriologica, v. 34, p. 37–53.

Overpeck, J. T., Webb, R. S., and Webb, T., III, 1992, Mapping eastern North American vegetation change of the past 18 ka: Non-analogs and the future: Geology, v. 20, p. 1071–1074.

Roy, K., Jablonski, D., and Valentine, J. W., 1995, Thermally anomalous assemblages revisited: Patterns in the extraprovincial latitudinal range shifts of Pleistocene marine molluscs: Geology, v. 23, p. 1071–1074.

Semken, H. A., Jr., 1984, Paleoecology of a late Wisconsinan/Holocene micromammal sequence in Peccary Cave, northwestern Arkansas, in Genoways, H. H., and Dawson, M. R., eds., Contributions in Quaternary vertebrate paleontology: Carnegie Museum of Natural History Special Publication 8, p. 405–431.

Semken, H. A., Jr., 1988, Environmental interpretations of the "disharmonious" late Wisconsinan biome of southeastern North America, in Laub, R. S., et al., eds., Late Pleistocene and early Holocene paleoecology and archeology of the eastern Great Lakes region: Buffalo Society of Natural Science Bulletin, v. 33, p. 185–194.

Simonetti, J. A., 1994, Impoverishment and nestedness in caviomorph assemblages: Journal of Mammalogy, v. 75, p. 979–984 .

Smirnov, N. G., 1995, Materials to the studies of historical dynamics of rodent diversity in the taiga regions of the middle Urals, in Bykova, G., ed., Materials to the history of the modern biota of the middle Urals: Ekaterinburg, Russia, Ekaterinburg Publishing, p. 24–57.

Stafford, T. W., Jr., Hare, P. E., Currie, L. A., Jull, A. J. T., and Donahue, D., 1991, Accelerator radiocarbon dating at the molecular level: Journal of Archaeological Sciences, v. 18, p. 35–72.

Printed in U.S.A.