Palaeontologia Electronica
http://palaeo-electronica.org

Polyphyly, paraphyly, provinciality, and the promise of intercontinental correlation: Charles Repenning's contributions to the study of arvicoline rodent evolution and biochronology

Christopher J. Bell and Christopher N. Jass

"The science of systematics has long been affected by profound philosophical preconceptions, which have been all the more influential for being usually covert, even subconscious."

George Gaylord Simpson, 1953

ABSTRACT

We review the history of Charles A. Repenning's contributions to the study of arvicoline rodents, with emphasis on his philosophical approach to the study of fossils, their taxonomic affinities, biostratigraphic distribution, and biochronologic significance. Rep viewed these issues in an explicitly evolutionary context under which gradational and anagenetic change was accepted as the dominant mode of evolution. He recognized a polyphyletic origin of five independent arvicoline lineages, and viewed paraphyletic higher taxa within those lineages as some of the best evidence of evolution. That perspective, combined with his view that the rock record preserved an adequate material history of population-level evolution in arvicolines, led him to adopt taxonomic practices that can be confusing and cumbersome to non-specialists. He used fossils of arvicolines as tools to develop an intercontinental correlation scheme extending across North America, northern Asia, and Europe. A core component of his correlation scheme was the hypothesis of a bi-directionally balanced history of dispersal events across the Arctic Ocean borderland that introduced comparable arvicoline taxa into Europe and North America from source areas in Asia. Within North America, his biochronology was structured around a concept of immigrant taxa, although definitive establishment of immigrant status often was an elusive goal. He worked diligently to accommodate new data into his biochronologic framework, and was actively engaged with major conceptual issues at the time of his murder. Rep sought to integrate diverse data sets and to explain evolutionary events in the context of fine-scale geologic and climatic history. Those efforts led to his exploration and eventual adoption of independent biochronologies for different faunal regions. The establishment of diachronous boundaries of land mammal ages within North America remains one of his most controversial and thought-provoking proposals.

PE Article Number: 14.3.18A

Submission: 15 June 2007. Acceptance: 5 October 2011

Bell, Christopher J., and Jass, Christopher N. 2011. Polyphyly, paraphyly, provinciality, and the promise of intercontinental correlation: Charles Repenning's contributions to the study of arvicoline rodent evolution and biochronology. *Palaeontologia Electronica* Vol. 14, Issue 3; 18A:15p;
palaeo-electronica.org/2011_3/28_bell/index.html

Christopher J. Bell, Department of Geological Sciences, 1 University Station C-1100, The University of Texas at Austin, Austin, Texas 78712, USA. cjbell@mail.utexas.edu
Christopher N. Jass, Royal Alberta Museum, 12845 – 102 Avenue, Edmonton, Alberta, T5N0M6, Canada. chris.jass@gov.ab.ca

Key Words: Arvicolinae; faunal provinces; biostratigraphy; biochronology; paraphyletic

INTRODUCTION

As the many contributions to this volume reflect, Charles A. Repenning ('Rep') is recognized widely as having made significant contributions in disparate disciplines of the geosciences. From his early career as a geologist studying and mapping extensive areas of the western United States, to his 'second' career addressing the evolutionary history of pinniped mammals, and his tangential studies of other mammal groups (e.g., shrews), Rep left a published record of data, thoughts, ideas, and suggestions that will stimulate geologists and paleontologists for many decades.

Most of our interactions with Rep centered on his third major research focus, the evolutionary history and biochronology of arvicoline rodents (voles, lemmings, muskrats, and their extinct kin). His contributions in this area were substantial and extend well beyond mere collection and identification of specimens and descriptions of new taxa. Rep's approach to his data (and those of other workers) often was controversial, and sometimes confrontational. He was passionate about his work, and could be obstinate, cantankerous, and caustic in interactions with colleagues and students, but his ideas and criticisms were almost universally stimulating. He was a prolific and inveterate correspondent. One of us (CJB) maintained a running postal (and subsequently, email) correspondence with Rep from 1990 through 2004, ending shortly before his murder. The correspondence encompasses hundreds of pages of material and is preserved (along with additional Repenning correspondence) in the Repenning Correspondence Archives of the Vertebrate Paleontology Laboratory at The University of Texas at Austin. Rep used his correspondence to develop ideas, to clarify thoughts, and to frame arguments. Much of what he published on arvicolines in the last decade of his life is revealed in inchoate form in his letters, and he openly admitted that this was his practice. In 1993 he wrote "Don't knock yourself out (or your car) to get here, we can always write letters. Gives me something to publish" (Repenning, letter to Christopher Bell, 22 July, 1993, p. 2). Our recent perusal of the correspondence files, combined with a review of his published works on arvicolines, provides an unparalleled opportunity to explore his thoughts about, and approaches to, the evolutionary history, biostratigraphy, and biogeography of extant and extinct arvicolines. The methodological and philosophical approaches under which he considered his work had enormous impacts on his results and the interpretations he drew from those results. We attempt to provide a broader perspective on Rep's work on arvicolines by summarizing the history and development of his ideas on arvicoline biochronology and elucidating some of the insights, assumptions, and underlying thought processes that influenced much of his research.

HISTORICAL OVERVIEW

The last 30 years of Rep's career were spent in large part in pursuit of a deeper understanding of the evolutionary history, classification, biostratigraphic distribution, and biochronologic significance of arvicoline rodents. The evolutionary history of arvicolines extends back to at least the early Pliocene, and is revealed through a rich and geographically widespread Holarctic fossil record and an impressive array of extant taxa, including at least 151 species distributed within 28 genera (Musser and Carleton 2005). The relatively rapid rate of evolutionary change within arvicolines, combined with their reproductive and dispersal capabilities, makes them one of the more important faunal groups for biostratigraphic correlation of Pliocene and Pleistocene deposits in the Holarctic (Repenning 1987; Repenning et al. 1990; Bell 2000; Bell et al. 2004b).

Rep recognized the possible significance of arvicolines for biostratigraphic correlation in the early 1960s, but his development of a fully mature research program did not occur until the 1970s. His first research study of arvicolines was conducted in pursuit of paleoenvironmental and habitat reconstructions of a late Pleistocene deposit in Alaska, but in that context arvicolines were simply listed as part of a larger faunal assemblage (Repenning et al. 1964). Within two years, he established the foundations of late Cenozoic intercontinental correlations between North America and Eurasia (Repenning 1966), a subject that would become one of the cornerstones of his research program in the later decades of his life.

His first paper that was centered entirely on arvicolines was an anatomical study of mandibular myology and osteology (Repenning 1968) that was prepared initially as a term paper for a comparative anatomy course at the University of California at Berkeley. That, his first immersion into arvicoline anatomy, was simultaneously his first major assessment of the evolutionary lineages within the group. Arvicoline rodents soon assumed a prominent role in Rep's attempts to establish intercontinental correlations between North America, Asia, and Europe. Initially, he used arvicolines in conjunction with other mammalian taxa (Repenning 1967), but they subsequently emerged in his thinking as prominent, if not dominant, biostratigraphic tools in that endeavor (Repenning and Fejfar 1977). In the decade between 1967 and 1977, Rep developed his ideas about trans-Beringian correlations, and struggled with the potential implications of his research for the established evolutionary and biogeographic framework then accepted in North America.

Early research on fossils of arvicolines in North America began in earnest in the 1940s, and was conducted mostly by Claude Hibbard and his students working in the central Great Plains. Hibbard recognized the value of arvicoline rodents for correlation and environmental reconstruction, but always centered his attention on local and regional correlations (e.g., Hibbard 1970a). His initial reticence to consider intercontinental correlations was a result of his conviction that correlations within North America were insufficiently understood to permit reliable correlations across continents, and he considered such attempts to be "unwise" (Hibbard 1941, p. 93), "futile" (Hibbard 1949, p. 1426), and contributory to additional confusion (Hibbard 1953, p. 410). By the mid 1960s Hibbard did recognize paleontological evidence for mammalian immigration into North America from Asia across the Bering Land Bridge (Hibbard et al. 1965), but he maintained that there was no evidence of immigration among arvicoline rodents (Hibbard 1970b). Instead, he conceived of the North American arvicoline fauna as being essentially an endemic radiation (Hibbard and Zakrzewski 1967). Rep took an opposite approach, seeking to explore the possibility of high-resolution intercontinental correlation through arvicoline rodents. However, he postponed publication of his ideas until after Hibbard's death in 1973, at least in part out of respect for Hibbard's accomplishments and Rep's concern that his new ideas were insufficiently well developed to contradict Hibbard's established reputation and authority (Repenning, email letter to Christopher Bell, 16 October, 1998, p. 1).

Repenning's first significant publication on arvicolines that post-dates Hibbard's death was prepared in collaboration with Oldřich Fejfar. They described the framework for an intercontinental correlation scheme based exclusively on arvicolines (Repenning and Fejfar 1977), and emphasized the hypothesis that the North American fauna achieved diversification not through endemic evolution, but through repeated pulses of immigration across the Bering Land Bridge. They openly acknowledged that their proposals would be controversial, and seemed to welcome the imminent challenge when they wrote "The thesis of this paper, as just outlined, is heresy according to the dogma of North American microtid paleontology which, for the past 35 years, has maintained that there were no successive invasions from the Old World" (Repenning and Fejfar 1977, p. 235). The omissions, awkward syntax, and typographic errors in that paper suggest it was a preliminary draft of a manuscript that saw print prematurely, but the paper was important because it preliminarily established the arvicoline rodent divisions of the Blancan North American land mammal age that would later figure prominently in Rep's correlation schemes.

In an extended abstract published in conjunction with the 1978 meeting of the American Quaternary Association, Rep expanded discussion of his divisions of the Blancan, and adopted the convention of using sequential roman numerals (e.g., Blancan I, Blancan II) to denote successive faunal changes that he recognized (Repenning 1978). Divisions of the younger Irvingtonian land mammal age were proposed, but not numbered, in that abstract, and Rep called specific attention to the importance of cave faunas for establishing a chronologic framework for the Pleistocene in North America. A fully developed and internally consistent presentation of an arvicoline biochronology appeared two years later in an expanded paper based on the 1978 abstract (Repenning 1980). In that paper, he established numbered divisions of the Blancan, Irvingtonian, and Rancholabrean land mammal ages, with a five-fold division of the Blancan, and two divisions each for the Irvingtonian and Rancholabrean. That scheme relied heavily on purported immigrant taxa, and the dispersal events responsible for introducing new taxa into North America were outlined in detail by 1984 (Repenning 1984). A full explication of this scheme, including the faunas and specific arvicoline occurrences upon which it was based, was published in 1987 (Repenning 1987) as a chapter in the influential *Cenozoic Mammals of North America* volume (Woodburne 1987a). At the time that book was conceived, the emergence of intercontinental arvicoline rodent biochronology was relatively new, justifying inclusion of a separate chapter dedicated entirely to the group (Woodburne 1987b). In that chapter, documented and/or purported dispersal events were sequentially numbered for the first time, and tied to the temporal divisions of each mammal age. That chapter became a standard reference for North American arvicoline rodent biochronology, and remained so even following the 1990 publication of substantial revisions in details of the timing of dispersal events, and the numbering sequence for the Irvingtonian and Rancholabrean divisions (Repenning et al. 1990). The later paper was missed, or ignored, by non-specialists for many years after its publication.

The establishment of a functional, biostratigraphically based biochronology for arvicoline rodents stands as one of Rep's most significant contributions to Neogene paleontology. In his many papers on arvicolines written subsequent to the core biochronology paper (Repenning 1987), Rep concentrated on refining, expanding, and updating his biochronology in light of new discoveries and interpretations emerging from various disciplines (e.g., Repenning 1989, 1990, 1992, 1998, 2001, 2003; Repenning and Grady 1988; Fejfar and Repenning 1992, 1998; Rogers et al. 1992, 2000; Repenning and Brouwers 1992; Repenning et al. 1995; Bell and Repenning 1999).

Taken as a complete body of work, Rep's publications concerning arvicolines reveal significant contributions that extend beyond the establishment of the biochronology itself. Many of those contributions were born from controversy surrounding Repenning's ideas, or because they stimulated additional work by a new generation of arvicoline enthusiasts. Some of those areas of controversy reveal not only the methodological and cognitive approaches Rep used in his work, but also his thoughts on the modern and continuing development of the evolutionary history, classification, temporal duration, and biogeography of arvicolines. We recognize and explore here three significant contributions Rep made to the study of arvicolines. We selected areas that encompass his philosophical approach to the study of fossils, taxonomy, and biostratigraphy, as well as his emphasis on intercontinental correlations, and the importance of faunal provinciality in establishing biostratigraphic correlations and their biochronologic implications.

EVOLUTIONARY BIOSTRATIGRAPHY

Rep learned and utilized evolutionary thinking in the context of the Modern Synthesis, and he always conceptualized his data in an evolutionary framework. Although he was most concerned with the application of fossils to geological problems, he thought about fossils as the remains of members of once-extant biological populations. He adopted a Simpsonian emphasis on population-level variation as a fundamental criterion for taxonomic allocation (thus exempting himself from one of Simpson's claims that biostratigraphers tended towards typological conceptualizations; Simpson 1953, p. 340). Rep struggled to strike a balance between his perspectives on the biological and geological relevance of fossils, and to integrate those perspectives into a holistic approach to biostratigraphy. The methods he used to achieve that integration changed through time, and had a powerful influence on his view of the classification, taxonomy, paleobiogeography, and stratigraphic utility of arvicoline rodents.

Polyphyly and Paraphyly as Organizing Principles

Rep was a strong proponent of classifications and taxonomies that reflected evolutionary history. He published three classifications of arvicolines, including a global classification (Repenning et al. 1990), and classifications of the "*Pitymys*" group (Repenning 1983a) and of *Allophaiomys* and its purported descendents (Repenning 1992). In subsequent papers he updated those classifications in light of new discoveries and taxonomic arrangements (e.g., Fejfar and Repenning 1998; Repenning 2003). Although published relatively late in his career, his classifications, and his taxonomic practices, were at odds with newly emerging contemporaneous philosophies that specifically sought classifications and taxonomies based upon nested sets of monophyletic taxa (e.g., Rowe 1987, Gauthier et al. 1988; de Queiroz and Gauthier 1990, 1992; de Queiroz 1992).

The ascendancy of monophyly as an organizing principle was anathema to Rep, and he eschewed the explicit recognition of monophyly, once remarking that monophyly (at least in taxa higher than the species) “is a myth” (Repenning, letter to Christopher Bell, 6 July, 1993, p. 3). Instead, he accepted the idea shared by many paleontologists of the Modern Synthesis that macroevolutionary dynamics were best exemplified by evolutionary hypotheses that postulated what we today call paraphyly. He recognized five independent originations of what he called a ‘microtine grade’ of dental specialization (Repenning 1987; rendered as ‘arvicolid grade’ by Repenning et al. 1990), and allocated the taxa from each independent lineage to a separate subfamily (Lemminae, Prometheomyinae, Arvicolinae, Ondatrinae, Dicrostonychinae). He considered the term ‘microtine’ to be an adjective with no taxonomic status (Repenning 1987, p. 238) and was perpetually frustrated by the variable taxonomic treatments (reviewed by Bell et al. 2004b) that used ‘microtine,’ ‘arvicoline,’ and their cognates as formal or informal taxonomic designations (alas, as we do here!) to unite what he conceptualized as five independent lineages. That frustration was especially acute when there was an implication of monophyly. He explicitly emphasized paraphyly of many recognized ‘microtine grade’ genera, and was a strong proponent of a polyphyletic origin of ‘microtine grade’ taxa as a whole (Repenning 1987; Repenning et al. 1990), and of some of the groups that achieved that ‘grade’ of dental specialization (Repenning 1992).

His efforts to trace the detailed evolutionary history of the members of those five lineages were strongly influenced by two related concepts. The first was that evolution was gradational and anagenetic at both higher and lower taxonomic levels within each lineage (e.g., Repenning 1992, p. 17). The second was that the fossil record of arvicolines can and does adequately preserve population-level evolutionary signals, as long as sample sizes are sufficiently high. Discrete time-slices of populations preserved in fossil deposits could, therefore, reflect various stages in the evolution of higher taxa that could be collated into a fairly complete history. A necessary complication was that a diagnostic feature of a given taxon (at any hierarchical level) must once have been present only as a morphological variant within an ancestral population (Simpson 1953). Such a feature would, with an adequate fossil record, be traceable as it increased in abundance within and between populations. Evaluation of population-level variation thus became a central focus for Rep and a key consideration for his taxonomic treatment of fossils.

Population-level Variation, Transitional Forms, and Taxonomic Practice

As a consequence of his views on evolutionary dynamics and classification, Rep came to recognize population-level variation as an essential consideration for both the identification of fossil specimens and the placement of those fossils in a taxonomic hierarchy. His thoughts on the issues developed over time and are reflected by shifts in his perspective on the importance of sample size for reliable determination of taxonomic affinity. As late as 1988 (Repenning and Grady 1988, p. 10), he was comfortable naming the new species *Phenacomys brachyodus* based on a relatively limited sample of six specimens, only two of which were lower first molars -- the arvicoline tooth accepted by Rep and other paleontologists as being the most diagnostic tooth in the head of arvicolines. By the early 1990s his standards became more rigorous, and he was adamant in his view that isolated arvicoline teeth could not reliably be identified. Instead, he insisted that a minimum sample size of 25 specimens was required to establish definitively the presence of a taxon in a fossil assemblage (Repenning 1992). It is not clear why he settled on 25 as the required number, but he emphasized the importance of that sample size to his colleagues and pushed for a wider adoption among paleontologists documenting fossils of arvicolines (e.g., Repenning, letter to James Mead, 11 January, 1993, pp. 2-3; letter to Anthony Barnosky, 9 March, 1993, p. 3).

In practice, his perspective resulted in complicated conventions for distinguishing between what he considered ‘primitive,’ ‘typical,’ and ‘advanced’ populations of particular genera or species; it also occasionally yielded awkward taxonomic treatments of what he considered to be transitional forms. His views on these issues were most thoroughly and explicitly discussed in his extensive analysis of the evolution of *Allophaiomys* and its many purported descendents (Repenning 1992). That discussion makes clear that an appreciation of his conceptual framework is essential for understanding the names he applied to fossils.

Rep utilized hyphenated taxonomies beginning in 1987, but without extensive explanation. That convention expressed his interpretation of the specimens in question as intermediate or transitional forms, unambiguously identified the taxa between which the transition was conceptualized, and simultaneously avoided cluttering the literature with additional binomial names (Repenning 1987). In his initial use, the hyphenated taxonomy was applied interspecifically within a genus (e.g., *Mimomys* (*Ophiomys*) *taylori*-*parvus*), and that convention also was followed by Repenning et al. (1990). By 1992 he applied hyphenated taxonomy intergenerically, but always with reference to species (conceptually, to populations *of* species) within sediments at a given locality. For example, he explicitly identified specimens from Cumberland Cave in Maryland as being intermediate between *Microtus paroperarius* and *Lasiopodomys deceitensis* (taxonomy rendered as *Microtus paroperarius-Lasiopodomys deceitensis* by Repenning 1992, p. 52). He continued to use hyphenated taxonomy until his death and it appeared in his last systematic work on arvicolines (Repenning 2003).

In addition to (and in conjunction with) his occasional use of hyphenated taxonomic nomenclature, Rep's writings on arvicolines are characterized by surprisingly frequent reference to the evolutionary origin of one genus from within a population of a species of another genus. Examples include his hypotheses of the evolutionary derivation of *Synaptomys* from within a southeastern population of an unspecified species of *Mictomys* (Repenning and Grady 1988), *Phenacomys* from within an unknown form of *Cromeromys* (Repenning et al. 1987), and *Microtus* (in part), *Lasiopodomys*, *Terricola*, *Pitymys*, *Pedomys*, *Lemmiscus*, and at least four other genera from within *Allophaiomys pliocaenicus* (Repenning 1992).

In two cases, he documented his view that origination events actually may have been captured in the fossil record; these are the possible derivation of *Lemmiscus* from within *Allophaiomys* at SAM Cave, New Mexico (Repenning 1992), and the evolution of *Microtus paroperarius* (in part) from within *Lasiopodomys* at Hamilton Cave, West Virginia (Repenning and Grady 1988). In both cases he later altered his opinion. He subsequently acknowledged that sufficient 'intermediate forms' were lacking between *Lemmiscus* and *Allophaiomys* in SAM Cave (Rogers et al. 2000). In the latter case, he reinterpreted specimens of *Microtus* in Hamilton Cave as representing extreme morphological variation within a new, but unnamed species of *Lasiopodomys* (Repenning 1992), but applied the awkward hyphenated taxonomy of '*Microtus paroperarius* - *Lasiopodomys deceitensis'* to indicate his conception of the anagenetic derivation of *Microtus paroperarius* from within a population of *Lasiopodomys deceitensis* in Cumberland Cave (Repenning 1992, p. 53).

His taxonomic decisions were predicated upon his assessment of the variation within a given sample of fossils relative to the known variation represented in the *typical* populations (literally, from the *type* populations) of species to which those fossils might be referable. His determination of 'typical' morphological condition was specifically framed on the basis of the type *population* (not solely the morphological configuration of the type *specimen*), ideally represented by a complete sample of specimens collected from the type locality. This was true regardless of the 'stage of evolution' of the type population relative to any other reference fauna or sample. He used hyphenated taxonomy if the relative abundances of different morphotypes in a fossil sample under study were between 40% and 60% of the sample (those percentages were not explicitly justified and appear to have been arbitrarily established). The dominant morphotype was listed first in the hyphenated name. Samples (interpreted by Rep to be *populations*) with greater than 60% of one morphotype were assigned to the genus and species whose typical morphotype they most closely approximated. Morphotypes in the remaining 39% (or less) of the sample were considered to be individuals of that taxon, but with a morphology that overlapped the morphology of another taxon.

It is, of course, possible to interpret such samples in alternative ways. It can be difficult (here, a possible euphemism for 'impossible') to distinguish between samples that reflect some stage of incipient speciation (characterized by relatively high levels of variation, but not sufficiently high to warrant a hyphenated name) from those that preserve remains of closely related taxa in differential relative abundance, especially if the type locality of a species includes a wide range of morphotypes. An example is represented by the type collection of *Microtus paroperarius* from Cudahy, Kansas. The holotype specimen was collected from the Sunbright Ash Pit, but paratypes were established from Sunbright as well as Cudahy Ash pits (Hibbard 1944). The species was diagnosed by having lower first molars with only four closed triangles (Hibbard 1944). An extensive subsequent collection from the Cudahy Ash Pit site yielded thousands of specimens of *Microtus paroperarius* and was accepted by Repenning as representing the 'typical' condition for the species (Repenning 1992; Bell and Repenning 1999). That 'typical' condition included m1s with five closed triangles, as well as those with four closed triangles. In addition, upper second molars with distinctive enamel fields typically referred to *Microtus californicus* (in faunas from California) or *Microtus pennsylvanicus* (in faunas from the Great Plains and eastern United States) were present in the collection. Initial discussions between Rep and one of us (CJB) about the Cudahy fauna and its interpretation were heated, and resolved only by joint re-examination of the thousands of relevant specimens. Rep pursued the re-examination willingly, but in the loan request he filed with University of Michigan Museum of Paleontology to borrow the specimens, he referred (good-naturedly?) to his "meddlesome associate" (i.e., Bell; Repenning letter to Philip Gingerich, 22 April, 1995, p. 2). However, in a departure from his previous bounds, Rep ultimately accepted that the low relative abundance of specimens with five closed triangles (7.3% of the total relevant sample of m1s) could plausibly represent a different, but unidentified, species of *Microtus* (Bell and Repenning 1999).

At the time of his death, Repenning was beginning to modify his percentage-based approach to taxonomic allocation. His motivation derived in part from the unusual discoveries within Porcupine Cave in Colorado (Barnosky and Rasmussen 1988) and Cathedral Cave in Nevada (Bell 1995; Jass 2007; Jass and Bell 2011). At both sites discrete stratigraphic levels contained specimens referable to *Allophaiomys pliocaenicus* and several of its purported descendants, including *Lemmiscus curtatus* (represented by specimens with both four and five closed triangles on m1), *Microtus paroperarius*, *Microtus meadensis*, and *Microtus* with five closed triangles on m1. The faunas from the initial excavations in Cathedral Cave and the renewed excavations by the Denver Museum in Porcupine Cave were under study simultaneously in 1994 and 1995, and the Porcupine Cave material excavated by the Denver Museum of Natural History (now Denver Museum of Nature & Science) was studied by Rep individually (e.g., Repenning letter to Elaine Anderson, 17 June, 1994) and in collaboration with others for over a decade (see Bell et al. 2004a). Much of the correspondence that we reviewed between Rep and Bell was dedicated to the significance of the faunas preserved in those caves. The cave faunas posed a vexing problem for Rep, whose model of anagenetic evolution was inconsistent with ancestors being found in direct association with descendents (see discussions by Gould 1982 and Barnosky 1987). The discoveries stimulated renewed discussions about taxonomic philosophies, and the operational practices he employed in correlating faunas without external (to the fauna) age control.

Rep's initial responses to the discoveries in Cathedral Cave and Porcupine Cave were dismissive; he simply did not accept that the co-occurrences could be valid. His starting position was that the relevant specimens were misidentified, either through ignorance of the relevant anatomical features or because of inadequate appreciation of the range of morphological variation that could be present within a single population. Getting him past the first inclination often meant providing an opportunity for him to personally view the material and pronounce his judgment. One of us (CJB) took advantage of Rep's invitation to visit him in Colorado with specimens from the two cave sites in hand. During the first afternoon of a five-day visit in August of 1994, anatomical ignorance was ruled out by the simple expedient of placing specimens (without reference to their known stratigraphic context) under a microscope and independently writing down the name that each person thought should be applied to the specimen based only upon its morphology. Comparison of answers revealed that there was no fundamental disagreement over the identity of species, although slight differences in higher-order taxonomic preference were revealed, saving much frustration in subsequent conversations. Once taxonomic parity was achieved, the discussion resolved into an in-depth assessment of the implications of the stratigraphic associations.

At the time that visit took place, Rep had been convinced for over a year that identification of *Allophaiomys* from Porcupine Cave was in error. He noted "There is no *Allophaiomys* or *Lasiopodomys* in Porcupine Cave, they both became extinct 830,000 years ago. The presence of *Allophaiomys* morphotypes in the fauna has to be an individual variant of *Microtus*..." (Repenning, faxed letter to Christopher Bell, 7 July, 1993, p. 3). No resolution was achieved during that first meeting, and discussions continued for over a decade. Rep's concerns were expressed clearly at the end of the first day when the question of dinner was raised: "How can you eat at a time like this – when the whole profession is in a crisis? Boy, you are putting a hole in biochronology" (Bell, "notes from microtine investigations with Repenning, Aug. 18-22, 1994", p. 7; in correspondence file).

By 2004 no final resolution on how to interpret the *Allophaiomys* morphotypes existed, but in a coauthored summary of the Porcupine Cave material the co-occurrence with purported descendents was noted as “perplexing “ (Bell et al. 2004a, p. 214), and the implications for taxonomy and evolutionary history were discussed briefly. This issue of taxonomic allocation of specimens with low sample sizes remained a perplexing problem for Rep, but was unresolved at the time of his death.

A WEB OF INTERCONTINENTAL CORRELATION

Arvicolines as Tools for Intercontinental Correlation

Rep dedicated extraordinary effort to establish intercontinental biostratigraphic and biochronologic correlations. During a time when many mammalian paleontologists focused on local, regional, or continental-scale correlation issues (the Great American Biotic Interchange being a notable exception), Rep centered his attention on intercontinental dispersal of mammals and the potential of such dispersals for forging correlations across vast distances. After initial explorations of the mammalian fauna *in toto* (Repenning 1967), he focused on using arvicolines to establish correlations across North America, Asia, and Europe. Rep's emphasis on the shared history of arvicolines from Eurasia and North America was pioneering in its attempt to establish intercontinental correlations for higher latitudes. His approach represented a clear departure from much of the earlier work by Hibbard and others that focused on regional patterns of change in the North American arvicoline fauna. Ironically, Rep was inspired in part (Repenning, personal commun. to C.J. Bell) by early comments published by Hibbard that arvicolines from the Cudahy fauna bore some resemblance to those from Norfolk, England (Hibbard 1944, 1950).

Immigrants, Boundary Definitions, and Dispersal Events

Rep's correlations of North American and Eurasian faunas were based on the interpretation that many North American arvicoline lineages were immigrant taxa (Repenning and Fejfar 1977; Repenning 1978, 1980, 1983a, 1983b, 1984, 1987, 1998, 2001, 2003; Repenning et al. 1990). The biogeographic context in which he conceptualized immigration to have occurred was complex and centered on the Arctic Ocean borderland. Rep framed, then set out to test, the hypothesis that similarities between North American and western European arvicoline faunas were a result of bidirectional and nearly simultaneous dispersal events along the Arctic Ocean borderland from source areas in Asia (e.g., Repenning 1983b; Repenning 1987; Repenning et al. 1990). Philosophically, he viewed immigrants as the best tools for the establishment of unambiguous definitions of biostratigraphic and biochronologic boundaries. He considered immigration (on a continental scale) to be a more readily recognizable phenomenon than intracontinental dispersals (Repenning 1998). He viewed correlations based on immigration events as a more reliable foundation for establishment of faunally based temporal divisions than stage-of-evolution correlations established based upon anagenetically evolving endemic lineages.

Nevertheless, stage of evolution of certain arvicoline lineages did play a role in the boundary definitions of two divisions he proposed for the Blancan North American Land Mammal Age (NALMA), both of which lacked evidence of North American immigrants (Blancan II, Blancan IV; Repenning 1987). Ultimately, the proposition and recognition of those boundaries was a result of his effort to recognize equivalent numbers of European and North American dispersal events (Bell et al. 2004b). That suggests to us that biogeographically balanced dispersal was a more important concept for him than was the exclusive use of immigrant taxa for the establishment of boundaries.

Purported North American immigrants in his final published formulations (Repenning 1998, 2001) included *Mimomys* (in two separate dispersals), *Pliopotamys*, *Mictomys*, *Plioctomys*, *Allophaiomys*, *Phenacomys* (*Paraphenacomys*), *Microtus* (in two separate dispersals), *Phenacomys* (*Phenacomys*), *Lasiopodomys*, *Clethrionomys*, *Terricola*, *Lemmus*, and *Dicrostonyx*. A persistent problem for Rep was the unambiguous establishment of immigrant status for many of those taxa. With the notable exception of one of the *Mimomys* dispersals (Repenning 2003), the immigrant status of arvicolines in North America was inferred rather than demonstrated (we note that he would disagree with this claim). Rep did acknowledge that in several cases earliest known occurrences of taxa in North America pre-dated known Eurasian occurrences. He attributed those, in part, to a lack of radioisotopic data from relevant Eurasian localities, or to misidentification of magnetic polarity events in the Eurasian sequence (Repenning 2001). In such instances, he invoked the occurrence of perceived primitive versus advanced forms (morphotypes) of lineages as a basis for his interpretation of dispersal from Eurasia to North America (Repenning 2001).

Many of the details of Rep's proposed biochronology would stand regardless of whether or not the taxa involved were actually immigrants. His purported immigration events were radiometrically dated or calibrated (e.g., Repenning 1967, 1998) and those data serve as useful anchors for any biochronology. As geologically 'instantaneous' events with global expression, magnetic polarity transitions were viewed by Rep as fundamentally important for intercontinental correlation. He utilized radiometrically dated magnetopolarity chronology (e.g., Mankinen and Dalrymple 1979) to calibrate the history of arvicoline rodents in North America and Eurasia throughout much his work (e.g., Repenning 1987, 1992; Repenning et al. 1990, 1995), but arvicolines themselves were often the ultimate arbiters for determination of *which* polarity event was represented in a stratigraphic section. Many of the North American arvicoline faunas he considered, particularly those in the western United States, were constrained by age control external to the fauna and independent of magnetic polarity assessment (Repenning 1987). Those faunas formed the backbone of his web of biochronologic correlations. Other faunas that were unconstrained by external age control were positioned on the basis of phylogenetic interpretation. In those instances, he seems to have evaluated population-level variation of component taxa, and by assuming a constant rate of evolutionary change, assigned an age range to those unconstrained faunas (see data and locality summaries provided by Repenning 1987, figure 8.1 [in pocket of book], and individual taxon discussions provided by Repenning 1992).

The hypothesized dispersal events that introduced purported immigrants were outlined early in Rep's work on arvicolines (e.g., Repenning 1980, 1983b, 1984), and were tightly integrated with his arvicoline divisions of the NALMAs. Those events were formally recognized and numbered by Rep in 1987 (dispersal events 1-10; Repenning 1987), but new data forced awkward modifications and revisions to the numbered system (e.g., Repenning et al. 1995). Formal, numbered, events were eventually abandoned in favor of nomenclatural practice tied to particular taxa or time intervals (e.g., Repenning 1998). Eventually, Rep came to recognize 16 arvicoline dispersal events, with all but one bringing immigrants from Asia into North America (Repenning 2001). The exception was the emigration of *Microtoscoptes* from North America into Asia (Repenning 1998, 2001; current phylogenetic hypotheses [not accepted by Rep] suggest that *Microtoscoptes* was not an arvicoline, but a cricetid exhibiting dental characteristics convergent with arvicolines; see comments by Musser and Carleton 2005, p. 957). The west-to-east predominance was obvious, unexpected, and eventually suggested, with some comedic flavor, as a biological phenomenon of unknown origin (Repenning 1998, p. 55, footnote).

For Rep, dispersal events and the immigrants they introduced were constrained by both geologic and paleoclimatic events, and represented opportunities to explain patterns of biological and evolutionary change in the broader context of geologic and climatic processes that led to periods of population-level isolation or, conversely, dispersals. He discussed extensively the relationship between climate, geology, dispersal events (or lack thereof), and dispersal routes (e.g., Repenning 1990, 1998, 2001). Elucidating those complex relationships was a major goal for Rep in much of his work.

Temporal Range Extensions and Youngest Known Occurrences

An interesting contrast to Rep's emphasis on first-appearance data (especially those associated with immigration) was a disinclination to explore the *youngest* known occurrences of many arvicolines. In addition, he found it difficult to accept radiometrically dated occurrences of arvicolines that conflicted with his conceptualization of arvicoline chronology. For example, conservative radioisotopic age estimates supported an age of 252,000±30 ka for the Salamander Cave locality in South Dakota (Mead et al. 1996), but Repenning, as a co-author of the paper, argued for an older, Cudahy-equivalent age (600,000±100,000 years old) for the site, based on the presence of *Microtus meadensis*, *Microtus paroperarius*, and *Mictomys meltoni*/*kansasensis*, taxa known to co-occur in the Cudahy faunas of west Kansas (Hibbard 1944). Rep was intransigent is his arguments, and the final publication proposed two alternative age interpretations, framed as hypotheses in need of additional testing (Mead et al. 1996). Although Repenning clearly recognized the importance of geologically young taxonomic occurrences, particularly in the context of faunal provinciality (Repenning letter to Jim Mead, January 11, 1993), the independent age data from Salamander Cave conflicted with his conception of the temporal distribution of *M. paroperarius*. His view on the age of Salamander Cave might be interpreted ungenerously only as an unwillingness to accept the possibility that his chronology was flawed, but other factors played a role in his thinking (Repenning letter to Jim Mead, January 11, 1993). Most important among those was the low sample size involved, when considered in light of the total range of variation in the relevant taxa as they were then understood.

Other reports of potentially young occurrences of *M. paroperarius* had reached Rep's attention as early as 1990. He argued that *M. paroperarius* was not likely to be present at Cathedral Cave, Nevada, based primarily on the initial late Pleistocene age assignment for the site: "I did not worry about your *Microtus* being *paroperarius* because I assumed that your fauna was less than 450,000 years old" (Repenning letter to Bell, December 17, 1990, p. 4). Although subsequent research pushed back the age assignment for the Cathedral Cave fauna, it is still significantly younger than would be expected given Rep's understanding of the temporal distribution of *M. paroperarius*. New age data on the Cathedral Cave fauna, which includes *M. paroperarius*, are consistent with the younger age interpretation for the Salamander Cave material (Jass 2007; Jass and Bell 2011).

Rep's initial reticence to embrace the younger ages is somewhat surprising given his acknowledgment of the paucity of data for faunas younger than Cudahy. In 1994 he wrote an informal report on the identification of some arvicoline specimens from the Denver Museum of Natural History excavation in the Velvet Room in Porcupine Cave. In that report he wrote

> "It is a Cudahy-type fauna and has a modern *Lemmiscus curtatus* in it. Not much *Mictomys*, but some. Cudahy is 0.61 Ma, *as you know, but we really do not know the temporal range of this sort of fauna...* Consideration of evolutionary rates would suggest that the fauna would not stay so much like Cudahy for more than about 100 kya, and then sometime about 450 kya we get an immigrant of Old World (modern species) of *Microtus*." (Repenning, letter to Elaine Anderson, 17 June, 1994, pp. 2-3; emphasis added).

Near the end of his life, Rep came into greater acceptance of young occurrences of some arvicoline taxa and to an acceptance of unexpected taxonomic associations of arvicolines that were discovered in several faunas from the western United States. Most notable were the repeated instances of *Allophaiomys* being found in direct stratigraphic association with some hypothesized evolutionary descendants (*Microtus paroperarius*, *Lemmiscus curtatus*, *Terricola meadensis*). Such occurrences were anathema to Rep when he first encountered them, but he began to incorporate them into his thinking and to modify his biochronologic schemes accordingly. He once wrote on a manuscript review "Things that we have discussed, such as Cathedral Cave and Porcupine Cave have cast considerable doubt in my assumptions about faunal change (which are easier to make when you know less)" (quoted by Christopher Bell, letter to Charles Repenning, 19 May, 1995, p. 4). Rep was intrigued by the possibility that the anomalous taxonomic assemblages found in high-elevation cave sites in the west might reflect the need for independent biochronologies at high elevations, comparable to the latitudinal and longitudinal differences he already recognized. Occurrences that were at first seen as anomalous (e.g., Salamander Cave) became the norm for western cave sites that preserved biotas from relatively high elevations (Porcupine Cave and Cathedral Cave). The interesting thing about these sites was no longer the 'anomalous' taxonomic associations, but rather that those associations were consistently recovered in western sites of the appropriate age and elevational range.

His accommodations in the face of these new data were based on his increasingly acute sense that North American arvicoline biochronology was sufficiently mature to permit recognition of fine-scale patterns of provincialism and, consequently, of independent biochronologies for relatively fine-scale geographic areas.

SHIFTING BOUNDARIES: BIOCHRONOLOGIC PROVINCIALITY

Rep recognized geographic distinction in biochronologic patterns of arvicoline rodents (i.e., provincialism) as early as 1980, when he noted that Alaskan arvicoline faunas retained a distinct biochronology relative to other portions of North America (Repenning 1980). By 1987, his thinking on the topic was clearly developing, and he indicated the necessity of using different lineages as time markers within distinct geographic regions (Repenning 1987). He thus merged faunal provinciality and biochronology of arvicolines into what was for him an inseparable conceptual whole. A preliminary attempt at a synthesis of provincialism in arvicoline rodent biochronology was published in a paper co-authored with Oldřich Fejfar, in which they outlined provincial distinctions in both Eurasia and North America (Fejfar and Repenning 1992).

Faunal regions were proposed by Fejfar and Repenning (1992) on the basis of similarity in known arvicoline faunas. Eurasia was broken into four broad faunal provinces identified as the Oriental, Beringian, Paratethyian, and Central and Northern European faunal regions. North America was split into the Beringian, Canadian, Western United States, Eastern United States, and Mexican faunal regions. Topography, climate, and latitude were seen as primary factors that controlled regional dispersal, and those factors were important in discussions concerning the evolutionary history of individual taxa (e.g., *Mimomys*; Repenning 1990, 2003; Repenning et al. 1995).

Specific aspects of dispersal patterns within North America were explored in detail by Rep and others (e.g., Fejfar and Repenning 1992; Repenning et al. 1995), and within these works he explored the diachronous nature of arvicoline biochronology within North America. As a specific example, he recognized differences in the faunal characterization of the Irvingtonian in the eastern and western conterminous United States (Repenning 1987; Repenning et al. 1990), and eventually came to open acknowledgment of diachroneity for the Blancan-Irvingtonian boundary (Repenning et al. 1995). Immigration of *Allophaiomys* into the United States was known only east of the Rocky Mountains and was interpreted to have occurred at 1.9 Ma. In the west, the Irvingtonian taxa *Microtus* and *Phenacomys* did not appear until 300,000 years later, and *Allophaiomys* was thought to be absent. Although new data now indicate the presence of *Allophaiomys* in the Rocky Mountains (Porcupine Cave, Bell et al. 2004a) and areas farther to the west (Cathedral Cave, Jass 2007; Jass and Bell 2011), those occurrences are younger in age than the eastern occurrences, and the principle discussion points of Rep's work are still salient.

Rep recognized mammal ages as faunal units in geographic space and not as indicators of specific time units (Repenning et al. 1995). He proclaimed that the co-occurrence of distinct mammal ages in geographically separated regions was a reality. That remains one of his more controversial and thought-provoking suggestions. It was within such a conceptual framework that he noted the 300,000 year time disparity in the Blancan-Irvingtonian boundary in the conterminous United States. He nonetheless concluded that application of a single faunal age name would still be acceptable in this particular situation (Repenning et al. 1995). The circumstances under which the usage of a single name would no longer be appropriate were not clearly outlined, but longer time frames (two million years) were alluded to (Repenning et al. 1995), implying that single names for faunal ages across broad geographic regions might obscure complex patterns of change in different regions (Repenning et al. 1995).

Differences in timing of immigration events in Beringia appear to have met the criteria for subdivision because Rep was not opposed to establishing separate mammal age names for Beringian faunas (Repenning et al. 1995). Philosophically, Rep appeared to approve of other attempts to create regional mammal age names (Sher 1986), even though some weaknesses were thought to exist in how those divisions were supported (Repenning and Brouwers 1992; Repenning et al. 1995). Other regions simply lacked sufficient data for mammal age terms to be applied (e.g., Mexican faunal region; Repenning et al. 1995).

One of the interesting aspects of the initial discussion of provinciality by Fejfar and Repenning (1992) was the stated potential for further sub-division of provinces, an issue re-emphasized in later publications (Repenning et al. 1995). We interpret this as an indication that they recognized the fluid nature of the boundaries that they proposed, and that future work likely would serve to test and refine their model. Rep had long recognized the potential influence of latitudinal climatic differences on faunal character, as well as longitudinal differences governed by physiographic barriers (e.g., the Rocky Mountains). In later years he openly embraced the idea that elevational differences could contribute to distinct and recognizable faunal histories as a logical extension of that thinking (e.g., Repenning 1998). Rep emphasized that the complexities of biotic history played out in the context of changing climatic conditions, geologic perturbations, and resultant modification to landscapes, all of which he considered to be tractable, understandable problems. The complications associated with teasing apart the complexities of such a mosaic were not lost on Rep, but he clearly viewed them as a challenge worth undertaking. They remain a significant challenge for future generations.

CONCLUSIONS

We selected and discussed what we view to be the most influential components of Charles A. Repenning's work on arvicoline rodents, particularly because those components will likely impact research in the field for years to come. Casual perusal of his published works and personal correspondence will reveal that we have only scratched the surface. Other aspects of his work elucidate additional complexities in his thinking about arvicolines. For example, Rep used taxonomy to express his concepts of biogeographic history. That is best exemplified by his persistent use of the name *Mimomys* as the proper generic assignment for arvicolines otherwise classified as *Cosomys*, *Ogmodontomys*, and *Ophiomys* (the latter he accepted at generic level in 2003). That was a taxonomic convention that emphasized his focus on a connection between the Eurasian and North American arvicolines. Specialists on arvicolines have a strong and general tendency to quibble over details of taxonomy, and many aspects of Rep's taxonomic practices remain controversial. Most notable are the status of *Mimomys* in North American Pliocene faunas, and the merits and drawbacks of inclusion within *Microtus* of the taxa he variously placed within *Allophaiomys*, *Lasiopodomys*, *Pedomys*, *Pitymys*, *Proedromys*, and *Terricola*.

An appreciation of his evolutionary approach to biostratigraphy and its influence on his taxonomic practices is essential for placing his work in its basic cognitive context. His emphasis on polyphyletic origins of arvicolines and his explicit claims of paraphyly of many lineages he recognized are not compatible with modern phylogenetic methods, nor are they supported by recent phylogenetic analyses of rodents. That much of his work withstood the ascendancy of cladistic methodologies is testament to the flexibility of his framework and to the fact that (despite his intransigence on philosophical matters) the details of his biochronological schemes are, to a substantial degree, immune to the philosophical context under which they were born.

Rep's extensive explorations of intercontinental correlations in the northern hemisphere forced new ways of thinking about the North American arvicoline fauna. The hypothesis of trans-Beringian dispersal is now amenable to new forms of testing that are independent of the distribution of fossils in the rock record. His claims that much of the North American arvicoline rodent fauna is the result of repeated pulses of immigration followed by endemic radiation is an obvious and fertile area for molecular phylogenetic assessments. Initial efforts to test those claims (e.g., for *Microtus*) found them to be wanting and recovered a monophyletic lineage of extant North American endemic species (Conroy and Cook 2000). A limitation of such methods is, of course, that they include only the extant representatives of a diverse clade that left a rich fossil record. That record was Rep's special purview and bailiwick, and he was skeptical that molecular data alone could yield an informative view of the evolutionary history of the arvicolines. The challenges he faced in establishing immigrant status for many North American arvicolines remain unresolved in many cases, but the promise of detailed Holarctic biostratigraphic correlations remains, and the clear integration of European, Asian, and North American chronologies remains a desirable goal.

Continuing investigations of Pliocene and Pleistocene fossil deposits across North America regularly yield new data on the evolutionary history and temporal and spatial distribution of arvicoline rodents. Pioneering efforts in the Great Plains by Hibbard and his colleagues and students provided a foundation upon which Rep built his more expansive biochronology. In addition to modifications based on his own extensive research, Rep constantly strove to update his chronology and his thinking in light of renewed efforts to establish reliable and detailed correlations of faunas in the Great Plains (e.g., Martin 2003; Martin et al. 2000, 2002, 2003a, 2003b) and new insights from west of the Great Plains (e.g., Barnosky and Rasmussen 1988; Bell 1995, 2000; Mou 1997; Gillette et al. 1999; Bell and Barnosky 2000; Barnosky and Bell 2003; Bell et al. 2004a, 2004b; Bell and Jass 2004). These new data revealed that some characteristics of proposed arvicoline provinces would be overturned by new data (e.g., the purported restriction of *Allophaiomys* and *Microtus paroperarius* to faunas east of the Rocky Mountains), that high-elevation sites might require independent biochronologies, and that formerly unexpected and anomalous taxonomic associations were becoming common in the west.

Although persistent health problems plagued him in his last years, Rep continued to struggle with new data and the challenges they raised to his arvicoline rodent biochronology. Even following his 'retirement' he was a formidable antagonist, a cantankerous collaborator, and an inspiring and thoughtful connoisseur of the interplay among geology, paleontology, climate change, and biotic history. None of the problems with which he struggled were resolved to his complete satisfaction, and his work stands in large part as a roadmap for future investigations. His published works leave a legacy of insights and proposals to lace the struggles of future practitioners who seek to follow his interests. Those who do follow will do so in the context of their times and under the scientific paradigms that govern their fields of inquiry. Some may at times be confronted with a temptation simply to dismiss Rep's ideas and proposals as anachronistic, born and developed as they were in a pre-cladistic, though firmly evolutionary, context. Any such dismissal would be unwarranted. Certainly, Rep's proposals are best understood in the context in which he framed them, but they can and should be modified and reshaped in modern contexts. We are confident that his ideas will continue to provide stimulating challenges for years to come. We regret that his arguments now must be carried largely by his formally published works, and not by the colorful, humorous, and sometimes biting wit that was a hallmark of his personal interactions and correspondence.

REFERENCES

Barnosky, A.D. 1987. Punctuated equilibrium and phyletic gradualism. Some facts from the Quaternary mammalian record, p. 109-147. In Genoways, H.H. (ed.), Current Mammalogy Volume 1. Plenum Press, New York, New York.

Barnosky, A.D. and Bell, C.J. 2003. Evolution, climatic change and species boundaries: perspectives from tracing *Lemmiscus curtatus* populations through time and space. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, 270:2585-2590.

Barnosky, A.D. and Rasmussen, D.L. 1988. Middle Pleistocene arvicoline rodents and environmental change at 2900-meters elevation, Porcupine Cave, South Park, Colorado. *Annals of Carnegie Museum*, 57:267-292.

Bell, C.J. 1995. A middle Pleistocene (Irvingtonian) microtine rodent fauna from White Pine County, Nevada, and its implications for microtine rodent biochronology. *Journal of Vertebrate Paleontology*, 15 (Supplement to 3):18A.

Bell, C.J. 2000. Biochronology of North American microtine rodents, p.379-406. In Noller, J.S., Sowers, J.M., and Lettis, W.R. (eds.), *Quaternary Geochronology: Methods and Applications*. AGU Reference Shelf 4. American Geophysical Union, Washington, D.C.

Bell, C.J. and Barnosky, A.D. 2000. The microtine rodents from the Pit locality in Porcupine Cave, Park County, Colorado. *Annals of Carnegie Museum*, 69:93-134.

Bell, C.J. and Jass, C.N. 2004. Arvicoline rodents from Kokoweef Cave, Ivanpah Mountains, San Bernardino County, California. *Bulletin of the Southern California Academy of Sciences*, 103:1-11.

Bell, C.J. and Repenning, C.A. 1999. Observations on dental variation in *Microtus* from the Cudahy Ash Pit fauna, Meade County, Kansas and implications for Irvingtonian microtine rodent biochronology. *Journal of Vertebrate Paleontology*, 19:757-766.

Bell, C.J., Repenning, C.A., and Barnosky, A.D. 2004a. Arvicoline rodents from Porcupine Cave – identification, spatial distribution, taxonomic assemblages, and biochronologic significance, p. 207-263. In Barnosky, A.D. (ed.), *Biodiversity Response to Climate Change in the Middle Pleistocene – the Porcupine Cave Fauna from Colorado*. University of California Press, Berkeley, California.

Bell, C.J., Lundelius, E.L., Jr., Barnosky, A.D., Graham, R.W., Lindsay, E.H., Ruez, D.R., Jr., Semken, H.A., Jr., Webb, S.D., and Zakrzewski, R.J. 2004b. The Blancan, Irvingtonian, and Rancholabrean mammal ages, p. 232-314. In Woodburne, M.O. (ed.), *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*. Columbia University Press, New York, New York.

Conroy, C.J. and Cook, J.A. 2000. Molecular systematics of a Holarctic rodent (*Microtus*: Muridae). *Journal of Mammalogy*, 81:344-359.

de Queiroz, K. 1992. Phylogenetic definitions and taxonomic philosophy. *Biology and Philosophy*, 7:295-313.

de Queiroz, K. and Gauthier, J. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. *Systematic Zoology*, 39:307-322.

de Queiroz, K. and Gauthier, J. 1992. Phylogenetic taxonomy. *Annual Review of Ecology and Systematics*, 23:449-480.

Fejfar, O. and Repenning, C.A. 1992. Holarctic dispersal of the arvicolids (Rodentia, Cricetidae), p. 205-212. In Koenigswald, W. v. and Werdelin, L. (eds.), *Mammalian Migration and Dispersal Events in the European Quarternary* {sic}. *Courier Forschunginstitut Senckenberg* 153.

Fejfar, O. and Repenning, C.A. 1998. The ancestors of the lemmings (Lemmini, Arvicolinae, Cricetidae, Rodentia) in the early Pliocene of Wölfersheim near Frankfurt am Main; Germany. *Senckenbergiana lethaea*, 77:161-193.

Gauthier, J., Kluge, A.G., and Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics*, 4:105-209.

Gillette, D.D., Bell, C.J., and Hayden, M.C. 1999. Preliminary report on the Little Dell Dam fauna, Salt Lake County, Utah (middle Pleistocene, Irvingtonian land mammal age), p. 495-500. In Gillette, D.D. (ed.), *Vertebrate Paleontology in Utah*. *Utah Geological Survey Miscellaneous Publication* 99-1.

Gould, S.J. 1982. The meaning of punctuated equilibrium and its role in validating a hierarchical approach to macroevolution, p. 83-104. In Milkman, R. (ed.), *Perspectives on Evolution*. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

Hibbard, C.W. 1941. Paleoecology and correlation of the Rexroad fauna from the upper Pliocene of southwestern Kansas, as indicated by the mammals. *The University of Kansas Science Bulletin*, 27, Part 1:79-104.

Hibbard, C.W. 1944. Stratigraphy and vertebrate paleontology of Pleistocene deposits of southwestern Kansas. *Bulletin of the Geological Society of America*, 55:707-754.

Hibbard, C.W. 1949. Pleistocene vertebrate paleontology in North America. *Bulletin of the Geological Society of America*, 60:1417-1428.

Hibbard, C.W. 1950. Mammals of the Rexroad Formation from Fox Canyon, Kansas. *Contributions from the Museum of Paleontology, University of Michigan*, 8:113-192, Plates 1-5.

Hibbard, C.W. 1953. The Saw Rock Canyon fauna and its stratigraphic significance. *Papers of the Michigan Academy of Science, Arts and Letters*, 38:387-411.

Hibbard, C.W. 1970a. Pleistocene mammalian local faunas from the Great Plains and central lowland provinces of the United States, p. 395-433. In Dort, W., Jr. and Jones, J.K., Jr. (eds.), *Pleistocene and Recent Environments of the Central Great Plains*. *Department of Geology, University of Kansas Special Publication 3*. The University Press of Kansas, Lawrence, Kansas.

Hibbard, C.W. 1970b. A new microtine rodent from the upper Pliocene of Kansas. *Contributions from the Museum of Paleontology, The University of Michigan*, 23:99-103.

Hibbard, C.W. and Zakrzewski, R.J. 1967. Phyletic trends in the late Cenozoic microtine *Ophiomys* gen. nov., from Idaho. *Contributions from the Museum of Paleontology, The University of Michigan*, 21:255-271.

Hibbard, C.W., Ray, C.E., Savage, D.E., Taylor, D.W., and Guilday, J.E. 1965. Quaternary mammals of North America, p. 509-525. In Wright, H.E., Jr., and D.G. Frey (eds.), *The Quaternary of the United States. A Review Volume for the VII Congress of the International Association for Quaternary Research*. Princeton University Press, Princeton, New Jersey.

Jass, C.N. 2007. *New perspectives on Pleistocene biochronology and biotic change in the east-central Great Basin: an examination of the vertebrate fauna from Cathedral Cave, Nevada*. Unpublished Ph.D. Thesis, The University of Texas at Austin, Austin, Texas, USA.

Jass, C.N. and Bell, C.J. 2011. Arvicoline rodent fauna from the Room 2 excavation in Cathedral Cave, White Pine County, Nevada, and its biochronologic significance. *Journal of Vertebrate Paleontology*, 31:684-699.

Mankinen, E.A. and Dalrymple, G.B. 1979. Revised geomagnetic polarity time scale for the interval 0-5 m.y. B.P. *Journal of Geophysical Research*, 84:615-626.

Martin, R.A. 2003. Biochronology of latest Miocene through Pleistocene arvicolid rodents from the central Great Plains of North America. *Coloquios de Paleontología*, 1 (Ext.):373-383.

Martin, R.A., Duobinis-Gray, L., and Crockett, C.P. 2003a. A new species of early Pleistocene *Synaptomys* (Mammalia, Rodentia) from Florida and its relevance to southern bog lemming origins. *Journal of Vertebrate Paleontology*, 23:917-936.

Martin, R.A., Honey, J.G., and Peláez-Camponanes {*sic*}, P. 2000. The Meade Basin rodent project: A progress report. *Paludicola*, 3:1-32.

Martin, R.A., Hurt, R.T., Honey, J.G., and Peláez-Campomanes, P. 2003b. Late Pliocene and early Pleistocene rodents from the northern Borchers Badlands (Meade County, Kansas), with comments on the Blancan-Irvingtonian boundary in the Meade Basin. *Journal of Paleontology*, 77:985-1001.

Martin, R.A., Honey, J.G., Peláez-Campomanes, P., Goodwin, H.T., Baskin, J.A., and Zakrzewski, R.J. 2002. Blancan lagomorphs and rodents of the Deer Park assemblages, Meade County, Kansas. *Journal of Paleontology*, 76:1072-1090.

Mead, J.I., Manganaro, C., Repenning, C.A., and Agenbroad, L.D. 1996. Early Rancholabrean mammals from Salamander Cave, Black Hills, South Dakota, p. 458-482. In Stewart, K.M. and Seymour, K.L. (eds.), *Palaeoecology and Palaeoenvironments of Late Cenozoic Mammals. Tributes to the Career of C. S. (Rufus) Churcher.* University of Toronto Press, Toronto, Ontario, Canada.

Mou, Y. 1997. A new arvicoline species (Rodentia: Cricetidae) from the Pliocene Panaca Formation, southeast Nevada. *Journal of Vertebrate Paleontology*, 17:376-383.

Musser, G.G. and Carleton, M.D. 2005. Superfamily Muroidea, p. 894-1531. In Wilson, D.E. and Reeder, D.M. (eds.), *Mammal Species of the World. A Taxonomic and Geographic Reference*. *Volume 2* (third edition). The Johns Hopkins University Press, Baltimore, Maryland.

Repenning, C.A. 1966. Palearctic-Nearctic mammalian dispersal during the later Cenozoic. *United States Geological Survey Professional Paper*, 550:A117-A118.

Repenning, C.A. 1967. Palearctic-Nearctic mammalian dispersal in the late Cenozoic, p. 288-311. In Hopkins, D.M. (ed.), *The Bering Land Bridge*. Stanford University Press, Stanford, California.

Repenning, C.A. 1968. Mandibular musculature and the origin of the subfamily Arvicolinae (Rodentia). *Acta Zoologica Cracoviensia*, 13:29-72.

Repenning, C.A. 1978. Faunal exchanges between Siberia and North America, p. 40-55. In *American Quaternary Association, Abstracts of the Fifth Biennial Meeting, September 2-4, 1978, University of Alberta, Edmonton, Alberta*.

Repenning, C.A. 1980. Faunal exchanges between Siberia and North America, p. 37-44. In Rutter, N.W. and Schweger, C.E. (eds.), *Special AMQUA Issue. The Ice-Free Corridor and Peopling of the New*

World. Proceedings of the Fifth Biennial Conference of the American Quaternary Association Edmonton, September 2-4, 1978. *Canadian Journal of Anthropology*, 1(1).

Repenning, C.A. 1983a. *Pitymys meadensis* Hibbard from the Valley of Mexico and the classification of North American species of *Pitymys* (Rodentia: Cricetidae). *Journal of Vertebrate Paleontology*, 2:471-482.

Repenning, C.A. 1983b. Faunal exchanges between Siberia and North America. *Schriftenreihe für geologische Wissenschaften*, 19/20:333-346.

Repenning, C.A. 1984. Quaternary rodent biochronology and its correlation with climatic and magnetic stratigraphies, p. 105-118. In Mahaney, W.C. (ed.), *Correlation of Quaternary Chronologies*. Geo Books, Norwich, England.

Repenning, C.A. 1987. Biochronology of the microtine rodents of the United States, p. 236-268. In Woodburne, M.O. (ed.), *Cenozoic Mammals of North America. Geochronology and Biostratigraphy*. University of California Press, Berkeley, California.

Repenning, C.A. 1989. Arctic microtine biochronology – current status, p. 99-102. In Carter, L.D., Hamilton, T.D., and Galloway, J.P. (eds.), *Late Cenozoic History of the Interior Basins of Alaska and the Yukon*. *United States Geological Survey Circular*, 1026.

Repenning, C.A. 1990. Of mice and ice in the late Pliocene of North America. *Arctic*, 43:314-323.

Repenning, C.A. 1992. *Allophaiomys* and the age of the Olyor Suite, Krestovka Sections, Yakutia. *United States Geological Survey Bulletin*, 2037:1-98.

Repenning, C.A. 1998. North American mammalian dispersal routes: Rapid evolution and dispersal constrain precise biochronology, p. 39-78. In Tomida, Y., Flynn, L.J., and Jacobs, L.L. (eds.), *Advances in Vertebrate Paleontology and Geochronology*. *National Science Museum Monographs (Tokyo)*, 14.

Repenning, C.A. 2001. Beringian climate during intercontinental dispersal: A mouse eye view, p. 25-40. In Elias, S.A. and Brigham-Grette, J. (eds.), *Beringian Paleoenvironments Festschrift in Honour of D. M. Hopkins*. *Quaternary Science Reviews*, 20(1-3).

Repenning, C.A. 2003. *Mimomys* in North America, p. 469-512. In Flynn, L.J. (ed.), *Vertebrate Fossils and Their Context: Contributions in Honor of Richard H. Tedford*. *Bulletin of the American Museum of Natural History*, 279.

Repenning, C.A. and Brouwers, E.M. 1992. Late Pliocene – early Pleistocene ecologic changes in the Arctic Ocean borderland. *United States Geological Survey Bulletin*, 2036:1-37.

Repenning, C.A. and Fejfar, O. 1977. Holarctic correlations of microtid rodents, p. 234-250, fold-out Table 3. In Šibrava, V. (ed.), *Project 73/1/24 Quaternary Glaciations in the Northern Hemisphere. Report No 4 On the Session in Stuttgart, Federal Republic of Germany, September, 5-13, 1976*. IUGS – UNESCO International Correlation Program. Geological Survey, Prague Czechoslovakia.

Repenning, C.A. and Grady, F. 1988. The microtine rodents of the Cheetah Room fauna, Hamilton Cave, West Virginia, and the spontaneous origin of *Synaptomys*. *United States Geological Survey Bulletin*, 1853:1-32.

Repenning, C.A., Fejfar, O., and Heinrich, W.-D. 1990. Arvicolid rodent biochronology of the Northern Hemisphere, p. 385-418. In Fejfar, O and Heinrich, W.-D. (eds.), *International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia), Rohanov (Czechoslovakia) May 1987*. International Geological Correlation Programme 216, Bio-Events, Global Biological Events in Earth History. Geological Survey, Prague, Czechoslovakia.

Repenning, C.A., Hopkins, D.M., and Rubin, M. 1964. Tundra rodents in a late Pleistocene fauna from the Tofty Placer District, central Alaska. *Arctic*, 17:177-197.

Repenning, C.A., Weasma, T.R., and Scott, G.R. 1995. The early Pleistocene (latest Blancan-earliest Irvingtonian) Froman Ferry fauna and history of the Glenns Ferry Formation, southwestern Idaho. *United States Geological Survey Bulletin*, 2105:1-86.

Repenning, C.A., Brouwers, E.M., Carter, L.D., Marincovich, L., Jr., and Ager, T.A. 1987. The Beringian ancestry of *Phenacomys* (Rodentia: Cricetidae) and the beginning of the modern Arctic Ocean borderland biota. *United States Geological Survey Bulletin*, 1687:1-31, Plate 1.

Rogers, K.L., Repenning, C.A., Luiszer, F.G., and Benson, R.D. 2000. Geologic history, stratigraphy, and paleontology of SAM Cave, north-central New Mexico. *New Mexico Geology*, 22:89-100, 113-117.

Rogers, K.L., Larson, E.E., Smith, G., Katzman, D., Smith, G.R., Cerling, T., Wang, Y., Baker, R.G., Lohmann, K.C., Repenning, C.A., Patterson, P., and Mackie, G. 1992. Pliocene and Pleistocene geologic and climatic evolution in the San Luis Valley of south-central Colorado. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 94:55-86.

Rowe, T. 1987. Definition and diagnosis in the phylogenetic system. *Systematic Zoology*, 36:208-211.

Sher, A.V. 1986. On the history of mammal fauna of Beringida. *Quartärpaläontologie*, 6:185-193.

Simpson, G.G. 1953. *The Major Features of Evolution*. Columbia University Press, New York, New York.

Woodburne, M.O. (ed.) 1987a. *Cenozoic Mammals of North America. Geochronology and Biostratigraphy*. University of California Press, Berkeley, California.

Woodburne, M.O. 1987b. Introduction, p. 1-8. In Woodburne, M.O. (ed.), *Cenozoic Mammals of North America. Geochronology and Biostratigraphy*. University of California Press, Berkeley, California.