

## INTRODUCTORY REMARKS: DOES *ALLOPHAIOMYS* EXIST?

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### ABSTRACT

We introduce this issue of *Paludicola* as a volume dedicated to the systematics and evolution of "*Allophaiomys*," a set of species representing the early phases of diversification of *Microtus*-like taxa. Some background information is provided and then we speculate, presenting two conflicting arguments, on the existence and nomenclatorial integrity of "*Allophaiomys*," considered as a new construct here defined as a metaregion. Metaregions, or ancestral taxa defined by a set of symplesiomorphies relative to their descendants, are viewed as genetically constrained developmental conduits and deserve investigation. However, their recognition as formal supraspecific taxonomic entities is precluded because of their polyphyletic condition, despite the interesting paradox that they represented a homogeneous and probably sibling set of species during their existence. We recommend that the use of *Allophaiomys* be discontinued.

### INTRODUCTION

Sometimes there is value in going backwards. Certainly, we can learn about evolutionary radiations by constructing branching trees, but there is a humbling value to retracing the steps, realizing that every branching event in a clade eventually regresses to a single fixed point, like the "Big Bang" event in our universe's history. And just like the Big Bang, as we get closer to the origin, the details become veiled. Thanks mostly to a number of diligent European paleontologists, we have an unparalleled opportunity to examine the early radiation of a speciose modern clade, the genus *Microtus*, an arvicoline rodent taxon with a distribution throughout the Holarctic. Most modern members of this genus have characteristically complex dental patterns, and as we examine fossil samples from progressively more ancient sediments we discover that these patterns become simpler, until they eventually merge in even older samples with those of the presumed ancestral genus *Mimomys*. The earliest ancestral species to *Microtus* that are not *Mimomys* are often lumped together in the taxon *Allophaiomys*, treated either as a subgenus of *Microtus* or as a separate genus. This special edition of *Paludicola* is dedicated to the systematics and evolution of *Allophaiomys*, and is a direct result of a conference on the same subject held in Moscow, Russia, September 22-26, 1997. In this essay

we will use *Allophaiomys* as a model for the early evolution of any speciose clade, and see if we can deduce principles that will lead to consistent and logical phylogenetic and nomenclatorial practice.

### BACKGROUND

Around two million years ago, during the late Villanyian, populations of arvicoline rodents with evergrowing molars began to appear throughout Eurasia. These fossil samples have been identified by various names, including *Arvicola*, *Allophaiomys*, *Mimomys* and *Microtus*. Long ago T. Kormos recognized the similarity of these fossil dentitions to those of modern *Phaiomys* from southeast Asia, and he coined the name *Allophaiomys* for them (Kormos, 1930). Martin (1989) could not identify any definitive characters to separate *Allophaiomys* from *Phaiomys*, and he referred some fossil material from North America to *M. (Phaiomys) pliocaenicus*. Nadachowski and Garapich (this volume) indicate the difficulty in allying an extinct taxon with a modern one if features of the ancestral taxon predominantly represent a set of symplesiomorphies that appear in a variety of modern taxa, and there are other cogent reasons why the reference of early *Microtus* material to *Phaiomys* may be inappropriate. Nevertheless, the problem of character recognition looms large and must be addressed.

Recently, Donoghue (1985), Archibald (1994) and others have recognized that the lack of resolution in a

given phylogenetic hypothesis (cladogram) may actually represent an accurate portrayal if the terminal taxa are *metaspecies*, or species without autapomorphies. We would like to expand this concept somewhat, and suggest that all speciose clades progress through an initial period of character change that we define as a *metaregion*. Although species in the metaregion may lack autapomorphies, being defined instead on the basis of unique combinations of symplesiomorphic features, if a modern or extinct species possesses the defining set of symplesiomorphies and yet also demonstrates one or more unique characters that represent a trajectory not found among its relatives, it may still be legitimately associated with the metaregion.

If we envision a two-dimensional cone to represent the morphospace available to a generic clade (Figure 1), and a series of lines emanating from the origin (=the common ancestral morphology), each representing a distinct evolutionary trajectory, then a metaregion becomes an arbitrarily defined level on the cone, close to the origin, before which it is difficult or impossible to determine the historical fate of a species, beyond which it is possible to do so (note also that as the lines move farther from the origin, they also move farther away from each other. This represents the full, and usually later, expression of individual trajectories; for instance, a species with T4-5 open on m1, versus a species with T4-5 closed. Within the metaregion only the potential for this expression is seen, and consequently the distance between the lines is less). Lengths of lines on the cone represent morphological complexity within lineages, not time (for example, changing from three to four to five triangles on m1; this change may have occurred at different times in different lineages). Moreover, there is no implicit requirement for the widest points to represent the longest-lived species (though this may be the case). The model can accommodate morphological disparity at any time during a clade's existence.

We recognize the arbitrariness of the metaregion boundary, but we believe the model has heuristic value. For instance, it may help explain why ancestral species in a clade tend to be so variable, and why speciation in subclades farther from the metaregion often results in more limited morphologies. As can be seen in Fig. 1, it is much easier to cross from one distinct part of clade morphospace to another if such change begins in the metaregion. These attributes of the model will be explored in greater detail elsewhere.

So how do we treat species in a metaregion? Can a group of ancestral species in a clade be legitimately lumped into a single taxon above the species level despite the fact that they are likely ancestral to different modern subgenera and genera? More specifically, does

the taxon *Allophaiomys* have any biological reality or utility?

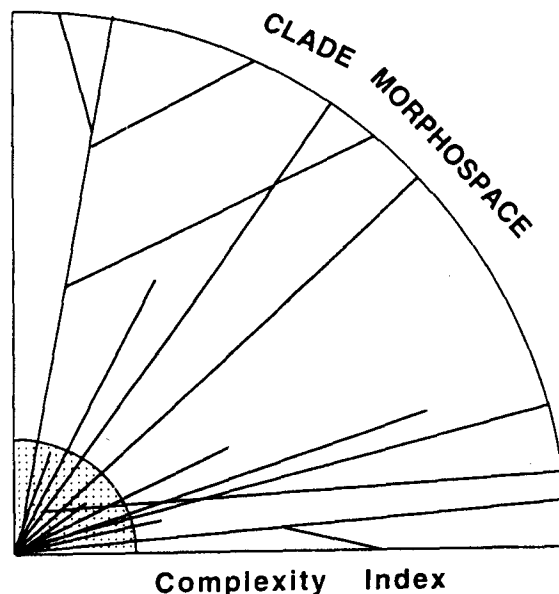


FIGURE 1. Theoretical model displaying the concept of a metaregion (shaded area). Note that the angle of lines relative to one another remains the same (=same epigenetic trajectory) but the distance between lines increases as morphology becomes more complicated. The model also expresses the idea that it is more difficult to change final morphology outside than from within the metaregion (compare bifurcations, representing speciation events). Modern as well as ancient species may exist in the metaregion if there has been stasis with regard to the character complex used to define the metaregion (e. g., *Microtus* [*Orthriomys*] *umbrosus* and *M.* [*Blandfordimys*] *bucharensis*).

#### DEFINITION OF *ALLOPHAIOMYS* AND THE EARLY EVOLUTION OF *MICROTUS*

*Allophaiomys* is a name applied in this volume to a related, even sibling set of species, treated as a metaregion (or metagenus), that existed throughout Eurasia and North America between about 2.2 -1.2 Ma. For a variety of reasons we prefer to restrict *Allophaiomys* to a monophyletic group ancestral to later *Microtus*-like species. Although there is a superficial resemblance of the rootless variants of the Spanish *Mimomys oswaldoreigi* to *Allophaiomys*, there is a combination of characters that allows this taxon to be separated with certainty from *Allophaiomys* (Agustí et al., 1993). Likewise, the evolution of *Arvicola* from *Mimomys savini* can be distinguished from that of early *Allophaiomys*, particularly by its much later occurrence in time and considerably greater size than related taxa.

The *Allophaiomys* metaregion is specifically defined on the following characters: 1) molars without roots and with crown cementum, 2) first lower molar with three basic triangles and a simple anteroconid complex (T4-5 may be incipient, but rarely completely developed), 3) M3 simple, with two closed triangles and a posterior loop with distinct LRA3, and 4) chronologically ordered progression of enamel differentiation, from negative - undifferentiated - positive (terms follow Martin [1987]; negative = thicker trailing edges and thinner leading edges of enamel on lower molars, reverse on uppers; positive = thinner trailing than leading edges on lowers, reverse on uppers). From a functional standpoint, *Allophaiomys* represents a genetically constrained developmental conduit through which all *Microtus*-like arvicolines had to pass on their way towards pastoral specialization during the late Villanyian - early Biharian of Europe and a bit later in North America, from the early to the middle Irvingtonian.

*Allophaiomys deucalion* is the first species seen in the fossil record. Reports in this volume suggest that *A. deucalion* had a very widespread geographic range, perhaps throughout Europe and into Siberia, during the late Villanyian and earliest Biharian. As Martin (this volume) indicates, there is a possibility that *A. deucalion* or a related species also dispersed to North America. Because there are extinct species of *Allophaiomys* with undifferentiated enamel (*A. chalinei*, *A. vandermeuleni*; Alcalde et al. 1981; Agustí et al., 1993) as well as living relic species of *Microtus* with negative and undifferentiated enamel (e.g. *M. umbrosus*; *M. guatemalensis*, *M. oaxacensis*; Martin, 1987), we know there were multiple radiations of species from *A. deucalion*. Another example of an early radiation from a *deucalion*-like species is North American *Microtus* (*Pitymys*) *pinetorum*. The extant *M. pinetorum* displays positive enamel differentiation, but its middle Pleistocene ancestor, *M. cumberlandensis* (van der Meulen, 1978), has thick and undifferentiated enamel.

But the most successful radiation of *Allophaiomys*, as measured by the number of resulting species, included those species that evolved from early descendants of *A. deucalion* with positive enamel differentiation. The first of these species is *A. pliocaenicus*, which appeared sometime in the early Biharian and also quickly developed a Holarctic distribution. The North American fossil record reveals the gradual evolution of the modern *Microtus* (*Pedomys*) *ochrogaster* from an early Pleistocene taxon that has been referred to *M. (Phaiomys = Allophaiomys) pliocaenicus* (Martin, 1989, 1993, 1995), and it is presumed that this is a good model for the evolution of most modern *Microtus* (e.g., van der Meulen, 1973, 1978; Rabeder, 1981; Chaline, 1990; Repenning, 1992). We do not claim that all extant *Microtus* with positive

enamel differentiation evolved from a single species, but we do suggest that many of them evolved from species closely related to *A. pliocaenicus*.

#### THE EXISTENCE AND NOMENCLATORIAL STATUS OF *ALLOPHAIOMYS*

*Allophaiomys* seems to be a set of related species, some of which were not likely ancestral to later species (e.g., *A. chalinei*) and some of which probably were. Both *Allophaiomys deucalion* and *A. pliocaenicus* may represent single, widely distributed species, but most likely represent sets of sibling species. Living species of *Microtus*-like voles evolved from both the *A. deucalion* and *A. pliocaenicus* complexes. If we assume that all *A. deucalion*-like populations recorded in the fossil record were descended from a single *Mimomys* species, then it is legitimate to recognize *A. deucalion* and its descendants as a clade which can be called the genus *Microtus*. But, can a metaregion of related ancient species have taxonomic integrity? Is there any sensible philosophical position that allows the formal recognition of a metaregion? Below, we present two arguments that take conflicting positions.

#### *Allophaiomys* as a legitimate taxon (Figure 2)

As a metaregion (or evolutionary grade, transition zone), *Allophaiomys* is defined on a set of symplesiomorphic features relative to later descendants. The set of species including *Allophaiomys deucalion* and its early relatives such as *A. pliocaenicus* represented a consistent and recognizable group during the time of its existence between about 2.2-1.2 Ma. One could argue, purely from the philosophical viewpoint, that taxonomic and biological reality is the reality of the moment, and that classifications through time are in essence another philosophical construct entirely. That is, it seems entirely reasonable that during the late Villanyian and early Biharian there existed a cohesive and even sibling set of species that would be classified by today's methods in a single taxon, and we could call that taxon *Allophaiomys*. The job then becomes to develop analytical techniques to determine which species of *Allophaiomys* gave rise to which later lineages of *Microtus*. With this option, the metaregion is given taxonomic recognition.

#### *Allophaiomys* n'exist pas (Figure 3)

The logic presented above for the formal recognition of *Allophaiomys* is not very compelling. Since most modern *Microtus* with positive enamel

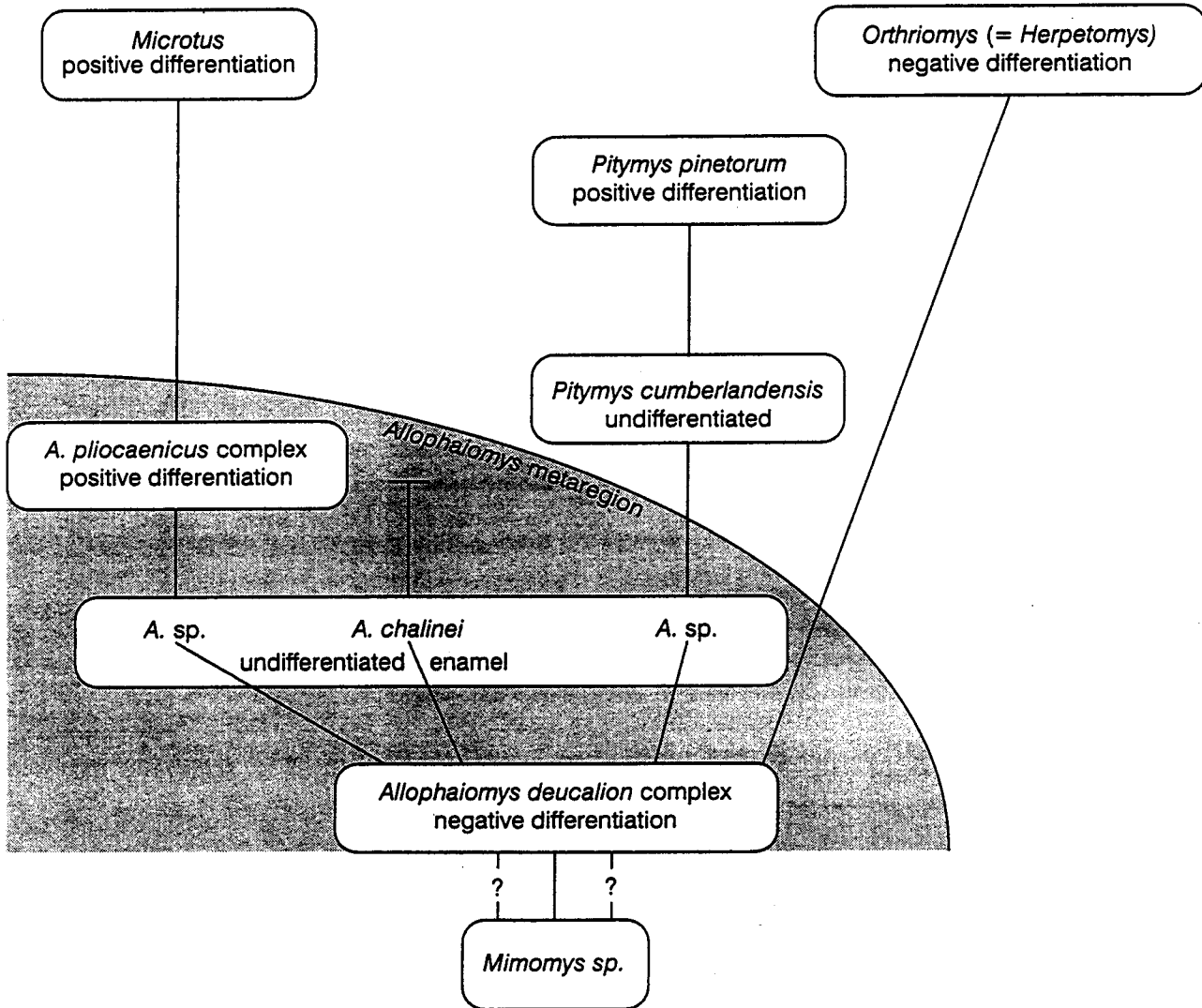


FIGURE 2. Evolutionary scenario for select lineages of *Microtus* with *Allophaiomys* recognized as a metaregion and related group of species (metagenus). Lineages can be viewed either as separate genera or subgenera of *Microtus*. Positive, negative and undifferentiated refer to the three conditions of enamel differentiation defined by Martin (1987).

differentiation are descended from "*Allophaiomys*" *pliocaenicus*, then "*A.*" *pliocaenicus* has already tipped its hand; it is already a member of a clade separate from those living species that evolved directly from *deucalion*-like species (with negative enamel differentiation) or those species, such as "*A.*" *vandermeuleni* or "*A.*" *chalinei*, with undifferentiated enamel. Similarly, as noted above, we already know that certain lineages, such as those leading to modern *Orthriomys* (see Martin, this volume) and *Pitymys* cannot be closely related to other modern *Microtus*. If we choose to classify organisms together based upon phylogeny, or ancestral-descendant relationships, then it is not appropriate to combine species we already know are on different evolutionary trajectories. Basically, "*Allophaiomys*" is a puzzle to be

solved by enterprising systematists. Each of its species, with the exception of the ancestral "*A.*" *deucalion*, belongs to a separate subclade, and it becomes our challenge to figure out the relationships among them. Perhaps a few, such as "*A.*" *chalinei* (Alcalde et al., 1981), are distinct enough to warrant their own clade.

There is no physical evidence at this point to conclusively show that fossil or extant *Microtus*-like species evolved from more than one *Mimomys* species. Modern karyological and immunological studies define *Microtus* as a fairly homogeneous group (Graf, 1982; Modi, 1987), although extant *Chionomys* shares some chromosomal features with *Arvicola* and *Clethrionomys* (Agadjanian and Yatsenko, 1984). Consequently, the most parsimonious taxonomic decision would be to drop

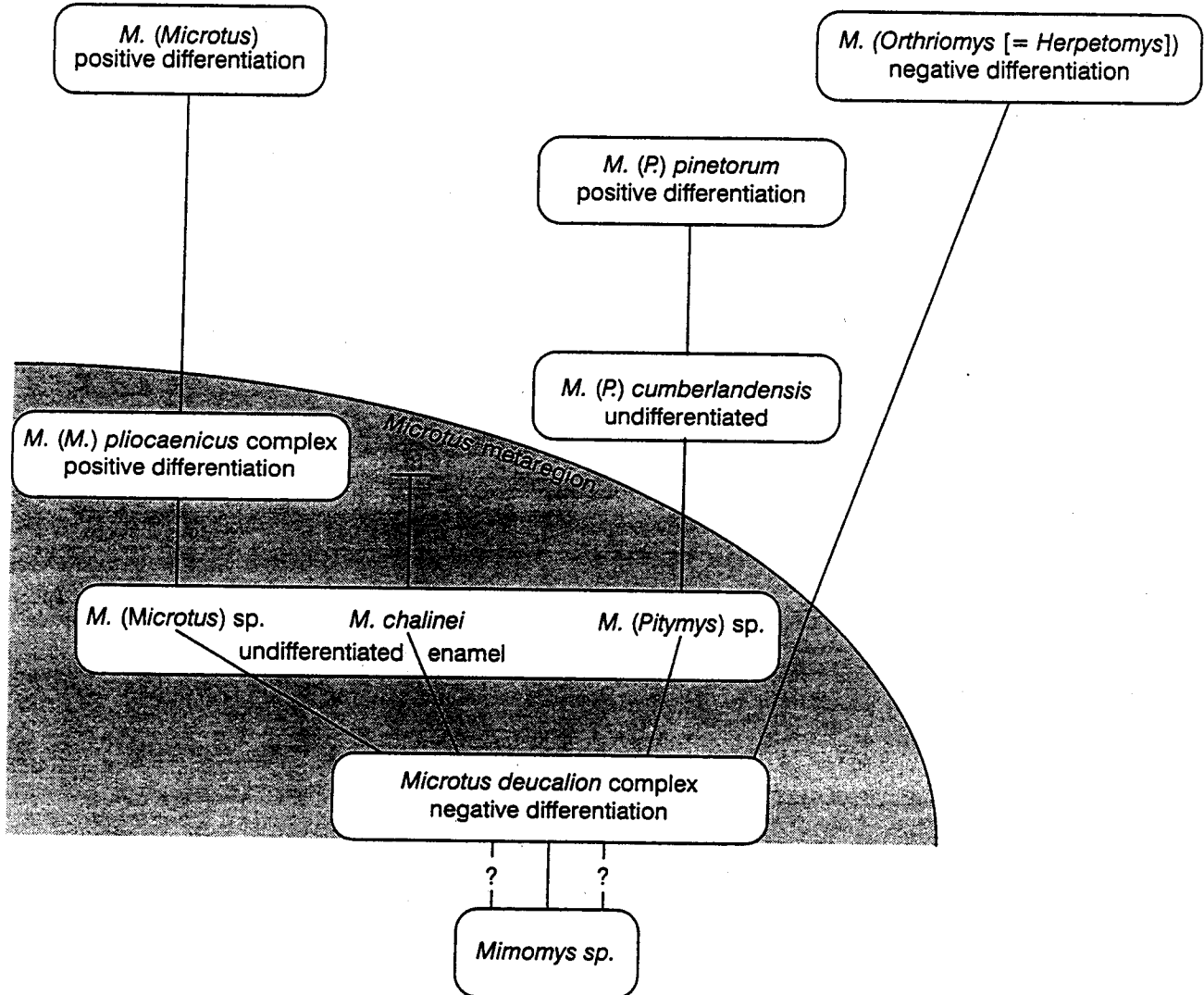


FIGURE 3. Evolutionary scenario for select lineages of *Microtus*, rejecting the *Allophaiomys* concept. All species descended from *Mimomys* treated as members of the clade genus *Microtus*. See Figure 1 for details.

*Allophaiomys* entirely, and use the name *Microtus* for all species with dental synapomorphies for the genus, assuming the decision was to treat these species as a single genus and not as a subfamily of related genera. But that is a logistical, not philosophical, problem we don't care to deal with here. Thus "*Allophaiomys*" *pliocaenicus* could become *Microtus (Microtus) pliocaenicus*, and its descendants would likewise be included within the subgenus *Microtus*. If a particular investigator feels that the relationships of an ancient species are not understood, then that species can simply be referred to the genus *Microtus*, without any subgeneric recognition. The use of *Microtus pliocaenicus*, *M. chalinei*, *M. vandermeuleni*, and *M. ruffoi* makes more intuitive sense than referring these

species to an amorphous taxon like *Allophaiomys*. Likewise, the term "*Allophaiomys*" metaregion loses its meaning, and we are better off referring to the zone as the *Microtus* metaregion (Figure 3), or whatever name the clade ultimately takes.

#### DISCUSSION AND CONCLUSIONS

Following modern cladistic precepts, every species or set of species descended from a different *Microtus deucalion* population must bear a different subgeneric name, if we choose to so designate them. Thus, North American *M. pinetorum* must be called *Pitymys* and Old World species not descended from *M. cumberlandensis* must be called something else,

enamel differentiation directly descended from *A. pliocaenicus* can be known as the subgenus *Microtus*. In the New World, *Microtus umbrosus* and *M. guatemalensis*, with negatively differentiated enamel, probably represent a distinct taxon *Orthriomys*, derived directly from a *deucalion*-like ancestor. These are just a few examples that flow from the logic presented here.

Metaregions are interesting, particularly from the standpoint of developmental biology. It is in this region where minor changes in developmental trajectories will result in major recognizable anatomical differences during later periods. And yet some species will remain unchanged, restricted to the metaregion for millions of years. The extant *Orthriomys umbrosus*, *Phaiomys leucurus* and *Blandfordimys bucharensis* may fall into this category (Martin, 1987; Nadachowski and Zagorodnyuk, 1996). It becomes the task of systematists to develop the techniques to tease apart the record and ally the taxa in the metaregion to later clades. As the papers in this volume dramatically attest, application of modern statistical techniques can play an important role, as can mechanical methods such as the *Schmelzmuster* work of von Koenigswald (1980) and the digital imaging of Viriot et al. (1993). Although we favor the use of *Microtus* over that of *Allophaiomys*, we have not tried to convince our colleagues in this volume of that position, and we look forward to their responses in the future.

#### ACKNOWLEDGMENTS

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