

Evolution, climatic change and species boundaries: perspectives from tracing *Lemmiscus curtatus* populations through time and space

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To provide empirical evidence of species boundaries and the role of climatic change in affecting evolution, we documented evolution of the sagebrush vole, *Lemmiscus curtatus*, through hundreds of thousands of years by following populations from the middle Pleistocene to the present. We found that: (i) extant representatives of the species culminate a morphological transition that was initiated within an unusually arid and warm interglacial period, perhaps related to the shift from glacial–interglacial cycles dominated by a 41 000 year periodicity to those dominated by a 100 000 year rhythm; and (ii) sympatry of extant and extinct morphotypes persisted for more than 800 000 years. This exceptionally detailed tracing of extinct populations into extant ones suggests that species such as the one we studied are real entities in space, that their boundaries become fuzzy (although potentially diagnosable) through time and that unusual climatic warming may initiate significant evolutionary change manifested at the morphological level.

Keywords: climate change; *Lemmiscus curtatus*; Pleistocene; species concepts

1. INTRODUCTION

Evolutionary biologists continue to debate models of speciation, especially with regard to the relative roles of allopatry, sympatry, selection, drift (Coyne & Orr 1998; Gavrilets *et al.* 1998; Barton 2001; Benton & Pearson 2001; Mallet 2001; Schluter 2001; Wu 2001; Via 2001; Rieseberg *et al.* 2002) and climatic change (Vrba 1995*a*; Bennett 1997; Alroy *et al.* 2000; Dynesius & Jansson 2000; Barnosky 2001; Barnosky & Carrasco 2002; Barnosky *et al.* 2003). Superimposed on these arguments about mechanism are confounding issues about species concepts and boundaries (de Queiroz & Donoghue 1988; Nadachowski 1993; Turner 1993; O'Hara 1994; Hey 2001; Miller 2001; to name but a few). Despite the rich literature on these topics (recent comprehensive treatments include: Howard & Berlocher 1998; Claridge *et al.* 1997; Levin 2000; Schluter 2000; Schilthuizen 2001), empirical data remain scarce for the organisms with which we deal in this study—mammals in natural ecological systems. Useful data have emerged in recent years; for example, extant populations have been traced back a few thousand years (Hadly *et al.* 1998, 2003), and the splitting of extinct species into succeeding extinct ones has been recognized (Lister & Sher 2001). What has been conspicuously lacking, however, is the tracing of populations of a modern mammal species back hundreds of thousands of years to a time near the species' origin. Here, we provide such data for the sagebrush vole, *Lemmiscus curtatus*, and use it to address three aspects of the many-faceted 'species problem' (O'Hara 1994; Miller 2001): (i) species boundaries in space and time; (ii) how long the speciation process

takes; and (iii) the role of climatic change in producing evolutionary change.

Such studies have been scarce because they are logistically difficult, requiring excavation of palaeontological sequences that extend back into at least the middle Pleistocene and that yield abundant evolutionarily significant remains of extant species, followed by parallel study of representative fossil and modern populations. The requisite palaeontological sequences are rare (Bell *et al.* 2004*a*), but the temporal extension to at least the middle Pleistocene is necessary for understanding speciation in mammals because the median lifespan of mammalian species is *ca.* 1.5 million years (Alroy 1996).

Our study organism, *Lemmiscus*, today ranges through areas of the North American West where sagebrush dominates (figure 1), occurring in habitats that are more arid than those typical for voles of the genus *Microtus* (Carroll & Genoways 1980). The distinctive morphology of *Lemmiscus* (Carroll & Genoways 1980; Carleton & Musser 1984)—characterized by pale grey fur dorsally; lighter grey on the sides; whitish, silver or buff ventrally; ears and nose commonly tinged buff; short furry tail; dental characteristics as detailed in § 3*a*—reflects genetic distinctiveness (Conroy *et al.* 2001).

2. MATERIAL AND METHODS

Data presented here come from one of the few known middle-Pleistocene richly fossiliferous stratigraphic sequences, Porcupine Cave Pit, Colorado, USA (Barnosky 2004), located at 38°43'45" N, 105°51'41" W, 2900 m elevation (figure 1). A combination of magnetostratigraphy and biostratigraphy places the Porcupine Cave Pit sequence (PCPS) at more than 600 000 years old at the top, near 780 000 years old at the middle and less than 1 million years old at the bottom. The sedimentological evidence suggests at least two glacial–interglacial cycles: the old-

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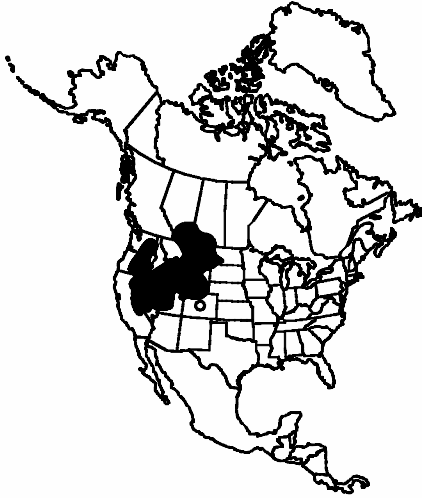


Figure 1. Location of Porcupine Cave (white dot) and modern geographical range of *Lemmiscus curtatus* (black area). Geographical range from Carroll & Genoways (1980).

est stratigraphical levels 14, 13, 12 and probably 11 indicate interglacial deposits; level 10 is glacial; levels 9, 8, 7 and 6 are interglacial; levels 5 and 4 are glacial; and the youngest levels 3, 2 and 1 are interglacial (figure 2) (Bell & Barnosky 2000; Barnosky 2004; Bell *et al.* 2004b). The youngest interglacial (levels 3, 2 and 1) was the warmest and most arid of all those represented in the PCPS, as indicated by the character of the sediments (a distinctive loose dry dust that occurs nowhere else in the sequence), the dominance of xeric taxa, such as the ground squirrel *Spermophilus*, and the highest diversity of reptiles and amphibians (Bell & Barnosky 2000; Barnosky 2004). The climatic change from interglacial level 6 to glacial level 5 was much less pronounced than the change from glacial level 4 to interglacial level 3 (Barnosky 2004). Palynological, invertebrate fossil and sedimentological data substantiate this inference for the coeval Hansen Bluff, Colorado (Rogers *et al.* 1992), located *ca.* 200 km south of the PCPS.

This study focuses on the fossil sample of sagebrush voles (genus *Lemmiscus*) from the PCPS; 52 other mammal species are also known from the locality (Barnosky 2004). The sagebrush vole fossils, which accumulated predominantly from wood rats collecting bone-laden carnivore scat and raptor pellets, and thus represent animals that lived within a *ca.* 10 km radius of the PCPS (Bell & Barnosky 2000; Barnosky 2004), came from levels 10 through 1. We examined a total of 233 fossil specimens (172 first lower molars and 61 third upper molars); out of these, 158 specimens of the first lower molar and 52 specimens of the third upper molar contained all of the requisite morphological features. We compared variation in the fossil sample with that in 363 specimens from extant *L. curtatus* populations distributed across the modern geographical range of the species, which is confined to the Great Basin and adjacent areas in association with dense stands of *Artemisia* (sagebrush) (figure 1; Carroll & Genoways 1980). For each first lower molar of *Lemmiscus*, we recorded the degree of closure in the fourth, fifth and sixth triangles, illustrated in figure 3. Triangles were defined as closed if the dentine field separating each from the next anterior triangle was less than one enamel bandwidth; incipient if the dentine field was between one and two enamel bandwidths; pinched if the dentine field was more than two and less than three enamel bandwidths; and confluent if the dentine field was more than

three enamel bandwidths. Modern specimens reside in the University of California Museum of Vertebrate Zoology and the Museum of Paleontology, and were from the following localities: California—Inyo Co., Lassen Co., Modoc Co., Mono Co. and Plumas Co.; Oregon—Crook Co., Deschutes Co., Harney Co. and Lake Co.; Nevada—Churchill Co., Elko Co., Esmeralda Co., Eureka Co., Humboldt Co., Lyon Co., Mineral Co., Nye Co., Washoe Co. and White Pine Co.; Idaho—Ringham Co.; Utah—Bryce Canyon National Park; Saskatchewan—‘Swift Current’. Fossil specimens reside in the University of California Museum of Paleontology and the Carnegie Museum of Natural History. Specimen numbers are listed in Appendix A.

3. RESULTS AND DISCUSSION

(a) *Species boundaries*

Living representatives of *L. curtatus* are morphologically (Carroll & Genoways 1980; Carleton & Musser 1984; Barnosky & Rasmussen 1988; Bell & Barnosky 2000; Bell *et al.* 2004b) and genetically (Conroy *et al.* 2001) distinct from all other species. Distinctive morphological attributes that characterize the first lower molars in extant populations include the presence of at least five completely closed triangles (figure 3b), as well as other details that are described elsewhere (Barnosky & Rasmussen 1988; Bell & Barnosky 2000; Bell *et al.* 2004b). The upper third molar is also diagnostic by its elongated posterior loop and simplified anterior half, which consists of at most two alternating triangles (figure 3c,d).

Seventy-five per cent of the modern specimens have only five triangles on the first lower molar; 8% have six; and 17% are transitional in morphology between five and six triangles (incipient-six or pinched-six morphology; figures 2 and 3). In the oldest PCPS sample (level 10) only three specimens are known: one of them falls within the range of variation of the modern sample (five triangles) and two are outside the modern range of variation (one with only four triangles, and one with intermediate morphology between four and five triangles). At level 6 an interesting trend begins (figure 2): an extinct four-triangle morphotype declines to its lowest proportions in level 1 as the extant five-triangle morphotype increases its numbers. In level 1, six-triangle morphotypes appear for the first time. Between the time represented by level 1 (more than 600 000 years old) and the present, the four-triangle and transitional four-to-five-triangle forms became extinct.

Changes in the third upper molar are consistent with those seen in the first lower molar. Most PCPS levels are dominated by third molars in which triangle one is incompletely closed (shallow re-entrant form, figures 3c and 4), whereas levels 1 and 2 shift to a predominance of closed triangle one (deep re-entrant form, figure 3d). Closure of triangle one characterizes 99% of the modern specimens.

The temporal pattern (figures 2 and 4) suggests two possibilities for population-level evolution. The first is that two species of *Lemmiscus* are represented, one characterized by only four triangles on the first lower molar, and the second by at least five triangles. Another possibility is that only one species is present, and its morphology has shifted through time from including four-triangle forms to having only morphologies with more than four triangles. We favour the single-species interpretation for the following reasons: (i) transitional morphologies are exhibited at

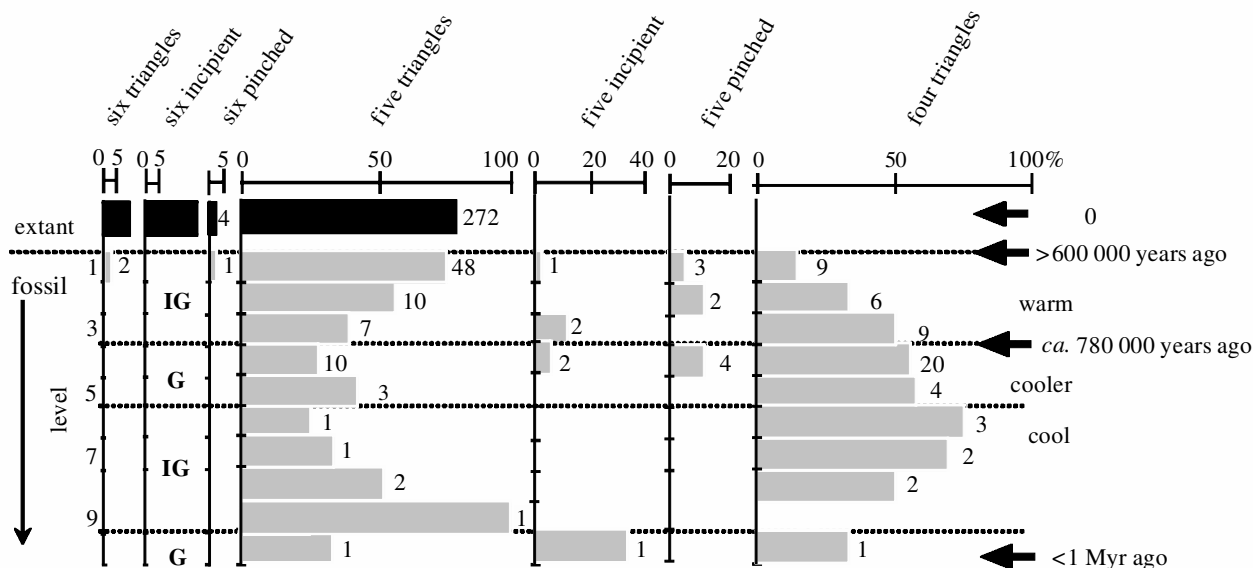


Figure 2. Stratigraphical sequence at Porcupine Cave and change in relative percentages of *Lemmyscus* first lower molar morphotypes. Relative percentages in the modern populations are shown as the black bars; fossil specimens are shown as the grey bars. The stratigraphical levels in the PCPS are arranged from the youngest at the top to the oldest at the bottom. Numbers to the right of the bars indicate numbers of specimens. See figure 3 for illustrations of the various morphotypes. G, glacial; IG, interglacial.

the PCPS levels with adequate sample sizes, which would suggest hybridization between species if more than one species were present; (ii) both five-triangle and six-triangle forms with intermediates exist in modern populations that are recognized as *L. curtatus*; and (iii) other species of extant arvicolines, notably *Microtus pennsylvanicus*, today exhibit spatial clines in the number of triangles on the first lower molar.

We therefore recognize as *L. curtatus* individuals that have a first lower molar exhibiting at least four triangles (and other features detailed in Barnosky & Rasmussen (1988), Bell & Barnosky (2000) and Bell *et al.* (2004b)) and third upper molars within the range of variation exhibited in figure 3. This diagnosis is consistent with regarding *L. curtatus* as an evolutionary species, a morphological species and a biological species. Although these different species concepts are not always mutually inclusive (de Queiroz & Donoghue 1988; O'Hara 1994; Miller 2001), they appear to be in this case. *Lemmyscus curtatus* as we recognize it appears to be monophyletic and based on shared derived characters (expressed as genetic distinctiveness (Conroy *et al.* 2001) and attainment of at least four triangles in contrast to arvicolines such as species of *Allophaiomys* (Bell & Barnosky 2000), which have only three triangles).

The PCPS data illustrate that evolution into present-day *L. curtatus* (populations characterized by exclusively the five-triangle and six-triangle forms) featured shifts in predominant morphology and changes in morphological variation (figure 2). At first, only four-triangle and five-triangle forms were present (levels 10 through 2); then, six-triangle forms were added (level 1); then, four-triangle forms were lost (subsequent to the PCPS; see § 3b). In this context, the species label masks important population-level change through time. Regarding the PCPS specimens as representing two species would also mask temporal population-level change, notably the apparent derivation of six-triangle forms from five-triangle forms.

(b) Duration of the morphological transition

How long did it take for the modern morphology to evolve? Answering this question is important because it suggests a lower limit on how long it takes for a modern species to become fully recognizable as such. The answer requires the addition of data from sites other than Porcupine Cave.

The bottom PCPS specimens are among the oldest known for *Lemmyscus*, which otherwise first appears *ca.* 820 000–840 000 years ago at San Antonio Mountain (SAM) Cave, New Mexico (Rogers *et al.* 2000), based on biochronology. The middle part of the SAM Cave sequence is probably about the same age as the middle of the PCPS, between 780 000 and 740 000 years old, based on magnetostratigraphic interpretations. However, a third locality of about the same age, Cathedral Cave, Nevada, also yielded four-triangle and five-triangle forms of *Lemmyscus* (Bell & Barnosky 2000). Given this approximately simultaneous appearance at sites in the Rocky Mountain West, it seems likely that *L. curtatus* originated just prior to 840 000 years ago, although it is controversial whether the origin was in the Old or New World (Carleton & Musser 1984; Rogers *et al.* 2000; Conroy *et al.* 2001). *Lemmyscus* is known from only North America, favouring a New World origin. The potential Old World relatives—suggested on dental morphological grounds that later were called into question (Carleton 1981; Carleton & Musser 1984)—include species within the genera *Lagurus* and *Eolagurus*. *Lagurus* first appears at least 900 000 years ago, and *Eolagurus* extends back as far as 2.5 million years (Repenning *et al.* 1990).

Populations containing the four-triangle and five-triangle morphologies of *Lemmyscus* are also known from Kennewick, Washington, which on the basis of calcrete formation rates and biochronology seems to be younger than *ca.* 330 000 years (Rensberger & Barnosky 1993). The geologically youngest four-triangle form, from Snake Creek Burial Cave, Nevada, was bracketed by radiocarbon and uranium series dates to between 9460 ± 160 and

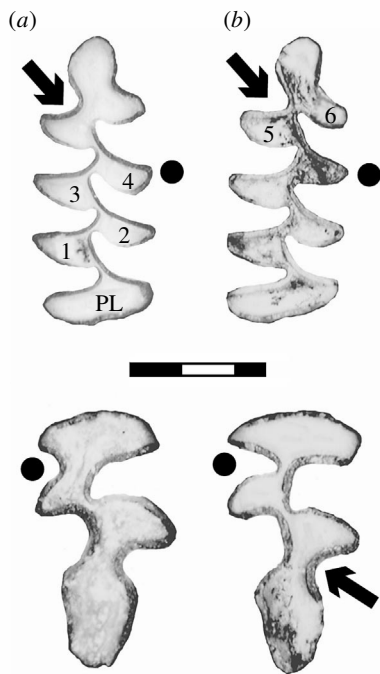


Figure 3. Salient morphological characteristics of *Lemmiscus curtatus* first lower (a,b) and third upper (c,d) molars. Anterior at top; (a), (c) and (d) are right molars; (b) is a left molar that was flipped in the program PHOTOSHOP to make visual comparison easier. The enamel perimeter forms the outline of the tooth; the cementum that fills the re-entrants in the actual specimens was removed from the photographs for clarity of illustration. In (a) and (b), black dots mark the fourth triangle; in (c) and (d), black dots mark the anterolabial re-entrant. AL, anterior loop; PL, posterior loop; 1, 2, 3, 4, 5, 6, triangles 1 to 6, respectively. (a) The four-triangle morphology; (b) the five-triangle morphology; (c) the shallow anterolabial re-entrant morphology; and (d) the deep anterolabial re-entrant morphology. Note that in (a), marked by the arrow, what would be the fifth triangle is widely confluent with the anterior part of the tooth. In (b) the arrow points to the same area, but note that the enamel bands touch such that triangle 5 is completely separated from the front part of the tooth. Transitional morphologies exhibit constriction intermediate between the extremes marked by the arrows in (a) and (b). Triangle 6 can show the same range from wide anterior confluence to complete closure. Note that in (d), the deeper anterolabial re-entrant has the effect of enhancing closure of triangle 1. The arrow in (d) points to a region that in some specimens becomes constricted to close off the posterior margin of triangle 2. All four teeth are from PCPS level 1. Scale bar, ca. 1 mm.

15 100 ± 700 BP (Bell & Mead 1998). Therefore it took at least 825 000 years for *L. curtatus* to attain the morphology and population structure characteristic of its modern representatives.

(c) Evolution and climatic change

To assess whether the population-level morphological changes corresponded with the transition from glacial to interglacial conditions, we searched for statistically significant differences in the numbers of four-triangle and greater-than-four-triangle specimens between levels and between glacial and interglacial intervals. Chi-squared and Fisher's exact tests both revealed significant ($p < 0.05$) differences between levels only when comparing the

uppermost interglacial level 1, which has a greater frequency of greater-than-four-triangle forms, with levels 3, 4, 5, 6 and 7. Level 1 also yields the first six-triangle forms. Comparisons between interglacial and glacial intervals indicated significantly more greater-than-four-triangle specimens in the uppermost interglacial compared with the preceding glacial and interglacial.

Some have viewed climatic change, especially cyclic climatic change evident from orbital variations over the past 2 million years of the Pliocene and Quaternary, as accelerating evolution and contributing to speciation (Vrba 1995a), or as dampening gradual evolution and enhancing abrupt speciation (Dynesius & Jansson 2000). Others regard such climatic oscillations as background noise within the magnitude of habitat change to which species are adapted (Bennett 1997; Alroy *et al.* 2000; Barnosky 2001; Barnosky *et al.* 2003). The *L. curtatus* data speak to both sides of this question. The lack of correspondence of morphological change with each glacial–interglacial transition argues against models that specify cyclic climatic changes as driving evolutionary change. However, the fact that the most pronounced morphological change takes place within the warmest driest interglacial period (level 3 to level 1) in the PCPS is consistent with an out-of-the-ordinary global-warming event accelerating the evolution of additional triangles on the teeth. This has the functional effect of adding enamel perimeter, which makes the tooth more resistant to abrasion. An increase in abrasive particles on food is correlated with increasing aridity (Fortelius *et al.* 2002), although more work needs to be done to assess the selective significance to *L. curtatus*.

The interglacial period during which evolution accelerated was different from the earlier ones in the PCPS not only in being drier and warmer but also in being the first interglacial in the sequence to occur after a new periodicity of glacial–interglacial cycles was well established. The periodicity transformed from a 41 000 year rhythm before 800 000 years ago to a 100 000 year rhythm after that time (Raymo 1998), and the 100 000 year periodicity became firmly established by ca. 640 000 years ago (Raymo 1998; Schmieder *et al.* 2000). Vrba (1995b) argued that such changes in periodicity stimulated biotic turnover. Although there was no marked 'turnover' event in the Porcupine Cave record (Barnosky 2004), transformation to the new periodicity would be consistent with stimulating morphological change in *Lemmiscus*.

4. CONCLUSIONS

In summary, these data provide exceptionally detailed insights into the evolutionary process that led to a modern mammal species. Species such as *L. curtatus* are real entities in space but through time demonstrate directional evolution (addition of triangles on teeth) at the population level. Therefore temporal species boundaries, although possible to define, are to some extent arbitrary and depend on the proclivities of the taxonomist. The biological reality in this case is that the speciation process itself—from splitting from an ancestor to attaining the characteristics of the living representatives (populations with mostly five-triangle and some six-triangle forms)—took at least ca. 825 000 years (or ca. 200 000 years if the two-species scenario discussed in § 3a applied). Speciation over

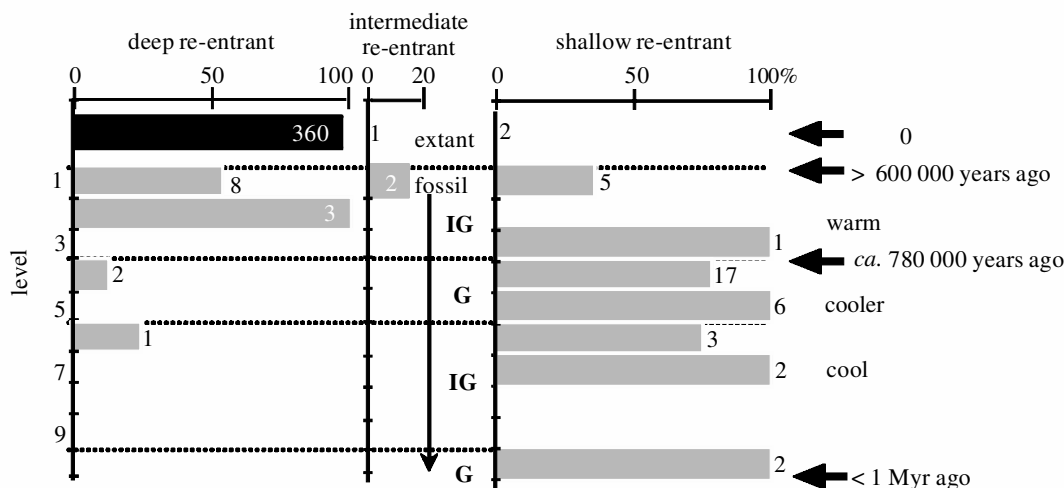


Figure 4. Change in relative percentages of *Lemmiscus* third upper molar morphotypes. See figures 2 and 3 for further explanation.

825 000 years is consistent with (although at the short end of) estimates based on molecular clocks derived from mtDNA (Avice *et al.* 1998). The major population-level change (attainment of six triangles and the decrease in frequency of four triangles) coincided with the transformation from a 41 000 year to a 100 000 year periodicity in glacial–interglacial cycles, during which there was an aberrantly arid warm period. Consistent with orbitally forced range-dynamics models (Dynesius & Jansson 2000; Jansson & Dynesius 2002), these considerations suggest that not every orbital-scale climatic change is evolutionarily significant to organisms, but those that are expressed atypically in critical geographical areas (in this case, through the range of *L. curtatus*) can stimulate evolution that results in obvious morphological change.

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APPENDIX A: SPECIMENS EXAMINED FOR THIS STUDY

CM, Carnegie Museum of Natural History; UCMP, University of California Museum of Paleontology; MVZ, University of California Museum of Vertebrate Zoology.

Fossil specimens (additional details including stratigraphical level are available in Bell *et al.* (2004b)). First lower molar: CM 45459–45472, 45506, 65233, 65481, 65556, 65557, 65562, 65578, 65579, 66190, 66194, 66201, 66214, 66220, 66239, 66242, 66255, 66267, 66268, 66277, 66279, 66281–66283, 66301, 66304, 66308, 66310, 66323, 66324, 66328, 66330, 66334, 66343, 66346, 66347, 66547, 66562, 66570, 66572, 66581, 66588, 66597. UCMP 155265–155319, 155329, 155331, 155333–155389. Third upper molar: CM 45410–45413, 45473, 65582, 65583, 65586, 66191, 66260, 66265, 66286, 66337. UCMP 155495–155542.

Specimens from extant populations (all complete skull and jaws, observations made on left and right sides; detailed information for each specimen available at <http://elib.cs.berkeley.edu/mvz/>). MVZ 3646, 7968–7972,

24024, 24025, 26425, 26425, 26426–26446, 31607, 35065, 36463, 37220, 37221, 38476, 38478–38501, 38505, 38724–38733, 42069, 42070, 45861–46383, 49455, 51928, 54471–54473, 58491, 58492, 64522, 64523, 65534, 66430, 68598–68602, 68604, 68756, 71137, 74268, 74270, 79544–79546, 79548–79553, 79560–79566, 84279, 89220, 95357–95360, 96749–96756, 97326–97344, 105518, 105519, 107307, 113295, 119363–119365, 121137–121140, 121206–121208, 121238–121240, 121523, 121840–121843, 126072, 126073, 165905–165907. UCMP 123793.

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