蟩擨鞼齝輍蝂赨榲誻鵋籡湁粅紨鞼鳨矆鍂鉳鵗逬۔逬漝鋠橁椚諎拢莂輧湁掘莂萷捁銆貟軵骩侸笻袧犐飰伅紶豘閁銆趶詴袑錽粻鳿輰鈗枩絑鈽嬒猹莥澾嬟抸褬潹蒭縔趪蛵鐱銆襓頀譝鵽**翑**霚抪厼坾

heating due to the net moisture convergence. Equation 6 shows that it is the derivative of the oceanic transport with respect to SST, not the magnitude of the oceanic transport, that determines the sensitivity of the tropical SST. This fact was overlooked by Ramanathan and Collins (10). The equation also shows that the effectiveness of the feedback from ocean currents depends crucially on the nature of other feedbacks. Over the warm pool region, $\partial E/\partial T$ is largely canceled by $\partial G_a/\partial T$, and $\partial C_1/\partial T$ is largely balanced by $\partial F_{as}/\partial T$ (3). There may be further cancellations between $\partial C_s/\partial T$ and $-\partial F_{al}/\partial T$ because increased cloudiness over the warm pool region is likely accompanied by enhanced moisture convergence (4). The larger cancellation among atmospheric feedbacks makes the feedback from ocean currents crucially important. Moreover, all of the feedback terms in Eq. 6 depend strongly on the Walker circulation (4, 5) and therefore more fundamentally on the dynamic coupling between the atmosphere and ocean. It is the dynamic coupling that gives rise to the east-west SST gradients and the accompanying Walker circulation.

REFERENCES AND NOTES

- T. J. Crowley and G. R. North, *Paleoclimatology* (Oxford Univ. Press, New York, 1991).
- S. G. H. Philander, *El Niño, La Niño, and the Southern Oscillation* (Academic Press, New York, 1989).
 V. Ramanathan and W. Collins, *Nature* 351, 27
- V. Hamanaman and W. Collins, *Nature* 331, 27 (1991).
 R. Fu, A. D. Del Genio, W. B. Rossow, W. T. Liu, *ibid*.
- **358**, 394 (1992).
- D. E. Waliser and N. E. Graham, J. Geophys. Res. 98, 12881 (1993); J. M. Wallace, *Nature* 357, 230 (1992); D. Hartmann and M. Michelsen, J. Clim. 6, 2049 (1993); R. T. Pierrehumbert, J. Atmos. Sci. 52, 1784 (1995).
- R. S. Lindzen and S. Nigam, J. Atmos. Sci. 44, 2418 (1987).
- 7. J. C. McWilliams and P. R. Gent, *ibid.* 35, 963 (1978).
- 8. The long-term coldness of the equatorial subsurface ocean is maintained by the meridional branch of the wind-driven circulation, which moves heat to the extratropical ocean (11).
- R. C. Pacanowski, K. W. Dixon, A. Rosati, "The GFDL Modular Ocean Model users guide," *GFDL Ocean Group Tech. Rep.* 2 (1991).
- H_w = S_c + C_s + G_a + C₁ E F_o F_{as} + F_{al}, where S_c is the clear-sky solar radiation. Ramanathan and Collins (3) dropped F_o from H_w before it was perturbed to obtain Eq. 6.
- J. McCreary and P. Lu, *J. Phys. Oceanogr.* 24, 466 (1994); Z. Liu, G. Philander, R. Pacanowski, *ibid.*, p. 2606.
- 12. D.-Z. Sun and A. H. Oort, J. Clim. 8, 1974 (1995).
- K. Bryan, J. Phys. Oceanogr. 14, 666 (1984).
 This estimate was obtained from Eq. 4. The upper limit for H₀ was taken as S_c + G_a(T₀) - σT₀⁴, where S_c = 370 W m⁻² (clear-sky solar radiation), G_a = 165 W m⁻², σ is the Stefan-Boltzmann constant, and T₀ = 300 K. The same values for S_c, G_a, and T₀ were used by Ramanathan and Collins (3). The value for
- water vapor feedback was from Sun and Oort (12).
 15. The ocean model domain spans 40° in longitude and 3000 m in depth from 2°S to 50°N, with a resolution of 2° in both latitude and longitude and 15 levels in the vertical. With no wind imposed on the ocean, we first spun up the ocean GCM for 1000 years for the surface layer and 5000 years for the bottom layer using an acceleration scheme given by Bryan (13).

The heat exchange between the atmosphere and ocean had the same form as in the box model, with $T_{\rm o}$ varying with latitude following a cosine profile from 319 K at the equator to 263 K at 50°N. The thermal relaxation time scale 1/c was chosen as 200 days. The salinity field was held constant. The spin-up was to allow the thermohaline circulation to set up a basic temperature structure for the ocean. Except near the western boundary, distributions of SST in such a state were essentially zonally symmetric. A perturbation to the upper ocean was introduced by imposing a weak wind stress for a year. The surface wind was then coupled to the east-west SST differences in a way similar to that for the box model: $\tau_{\rm x} = \lambda_0 [\eta(y)](T_1 - T_2)$, where $\tau_{\rm x}$ is the east-west wind stress, λ_0 is the

coupling strength, and $\eta(y)$ is a specified function of latitude *y* that gives easterly wind in the tropics and westerly wind in the extratropics. The domains over which T_1 and T_2 were obtained spanned latitudes of 0° to 10°N and longitudes of, respectively, 0° to 15° and 25° to 40° of our 40° region. Thirteen experiments with different λ_0 were conducted. For small λ_{p_1} no significant east-west SST gradients were de-

veloped, and the ocean returned to the basic state without wind. When λ_0 was sufficiently large, however, the ocean drifted quickly to a new state with significant east-west SST differences. No significant changes were found after the first two decades of integration, indicating that the heat transfer is mainly a balance between the radiative convective processes and the wind-driven circulations. In the GCM experiments, heat was gained in the tropics and lost in the extratropics, as in the observations. Plotted in Fig. 4 are values of T_1 and T_2 at the end of 50 years of integration. (A few experiments were extended to 1000 years of integration, and no significant differences from the corresponding 50 years of integration ()

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Fossil Evidence for a Late Cretaceous Origin of "Hoofed" Mammals

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Seventeen of eighteen orders of living placental mammals are not known before 65 million years ago. The monophyly of each order is well established, but interrelations have been less certain. A superordinal grouping of up to seven extant orders plus a variety of extinct orders, all included within Ungulata ("hoofed" mammals), can be linked to Late Cretaceous mammals from the 85-million-year-old Bissekty Formation, Uzbekistan (and, less certainly, North America and Europe), thus pushing the origin of this major clade back by 20 million years. Ungulatomorphs are not closely related to primates, rodents, or rabbits.

Whether they include one (aardvarks) or 1750 (rodents) extant species, orders are the most inclusive groupings for which there is certainty of monophyly within Mammalia. The monophyly of superordinal taxa such as Ungulata has been much less certain (1). The mammalian division Ungulata is usually argued to include archaic ungulates ("Condylarthra") (2), South American native ungulates (3), Desmostylia, and Embrithopoda, and the extant Artiodactyla, Cetacea, Hyracoidea, Perissodactyla, Proboscidea, Sirenia, and questionably Tubulidentata, but it excludes the extinct Pantodonta, Tillodontia, and Dinocerata (4). None of these orders had been known from before the earliest Tertiary [65 million years ago (Ma)] except for questionable Late Cretaceous occurrences in North and South America (5). Fossils recovered from the 85-million-year-old Bissekty Formation, Uzbekistan (6), however, appear to have ungulate affinities (7, 8) on the basis of dental morphology that seems to mark the beginnings of herbivory in placental mammals. These fossils, plus possibly others from North America and Europe, comprise

the family "Zhelestidae" (9). A review of the biostratigraphy of the Bissekty Formation (10) corroborates the ~85-millionyear age estimate and also suggests that various of its named and unnamed mammalian species are best referred to "Zhelestidae." In this report, I present the results of a species-level phylogenetic analysis of better known, Late Cretaceous placental mammals, including the "zhelestids," plus Ungulata. Trends in increased herbivory among "zhelestids" compared to other Late Cretaceous placental mammals are also discussed.

The phylogenetic analysis (Fig. 1) of all species of better known Late Cretaceous placental mammals (Table 1) shows that "zhelestids" are monophyletic relative to other Late Cretaceous eutherians. The upper and lower dentitions of the mid-sized Asian "zhelestids" cannot at this time be matched; thus, the study was limited to the better known upper dentition. As shown in Fig. 1, the analysis includes Tertiary Ungulata represented by Protungulatum (or Oxyp*rimus*) as an exemplar. Because some "zhelestids" have a more recent common ancestry with Ungulata than with other "zhelestids," "Zhelestidae" is paraphyletic (and thus the quotation marks). With Ungulata, however, "Zhelestidae" forms a clade

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relative to all Late Cretaceous mammals that is here named Ungulatomorpha (11). "Zhelestids" are of particular interest because they evolved character states leading toward herbivory, which are even more strongly developed within Ungulata. The only other extant orders of placental mammals that show similar overall tendencies toward herbivory are rodents, rab-

Fig. 1. Phylogenetic tree of placental mammals [after (1)] compared to a cladistic analysis (22) of ungulatomorphs ("zhelestids" and Ungulata) including the 10 Late Cretaceous eutherians listed in Table 1. The more important morphological shifts (some of which are found as homoplasies in other taxa) are as follows: Node 1, Ungulatomorpha: stylar shelf narrow, ultimate premolar (P5) with metacone or swelling (Fig. 2, C, E, and H), pre- and postcingula reach or extend below conules, and two cus-





pules in the parastylar region. Node 2, Gen. et sp. nov. (Fig. 2, C and D) plus Ungulata: substantial anteroposterior expansion of protocone, substantial labial shift of protocone, and molar crown shape at least subrectangular. Node 3, Ungulata (*Protungulatum donnae* as exemplar): molar conules with little or no internal wings, metacingulum formed by postmetaconular crista continuing on to metastylar region, parastylar region reduced with one cusp, four or fewer premolars [sirenians have five premolars (23)], upper molars rectangular in occlusal view, parastylar groove (and lobe) reduced, and conules closer to protocone than to midposition of the crown. Four other Ungulata autapomorphies have been noted (2): more bunodont, lower crowned teeth; molar trigonids anteroposteriorly shortened; M₃ with a large posteriorly projecting hypoconulid; and astragalus with a shorter, robust head. Of these, the first two are in all ungulatomorphs, and the second is hinted at in the M₃ tentatively referred to the new genus and species (Fig. 2B). The fourth was not evaluated. *lestes* are not closely related to ungulates. The earliest known primatomorphs (13) such as *Purgatorius* retain primitive features, especially in their lower dentition (such as less anteroposteriorly compressed trigonid than in "zhelestids"), that argue against membership in Ungulatomorpha.

Some of the 85-million-year-old "zhelestids" resemble the 65-million-year-old archaic ungulates (so-called condylarths). For example, the largest "zhelestid," gen. et sp. nov. (Fig. 2, A through D, and Fig. 3D), at first could be mistaken for an archaic ungu-



Fig. 2. Occlusal views: cf. gen. et sp. nov. (**A**) right M₂ (Chernyshev's Central Museum of Geological Exploration of Saint Petersburg or CC-MGE 17/12953), (**B**) left M₃ (CCMGE 16/12953), (**C**) right P⁵ (CCMGE 35/12176); gen. et sp. nov. (**D**) left M² (CCMGE 2/12455, type); *Aspanlestes aptap* (**E**) left P⁵ and M¹⁻² (CCMGE 1/12455, cast of type of *Zhelestes bezelgen*), (**F**) right P₅ and M¹⁻² (CCMGE 4/12176, type); *Parazhelestes* sp. nov. (**G**) right M¹ (CCMGE 11/12953, type), (**H**) P⁵ and M¹⁻² (CCMGE 11/12176, cast). Scale bar, 2 mm.

Table 1. Matrix of taxon and the characters and states defined in (24), which were used in the phylogenetic analysis in Fig. 1.

Species	Character																	
	a	b	с	d	е	f	g	h	i	j	k	I	m	n	0	р	q	r
Hypothetical ancestor Late Cretaceous eutherians represented by upper teeth	0	0	0	0	Ó	0	0	0	0	0	0	0	0	0	0	0	0	0
Asioryctes nemegetensis	0	0	1*	0	0	0	1	0	?	1	0	0	0	0	0	0	0	0
Batodon tenuis	0	0	0	0	0	0	1	0	0	1	0	1	1	?	0	0	0	0
Barunlestes butleri	0	0	1	0	1?	0?	0	0	0	1†	0	0	0,1	1	0	0	0	0
Cimolestes spp.	0	0	0	0	0	0	0,1	0	0	1	0	0,1	0,1	0	0	0	0	0
Gypsonictops spp.	0	0	0	0	1	0	1	0?	1	0,1	0	1	0,1	0	0	0	0	0
Kennalestes gobiensis	0	0	0	0	0	1	1	0	0,1	0,1	0	1,2	0	0	0	0	0	0
Paranyctoides maleficus	1,2	0	0	0	0	0	1	1	0	?	1	1,2	0	0	0	1	0	0
Otlestes meiman	0	0	0,1	0	0	0?	0	0	?	0	0	0	0	0?	0	1	0	0
Sailestes quadrans	1	0	0	0	0	1	1	0?	?	?	0	2	1	?	0	1	1	0
Zalambdalestes lechei	0	0	1?	0	0,1	0	0	0	1?	1	0	0	0	1	0	1	0	0
Ungulatomorphs																		
Ălostera																		
saskatchewanensis	1	0	0	1	1	0	2	1	1	?	1	2	2	?	1	1	1	0
Avitotherium utahensis	1	0	0	0	1	1	1,2	1	. 1	?	1	2	0,1	?	0	1	1	0
Aspanlestes aptap	1	0	0	0	1	1	2	1	1	0?	1	2	0,1	0	0	1	0	0
Zhelestes temirkazyk	1	0?	0	0	1	1	2?	1?	1	0	1	3	1	0	0	1?	2?	0
Parazhelestes robustus	2	1	0	0	1	1	2	1	1	0?	1	3	1	1	0	1	2	1
Parazhelestes sp. nov.	1,2	1	0	0	1	1	2	1	0,1	0?	1	2	1	?	0	1	2	0
Gen. et sp. nov. Ungulata (for example,	3	2	0	0	1	1	2	1?	1?	?	2	3	2	?	0	1	2	0
Protungulatum)	3	2	1	1	1	0	2	1	0,1	1**	3	3	1,2	0	1	1	2	1

late from the Paleocene of North America (Fig. 3E). In this new taxon (Fig. 3D) and in ungulates (Fig. 3E), the protocone on the upper molars (and last premolar) (Fig. 2C) is greatly expanded and shifted labially, squaring the crown, as compared to the narrower, more triangular shape found in Late Cretaceous eutherians such as Kennalestes or Gypsonictops (Fig. 3, A and B). In addition, in "zhelestids" the pre- and postcingula, although narrow, extend labially below the conular region; the bases of the paracone and metacone are separated; the parastylar region is weak because shearing in this area is reduced; and the stylar shelf is narrower, with little or no ectoflexus. These changes facilitate the crushing function of the protocone-talonid and the transverse chewing motion found in herbivores versus the shearing crests on the molars and the more vertical chewing motion in carnivores (14). Even the smallest "zhelestid," Aspanlestes aptap (Figs. 2, E and F, and 3C), heralds the beginning of these trends, which are more obvious in intermediate-sized species (Parazhelestes sp. nov.) (Fig. 2, G and H).

These changes are mirrored in the lower dentition (Fig. 2, A, B, and F), in which a widened talonid receives the expanded protocone, the entoconid-hypoconulid are closely approximated, trigonid height is lowered relative to the talonid, the trigonid has some anteroposterior shortening, and the ultimate premolar has a metaconid or swelling (shared with other Late Cretaceous eutherians). The twinning of entoconid-hypoconulid could be unique for "zhelestids," but it is more likely that this resulted from expansion of the protocone, as the hypoconid moved away from the other talonid cusps. A different twinning of these cusps occurred in marsupials (15). In species of Ungulata that first appear some 65 Ma, further talonid expansion pushed the entoconid and hypoconulid apart. Continued anteroposterior shortening and lowering of the trigonid squared up the



Fig. 3. Occlusal views of left upper second molars: (**A**) *Kennalestes gobiensis*; (**B**) *Gypsonictops illuminatus*; (**C**) *Aspanlestes aptap*; (**D**) gen. et sp. nov.; and (**E**) *Protungulatum donnae*. [(A, B, and E) after (25)]. Molars drawn at same width. Scale bars, 1 mm.

molars, which is correlated with the continued shift to herbivory.

Although "zhelestids" show clear links to ungulates, they retain some character states primitive for Late Cretaceous eutherians. The more obvious and important of these are (i) retention of strong internal wings on the upper molar conules (Fig. 2, D, E, G, and H, and Fig. 3, A through D) that are reduced or lost in the earliest ungulates (Fig. 3E) as more transverse occlusion evolves; (ii) retention of five premolars with relative size 5>4>2>3>1 (Fig. 4, A and B) that are reduced to four or fewer in most ungulates; and (iii) retention of a more ventrally placed mandibular condyle (Fig. 4C) as compared to a more dorsal position in even the earliest known archaic ungulates (Fig. 4D). This latter transformation is correlated with herbivory in which there is increased emphasis on the masseter and pterygoid musculature with concomitant deemphasis on the temporalis (16) and the development of a simultaneous rather than a sequential occlusion of the teeth (17)

Near the Cretaceous-Tertiary boundary (65 Ma), archaic ungulates appear in North America and shortly thereafter in South America (18), thus beginning a tremendous taxonomic and ecological radiation leading to the present ungulate diversity that ranges from antelope to elephants to whales. The discovery of ungulate precursors 85 Ma in



Fig. 4. Reconstructed left labial view of the snout region based on (**A**) maxilla of *Zhelestes temirkazyk*, canine (C), P^{1–5}, M^{1–3} (CCMGE 10/12176, type); and (**B**) dentary of *Sorlestes budan*, canine, P₁₋₄ (CCMGE 15/12953), demonstrating the presence of five premolars and the relative sizes of the premolars 5>4>2>3>1; stippling shows reconstructed teeth. Left labial views of reconstructed teeth and views of reconstructed teeth above dentary: (**C**) "zhelestid" based on *Sorlestes budan* (Zoological Institute of the Academy of Sciences of Uzbekistan or IZANUz P2155-M-1), and *S. kara* (CCMGE 106/12455, type) (26); and (**D**) the ungulate *Protungulatum donnae* (27). Scale bars, 2 mm.

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western Asia ("zhelestids"), North America, and possibly Europe provides evidence for rooting the ungulate radiation much farther back in time. This older time of origin for major eutherian superordinal clades bolsters the argument that fossils can be key in clarifying evolutionary relationships (19). It also serves as an additional, older tie point for molecular studies of higher level relations among eutherians (20) and argues that soft tissue structures unique and universal to all extant eutherians, such as the chorioallantoic placenta (21), must have arisen by 85 Ma.

REFERENCES AND NOTES

- 1. M. J. Novacek, Nature 356, 121 (1992).
- D. R. Prothero, in *Placentals*, vol. 2 of *Mammal Phylogeny*, F. S. Szalay, M. J. Novacek, M. C. McKenna, Eds. (Springer-Verlag, New York, 1993), pp. 173– 181.
- 3. R. L. Cifelli, ibid., pp. 195-216.
- 4. S. G. Lucas, ibid., pp. 182-194.
- J. D. Archibald, in *Evolution of Tertiary Mammals of North America*, C. M. Janis, K. M. Scott, L. L. Jacobs, Eds. (Cambridge Univ. Press, Cambridge, in press).
- L. A. Nessov, *Ezheg. Vses. Paleontol. O-va.* 25, 228 (1982).
- 7. ____, Vestn. Zool. 2, 60 (1984).
- 8. P. M. Butler, *Biol. Rev.* 65, 529 (1990).
- L. A. Nessov, Vestn. Leningr. Univ. Ser. 7 17, 8 (1985).
- 10. _____, J. D. Archibald, Z. Kielan-Jaworowska, Bull. Carnegie Mus. Nat. Hist., in press.
- 11. Mammalia Linnaeus, 1758; Placentalia Owen, 1837. Ungulatomorpha, new. Taxa included. Zhelestidae [eight species, western Asia; three, North America; questionably three, Europe. See (10) for complete list] and Ungulata (taxa noted above). Definition. The most recent common ancestor of Zhelestidae and Ungulata and all of its descendants, Diagnosis, Various Late Cretaceous or later eutherians have some of the following character states, but only ungulatomorphs have them (or subsequent transformations) in combination. Those character states labeled with a dagger (†) appear to be apomorphic for Ungulatomorpha, whereas those not so labeled appear to be plesiomorphic or their polarity cannot be determined. Protocone is anteroposteriorly expanded, if only slightly; upper molar crown in occlusal view is at most only slightly constricted through the conular region, and the crown shape is trapezoidal, subrectangular, or rectangular, but not triangular; the parastylar region has two cuspules (†); the paraconemetacone and protocone are relatively far apart with conules closer to paracone-metacone; the stylar shelf is narrow (†); pre- and postcingula are consistently present; pre- and postcingula reach or extend below conules (†); para- and metacone are of similar height and are separate at the base; ultimate upper premolar has metacone or swelling (metaconid or swelling on lower) (†); paraconid is lingual to sublingual with some appression to metaconid (†); entoand hypoconulid are twinned (†); trigonid height is lower relative to talonid height (†); talonid is expanded to the same or greater width than trigonid (†).
- R. K. Stucky and M. C. McKenna, in *The Fossil Record II*, M. J. Benton, Ed. (Chapman and Hall, London, 1993), pp. 739–771.
- 13. K. C. Beard, in (2), pp. 129-150.
- P. M. Butler, in *Structure, Function, and Evolution of Teeth*, P. Smith and E. Tchernov, Eds. (Freund Publishing, Tel Aviv, 1992), pp. 125–138.
- L. G. Marshall and Z. Kielan-Jaworowska, *Lethaia* 25, 353 (1992).
- C. M. Janis, in *Functional Morphology in Vertebrate* Paleontology, J. J. Thomason, Ed. (Cambridge Univ. Press, Cambridge, 1995), pp. 76–98.
- 17. W. S. Greaves, ibid., pp. 99-115.
- C. de Muizon, *Rev. Téc. Yaciminetos Petrolíferos Fiscales Bolivianos* 12, 575 (1991).

- J. Gauthier, A. G. Kluge, T. Rowe, *Cladistics* 4, 105 (1988).
- 20. D. M. Irwin and A. C. Wilson, in (2), pp. 257-267.
- J. A. Lillegraven, S. D. Thompson, B. K. McNab, J. L. Patton, *Biol. J. Linnean Soc.* **32**, 281 (1987); M. B. Renfree, in *Mesozoic Differentiation; Multituberculates, Monotremes, Early Therians, and Marsupials*, vol. 1 of *Mammal Phylogeny*, F. S. Szalay, M. J. Novacek, M. C. McKenna, Eds. (Springer-Verlag, New York, 1993), pp. 4–20.
- 22. All terminal taxa except the hypothetical ancestor were run as a single polytomy in order to assess the monophyly of Ungulatomorpha. In Table 1, all multistate characters were run unordered; all numbered states followed by a question mark were run as the state indicated: those given only as a question mark were run as missing data. The default settings of the branch-and-bound method of PAUP [D. L. Swofford, PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1 (Illinois Natural History Survey, Champaign, IL, 1993)] were used. The results were four equally parsimonious trees with a tree length of 67 steps, in which only the position of the various nonungulatomorphs changed, thus the strict consensus tree in Fig. 1. The measures for each tree were as follows: (i) consistency index = 0.701; (ii) homoplasy index = 0.582; (iii) retention index = 0.773; and (iv) rescaled consistency index = 0.542. I ran a second analysis, using the heuristic method to determine the shortest tree, that did not hold Ungulatomorpha as monophyletic. The run yielded 2047 equally parsimonious trees, each of 69 steps. The measures for each of these trees were as follows: (i) consistency index = 0.681; (ii) homoplasy index = 0.594; (iii) retention index = 0.750; and (iv) rescaled consistency index = 0.511.
- P. D. Gingerich, D. P. Domning, C. E. Blane, M. D. Uhen, *Contrib. Mus. Paleontol. Univ. Mich.* 29, 41 (1994).
- 24. Upper dentition characters and character states for taxa shown in Table 1 and used in the phylogenetic analysis in Fig. 1 are as follows: Primitive or ancestral state = 0, derived = 1 to 3, and missing = ? *Metaconule reduced. **Usually only four premolars at most, #Has only three premolars. Characters are as follows: (a) Amount of anteroposterior expansion of protocone: none (0), slight (1), moderate (2), substantial (3). (b) Amount of labial shift of protocone: none (0), moderate (1), substantial (2). (c) Postparaconular and premetaconular cristae: strong and winglike (0), weak or absent (1). (d) Metacingulum: formed only of the postmetaconule crista and terminates dorsal of postmetacrista, which is continuous with the metastylar lobe (0), formed of the postmetaconule crista continuing on to the metastylar lobe (1). (e) Stylar shelf: wide (0), narrow (1). (f) Number of cuspules in parastylar region: one (0), two (1). (g) Pre- and postcingula: do not have or have only a hint of cingula (0), cingula do not reach or extend below the conules (1), cingula reach or extend below the conules (2). (h) Height and size of para- and metacone: paracone higher and larger (0), cusps of similar height and size (1). (i) Metacone or metaconal swelling on P⁵ (or ultimate upper premolar): absent (0), present (1). (j) Number of premolars: five (0), four or fewer (1). (k) Shape of molar crown in occlusal view: triangular (0), trapezoidal (1), subrectangular (2), rectangular (3). (I) Constriction of crown through conular region without or without cingula present: no constriction and no cingula (0); marked constriction and with cingula (1), slight constriction and with cingula (2), no constriction with cingula (3), (m) Ectoflexus: deep (0), shallow (1), none (2). (n) M³ linguolabial width relative to other molars; not markedly narrowed (0), markedly narrowed (1), (o) Parastylar groove: well developed (0), very reduced or absent (1). (p) Base of paracone and metacone: merged (0), separate (1). (q) Distance between paracone or metacone and protocone relative to total anterior or posterior width, respectively: between 45 and 55% of crown width (0), more than 55% of crown width (1), less than 45% of crown width (2). (r) Position of conules (especially paraconule) relative to paracone and metacone versus protocone: conules closer to mid-position (0), conules closer to protocone than to the mid-position (1).

- Z. Kielan-Jaworowska, T. M. Bown, J. A. Lillegraven, in *Mesozoic Mammals: The First Two-Thirds of Mammalian History*, J. A. Lillegraven, Z. Kielan-Jaworowska, W. A. Clemens, Eds. (Univ. of California Press, Berkeley, 1978), pp. 99–149.
- 26. L. A. Nessov, *Tr. Zool. Inst. Ross Akad. Nauk SSSR* **249**, 105 (1993).
- R. L. Carroll, Vertebrate Paleontology and Evolution (Freeman, New York, 1988).
 Itbank L. A. Nessov, O. L. Tsaruk, and B. G. Vereten-
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Bacteria as Mediators of Copper Sulfide Enrichment During Weathering

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Supergene chalcocite enrichment during weathering is an economically vital natural process that may lead to severalfold increases in the copper content of sulfide deposits. A scanning electron microscope study of chalcocite (Cu_2S) from major enriched copper deposits in northern Chile revealed myriad bacterioform bodies in original growth positions near replacement interfaces with remnant hypogene sulfide grains. These minute (0.03 to 0.2 micrometers) chalcocite bodies are interpreted as fossilized and metallized nannobacteria that promoted the fixation of mobilized copper ions. Bacterial activity may thus be a fundamental factor in supergene enrichment of copper deposits.

Many of the world's major Cu deposits were formed by supergene enrichment during weathering. Enrichment took place at and beneath the ground-water table under reducing conditions and involved the progressive replacement of hypogene sulfides, especially chalcopyrite (CuFeS2) and pyrite, by Curich sulfides of the chalcocite (Cu₂S) group (1-3). The necessary Cu, supplied by descending acidic solutions at ambient temperatures, was obtained by oxidative dissolution of cupriferous sulfides in the vadose zone above the ground-water table (Fig. 1). Sulfide oxidation is promoted by acidophilic bacteria, both in the natural environment and in commercial beneficiation of chalcocite and other ores (4, 5), but Cu enrichment typically has been modeled as an abiotic process. Here we present results from a scanning electron microscope (SEM) study of representative samples of enriched sulfides from major Cu deposits in northern Chile that suggest that supergene enrichment, like sulfide oxidation, is a bacterially mediated process. Bacteria were shown recently to nucleate placer Au formation (6).

Northern Chile–southern Peru is the world's premier Cu province and contains at least 12 major porphyry-type Cu deposits that display well-developed zones of supergene enrichment (7); ten of them are or have been exploited and the other two will be soon. The enrichment zones, ranging from 50 to 300 m thick (Fig. 1), were generated cumulatively as ground-water tables descended (2, 7) under semiarid climatic conditions during the mid-Tertiary.

Representative samples of supergene enriched Cu ores were collected from highgrade veins in three of the major porphyrytype deposits mined in northern Chile: Chuquicamata (8) (Fig. 1), Quebrada Blanca (9), and El Salvador (10). The samples, from the uppermost 40 m of the respective enrichment zones, contain mas-



Fig. 1. Representative section of the Chuquicamata porphyry Cu deposit (8), northern Chile, that shows the position of supergene enrichment. Symbols: LC, leached capping, which was depleted of Cu by downward-migrating solutions; OZ, oxidized zone, where Cu was partially fixed as oxidized minerals, separated by a paleogroundwater table from the enrichment zone (EZS, strong enrichment zone; EZW, weak enrichment zone); and HZ, hypogene zone, containing chalcopyrite, pyrite, and other sulfide minerals.

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