

significantly higher than that of the corresponding thin-film sample in L1 (30%). The x-ray analysis of this sample confirmed the cubic perovskite structure with $a = 3.82 \text{ \AA}$.

It has been suggested (3) that the CMR effect in the Ca-doped LaMnO_3 system originates from "double exchange" electron-hopping processes between Mn^{3+} and Mn^{4+} neighboring sites through the O^{2-} anion between them (10). In these processes, the e_g itinerant electron conduction or hopping rate $t_{ij} = t_0 \cos(\theta_{ij}/2)$, where θ_{ij} is the angle between local spin directions of electrons on neighboring sites i and j , and t_0 is the hopping rate in a perfect ferromagnetic state. The application of an external field may align the disordered local spins during a ferromagnetic transition and thereby increase electron conduction or even induce an insulator-metal transition through strong interaction between itinerant electron and local spins. In this model, the MR effect may be induced by an external field when the system is in transition toward the ferromagnetic state. In this aspect, our data are consistent with this model, that is, MR effects appear only below the Curie temperature ($T_c \sim 150$ to 200 K) and decrease below the saturation field (~ 30 to 40 K) (Fig. 3). However, the role of alkaline earth ion size in the MR effect remains unclear. In doped LaMnO_3 systems, it appears that smaller dopant size favors the MR effect (5), whereas in doped LaCoO_3 systems, the opposite effect is observed.

REFERENCES AND NOTES

1. See, for example, R. M. Kusters, J. Singleton, D. A. Keen, R. McGreevy, W. Hayes, *Physica B* **155**, 362 (1989); K. Chahara, T. Ohno, M. Kasai, Y. Kozono, *Appl. Phys. Lett.* **63**, 1990 (1993); H. L. Ju, C. Kwon, R. L. Greene, T. Venkatesan, *ibid.* **65**, 2108 (1994); R. von Helmolt, J. Wecker, K. Samwer, L. Haupt, K. Bärner, *J. Appl. Phys.* **76**, 6925 (1994).
2. S. Jin, H. M. O'Bryan, T. H. Tiefel, M. McCormack, W. W. Rhodes, *Appl. Phys. Lett.* **66**, 382 (1995).
3. S. Jin *et al.*, *Science* **264**, 413 (1994).
4. G. C. Xiong *et al.*, *Appl. Phys. Lett.* **66**, 1427 (1995).
5. X.-D. Xiang *et al.*, *Science* **268**, 1738 (1995).
6. Sputtering was carried out at 5 to 15 mtorr, with Ar as the sputtering gas; deposition rates were 0.1 to $1 \text{ \AA s}^{-1}$. Film thickness was monitored with a crystal microbalance and calibrated independently with a profilometer. The uniformity of the deposited films varied less than 5% over an area $\sim 2.5 \text{ cm}$ in diameter.
7. Library L1 was treated as follows: heated from room temperature (RT) to 200°C , heated to 300°C over 12 hours, and cooled to RT; it was then heated to 650°C over 1 hour, heated to 850°C over 3 hours, heated to 900°C over 3 hours, and cooled to RT over 2 hours. Library L2 was treated as follows: heated from RT to 200°C , heated to 350°C over 15 hours, and cooled to RT; it was then heated to 650°C over 2 hours, heated to 740°C over 13 hours, heated to 850°C over 1 hour, heated to 900°C over 0.5 hour, cooled to 650°C over 2 hours, and cooled to RT.
8. G. Briceño, X. Sun, H. Chang, X.-D. Xiang, P. G. Schultz, unpublished material.
9. F. Askham, I. Fankuchen, R. Ward, *J. Am. Chem. Soc.* **72**, 3799 (1950).
10. C. Zener, *Phys. Rev.* **82**, 403 (1951); P. W. Anderson and H. Hasegawa, *ibid.* **100**, 675 (1955); P.-G. de Gennes, *ibid.* **118**, 141 (1960).

11. We are grateful for financial support for this work from the Laboratory Directed Research and Development Program of Lawrence Berkeley Laboratory under U.S. Department of Energy contract DE-AC03-76SF00098 and the Office of Naval Research (grant N00014-95-F-0099). G.B. acknowledges

support from a University of California President's Postdoctoral Fellowship. We thank J. Torrance for helpful advice and E. Granlund and J. Wu for technical support.

25 May 1995; accepted 22 August 1995

Molluscan Diversity in the Late Neogene of Florida: Evidence for a Two-Staged Mass Extinction

Edward J. Petuch

Analyses of recent data show that Floridian molluscan diversity declined markedly during the Pliocene-Pleistocene mass extinction. This decline in diversity was seen at all trophic levels, indicating a complete collapse of the ecosystem. These findings contradict the notion that there was a species diversity stasis throughout the Pliocene-Pleistocene and that the diversity of Pliocene Florida was equivalent to that of Recent Florida. The mass extinction was a two-staged, sequential event. A similar two-staged mass extinction occurred in the Miocene, indicating that two ecological catastrophes in quick geological succession may have produced this mass extinction as well.

Studies of tropical western Atlantic Pliocene (Plio)-Pleistocene molluscan mass extinctions (1–8) have resulted in two conflicting conclusions. The main data source used to arrive at these antitheses was the rich upper Neogene molluscan fossil beds of southern Florida (deposited within the Floridian component of the Plio-Pleistocene Caloosahatchee Molluscan Province) (2, 6, 9). One conclusion (4) was that diversity (at both the generic and specific levels) decreased dramatically in Florida during late Pliocene–early Pleistocene time, producing an impoverished middle and late Pleistocene fauna and a reconstituted but less diverse Recent Floridian fauna. The other conclusion (8) was that although Plio-Pleistocene rates of extinction were high in Florida, the overall diversity (species level) has remained relatively constant from the Pliocene to the Recent. This was explained by a high rate of recruitment (origination), produced by invasion and speciation, that balanced the net loss due to extinction. Both notions, however, were hampered by incomplete museum collections and by variable reporting in the literature.

Data sources and compendia have recently become available that offer a more complete database of molluscan diversity (10, 11). When put into a new stratigraphic and geochronological scheme (12, 13), the data on macrogastropod diversity reveal patterns of extinction and faunal impoverishment. In an attempt to illustrate such patterns, I selected eight dominant macrogastropod families for analysis, with each representing a major trophic level within its

respective molluscan community. Included are algal film grazers (Potamididae), sea grass and epibiont feeders (Cypraeidae), suspension and detritus feeders (Turritellidae), large general carnivores (Busynconidae), small general carnivores (Buccinidae), molluscivores (Muricidae), vermivores (Conidae), and specialized suctorial feeders (Cancellariidae). If a mass extinction truly occurred, with a corresponding drop in species diversity, it would be safe to assume that many, if not all, trophic levels within an ecosystem would suffer.

As can be seen in Table 1 and Fig. 1, all eight families reached a peak of species diversity during the middle Pinecrest Beds (PB2, units 5, 6, 7) at approximately 3 million years ago (Ma) (14). Species diversity declined at the end of Pinecrest Beds time, rose again during Caloosahatchee time, at approximately 1.5 to 2 Ma, and then dropped precipitously during the late Pleistocene (Bermont to Fort Thompson interval). With the exception of the Conidae, with five additional species, and the Potamididae, with an equivalent number of species, all other families show a much lower species diversity in Recent Florida. If all three Pinecrest Beds faunas are considered in unison, as in (8), then the total number of Pinecrest Beds species is much larger for all eight families. In the case of some families, such as the Busynconidae, the difference between the late Pliocene Pinecrest Beds and the Recent fauna is over eightfold. Other families, such as the Cypraeidae, Turritellidae, and Cancellariidae, all exhibit differences ranging from factors of 4 to over 5. The same pattern is seen at the generic level, as shown in Table 2. With the exception of the Cypraeidae (because of late Pleistocene inva-

Division of Geological Oceanography, Department of Geology, Florida Atlantic University, Boca Raton, FL 33431, USA.

sion and recruitment) (10), seven families are shown to have had more genera during the late Pliocene than are found in Recent Florida.

These data all indicate that the late Pliocene molluscan mass extinction was a real event, and they substantiate the findings of Stanley (3, 4) and Stanley and Campbell (1). The sharp drop in the number of genera between the late Pliocene and Recent, particularly in such stenothermal tropical and subtropical indicator families as the Potamididae and the Conidae, also supports the extinction model of Stanley (4). Of all eight families, the Buccinidae seems to have suffered the greatest extinction at both the specific and generic levels, and it seems never to have fully recovered after the mass extinction. High tropical genera such as *Cymatophos* and *Trajana* all became regionally extinct after Pinecrest Beds time but have survived in the tropical Eastern Pacific. These, and many other ex-

amples, imply that abrupt cooling and an accompanying reduction in productivity (as shown by the corresponding drop in diversity in the detritivore–suspension-feeding family Turritellidae) caused this extinction event. The present data do not support the proposition of a Plio-Pleistocene species diversity stasis (8).

The data show that the Plio-Pleistocene mass extinction was not a single, one-time event but a two-staged, sequential event. Both extinction episodes occurred in close geochronological succession, and the extinction couplet is seen on the graph shown in Fig. 1. On the basis of the data in Tables 1 and 2, the first and strongest extinction event took place at the end of Pinecrest Beds time (PB3) and resulted in a much lowered species diversity. Although such genera as *Rhipophos*, *Extractrix*, and *Virgiconus* and many others became extinct in Florida, some groups such as *Pterorhytis*, *Acantholabia*, *Solenosteira*, and *Massyla* sur-

vived on into the Pleistocene (as new and different species). By Caloosahatchee time, climatic conditions apparently returned to those of Pinecrest Beds time, as evidenced by incipient species radiations of several main groups such as *Siphocypraea* and *Contraconus* (10). At the end of Caloosahatchee time (early Pleistocene) a second extinction event took place, and this acted as the “coup de grâce” for even these last remnants of the great Pliocene eastern American molluscan fauna.

This pattern of a two-staged molluscan mass extinction may not be unique to the Plio-Pleistocene event. A similar but more widely spaced couplet is seen in the middle and late Miocene of the Atlantic coastal plain. Here, a Serravalian extinction event was recently documented (15) and was shown to have resulted in a drop in diversity and a loss of such distinctive gastropod genera as *Ecphorosycon*, *Stephanosalpinx*, *Trisecphora*, and *Patuxentrophon*. Climatic conditions became more tropical by the early Tortonian, as evidenced by the first appearance of genera such as *Leptoconus*, and both specific and generic diversity climbed to former levels. By the late Tortonian and Messinian, however, a second extinction event occurred (6) and most pre-Serravalian survivors, as exemplified by the busyconids *Turritulur* and *Sycopsis*, died out. Another recent analysis of a mass extinction at the end of the Permian (16) has, again, revealed a similar two-staged pattern. Detailed studies of other faunal impoverishments throughout time may show that these couplets are recurrent events and that they may be typical, if not necessary, components of mass extinctions.

Table 1. Number of species in predominant macrogastropod families found in southern Floridian Plio-Pleistocene faunozones (arranged by ecology). PB1, Pinecrest Beds fauna, units 8, 9, and 10; PB2, Pinecrest Beds fauna, units 5, 6, and 7; PB3, Pinecrest Beds fauna, units 2, 3, and 4; C, Griffin Pit and Caloosahatchee fauna; BE, Bermont and Holey Land fauna; FT, Fort Thompson fauna; R, Recent fauna. Data taken from (10) and (17).

Family and ecology	Number of species in faunozones						
	PB1	PB2	PB3	C	BE	FT	R
Potamididae, algal film grazers	0	3	8	5	5	2	3
Cypraeidae, sea grass feeders*	3	13	5	3	3	1	5
Turritellidae, suspension-detritus	8	18	3	10	4	2	5
Busyconidae, general carnivores, large	15	20	7	17	6	5	5
Buccinidae, general carnivores, small	4	27	5	6	7	4	11
Muricidae, molluscivores	11	47	11	26	27	9	38
Conidae, vermivores	4	18	7	20	12	4	23
Cancellariidae, specialized suctorial	5	23	6	13	6	2	6

*Based on living relative *Cypraea mus* and paleoenvironmental inferences.

Table 2. Number of genera in predominant macrogastropod families found in southern Floridian Plio-Pleistocene faunozones, showing times of extinction (both regional and complete). P_0 , total number of genera at beginning of Pinecrest Beds time; E_p , number of genera that became extinct at end of Pinecrest Beds time; E_c , number of genera that became extinct at end of Caloosahatchee time; E_b , number of genera that became extinct at end of Bermont time; E_t , number of genera that became extinct at end of Fort Thompson time; R , number of genera found in Recent Floridian neritic fauna. Data taken from (10) and (17).

Family	Number of genera					
	P_0	E_p	E_c	E_b	E_t	R
Potamididae	4	2	0	0	1	1
Cypraeidae	2	0	1	1	0	3*
Turritellidae	7	2	2	0	0	3
Busyconidae	7	0	2	0	0	5
Buccinidae	15	7	2	0	0	6
Muricidae	21	3	5	1	0	15†
Conidae	8	1	1	0	0	4
Cancellariidae	9	2	3	0	0	5‡

*The genera *Erosaria*, *Luria*, and *Macrocypraea* appear in the early and late Pleistocene. †The genera *Caribiella* and *Tripterotyphis* appear in the Recent fauna and *Trachypollia* first appears in the Bermont fauna. ‡The genus *Bivertopsis* appears in the Bermont fauna.

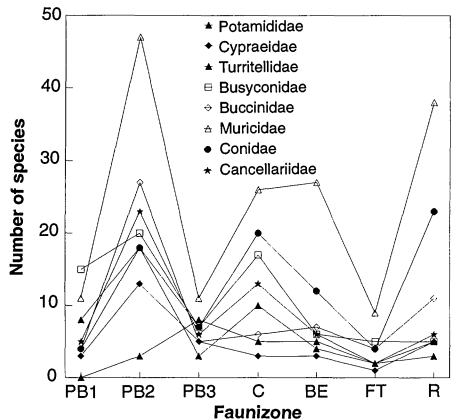


Fig. 1. Number of species in eight ecologically exclusive gastropod families, arranged geochronologically by faunizone. Data points are listed in Table 1. PB1 (3.5 Ma), PB2 (3 Ma), and PB3 (2.5 Ma) (Pinecrest Beds 1, 2, 3), late Pliocene; C (Caloosahatchee) (1.5 to 2 Ma), Plio-Pleistocene boundary and early Pleistocene; BE (Bermont) (1 Ma), middle Pleistocene; FT (Fort Thompson) (150,000 years), late Pleistocene; R, Recent Florida fauna. Dating listed under (14).

REFERENCES AND NOTES

1. S. M. Stanley and L. D. Campbell, *Nature* **293**, 457 (1981).
2. E. J. Petuch, *Proc. Acad. Nat. Sci. Phila.* **134**, 12 (1982).
3. S. M. Stanley, *Geology* **12**, 205 (1984).
4. ———, *Palaos* **1**, 17 (1986).
5. G. J. Vermeij and E. J. Petuch, *Malacologia* **27**, 29 (1986).
6. E. J. Petuch, *Neogene History of Tropical American Mollusks* (Coastal Education and Research Foundation, Charlottesville, VA, 1988).
7. J. B. C. Jackson, P. Jung, A. G. Coates, L. S. Collins, *Science* **260**, 1624 (1993).
8. W. D. Allmon, G. Rosenberg, R. W. Portell, K. S. Schindler, *ibid.*, p. 1626.
9. D. S. Jones and P. F. Hasson, in *The Great American Biotic Interchange*, F. G. Stehli and S. D. Webb, Eds. (Plenum, New York, 1985), pp. 325–355.
10. E. J. Petuch, *Atlas of Florida Fossil Shells (Pliocene and Pleistocene Marine Gastropods)* (The Graves Museum of Archaeology and Natural History, Dania, FL, 1994).
11. ———, in "The Neogene of Florida and adjacent regions," V. A. Zullo, W. B. Harris, T. M. Scott, R. W. Portell, Eds. (Spec. Publ. 37, Florida Geological Survey, 1993), pp. 73–85.
12. T. M. Scott in "The Plio-Pleistocene stratigraphy and paleontology of southern Florida," T. M. Scott and W. D. Allmon, Eds. (Spec. Publ. 36, Florida Geological Survey, 1992), pp. 21–25. The terms Pinecrest Beds, Caloosahatchee Formation, Bermont Formation, and Fort Thompson Formation were never formally proposed as lithostratigraphic units but are, in actuality, simply faunozones. In anticipation of a formal biozonational scheme for southern Florida, I have adopted a transitional nomenclature, referring to the previous "formations" as "faunas" within Scott's proposed "Okeechobee Formation" and within a redefined Tamihi Formation. With this scheme, the Sarasota Unit, Buckingham "Formation," the Ochopee "Member," and the Pinecrest Beds are included within the Tamihi Formation, and the Caloosahatchee "Formation," Griffin Pit Unit, Holey Land Unit, Bermont "Formation," and Fort Thompson "Formation" are included in the new Okeechobee Formation.
13. Although Allmon *et al.* (8) included the Pinecrest Beds as a single faunal unit, chronologically equivalent to the Caloosahatchee and Bermont Formations, recent geochronological data [D. S. Jones *et al.*, *J. Geol.* **99**, 637 (1991)] and faunal analyses (10) have shown that the Pinecrest Beds contain three separate sequential faunas and that the total unit is chronologically three times as large as either the Caloosahatchee, Bermont, or Fort Thompson faunozones. As shown in (10), Pinecrest Beds unit 10 (and the thinner units 8 and 9) contains a base set of species (essentially the same fauna as contained in the "Ecphora zone" of the Jackson Bluff Formation of northwestern Florida), whereas Pinecrest Beds unit 7 (and the thinner units 5 and 6) contains a separate suite of species descended from the unit 10 fauna, and Pinecrest Beds unit 3 (and also units 4 and 2) (this fauna has also been collected in the Mule Pen quarry in Naples, Collier County, Florida) contains yet another separate suite descended from the unit 7 fauna. The highly endemic Kissimmee River valley fauna is here included with the stratigraphically equivalent Pinecrest Beds.
14. On the basis of (10, 13), Pinecrest Beds unit 10 is now dated at 3.5 Ma, Pinecrest Beds unit 7 at 3 Ma, Pinecrest Beds unit 3 at 2.5 Ma, the Caloosahatchee and Griffin Pit faunas at 1.5 to 2 Ma, the Bermont fauna at 1 Ma, and the Fort Thompson Fauna at 150,000 years before present.
15. E. J. Petuch, *Nautilus* **106**, 155 (1993).
16. S. M. Stanley and X. Yang, *Science* **266**, 1340 (1994).
17. R. T. Abbott, *American Seashells* (Reinhold, New York, ed. 2, 1974).

12 June 1995; accepted 16 August 1995

Geomorphically Driven Late Cenozoic Rock Uplift in the Sierra Nevada, California

Eric E. Small* and Robert S. Anderson

Geologists have long accepted that the Sierra Nevada, California, experienced significant late Cenozoic tectonically induced uplift. A flexural-isostatic model presented here shows, however, that a large fraction of the primary evidence for uplift could be generated by the lithospheric response to coupled erosion of the Sierra Nevada and deposition in the adjacent Central Valley and therefore requires less tectonic forcing than previously believed. The sum of range-wide erosion and the resultant isostatic rock uplift would have lowered Sierra mean elevation by 200 to 1000 meters since 10 million years ago and could also have increased summit elevations during the current period of relief production.

For a century, geologists have thought that the Sierra Nevada (Sierra) crest (Fig. 1) has been uplifted about 2000 m by tectonic forces in the late Cenozoic (1–3). This uplift event is enigmatic because it occurred 100 million years after arc-related crustal thickening in the Sierra (4). England and Molnar (5) proposed that much evidence used to infer mountain uplift, similar to that reported for the Sierra, may actually reflect either exhumation or isostatically driven

rock uplift rather than tectonically driven surface uplift. In addition, they hypothesized (6) that much of the data interpreted as evidence for late Cenozoic uplift events could instead have been generated by global cooling, thereby challenging proposals that the reputed late Cenozoic uplift had caused global cooling (7).

Surface uplift is the change in mean elevation with respect to the geoid averaged over $>10^3$ km², rock uplift is displacement of individual points (rocks) with respect to the geoid, and exhumation is displacement of points with respect to the surface (5). These terms are related: surface uplift equals rock

uplift minus exhumation. Rock uplift can be driven by tectonic forcing or by the isostatic response to exhumation. Before using any geologic data to constrain the amount of surface uplift attributable to tectonic forcing, one must first assess how much of this geologic signal was generated by exhumation and the resultant isostatically driven rock uplift. Here, we quantify what fraction of the evidence for late Cenozoic Sierra uplift was produced by these latter processes.

The primary evidence previously used to calculate the magnitude and timing of Sierra uplift was the westward tilt of markers (Fig. 2) (1–3), including stratigraphic horizons in the eastern Great Valley sedimentary sequence and abandoned fluvial channels filled with dated volcanic flows and alluvium along the western Sierra margin. Most studies, as well as our own, have focused on uplift north of 36.5°N because tilted markers do not exist farther south (Fig. 1). In previous studies, crestal uplift was calculated by simple linear projection of tilted markers to the crest (Fig. 2). Four assumptions were made in these studies: (i) the Sierran block rotated rigidly, (ii) there was a constant hinge line position, (iii) all tilt exceeding modern stream gradients indicates deformation, and (iv) there was no erosion (2, 3). The last assumption was not explicitly stated. The tilt rate deduced from stratigraphic markers more than doubles 3 to 4 million years ago (Ma); this observation lead researchers to argue for accelerated uplift toward the present (2). Huber (2) calculated about 2000 m of crestal uplift since 10 Ma, with 1000 m of this uplift occurring since 3 Ma. This crestal uplift corresponds to a 1000-m increase in mean elevation (surface uplift) since 10 Ma if all four of these assumptions are valid. Secondary evidence used to argue for late Cenozoic uplift comes from studies of paleobotany (8), sediment provenance (9), and the depletion of deuterium in Great Basin ground water (10).

The tilt of western Sierra geologic markers unambiguously records differential rock uplift, with greater rock uplift occurring within the Sierra than in the adjacent Central Valley. Rock uplift could have been driven by tectonic forcing or by the isostatic response to geomorphic forcing, or both. Tilt observed at the western Sierra margin can be used to quantify tectonically driven surface uplift of the range only in the absence of exhumation (5), that is, when surface uplift equals rock uplift. Previous researchers have implicitly assumed that tilt indicates differential surface uplift and, therefore, that it is both tectonic in origin and has increased Sierra mean elevation. Several time-dependent tectonic mechanisms have been proposed to explain the accelerating increase in mean elevation

Department of Earth Sciences and Institute of Tectonics, University of California, Santa Cruz, CA 95064, USA.

*To whom correspondence should be addressed.