have at least some information about the relative orientation of the two eyes. The most useful applications of the eight-point algorithm will probably be found in computer vision systems, where there is still a need for fast and accurate methods of converting two-dimensional images into three-dimensional interpretations.

I thank Drs A. L. Allan and K. B. Atkinson for the reference to Thompson¹, and the RS and SRC for support.

Received 13 April; accepted 13 July 1981.

1. Thompson, E. H. *Photogrammetric Record* 3(14), 152–159 (1959).
2. Ogle, K. N. *Researches in Binocular Vision* (Hafner, New York, 1964).
3. Ullman, S. *The Interpretation of Visual Motion* (MIT Press, Cambridge, 1979).
4. Marr, D. & Poggio, T. *Science* 194, 283–287 (1976).

Local extinction and ecological re-entry of early Eocene mammals

David M. Schankler

Department of Geological and Geophysical Sciences,
Princeton University, Princeton, New Jersey, USA

The use of high-resolution stratigraphical control in studying the species sequencing patterns of early Eocene mammals has recently been demonstrated by Gingerich *et al.*^{1–5}. These studies have documented the nature of the tempo and mode of evolution and have stimulated the debate between adherents of phyletic gradualism and punctuated equilibria⁶. All studies have been largely verticalist (evolutionary) in outlook, equating change within a single basin of deposition with evolution. However, when I applied these techniques to the early Eocene condylarth, *Phenacodus*, I found a strong lateral (biogeographical and ecological) component influencing the sequencing of species in a single basin. I report here that *Phenacodus* species are relatively static in size and morphology throughout the local section studied, and two of these show statistically significant discontinuities in temporal range. The clumped re-entry of these species after local disappearance along with the introduction of other new taxa points to ecological control of vertical events within a local section.

I used high-resolution stratigraphy to study mammalian evolution at the species level, concentrating on early Eocene Willwood Formation of northwestern Wyoming because of the density and continuity of the fossil record preserved in these sediments. The Elk Creek Section through the Willwood

Formation of the central Bighorn Basin is 773 m thick⁷, and represents an estimated 3.5 Myr (ref. 8). Using a 10-m resolution interval, over 240 fossil localities can be related to this section. These localities, distributed over a 650-km² area, so far have produced over 15,000 specimens and are distributed vertically through the section so that more than 50 of the 77 10-m intervals are fossiliferous; half of these have total mammalian sample sizes (minimum number of individuals) of over 75.

In a recent review of the systematics of the genus *Phenacodus*, West⁹ recognized three species from the early Eocene, *P. brachypternus*, *P. vortmani* and *P. primaevus*; his study predates publication of the Elk Creek Section and the stratigraphical resolution used was at the level of the zone, that is, early Eocene *Phenacodus* were divided into three samples corresponding to Graybullian (base–530 m), Lysitian (530–660 m) and Lostcabinian (660–770 m) zones. *P. brachypternus* was recorded as being almost wholly restricted to the Graybullian, whereas the other two species were distributed through the entire Wasatchian. *P. brachypternus* and *P. vortmani* are relatively well defined fossil species that have always been easily identified in collections on the basis of size and morphology, whereas *P. primaevus* has usually been characterized by a fairly large variation that has made it difficult to define the bounds of the species. This has led to the subdivision of *P. primaevus* into two to four species^{10,11}. West⁹ did not subdivide this species even though the recorded ranges of variation (coefficients of variation of ~10 for most linear measures) and a range of ln 0.8 for tooth crown area of M₂ (lower second molar) are almost double those expected for a single species^{12–14}.

Inclusion of all large specimens of *Phenacodus* in a single species is untenable, and on the basis of data shown in Fig. 1, the large phenacodontids have been subdivided into two species, *P. intermedius* and *P. primaevus*. As previously shown by Gingerich^{12,13} and observed in the two smaller species of *Phenacodus*, the normal range of variation of ln of the crown area of a molar tooth is of the order of 0.4. In the interval 100–190 m, almost all specimens fall neatly within the expected range of a single species, the size of which agrees well with the type of *P. intermedius*; thus these specimens are referred to that species. The single outlier at the 100-m level has a value that differs by 4 standard deviations from the mean of *P. intermedius* specimens, and is therefore too large to be included in that species. In the interval 200–380 m there is a second well defined

Fig. 1 Species-sequencing pattern of early Eocene *Phenacodus* in the central Bighorn Basin, Wyoming. Stratophenetic plot shows the distribution in size and time of the four species, and illustrates the discontinuity in the temporal ranges of *P. brachypternus* (□) and *P. vortmani* (◆), and the transition in dominance between *P. intermedius* (○) and *P. primaevus* (●) at the base of the Upper *Haplomylus*–*Ectocion* Zone. Size is measured on the abscissa as ln of the crown area of the lower second molar (M₂) and time is shown on the ordinate as metres above the base of the Elk Creek Section. The horizontal lines at the 730-m level are the maximum ranges of the two species of *Phenacodus* from the Lostcabinian of the Wind River Basin. Note the similarity between the size range of the larger species from the Wind River Basin and *P. intermedius* from the Elk Creek Section.

sample of large phenacodontid. The size of this species is similar to that of Granger's¹⁰ plesiotype of *P. primaevus* and this sample is referred to as that species, as is the 100-m level outlier already mentioned. *P. primaevus* could not be derived by gradual size transformation from *P. intermedius* because both species occur together at YPM Locality 351 (evidence provided by the large variation at the 240-m level) and *P. primaevus* occurs earlier at the 100-m level. This early occurrence of *P. primaevus* also tends to rule out a speciation event as an explanation for the size

discontinuity at the 240-m level. It seems more likely that the observed pattern is the result of a shift in dominance between the two species, with the zone of transition in the interval 200–240 m. Above the 420-m level all large phenacodontids become exceedingly rare in the central Bighorn Basin. Although no M_2 values substantiate this point in Fig. 1, other elements indicate that *P. intermedius* returns as the primary species of large phenacodontid in the highest part of the section. This also seems to be the case in the Wind River Basin¹⁵ (Fig. 1).

Table 1 Distribution of abundances of the five species of phenacodontid condylarths through the Elk Creek Section

Metre level	<i>P. intermedius</i>	<i>P. primaevus</i>	<i>P. vortmani</i>	<i>P. brachypternus</i>	<i>E. osbornianus</i>	Sample size
720	—	—	—	—	—	4
710	—	—	—	—	—	1
700	—	—	—	—	—	—
690	—	—	2	—	—	28
680	1	—	1	—	—	112
670	—	—	—	—	—	65
660	—	—	—	—	—	—
650	—	—	1	—	—	53
640	—	—	1	?	—	80
630	—	—	—	—	—	82
620	—	2	8	1?	—	546
610	—	—	3	?	—	387
600	—	1	3	—	—	109
590	1?	1	5	?	—	154
580	—	—	13	6	—	359
570	—	—	8	?	—	260
560	—	—	19	1	—	395
550	—	—	1	—	—	17
540	—	1	—	—	—	17
530	—	1	9	—	—	424
520	—	—	1	—	—	8
510	—	—	—	—	—	—
500	—	—	—	—	—	—
490	—	—	—	—	—	21
480	—	—	—	—	—	—
470	—	—	2	—	—	62
460	—	—	2	2	—	83
450	—	1	—	5	—	69
440	—	—	1	—	—	38
430	—	—	—	1	—	16
420	—	2	1	2	—	68
410	—	3	—	1	—	52
400	—	—	—	—	—	—
390	—	3	—	7	—	98
Upper Haplomylus-Ectocion Zone						
380	—	1	—	—	—	5
370	—	9	—	—	1	195
360	—	11	—	—	3	209
350	—	—	—	—	—	—
340	—	—	—	—	—	—
330	—	—	—	—	—	—
320	—	—	—	—	—	—
310	—	1	—	—	1	45
300	—	—	—	—	—	—
290	—	6	—	—	1	153
280	—	2	—	—	2	80
270	—	1	—	—	4	111
260	—	—	—	—	—	—
250	—	—	—	—	—	7
240	1	5	—	—	5	190
230	1	1	—	—	—	13
220	2	1	—	—	2	69
210	1	—	—	—	2	29
200	—	—	—	—	—	—
190	4	—	2	1	6	209
180	7	—	1	—	2	96
170	—	—	—	—	—	25
160	8	—	1	—	1	109
150	2	—	—	1	—	22
140	11	—	6	8	8	464
130	2	—	1	—	—	26
120	—	—	—	—	—	—
110	—	—	—	—	—	—
100	2	1	1	3	4	157
90	1	—	1	—	5	74
80	—	—	—	—	1	14
70	—	—	—	—	—	—
60	—	—	—	—	—	—
50	—	—	—	—	—	20
40	—	—	—	—	—	—

The abundances of the five species and the total sample size at each level are given as minimum number of individuals. Note the absence of *P. brachypternus* and *P. vortmani* from the entire Upper Haplomylus-Ectocion Zone (200–380 m).

This temporal discontinuity in the range of *P. intermedius* is even more evident in the ranges of *P. brachypternus* and *P. vortmani*. *P. brachypternus* is distinguished from all other species of *Phenacodus* by its small size and elongate lower fourth premolar (P_4) (Fig. 2). This condition of P_4 is present in the samples from all levels. As indicated in Fig. 1, there are no specimens of *P. brachypternus* from the entire 200–380-m interval (Upper *Haplomylus*–*Ectocion* Zone). The relative abundance of *P. brachypternus* through the entire section is 0.006 (Table 1). Using this as the most conservative estimate the probability of *P. brachypternus* not being found in the Upper *Haplomylus*–*Ectocion* Zone, if it were in fact present, is 0.0007. Of course, the higher frequency of *P. brachypternus* in the two zones bounding the zone of absence gives a lower probability that the species was in fact present in the intervening zone and has not yet been found. It is possible that the species present in the Lower *Haplomylus*–*Ectocion* Zone became extinct and a totally new species appeared at the beginning of the *Bunophorous* interval zone; this is highly unlikely in this particular case because of the presence of the unique P_4 in both the lower and upper samples, as noted above. The pattern for *P. vortmani* is very similar to that of *P. brachypternus* and an equally convincing argument can be made for its absence from the Upper *Haplomylus*–*Ectocion* Zone. However, for *P. vortmani* there is no unifying morphology between the lower and upper samples, and the positing of the discontinuity in the temporal range of this species is based on inference from *P. brachypternus*.

The temporal gap in the range of *P. brachypternus* is on the order of 200 m (slightly more for *P. vortmani*) and probably represents a time interval of ~1 Myr. In searching for an explanation for the species-sequencing patterns of these two species, it is necessary to consider the changes occurring in the entire fauna as well as aspects of the history of the Phenacodontidae. Phenacodontids experienced a severe decrease in relative abundance across the Clarkforkian–Wasatchian boundary¹⁶. This decline continued through the Wasatchian and correlates with the appearance and rise of the more advanced Perissodactyla. During the Wasatchian, larger condylarths are characterized by a patchy distribution such that the presence of one often means the exclusion of others¹⁷. In the central Bighorn Basin, the lower and upper boundaries of the Upper *Haplomylus*–*Ectocion* Zone (Biohorizons A and B respectively) are times of increased faunal turnover⁷. Biohorizon B also seems to correlate with a shift in the environmental regime as indicated by changes in the depositional environments and palaeoflora across this boundary¹⁸. No significant shift in the palaeoflora has been documented across Biohorizon A, although a slight shift is observed in the depositional environment.

It is informative to consider the distribution of a fifth species of phenacodontid, *Ectocion osbornianus*. At the base of the Wasatchian, *Ectocion* is equal in size with *P. brachypternus*. It increases slightly in size through the *Haplomylus*–*Ectocion* Zone such that at the top of its range it is intermediate in size between *P. brachypternus* and *P. vortmani*. During the Lower *Haplomylus*–*Ectocion* Zone, *P. brachypternus* and *P. vortmani* decrease in abundance just before their disappearance from the central basin—this decrease is matched by an increase in abundance of *Ectocion*. The reciprocity of abundances is not continued into the Upper *Haplomylus*–*Ectocion* Zone, when *Ectocion* abundance is also reduced. *Ectocion* becomes locally extinct in the central basin at the top of the Upper *Haplomylus*–*Ectocion* Zone, just before the return of *P. brachypternus* and *P. vortmani*.

Thus it seems that during the Wasatchian, phenacodontid condylarths became relatively sensitive environmental indicators. The general increase in open habitats through the Wasatchian (L. Hickey and S. Wing, personal communication) was probably responsible for the decline in abundance of the phenacodontids and the rise of the perissodactyls. Due to their dietary preferences (frugivore–foliivores), the phenacodontids were better adapted to a closed canopy forest habitat, whereas the perissodactyls (foliivores) were favoured in more open habitats (C. Janis and P. Gingerich, personal communication).

Fig. 2 Comparison of the five species of phenacodontid condylarths from the Elk Creek Section of the central Bighorn Basin. a, *Ectocion osbornianus* (YPM 21211); b, *Phenacodus vortmani* (YPM 31949); c, *P. brachypternus* (YPM 22963); d, *P. intermedius* (YPM 32416); e, *P. primaevus* (YPM 25502). All specimens show right P_4 – M_1 or P_4 – M_2 in occlusal view and represent only a portion of the preserved specimen. Note the similarity in size between *Ectocion* and *P. brachypternus*, and the elongated P_4 of *P. brachypternus*.

The exclusion and subsequent return of the two small *Phenacodus* species may be attributed to an increase in competition with *Ectocion*. That this increase in competition was influenced by external factors is seen in the later decline of *Ectocion*, and the correlation of the species-sequencing events with high species turnover rates and changing environments at Biohorizons A and B. The shifts in the environment that led to these events were probably of a more subtle nature than those that led to the general decline of the Phenacodontidae.

Documentation of the discontinuity in the temporal range of *Phenacodus brachypternus*, with its unifying morphology of disjunct samples, is important because it allows recognition of gaps in the distribution of species where the morphology is ambiguous, as is the case for *P. vortmani*. Preliminary work indicates that coincident gaps also occur in the ranges of the condylarth *Hyopsodus* cf. *simplex*, in a species of the perissodactyl genus *Hyracotherium*, and to a lesser degree in the primate *Pelycodus mckennai* and the arctocyonid *Thryptacodon antiquus*.

More significantly, perhaps, the temporal gaps demonstrate the importance of the biogeographical or environmental component in influencing the species-sequencing patterns in a single basin. The first appearance of a lineage within a stratigraphical sequence cannot necessarily be treated as a speciation event but might be regarded rather as immigration, either from a different geographical area or a previously unsampled habitat. The phyletic linkage of a species with its nearest stratigraphical congener is not necessarily the most parsimonious of possible evolutionary patterns. Documentation of discontinuities in the morphology of successive species within a single basin offers no real evidence for either phyletic gradualism or punctuated equilibria. The long-term stasis in morphology and size shown by the four species of *Phenacodus* conforms to the pattern expected in a model of evolution by punctuated equilibria. However, shifting geographical ranges under the influence of a changing environment, rather than speciation, seems to be an adequate explanation for the observed pattern.

I thank P. Gingerich, R. Bakker, D. Rubenstein, D. Baird and J. Horner for reviewing the manuscript and for constructive criticism. Support for this project was provided in part by NSF Doctoral Dissertation Improvement Grant DEB76-22769 and a Sigma Xi research grant.

Received 5 May; accepted 17 July 1981.

- Gingerich, P. D. *Nature* **248**, 107–109 (1974).
- Gingerich, P. D. *Am. J. Sci.* **276**, 1–28 (1976).
- Gingerich, P. D. & Simons, E. L. *Contr. Mus. Paleont. Univ. Mich.* **24**, 245–279 (1977).
- Gingerich, P. D. & Gunnell, G. *Contr. Mus. Paleont. Univ. Mich.* **25**, 125–153 (1978).
- Bookstein, F. L., Gingerich, P. D. & Kluge, A. G. *Paleobiology* **4**, 120–134 (1978).
- Gould, S. J. & Eldredge, N. *Paleobiology* **3**, 115–151 (1977).
- Schankler, D. M. *Univ. Mich. Pap. Paleont.* **24**, 99–114 (1980).
- Bown, T. & Kraus, M. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **34**, 1–30 (1981).
- West, R. M. *Contr. Biol. Geol. Milwaukee publ. Mus.* **6**, 1–78 (1976).
- Granger, W. *Bull. Am. Mus. nat. Hist.* **34**, 329–361 (1915).
- Simpson, G. G. *Am. Mus. Novit.* **954**, 1–24 (1937).
- Gingerich, P. D. *J. Paleont.* **48**, 895–903 (1974).
- Gingerich, P. D. & Winkler, D. A. *J. Mammal.* **60**, 691–704 (1979).
- Gingerich, P. D. & Ryan, A. S. *Primates* **20**, 141–159 (1979).
- Guthrie, D. A. *Ann. Carneg. Mus.* **43**, 47–113 (1971).
- Rose, K. *Univ. Mich. Pap. Paleont.* (in the press).
- Gazin, C. L. *Smithson. misc. Collns* **149**, 1–98 (1965).
- Wing, S. *Univ. Mich. Pap. Paleont.* **24**, 119–125 (1980).

Abolition of seasonal embryonic diapause in a wallaby by pineal denervation

Marilyn B. Renfree*, D. W. Lincoln†, O. F. X. Almeida‡ & R. V. Short‡

* School of Environmental and Life Sciences, Murdoch University, Western Australia 6150, Australia

† Department of Anatomy, The Medical School, University of Bristol, Bristol BS8 1TD, UK

‡ MRC Reproductive Biology Unit, 37 Chalmers Street, Edinburgh EH3 9EW, UK

Embryonic diapause is a widespread phenomenon in mammals and may be controlled either by lactation or by seasonal environmental factors¹. A few species, such as the tamar wallaby, *Macropus eugenii*, use both mechanisms, depending on the time of year. On Kangaroo Island, South Australia (latitude 36° S), female tamar wallabies give birth to a single young in late January or early February². Mating occurs on the day after birth and the resulting conceptus grows to a 100-cell blastocyst before entering a state of embryonic diapause. This arrest of embryonic growth is due to a suppression of the corpus luteum by prolactin induced by the young in the pouch sucking the teat (lactational diapause)^{3,4}. If the young is removed from the teat between February and early June, the corpus luteum hypertrophies, the blastocyst resumes growth and birth occurs 27 days later⁵. In the second half of the year (June to December), diapause is not solely dependent on the sucking stimulus as it is maintained after weaning, which usually occurs in October, or following experimental removal of the pouch young. This is referred to as seasonal diapause⁵. Reactivation occurs on or about the summer solstice (22 December) and there is evidence that it is photo-periodically induced⁶ (Fig. 1). We report here that bilateral removal of the superior cervical ganglion in female tamar wallabies eliminates seasonal embryonic diapause, but has no effect on lactational diapause. This is the first evidence that the pineal gland may be involved in regulation of embryonic diapause in mammals.

Twelve wallabies in lactational diapause with pouch young of similar ages were operated on in March and April and the first week in May 1980. In eight of these animals, the superior cervical ganglia were removed bilaterally, fixed in glutaraldehyde and examined histologically to confirm the presence of ganglion cells. Four animals served as sham-operated controls and a further nine unoperated animals were maintained in parallel. The animals were kept in a large outdoor enclosure together with three males at Murdoch University, Western Australia (latitude 32° S). To examine the effects of ganglionectomy on pineal function, blood samples were collected from a lateral tail vein at 12.00 and 24.00 h on the day before surgery and again some weeks after the operation, and the levels of melatonin determined by a modified radioimmunoassay⁷.

Table 1 Effect on embryonic diapause of the bilateral removal of the superior cervical ganglia from the tamar wallaby

Treatment group	No. of mothers with small pouch young in February 1980	No. of young born May to July 1980, pouch young of February left <i>in situ</i>	No. of young born August to November 1980	Mothers giving birth to new young in February 1981
Ganglionectomy (March to early May)	8	0	24	(Young of November left <i>in situ</i>)
Sham-operated* (March to early May)	4	0	0	9/12
Unoperated	9			

* Number reduced to three in September when one wallaby was culled due to an eye infection.

Further plasma samples were taken every 3 h over a 27-h period in August and November.

The removal of the superior cervical ganglia had no effect on lactational diapause. In late July, four of the ganglionectomized wallabies lost their pouch young, two of which were recovered dead; these two were small for their age. This was also the case for all the pouch young still carried by the other ganglionectomized animals. All eight ganglionectomized animals had smaller mammary glands than did control animals, suggesting that the operation had interfered with mammary development.

To determine whether ganglionectomy had affected seasonal diapause, pouch young were removed from the wallabies on 1 August (Table 1). This resulted in the immediate resumption of blastocyst growth in seven of the eight ganglionectomized wallabies, and they gave birth 27–28 days later. They subsequently came into oestrus, ovulated and their blastocysts entered lactational quiescence. By contrast, none of the 13 controls gave birth. During the next 4 months of seasonal diapause, any new pouch young were removed every 30–35

Fig. 1 Diagrammatic illustration of the reproductive pattern of the tamar wallaby *M. eugenii*, and the experimental protocol used to study the effect of removing the superior cervical ganglia on embryonic diapause. Ovulation, mating and fertilization (O) occur within 24 h of giving birth (B) but the blastocyst so formed normally remains in a state of diapause (suspended animation) for 11 months induced initially by the sucking of the pouch young ('lactational diapause'). Later in the year diapause is maintained in the absence of a pouch young by seasonal constraints ('seasonal diapause'). At about the time of the summer solstice, the blastocyst recommences growth (A) and a baby weighing <0.5 g is born 27 days later (B). The object of the experiment was to determine whether removal of the superior cervical ganglia (SCG) from the mother would influence the duration of seasonal diapause after the removal of the sucking pouch young (RPY).