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Table 1 Results of depth tracking for four specimens of *Nautilus*

Name	Sex	Dates of observation	Time	Mean day depth† (m)	Mean night depth† (m)
Yellow	M	24–30 June 1983	152	290	153
Blue	F	4–15 July 1983	266	329	260
Green	M	26–27 June 1983	34	441	321
Red	F	7–15 July 1983	32	120	87

* Hours under observation.

† Derived from daytime and nighttime depth figures, with a maximum of two readings during any single hour being included. In the case of Yellow the mean depth figures were computed by integrating the depth curves.

on this southwestern horizontal movement was vertical movement, which was accomplished by inshore and offshore motion. Because of the steepness of the Palauan reefs, very short horizontal distances resulted in large vertical displacements. The Blue animal, followed for the longest period, travelled a total of 16 km along the reef front during the 10-day observation period. Horizontal movements of a similar magnitude have been observed previously for longer time periods in this population of *Nautilus*⁸.

The depths at which *Nautilus* were found, as computed from the ultrasonic emissions, were compared with the bottom depth recorded nine times using a fathometer. The two depths differed significantly in only two cases, both involving the Blue transmitter. On 7 October 1983 Blue was followed for about 6 h as it ascended from 250 m depth to 150 m. At the end of this period the animal resettled to the bottom, after having travelled ~1 km horizontal distance. Although *Nautilus* appear to move mainly on the bottom, there does seem to be some movement within the water column.

We thank James McKibben for construction of the transmitters. This work was carried out at the Marine Mariculture Demonstration Center, Palau. Mr Tosh Paulis helped with boat acquisition. This work was supported by NSF grant PCM 8202891.

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1. Wiley, A. *Proc. zool. Soc. Lond.* 7–9 (1899); *Zoological Results* Part IV, 750–830 (Cambridge University Press, 1902).
2. Stenzel, H. *Treatise on Invertebrate Paleontology*, (ed. Moore, R. C.) 59–93 (University of Kansas Press, 1964).
3. Heptonstall, W. *Lethaia* 3, 317–328 (1970).
4. Mutvei, H. & Reymont, R. *Paleontology* 16, 623–636.
5. Denton, E. & Gilpin-Brown, J. *Adv. mar. Biol.* 11, 197–268 (1973).
6. Ward, P. *Paleobiology* 6, 32–43 (1980).
7. Ward, P. *Paleobiology* 5, 415–422 (1979).
8. Saunders, W. B. & Spinosa, C. *Science* 204, 1199–1201 (1979).

Gradual phyletic evolution at the generic level in early Eocene omomyid primates

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Analysis of dental morphology in over 600 stratigraphically controlled specimens of tarsier-like primates from early Eocene strata in the Bighorn Basin, Wyoming, provides important new data for understanding the tempo and mode of evolution in primates. Here we describe two evolutionary transitions at the generic level in separate lineages of the family Omomyidae. In both lines transformation occurred not only continuously (rather

than by abrupt appearance of new morphologies followed by stasis), but also in mosaic fashion, with greater variation in certain characters preceding a shift to another character state. In one lineage this resulted in a significant change in dental adaptation. These data support a gradual model of dental evolution and are inconsistent with the punctuated equilibria model. Together with other reported cases, the data suggest that gradualism is much more prevalent than proponents of punctuated equilibria have argued.

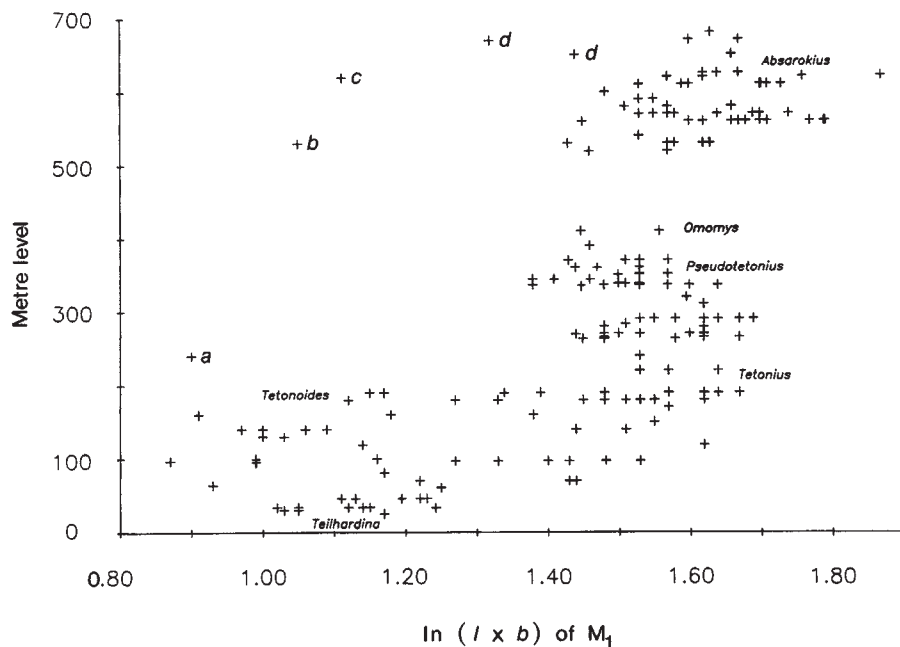
The early Eocene sequence of the Willwood Formation in the Bighorn Basin, Wyoming, is more than 700 m thick, spans about 4 Myr and is among the richest areas for fossil vertebrates in the world. Because of excellent stratigraphical control, samples from these deposits constitute some of the most important data for studies of mammalian evolution^{1–12}, including the largest and most diverse collection of omomyid primates known from any basin. This collection is now several times larger than the largest sample studied by previous workers, and nearly all specimens are tied into measured stratigraphical sections.

The omomyid samples have been assigned to at least six species in as many as six genera: *Teilhardina americana*, *Tetonoides tenuiculus*, *Tetonius homunculus*, *Pseudotetonius ambiguus*, *Absarokius abbotti* and *Omomys vespertinus*^{7,13–20}, and several undescribed species (Fig. 1). The systematics of these fossils is still under study, and it is clear that previous understanding of most of them was very incomplete. Our studies indicate that all of these species are valid, but it is debatable how many genera are represented. Here we provide evidence for the transitions between *Tetonius homunculus* and *Pseudotetonius ambiguus* and between *Teil. americana* and *Tetonoides tenuiculus*. Detailed justification will be provided elsewhere for recognition of *Teil. americana* and *P. ambiguus*, the validity of both of which has been questioned^{20–22}, but for this report, the taxonomy of the fossils is of less consequence than the evolutionary patterns they show.

All omomyids from the Bighorn Basin are conservative in molar morphology, differing consistently only in absolute size or relative breadth. Figure 1 shows that the molars separate to some extent on size alone. *Teilhardina* and *Tetonoides* are about the same size and are significantly smaller than *Tetonius* or *Pseudotetonius*, whereas the latter and *Omomys* are slightly smaller than *Tetonius*, and *Absarokius* is somewhat larger than *Tetonius*. Even so, the latter four taxa overlap substantially in molar size. To distinguish between them, differences in crown morphology, size and configuration of antemolar teeth are more important than molar size. Within each size group (Fig. 1), different morphologies are recognized under the specific names listed above, and our studies demonstrate that each comes from a restricted stratigraphical interval. Precise stratigraphical documentation has, therefore, been indispensable in determining relationships between species.

In the lineage from *Tetonius homunculus* to *P. ambiguus*, the anterior dentition evolved dramatically, while the molars and the last lower premolar (P_4) remained conservative. Here we apply the name *Tetonius homunculus* to the most primitive specimens (see also ref. 19), which have a relatively large, two-rooted P_3 , a very small, one-rooted P_2 , a moderate sized canine and second incisor (I_2), and an enlarged medial incisor (I_1). All such specimens (stage 1 in Fig. 2) are confined to the 180–190 m interval of the Willwood Formation in the principal study area (central and southern Bighorn Basin). *Tetonius* first appears at about 65 m but its anterior dentition is unknown below 180 m. Not all specimens in this lineage possess P_2 ; but from the stratigraphy it became clear that P_2 was lost after stage 1, beginning a trend toward progressive compaction and reduction of anterior teeth, except for I_1 which became larger with time. The name *Tetonius ambiguus* was first applied to a specimen showing extreme compression of the anterior dentition¹⁷, but with increasing knowledge of variation in samples allocated to *Tetonius*, *Tetonius ambiguus* was transferred to a new genus, *Pseudotetonius*¹⁴. *P. ambiguus*, here shown to be the end point of the lineage, is characterized by a much reduced P_3 with one

Fig. 1 Stratigraphical distributions of omomyid primates in the central and southern Bighorn Basin (Elk Creek, Fifteen-mile Creek and Sand Creek sections). Abscissa show the natural logarithm of crown area (mm^2) of the first lower molar; the ordinate represents the stratigraphical level in Willwood Formation. Some points represent more than one individual. Names are placed near clusters of specimens that can be referred on morphological grounds to the species listed in the text and points situated stratigraphically between them represent evolutionary intermediates. Points *a-d* denote individuals belonging to undescribed taxa. Some taxa overlap considerably in size range of M_1 , but their means may differ: for example, mean area of M_1 in *P. ambiguus* is less than in *Tetonius homunculus* and both are smaller than the mean for *A. abbotti*. Plots for other teeth show a similar pattern except that those based on P_3 and M_2 show greater separation between *Tetonius homunculus* and *P. ambiguus*, and that based on P_4 segregates *A. abbotti* more from other samples.



root or coalesced roots, absence of P_2 , diminutive canine and I_2 , and much enlarged I_1 (stages 4 and 5 in Fig. 2). The dentary anterior to P_4 is much shorter than in *Tetonius homunculus*. This morphology occurs in the 350–390 m interval in the study area, at the top of which *P. ambiguus* apparently became extinct (coinciding with an extinction-immigration event termed biohorizon B²³). Intervening strata have revealed morphologically intermediate specimens that record a gradual transition from *Tetonius homunculus* to *P. ambiguus* (Fig. 2).

Of particular interest is the mosaic pattern of change. Modi-

fications that characterize *Pseudotetonius* did not appear synchronously, and certain characters (for example, P_3 root configuration) were more variable during periods of change. P_2 disappeared between stages 1 and 2; P_3 gradually diminished in size throughout the sequence while its two roots became closely appressed and merged into one from stages 2 to 5; the canine and I_2 became gradually smaller up-section; and I_1 enlarged, principally in stages 3 to 5. There was also a slight reduction in mean lengths of P_4 and the lower molars in stages 3–5. The sum of changes during this transition reflect an adaptive

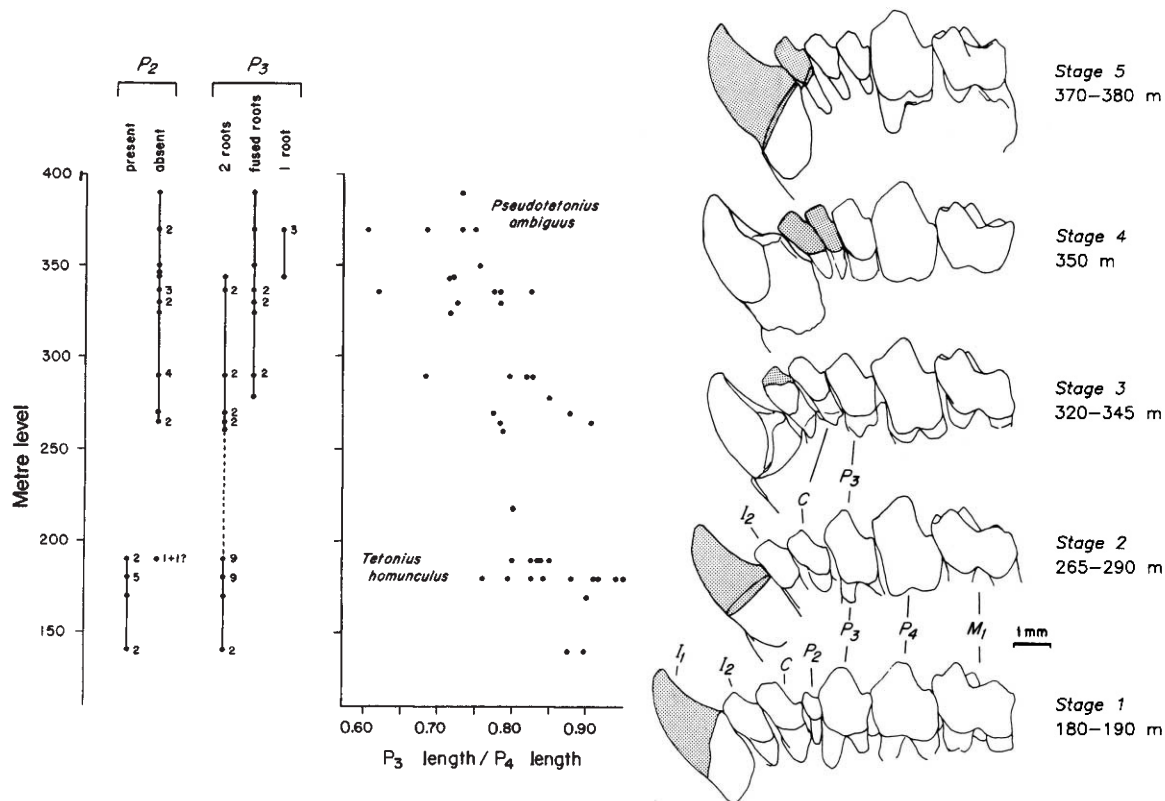


Fig. 2 Evolution of the anterior lower dentition in the *Tetonius homunculus*–*P. ambiguus* lineage from the central and southern Bighorn Basin. Stages in the transition are arbitrarily delimited by slight morphological differences and/or intervals with little or no data, and each is a composite dentition (M_{2-3} omitted) based on all known material from the indicated interval. Shaded parts are reconstructed from root size and known structure in other stages. The stratigraphical distribution of certain character states is shown on the left; numbers of individuals are indicated except where data points represent single specimens.

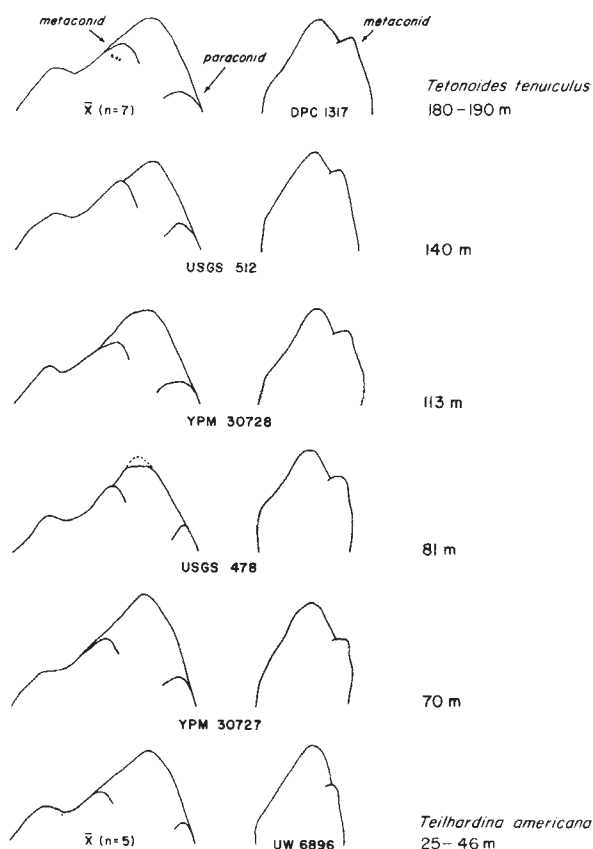


Fig. 3 Transformation of lower fourth premolar (P_4) in the *Teilhardina americana*-*Tetonoides tenuiculus* lineage. Left, computer-generated digitized lingual profiles, standardized to the same length so as to indicate only structural differences. Note the progressive enlargement and elevation of the metaconid and the elongation of the paraconid in successively higher strata. Right, camera lucida tracings, at constant magnification, of the back of the P_4 trigonid, showing the increase in size and height of the metaconid as well as increase in absolute breadth. Profiles for *Teilhardina americana* and *Tetonoides tenuiculus* are means computed from only complete, unworn specimens; other profiles depict individual specimens. Other known specimens from these levels conform to the morphologies shown.

shift to shorter-jawed omomyids with enhanced emphasis of the anterior grasping teeth and declining importance of the teeth just behind them.

Also found is a gradual transition from *Teilhardina americana* to *Tetonoides tenuiculus*, best documented in the morphology of the posterior lower premolars (P_{3-4}). *Teilhardina americana* is the oldest and most conservative North American omomyid^{13,24} and, as in European *Teilhardina belgica* [clearly its congener (K.D.R., T.M.B. and M. Godinot, in preparation)], the P_3 and P_4 are relatively high-crowned, pointed and bear small, low conids, which are more pronounced on P_4 ; the cheek teeth are not basally inflated. These features occur only in the lowest 50 m (25–50 m interval) of the study area. *Tetonoides tenuiculus* differs from *Teilhardina* chiefly in having relatively broader and lower cheek teeth and a more molariform P_4 , best illustrated by the higher, more salient paraconid and metaconid. Specimens in which this morphology is fully developed come from the 180–190 m interval in the study area. Fossils from intervening strata are intermediate between the two morphologies and become progressively more like *Tetonoides* up-section, the cheek teeth increasing in relative breadth and the paraconid and metaconid increasing in prominence with time (Fig. 3). At

no level in the section is there an obvious morphological shift (punctuation); rather, change appears to be continuous and gradual. *Tetonoides tenuiculus* was short-lived in the Bighorn Basin (but a few stratigraphically higher specimens may be related to it: Fig. 1a–c), although the genus is known from younger rocks in other basins^{25,26}.

Both of the phyletic transitions described here are also recorded in samples from the Clark's Fork Basin, 100 km north of the study area. Those samples show the same sequence of changes in both lineages as observed in the study area, thus providing independent confirmation of the patterns reported here.

The tempo and mode of evolutionary change continue to be among the most actively debated issues in evolutionary biology, with particular attention currently focused on punctuational and gradual models of evolution^{3,11,12,27–35}. The most convincing evidence for gradual evolution in fossil mammals has been advanced by Gingerich and colleagues^{1–6}, but these studies concentrate primarily on changes in molar size, and advocates of the punctuated equilibria model largely discount them^{11,12}. The transitions in two lineages of omomyid primates detailed here involve a mosaic of continuously changing features that document the gradual evolution of new morphological types of generic rank. Together with Gingerich's examples and other detailed cases of gradual evolution^{36–38}, our data suggest that phyletic gradualism is not only more common than some would admit but also capable of producing significant adaptive modifications.

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- Gingerich, P. D. *Nature* **248**, 107–109 (1974).
- Gingerich, P. D. *Am. J. Sci.* **276**, 1–28 (1976).
- Gingerich, P. D. *A. Rev. Earth planet. Sci.* **8**, 407–424 (1980).
- Gingerich, P. D. & Simons, E. L. *Contr. Mus. Paleont. Univ. Mich.* **24**, 245–279 (1977).
- Gingerich, P. D. & Gunnell, G. F. *Contr. Mus. Paleont. Univ. Mich.* **25**, 125–153 (1979).
- Bookstein, F. L., Gingerich, P. D. & Kluge, A. G. *Paleobiology* **4**, 120–134 (1978).
- Bown, T. M. *Mem. geol. Surv. Wyo.* **2**, 1–151 (1979).
- Bown, T. M. & Kihm, A. J. *J. Paleont.* **55**, 257–270 (1981).
- Rose, K. D. *Univ. Mich. Pap. Paleont.* **26**, 1–197 (1981).
- Schankler, D. M. *Nature* **293**, 135–138 (1981).
- Gould, S. J. & Eldredge, N. *Paleobiology* **3**, 115–151 (1977).
- Stanley, S. M. *Macroevolution* (Freeman, San Francisco, 1979).
- Bown, T. M. *Folia primatol.* **25**, 62–72 (1976).
- Bown, T. M. *Univ. Wyo. Contr. Geol.* **13**, 19–26 (1974).
- Jepsen, G. L. *Proc. Am. phil. Soc.* **69**, 117–131 (1930).
- Cope, E. D. *Proc. Am. phil. Soc.* **20**, 139–197 (1882).
- Matthew, W. D. *Bull. Am. Mus. nat. Hist.* **34**, 429–483 (1915).
- Simons, E. L. *Primate Evolution* (Macmillan, New York, 1972).
- Szalay, F. S. *Bull. Am. Mus. nat. Hist.* **156**, 157–450 (1976).
- Gingerich, P. D. *J. hum. Evol.* **10**, 345–374 (1981).
- Szalay, F. S. & Delson, E. *Evolutionary History of the Primates* (Academic, New York, 1979).
- Szalay, F. S. *Folia primatol.* **37**, 153–162 (1982).
- Schankler, D. M. *Univ. Mich. Pap. Paleont.* **24**, 99–114 (1980).
- Savage, D. E., Russell, D. E. & Waters, B. T. *Géobios Mém. spéc.* **1**, 159–164 (1977).
- Gazin, C. L. *Smithson. misc. Collns* **144**, no. 1, 1–98 (1962).
- Savage, D. E., Waters, B. T. & Hutchison, J. H. in *Field Conference on Tertiary Biostratigraphy of Southern and Western Wyoming* (ed. West, R. M.) (1972).
- Eldredge, N. & Gould, S. J. in *Models in Paleobiology* (ed. Schopf, T. J. M.) (Freeman, San Francisco, 1972).
- Vrba, E. S. *S. Afr. J. Sci.* **76**, 61–84 (1980).
- Stebbins, G. L. *Evolution* **36**, 1109–1118 (1982).
- Mayr, E. *Evolution* **36**, 1119–1132 (1982).
- Schopf, T. J. M. *Evolution* **36**, 1144–1157 (1982).
- Levinton, J. S. & Simon, C. M. *Syst. Zool.* **29**, 130–142 (1980).
- Williamson, P. G. *Nature* **293**, 437–443 (1981).
- Stanley, S. M. *Evolution* **36**, 460–473 (1982).
- Charlesworth, B., Lande, R. & Slatkin, M. *Evolution* **36**, 474–498 (1982).
- Ozawa, T. *Mem. Fac. Sci. Kyushu Univ., ser. D. Geol.* **23**, 117–164 (1975).
- Dzik, J. & Trammer, J. *Acta palaeont. pol.* **25**, 55–89 (1980).
- Malmgren, B. A. & Kennett, J. P. *Paleobiology* **7**, 230–240 (1981).