on the palate (J.A.H., unpublished). All of the above genera are similar in possessing the presumably derived condition of a short snout lacking a constriction behind the incisor region. *Tritylodon* (J.A.H., unpublished) and *Oligokyphus*[9] have a short premaxilla and a long narrow snout with a mid-length constriction; these features are found both in early mammals[21] and in gomphodont cynodonts (J.A.H., unpublished) and thus are considered primitive for tritylodontids. The interrelationships of tritylodontid genera (Fig. 4) suggest that a small number of cusps in the upper postcanine teeth is a derived condition.

The close relationship of *Bocatherium* to *Bienotheroides* and *Stereognathus* suggests that the Mexican form may also be post-early Jurassic in age; it is certainly younger than late Triassic. A Jurassic age for the upper part of the La Boca Formation is consistent with the stratigraphical[18] and palaeomagnetic[19] evidence. We believe *Bocatherium* to be the oldest terrestrial vertebrate known from Mexico. If the upper part of the La Boca Formation proves to be middle Jurassic in age, *Bocatherium* will be the first terrestrial vertebrate of this age in North America[22,23].

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# Neo-darwinian evolution implies punctuated equilibria

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**The two central elements of neo-darwinian evolution[1,2] are small random variations and natural selection. In Wright's view, these lead to random drift of mean population characters in a fixed, multiply peaked 'adaptive landscape', with long periods spent near fitness peaks[3,4]. Using recent theoretical results[5], we show here that transitions between peaks are rapid and unidirectional even though (indeed, because) random variations are small and transitions initially require movement against selection. Thus, punctuated equilibrium[6,7], the palaeontological pattern[8,9] of rapid transitions between morphological equlibria, is a natural manifestation of the standard wrightian evolutionary theory and requires no special developmental, genetic or ecological mechanisms[10–13].**

The simplest neo-darwinian model for the evolution of the population mean $\bar{x}$ of a genetically determined character expresses the change $d\bar{x}$ in time interval $dt$ as the sum of a natural selection term and a random variation term:

$$d\bar{x}(t) = F'(\bar{x}(t)) + \alpha \, dW(t) \quad (*) \qquad (1)$$

$F(\bar{x})$, a one-dimensional genotypic[3] or phenotypic[14] adaptive landscape, describes the mean population fitness. If, for example, the slope $F'$ is positive (a rising landscape) at $\bar{x}(t)$, natural selection pushes $\bar{x}$ towards larger values. The parameter $\alpha$ gives the magnitude of random variations relative to that of natural selection. The random process $W(t)$, a standard brownian movement with zero mean drift, represents, for example, genetic drift and short-term environmental fluctuations showing no obvious trend. We assume, for simplicity, that $\alpha$ is independent of $\bar{x}$.

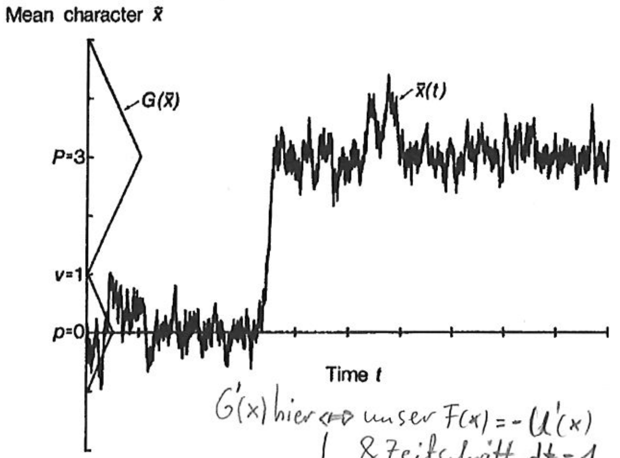


**Fig. 1** Punctuated equilibria in a numerical solution of the discrete time equation, $\bar{x}(t+1) - \bar{x}(t) = G'(\bar{x}(t)) + sw_t$. The landscape $G$ has a lower peak at $\bar{x}=0$, a valley at $\bar{x}=1$ and a higher peak at $\bar{x}=3$; its slope, $G'$, takes only the values +0.01 or −0.01. $w_t$ Represents the sign of random variables, $s$ their magnitude. For each $t$, $w_t$ is independently +1 or −1 with equal probability; $s=0.07$. The jagged line plots $\bar{x}(t)$ for 5,000 time units. As theory predicts, during the transition between peaks, $\bar{x}$ moves from 0 to 1 as if the direction of natural selection were reversed, that is, at the same speed that $\bar{x}$ moves by natural selection from 1 to 3.

Suppose that the landscape is doubly peaked: as $\bar{x}$ increases, $F$ rises to a peak at $\bar{x}=p$, declines to a valley at $\bar{x}=v$, rises to a second higher peak at $\bar{x}=P$, then declines. Let the initial value $\bar{x}(0)$ be smaller than $v$. To mimic the fossil record, suppose $\bar{x}(t)$ is observed, not continuously, but at some finite (perhaps large) number $N$ of epochs $0 < t_1 < \ldots < t_N$, perhaps chosen by another random process modelling stratigraphic sampling. There is a natural timescale $\tau_\alpha$ associated with transitions from the smaller to the larger peak which increases dramatically as $\alpha$ decreases. We suppose that the intervals between observations are, for small values of $\alpha$, proportional to $\tau_\alpha$.

Under these assumptions[5], for small $\alpha$, the observed $\bar{x}(t_i)$ values behave quite differently from $\bar{x}(t)$ itself, which is intrinsically continuous. As $\alpha$ approaches 0, the observed values become fixed exactly at $p$ for some random (exponentially distributed) time, then jump (apparently) instantaneously to $P$

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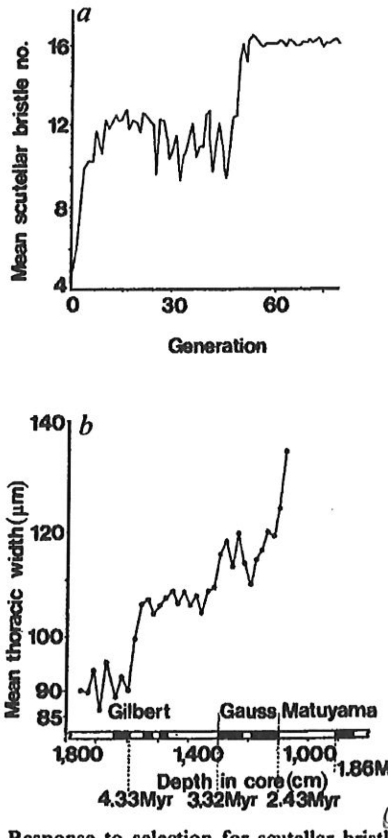
(*) $\frac{F'(x)}{dt}$ hier ⟺ unser $F(x) = -U'(x)$




(*)

**Fig. 2** *a*, Response to selection for scutellar bristle number in female *Drosophila* (presumably *melanogaster*; species not given[16]) according to MacBean *et al.*[16], as simplified by Parsons[18]. *b*, Increase in thoracic width of the Antarctic radiolarian *Pseudocubus vema* during ~2.5 Myr according to Kellogg[17], as simplified by Parsons[18].

(**)

and remain there (apparently) indefinitely. Analogous results hold if $F$ has more than two peaks[5] or if $\bar{x}$ is multidimensional[15].

To understand this result, note that a movement of $\bar{x}$ from $p$ to $v$ goes against the influence of natural selection and, for small $\alpha$, is very improbable. Improbable events eventually occur (with timescale $\tau_\alpha$) and then by the most likely of the improbable alternatives. Here it is most likely[5] that small random variations combine to push $\bar{x}$ from $p$ to $v$ as if the direction of natural selection were reversed, hence rapidly and unidirectionally. Once at $v$, the move to $P$ is by natural selection. The rapidity of the second part of the transition is well recognized[4], whereas that of the first part seems largely unknown.

Figure 1 is a computer simulation illustrating the theoretical results about equation (1). For comparison, Fig. 2 shows examples[16,17] (from ref. 18) of observed punctuated equilibria with two different timescales.

In a changing landscape, punctuation can be triggered by selection, rather than drift, either by a rapid (for example, environmental) change[19] or after a gradual change eliminates the currently occupied peak[13]. The introduction of a rare selectively superior mutant into a population from which it was previously absent can lead to punctuation[20,21] corresponding to transition from an unstable equilibrium in a fixed landscape. Our analysis is the first to show that transitions between stable equilibria, triggered by drift in an unchanging adaptive landscape, should have fossil records indistinguishable from punctuations triggered by selection.

Gradual evolution is only possible in an unchanging landscape either if $\alpha$ is not small (violating neo-darwinian assumptions) or if sampling intervals are as short as the timescale of natural selection (unusual in fossil records). Even assuming many peaks, the suggestion[20,22] that stepwise changes will appear to be gradual on a coarse timescale seems to be inconsistent with Wright's model: an increased timescale of observation implies[5] that more local peaks are skipped over apparently instantaneously and stasis is observed only at higher fitness levels.

Gradual evolution is possible in a changing landscape if peaks shift gradually and unidirectionally. Our analysis suggests a resulting palaeontological pattern of 'punctuated shifting equilibria' as the gradual evolution of a population following a moving peak is punctuated by rapid transitions between peaks. It is unclear whether such changing landscapes should occur commonly.

Models similar to that described in equation (1) are applicable directly to populations that are panmictic or have much migration and hence are geographically homogeneous. Because the timescale $\tau_\alpha$ is a rapidly increasing function of population size, equation (1) predicts stasis and punctuation for a small to moderate population but only stasis for a large population.

The model in equation (1) may be applied to an isolated subpopulation with a smaller $\tau_\alpha$ than the larger parent population. Allopatric speciation will occur if the subpopulation, after transition to a new peak, cannot interbreed with the parent population. Without requiring special 'genetic revolutions',[23] our analysis predicts that punctuated equilibria will be associated with the branching speciation of isolated subpopulations.

Generalizations of equation (1) incorporating spatial inhomogeneity in a local mean character correspond to Wright's notion of local populations in his shifting balance model[3,4], in which he suggested that speciation could occur without physical barriers to migration and gene flow[23]. Mathematically nonrigorous[24,25] and rigorous[26] results suggest that punctuation occurs on the timescale $\tau$ needed to form by random drift (against natural selection) a 'critical droplet' (that is[23], a geographical region where transition to a higher peak of fitness occurs) which is of sufficient size to resist swamping by gene flow; such a critical droplet spreads rapidly by selection. The timescale $\tau$ is a slowly decreasing function of population size[27] (for fixed spatial density) because a critical droplet can form in each local subrange[4,23]. Unlike $\tau_\alpha$, this $\tau$ need not exceed geological timescales even for very large populations.

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