

divided by 79 sample points). If a typical replacement time is significantly less (selective advantages of 10^{-4} – 10^{-5} per year), our hypothesis may well be correct. Note that other well-documented studies claiming support for gradualism appear to have scale resolutions significantly greater than this. These researchers may be sampling at too coarse a time scale to detect 'punctuational' events (See Table below).

Table

| | Studies in support of gradualism | Time-scale resolution (total time span/total no. of samples)(yr) | Organism |
|---|-----------------------------------|--|----------------|
| a | Cronin <i>et al.</i> ² | 625,000 | Hominids |
| b | Ozawa ³ | 440,000 | Foraminiferans |
| c | Gingerich ⁴ | 90,300 | Condylarths |
| d | Kellogg ⁵ | 74,700 | Radiolarians |

a, 625,000 = 2.5 Myr time span divided by four sample points (measuring cranial capacity). Includes specimens of *Australopithecus africanus*, *Homo habilis*, *Homo erectus* and *Homo sapiens*. b, 440,000 = 15 Myr time span divided by 34 sample points. c, 90,300 = 3.07 Myr time span divided by 34 sample points; *Hyopsodus*. d, 74,700 = 2.54 Myr time span divided by 34 sample points. All total time spans were estimated from author's graphs.

1. Ginzburg, L.R. *Paleobiology* xxx.

2. Cronin, J.E. *et al.* 1981. *Nature* 292, 113 (1981).

3. Ozawa, T. *Mem. Fac. Sci. Kyushu Univ. Ser. D. Geol.* 23, 117 (1975).

4. Gingerich, P.D. *Am. J. Sci.* 276, 1 (1976).

5. Kellogg, D.E. *Paleobiology* 1, 359 (1975).

Punctuated equilibria and punctuated environments

from D.W. Lindsay

EVOLUTION is not an event which occurs without external agency. A selective pressure is necessary for evolution to occur and must be an important determinant of the rate of evolution. Where such rates appear to vary, as Williamson's study shows, surely the first aspect of the problem to receive attention should be the selective pressures involved. In a stable lacustrine environment, as seems to have existed between the bouts of 'speciation' described by Williamson, selective pressures may have been low or minimal so that a lack of change in a few correlated characters seems rather unsurprising. Equally unsurprising are sudden series of changes coinciding with 'major lacustrine regressions'. These would clearly introduce marked selective pressures and a consequent flurry of genotypic and phenotypic experimentation until adaptation had been attained, or not,

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and the environment stabilised. Thus, observations of stasis interspersed with rapid change may simply reflect changes in the direction and intensity of the selective pressures which are implied by the stratigraphic record. Generally, we ought to consider a punctuated environment in thoughts on punctuated evolution. It is a sad fact of paleontology that the conditions of stable, prolonged sedimentation which favour preservation may lead to low rates of evolution, while periods of environmental hiatus which would have accelerated the process may often be lost in the unconformities. □

Williamson replies:

In answer to Mayr's first point: It is surely unnecessary to postulate that *all* the clones of *Melanoides* present in the Turkana Basin underwent parallel genetic changes during the episodes of morphological transformation at the Suregei and Guomde levels. It seems more probable that one, or a few, such clones made an appropriate evolutionary response to the relevant selective pressures, and that, as these few clones evolved, they proceeded to outcompete other 'conspecific' clones. Such interclonal competition is well documented¹, and Mayr himself has suggested competitive elimination of inferior clones as the probable mechanism whereby discontinuities between closely related asexual 'species' arise². I address Mayr's further suggestion (that the morphological transformations documented in the Turkana sequence are purely ecophenotypic reactions) below.

In response to Mayr's second point: The variability (c.v.) of all measured traits in populations of the asexual taxon *Melanoides tuberculata* are quite comparable to the variabilities documented in typical populations of the gonochoristic gastropod taxa³.

Mayr's third point: The details surrounding the sudden reinvasion of parental stocks into the basin above the Suregei Tuff level speciation event, synchronous with a major lacustrine transgression, are at present poorly understood. Some 2-3 metres of fossiliferous sediment separates the last of the novel Suregei level forms from the first of the returning ancestral stocks. No hybrids, sympatric faunas or intermediates are currently known. It is not therefore possible to distinguish between Mayr's options (a), (b) and (c). But as discussed below, Mayr's option (d) appears untenable.

Mayr is correct in noting a set of speciation events in certain lineages in the Lower Member of the Koobi Fora Forma-

tion. These new forms appear suddenly in the record and coexist with their ancestral stocks; the event is therefore a modest adaptive radiation typical of that seen in many modern rift lakes. All these new endemics become extinct by the top of the Lower Member, due to a climatically induced regression — and consequent increase in alkalinity — well documented in the uppermost part of the Lower Member. It is indeed likely, that these new endemics arose in peripheral isolates of the large Lower Member lake, perhaps in the manner suggested by Hubendick⁴.

With reference to Mayr's last paragraph: I believe that it is indeed possible to resolve the conflict between Mayr's model of peripatric speciation and my observations in the Turkana Basin. I hope to address this topic in a forthcoming paper.

Boucot — and also Mayr — suggest that the novel forms I document as arising at the Suregei, Guomde, and Lower Member levels may simply be ecophenotypic 'reactive forms' of the 'ancestral' lineages. Several factors strongly indicate that this is not the case: (1) the novel forms arising in the Lower Member *coexist* with their presumed ancestral forms, and occur with them in the same 'life-assemblages'. The Lower Member novelties at least can not be simple ecophenotypic variants⁵. (2) The principle stem lineages in the Turkana Basin sequence are still extant and widely distributed in Africa, but even the most extreme modern environments in which these lineages occur at present produce a simple dwarfing of characteristic morphology (or *in extremis*, extinction of local populations), they never produce the striking reorganization of phenotype documented in the Turkana Basin sequence⁵. (3) The morphological transformations documented at the Suregei Tuff level are invariably unidirectional in character space, and required some 10^3 – 10^4 generations to accomplish⁶. This is hardly the nature or time-scale of a conventional ecophenotypic response⁵. The *magnitude* of phenotypic change during the Suregei and Guomde Level episodes is striking. In the bivalves, these changes involve a radical restructuring of shell form and hinge dentition, and major changes in the disposition of the muscle scars. The magnitude of the changes documented in both bivalves and gastropods is generally far greater than that observed in the ecophenotypic transformations of even the most plastic of modern African freshwater molluscs³. I do not therefore believe that the profound morphological transformations documented in the Turkana Basin sequence can be simply 'written off' as an ecophenotypic response.

Boucot expresses surprise that *all* lineages at the Suregei and Guomde levels speciate. But it has long been acknowledged that two major 'triggers' for speciation events within peripheral isolates are (1) isolation *per se* and (2)