Speciation in molluscs from Turkana Basin

SEVERAL of Williamson's conclusions on speciation in the freshwater molluscs of the Turkana Basin[1] are based on assumptions which need further examination. Here we comment on some relevant research in the Koobi Fora area.

Although the snail faunas collected by Williamson represent 'life and death assemblages'[1], he does not discuss the implications of this. We feel that the nature of the process of preservation may explain some morphological patterns in these fossil snails as well as the "instantaneous speciation" model proposed by Williamson. Our (A.C.) extensive bottom dredging of Lake Turkana shows that its modern molluscan assemblage consists of a mixture of stunted, transparent, living forms and long-dead, robust (bleached) specimens (with a few intermediate shells). The dead shells have been eroded from elevated Holocene and pre-Holocene lake beds. They occur both in shallow water (in which case most of the shells are broken) and in deeper water (where both broken and whole shells are present). The same patterns of deposition are found in Lake Naivasha (central Kenya rift valley).

Transported molluscan deposits in these lakes may therefore be mixed faunas containing individuals derived from sediments of different ages and of differing environmental origin. Assemblages of living snails in these modern lakes are much rarer than are such transported assemblages, and our observations have convinced us that the fossil deposits of Turkana Basin resemble those of the modern lake in this respect. We therefore challenge Williamson's statement[2] that "the faunal units concerned seem to be undisturbed life assemblages with no evidence of reworking" and note that in his original article[1] he states that they "represent both life and death assemblages". Given both the lack of information on the ancient environment and the nature of the evidence from the modern lake, we feel that Williamson's morphologically deviant populations (at the Suregei Complex, Lower Member and Guomde levels) may not represent instantaneous speciation as he suggests; if the deposits sampled at these horizons consist of transported assemblages the faunas could represent a mixture of individuals from geologically different periods or from geographically separated environments. Morphological deviants from one horizon would then reflect morphological change over extended periods of time or over long distances, and could say little about the nature of morphological changes in the single fossil populations.

Williamson bases his argument for rapid speciation on his observations of rapid morphological change at three stratigraphic levels. However, we believe that 'rapid' morphological shifts are not well substantiated for at least two of these. He documents his lineages using evidence from *Bellamya unicolor*. A summary of a canonical variate analysis for this lineage (p. 440 of ref. 1) illustrates increased phenotypic deviance at three levels, between populations 8–12c (Suregei Complex), 27–29 (Lower Member) and at 88 (Guomde Formation). There are several potential problems of interpretation here. In particular, Williamson's assertion that the periods of character variation begin and end abruptly (Fig. 4 of ref. 1) is not well supported by his data. Lengthy intervals of time may exist between those horizons exhibiting character deviance and those which precede and follow them. Nothing is known about the mode of evolution during these intervals. For example, Williamson's Figs 1 and 2 show that the first fauna which precedes fauna 8 and which contains *B. unicolor* (fauna 5b) lies 4.5 m below fauna 8. The next youngest fauna above 12c to contain *B. unicolor* (fauna 17) lies at least 30 m above the deposits containing highly deviant populations (fauna 17 actually lies much more than 30 m above fauna 12c, as an unspecified interval is shown between subsections 2 and 3 in Fig. 1). Similarly, in the next anomalous populations (faunas 27–29) no *B. unicolor* occur for about 12 m below or 1 m above deviant population 27.

Deviant population 88 has no stratigraphically close, nondeviant neighbours, and Fig. 4 is misleading in illustrating 'punctuated' shifts of morphology at this (the Guomde Formation) horizon; chronological gaps of unknown length lie at its upper and lower boundaries[3] so that it is difficult to estimate evolutionary rates from a comparison of the Guomde populations with their neighbours. The faunas at the Guomde level do not "clearly document speciation within peripheral isolates" as Williamson claims.

Williamson's Fig. 1 shows the stratigraphic positions of his molluscan faunas and that they were collected from geographically separate areas with most of the faunas (including two morphologically deviant populations, faunas 27 and 29) stratigraphically located between tuffaceous marker horizons. Williamson determined the stratigraphic placement of inter-tuff faunas by measuring the vertical distance from each faunal locality to the base of the nearest marker horizon, and assuming similar sedimentation rates in each area. However, sedimentation is known to be extremely variable in rate and character in lake deltas—a common palaeoenvironment in the north-east Turkana stratigraphic section[4,5]. We therefore question the accuracy of the ordering faunas in this area. For example, faunas collected from 2 m above the same tuff horizon, in separate areas, could be of different ages if they occur in different interfingering lithological units. Widely separated faunas would be more susceptible to ordering error, and this reduced stratigraphic resolution might further reduce the capacity of this to document episodes of speciation.

Williamson believes that lake regression was the primary cause of speciation events in the Turkana Basin. However, the fossil evidence does not support the view that a major regression occurred at the Suregei Complex horizon. In area 202, the Suregei Complex contains the diatoms *Melosira granulata*, *Melosira agassizi* and *Cyclotella meneghinana* (ref. 6 and J. Richardson, personal communication). In area 102 this complex comprises an open, deep-water (30 m) ostracod fauna, *Sclerocypris exserta* and *Gomphocythere* sp. Both of these are indicators of low to moderate alkalinity water[6], and therefore suggest accumulation during a period of high (rather than low) lake level. The following model may be a more satisfactory explanation of the appearance of derived morphotypes at the Suregei Complex horizon.

Deep lake populations of many sexual and asexual molluscs are commonly more variable than are littoral populations[7–9]. Organisms in deeper water tend to lose the dispersal capabilities found in shallow water species and normally exist as highly localized populations with restricted gene flow[10–12] and increased morphological divergence and speciation. For example, in old deep lakes, cosmopolitan molluscan taxa are generally restricted to littoral environments, whereas more derived, descendant forms are more abundant in deeper water[13].

Because most of the Turkana sediments represent marginal nearshore deposits, few of these ancient deep-water faunas have been observed. Williamson's 'speciation events' might represent incursions of deep water-derived morphotypes (perhaps even of different species) into shallow areas during brief periods of high lake level. Subsequent disappearance of such

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forms might indicate a return to shallower conditions.

This model of the environmental conditions associated with the appearance of novel forms is quite different from that of Williamson. It suggests that although changes in lake level may coincide with morphological change they are not the causes of speciation. Instead it suggests that the occasional invasion of deep water populations into the East Turkana fossil records, means that it is impossible to use them to estimate the rate of morphological change and hence to distinguish between punctuated and gradual evolution.

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1. Williamson, P. G. *Nature* **293**, 437–443 (1981).
2. Williamson, P. G. *Nature* **296**, 611–612 (1982).
3. Findlater, I. C. in *Koobi Fora Research Project Monogr.* **1**, (eds Leakey, R. E. F. & Leakey, M.) (Clarendon, Oxford, 1978).
4. Findlater, I. C. thesis, Univ. London (1976).
5. Johnson, G. D. & Raynolds, R. in *Earliest Man and Environments in the Lake Rudolph Basin* (eds Coppens, Y., Howell, F. D., Isaac, G. & Leakey, R. E. F) 115–122 (University of Chicago Press, 1976).
6. Cerling, T. E. thesis, Berkeley Univ. (1979).
7. Crowley, T. E., Pain, T. & Woodward, F. R. *Annls Mus. r. Afr. cent. Sér.* 8.
8. Stankovic, S. *Int. Ass. theor. appl. Limnol.* **12**, 478–507 (1953).
9. Khozov, M. *Monogr. Biol.* **11** (1963).
10. Mayr, E. in *Evolution as a Process* (eds Huxley, J., Hardy, A. C. & Ford, E. B.).
11. Greenwood, P. H. *Bull. Br. Mus. nat. Hist. Zool.* Suppl. 6 (1974).
12. Brooks, J. L. *Q. Rev. Biol.* **25**, 30–60 131–176 (1950).
13. Brown, D. S. *Freshwater Snails of Africa and their Medical Importance* (Taylor & Francis, London, 1980).

THERE are two views of evolutionary pattern and process: either that most change occurs during relatively brief periods of speciation (the punctuation model) or that such changes occur gradually in established lineages (the gradualistic model). Williamson[1] concludes from his study of fossil freshwater molluscs in Lake Turkana that evolutionary patterns correspond to the punctuation model. A major problem in the taxonomy of freshwater molluscs is that of extensive intra- and interpopulation variability, which is presumably of ecophenotypic origin. Most morphological characters chosen by Williamson to describe shell shape are indeed very variable. In consequence, what he describes as the simultaneous origin of new lineages could be no more than the simultaneous origin of new environmentally induced variants. In addition, Williamson's reconstruction of events underlying speciation largely ignores much previous evidence.

The systematics of freshwater molluscs has recently greatly been clarified by the study of soft parts such as the reproductive and digestive tracts, the mantle edge and the radular teeth[2,3]. Enzymatic, chromosomal and shell microstructural analyses are also invaluable in determining taxonomic identity in difficult groups[4–6]. The use of such taxonomic characters (which have high heritability) has had two effects on freshwater mollusc systematics; it has led to an appreciation of the degree of environmentally modified variability to which most freshwater molluscs are subject, and has led to the rejection of systems of classification based exclusively on shell characters such as shape, size, ornamentation or dentition. This poses a problem for fossil material because the taxonomically valuable characters are not preserved, and so identification must be based on characters with high levels of ecophenotypic variability.

Classification will then be prone to two errors; underestimation of the number of species in a fauna because of convergence of shell shape, and overestimation of species number because of extensive intraspecific variability (Fig. 1).

Convergence in shell shape and ornamentation is common among freshwater molluscs. For example, there is convergence on a particular shell sculpture and shape among gastropods of the families Hydrobiidae, Pomatiopsidae and Viviparidae[2,7]; chromosomal and molecular genetic analyses demonstrate parallel evolution in shell shape in pleurocerid gastropods[8,9]; and there is parallel evolution towards a lanceolate shape among species of the genus *Elliptio* (Fig. 2). Wetherby[10] discussed intraspecific variability a century ago, and a multitude of factors such as sediment type, water depth and composition, habitat type, wave exposure and currents, have now been shown to affect shell shape to a sufficient degree to cause species sampled from different habitats in the same drainage to exhibit a variety of non-overlapping phenotypes[11–14].

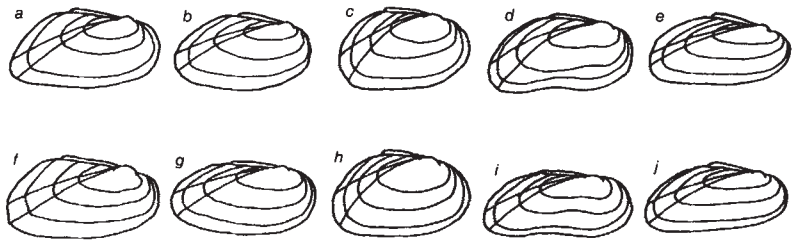

Fig. 1 An example of the wide range of phenotypic variability that can be present among species of the freshwater bivalve family Unionidae. In this case, variability expressed by *Elliptio complanata* (*a–e*) overlaps shapes typical of *Elliptio hopetonensis* (*f*), *Elliptio icterina* (*g*), *Elliptio congarea* (*h*), *Elliptio arctata* (*i*) and *Elliptio lanceolata* (*j*).

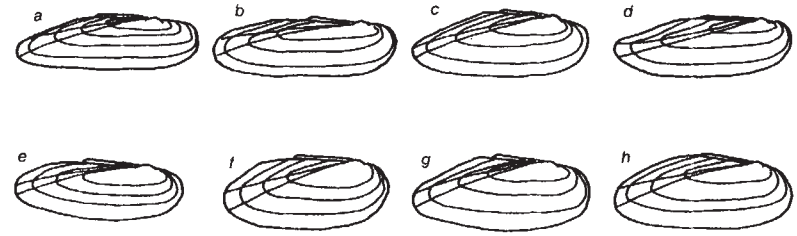

Fig. 2 Convergence on a lanceolate shape among unionid bivalves. *a*, *Elliptio shephardiana*; *b*, *Elliptio folliculata*; *c*, *Ligumia nasuta*; *d*, *Elliptio producta*; *e*, *Ligumia recta*; *f*, *Elliptio jayensis*; *g*, *Elliptio fisheriana*; *h*, *Elliptio lanceolata*.

However, Williamson[15] simply dismisses most of these problems of phenotypic variability. He devotes much attention to change in the *Bellamya unicolor* lineage, which is stated to correspond to patterns of change in the other lineage examined. The divergent forms of this species which arose during periods of lake regression are considered by Williamson to lie outside his conception of the narrow phenotypic range of *B. unicolor* and thus to constitute descendant species. However, it is clear in the context of the extensive information available on European and North American freshwater snails that the range of phenotypic variability expressed in these lineages is not at all narrow[16–19]. In addition, the Lake Tanganyika viviparid *Neothauma tanganyicense*[20,21] (which is closely related to *B. unicolor*) shows a range of variability within a single species in various habitats which completely overlaps that exhibited by the various phenotypes of fossil *B. unicolor* which Williamson considers to be distinct species (Fig. 3). Finally, Rohrbach[22] examined several variants of *B. unicolor* itself using reproductive tract anatomy, and rejected shell shape as a valid means of classification for the group.

Williamson stresses that speciation in the Lake Turkana fossil fauna coincides