E-MAIL CONTRIBUTIONS

One of this week's email contributors takes to task those who would hold up the *foraminifera* as an example of a gap free fossil record.

NORMAN MACLEOD

"Contrary to statements by [Pearson](#) and [Pawłowski & de Vargas](#) in this debate it should be noted that three decades of intense oceanographic and marine geological research have shown the (once) traditional model of deep-sea ocean basins as ultimate sediment traps to be an illusion¹⁻³. The deep-sea stratigraphical record is replete with hiatuses on all time scales³⁻⁵, intervals of wildly fluctuating sediment accumulation rates^{6,7}, and instances where the first and/or last appearance of microfossil species occurs at different time horizons in different sections/cores (diachrony) ⁸⁻¹¹.

Traditional microfossil biostratigraphy works not because all deep-sea stratigraphical successions contain the same sequence of first and last appearances (they do not), but because biostratigraphical zones are defined over relatively long time intervals (typically 10's of thousands of years, often 100's). Over these time scales the inherent diachrony of most zone-defining fossils is not noticed.

Zone-based biostratigraphical correlation presents a digital (not an analogue) representation of geological time that is punctured by many holes in sampling as well as recovery. Moreover, in the comparatively few cases in which a quasi-continuous and constant record of sediment accumulation might be preserved, the failure of most biostratigraphers to make detailed and internally-consistent comparisons with the stratigraphical records of other ocean basins means that speciation and migration events could become confused, as they often do in studies of other biotic groups.

Also, contrary to statements made by the above authors, recent molecular evidence from living planktonic foraminifera suggests that traditional stratophenetically-defined foraminiferal phylogenies are seriously in error. [Pearson](#) cited the study of de Vargas *et al.*¹² in support of his statement that "the genetic and fossil data [for planktonic foraminifera] are in broad agreement." However, a strict consensus analysis of the "molecular" and "fossil record" phylogenies shown in Figure 3 of de Vargas *et al.*¹² tells a different story (Fig. 1).

Figure 1 Strict consensus analysis of compatibility between molecular and "fossil record".

[High resolution image and legend](#)
(12k)

All of the deeper nodes in the globigerinid phylogeny are inconsistent between the two trees as are all of the globorotalid nodes. Since deep-level structure is almost always the primary

target of a phylogenetic analysis one must conclude (contrary to [Pearson](#)) that these data do not represent a justification for stratophenetics. In addition (as originally pointed out by de Vargas *et al.*¹²), these molecular data imply an independent origin for globorotalid and globogerinid clades from benthic ancestors; a hypothesis that has been consistently rejected by stratophenetic inference^{13,14}.

Last, but certainly not least, the temporal uncertainty associated with the divergence times of these stratophenetically-defined lineages (and shown in Fig. 3 of de Vargas *et al.*¹²) is typically on the order of several million years (for Neogene species!) and in many cases prevents an unambiguous assessment of ancestor-descendent relationships. This uncertainty is plainly at odds with the claims of [Pearson](#) and [Pawlowski & de Vargas](#) regarding the "precise calibration" of foraminiferal biostratigraphy to "radiometric" (or rather radioisotopic) time.

The microfossil record contains several striking and morphologically well-documented examples of undisputed continuous evolution with a lineage (anagenesis)¹⁵. However, the vast majority of described microfossil lineages exist as little more than names on diagrams joined by various types of lines. Often, these lineages are proposed without any formal reference to unique character-state transitions whatsoever^{14,16-19}. As a result, it is not unusual to find glaring disagreements between researchers with respect to the composition and/or structure of microfossil lineages²⁰.

If the tracing of microfossil lineages by stratophenetics were as simple as described by [Pearson](#) and [Pawlowski & de Vargas](#) this should not be the case. In addition, Pearson's suggestion that microfossil morphologies are so highly convergent that a formal character analysis is all but impossible seems very odd in the context of his argument. If convergence really were complete planktonic foraminiferal biostratigraphy (as well as phylogeny) would be hopeless. In point of fact, even character complexes that seem superficially identical contain unique morphological character states²¹ and many more characters are available in the so-called simple morphologies of microfossil shells than is evident at first glance^{20,22}.

Microfossils and the deep-sea fossil record may have much to teach us about evolutionary processes, but the fundamental nature of that record-rife with hiatuses and stratigraphical uncertainty, containing sets of morphologies, many of doubtful homology, with conflicting character-state distributions-is no different in kind than the stratigraphical records of many other fossil groups. The true evolutionary lessons of the microfossil record will likely remain obscure until micropaleontologists abandon their ill-advised adherence to stratophenetics and adopt a more rigorous approach to phylogenetic analysis based on well-tested cladistic principles."

Norman MacLeod

Division of Micropalaeontology, The Natural History Museum, London, U.K.

References

1. Keller, G. & Barron, J. A. Paleooceanographic implications of Miocene deep-sea hiatuses. *Geol. Soc. Am. Bull.* **94**, 590-613 (1983).
2. Keller, G. & Barron, J. A. Paleodepth distribution of Neogene deep-sea hiatuses. *Paleoceanography* **2**, 697-713 (1987).

3. Kennett, J. P. *Marine Geology* (Prentice Hall, Englewood Cliffs, New Jersey, 1982).
4. Sadler, P. M. Sediment accumulation rates and the completeness of stratigraphic sections. *J. Geol.* **89**, 569-584 (1981).
5. Schindel, D. E. Resolution analysis: a new approach to the gaps in the fossil record. *Paleobiol.* **8**, 340-353 (1982).
6. Vail, P. R., Mitchum, R. M. J. & Thompson, S. Seismic stratigraphy and global changes in sea level, part three: Relative changes of sea level from coastal onlap. *American Association of Petroleum Geologists Memoir* **26**, 83-98 (1977).
7. Loutit, T. S., Hardonbol, J., Vail, P. R. & Baum, G. R. in *Sea-Level Changes: An Integrated Approach* (Wilgus, C. K. *et al.* eds) 183-213 (Society of Economic Paleontologists and Mineralogists Special Publication 42, Tulsa, Oklahoma, 1988).
8. Dowsett, H. J. Diachrony of Late Neogene microfossils in the southwest Pacific Ocean: Application of the Graphic Correlation method. *Paleoceanog.* **3**, 209-222 (1988).
9. Dowsett, H. J. Application of graphic correlation to Pliocene marine sequences. *Marine Micropaleontol.* **14**, 3-32 (1989).
10. MacLeod, N. Punctuated anagenesis and the importance of stratigraphy to paleobiology. *Paleobiol.* **17**, 167-188 (1991).
11. MacLeod, N. & Keller, G. How complete are Cretaceous/Tertiary boundary sections? A chronostratigraphic estimate based on graphic correlation. *Geol. Soc. Am. Bull.* **103**, 1439-1457 (1991).
12. de Vargas, C., Zaninetti, L., Hilbrecht, H. & Pawloski, J. Phylogeny and rates of molecular evolution of planktonic foraminifera: SSU rDNA sequences compared to the fossil record. *Molec. Evol.* **45**, 285-294 (1997).
13. Cifelli, R. Early occurrences and some phylogenetic implications of spiny, honeycomb textured planktonic foraminifera. *J. Foraminiferal Res.* **12**, 105-115 (1982).
14. Pearson, P. N. A lineage phylogeny for the Paleogene planktonic foraminifera. *Micropaleontol.* **39**, 193-232 (1993).
15. Bolli, H. M. Evolutionary trends in planktic foraminifera from early Cretaceous to Recent, with special emphasis on selected Tertiary lineages. *Bulletin Centres Recherches Exploration-Production, Elf-Aquitaine* **10**, 565-577 (1986).
16. Hart, M. B. A water depth model for the evolution of the planktonic Foraminiferida. *Nature* **286**, 252-254 (1980).
17. Caron, M. La spéciation chez les foraminifères planctiques: une réponse adaptée aux contraintes de l'environnement. *Zitteliana* **10**, 671-676 (1983).
18. Kennett, J. P. & Srinivasan, S. *Neogene Planktonic Foraminifera: A Phylogenetic Atlas* (Hutchinson Ross, Stroudsburg, PN, 1983).
19. Tappan, H. & Loeblich, A. R., Jr. Foraminiferal evolution, diversification, and extinction. *J. Paleo.* **62**, 695-714 (1988).
20. MacLeod, N. The Maastrichtian-Danian radiation of triserial and biserial planktic foraminifera: Testing phylogenetic and adaptational hypotheses in the (micro)fossil record. *Marine Micropaleontol.* **21**, 47-100 (1993).
21. Norris, R. D. Parallel evolution in the keel structure of planktonic foraminifera. *J. Foraminiferal Res.* **21**, 319-331 (1991).
22. Berggren, W. A. & Norris, R. D. Biostratigraphy,

phylogeny and systematics of Paleocene trochospiral planktic foraminifera. *Micropaleontol.* **43**, 1-116 (1997).

Contributions to this debate from readers are encouraged, by e-mail only, please, to debates@nature.com.

The rules are simple: contributions should be short and to the point. The moderator reserves right to select contributions to be posted on the site, and to normal editing for style, sense, length and, of course, good taste.

Nature © Macmillan Publishers Ltd 1998 Registered No. 785998 England.