the submandibular gland showed that in the experimental animals there is a similar increase in the number of myelinated axons, compared with controls, all along the nerve, consistent with their arising from cells within the ganglion. Second, for both experimental and control animals, applying horseradish peroxidase to the nerve at the site near the gland where a sample was taken for electron microscopy resulted in an almost one-to-one agreement (95 per cent) between the number of axon profiles counted in electron micrographs and the number of retrogradely labelled neurons in the superior cervical ganglion. The source of the 5 per cent of axons that could not be accounted for by this labelling method is unknown and may well include the subpopulation of axons

that Garrett mentions persist after ganglionectomy.

In my experiments this 5 per cent fraction was far too small to explain the large numbers of myelinated axons, more than half the axons in the nerve in some cases, seen after increasing peripheral target size by partial denervation of the gland. Clearly, most of the myelinated axons in the nerve must be axons of superior cervical ganglion cells, which became myelinated as a result of the experimental manipulation.

JAMES T. VOYVODIC

Department of Biology,
University College London,
Gower St, London WC1E 6BT, UK

1. Garrett, J.R. *Nature* **345**, 28 (1990).
2. Voyvodic, J.T. *Nature* **342**, 430–433 (1989).

Shaking up evolutionary patterns

SIR—My report on parallel gradualistic evolution of Ordovician trilobites¹ kindled a lively discussion (see refs 2, 3). My findings were, of course, not an argument for the universality of gradualism, but suggested that many cases of gradualism are obscured by descriptive biases that generate an impression of punctuation and stasis, irrespective of the real pattern.

Punctuated equilibrium and phyletic gradualism are theoretical ends of a wide spectrum of possible evolutionary patterns. Nature will have found a great many ways of getting from A to B; at issue is the relative frequency of particular patterns. Undeniably, the net changes that the Builth trilobites show in about 3 million years¹ seem very slow on a geneticist's timescale. Nevertheless, the pattern of persistent phyletic evolution resembles the gradualism model far more than stasis. And as finer timescales are resolved the patterns become increasingly dynamic, with frequent short-term reversals of overall trends.

The Builth trilobites lived in a stable, narrowly fluctuating environment¹. One might expect a changing environment to lead to changing morphology, and a stable environment to stable morphology. But over long intervals the opposite may often occur. I suggested¹ that “perhaps . . . gradual phyletic evolution can only be sustained by organisms living in or able to track narrowly fluctuating, slowly changing environments, whereas stasis, almost paradoxically, seems to prevail in more widely-fluctuating, rapidly changing environments”. Evidence for this generalization is growing. It applies mainly to long-term physical variables such as sea level, substrate and climate, rather than ecological ones such as food availability and seasonal differences.

As Maynard Smith said³, “Stasis is a real phenomenon, and a fascinating one”. Morphological stasis lasting millions of years is common in shallow marine shelly

organisms such as bivalves, bryozoans and limulids. Cenozoic marine ostracods and Pleistocene beetles exhibit most stasis during major climatic oscillations.

Perhaps more widely fluctuating environments (on geological rather than ecological timescales) maintain their own kind of stability within wide reflecting boundaries, and selection soon favours lineages with ‘all-purpose’ hard-part morphologies that are relatively inert to each environmental twist and turn (see figure).

The saying “*Plus ça change, plus c'est la même chose*” may be very apt for the relationship between physical environment and phyletic evolution. In conditions that produce complex sedimentary sequences (with many lithological changes and hiatuses) the ability to track preferred environments would be a prime selection pressure, especially on benthic lineages. Whether by selection for habitat tracking or for eurytopy, such lineages might then experience widely fluctuating environments as stable until thresholds are

Model illustrating the hypothesis that persistent phyletic evolution is more characteristic of narrowly fluctuating, slowly changing environments (right), whereas stasis tends to prevail in more widely fluctuating, rapidly changing environments (left). The frequent reversals during gradual evolution are predicted on theoretical grounds¹. Env., some long-term aspect of environment, such as sea level or temperature. Mor., some aspect of hard-part morphology, such as mean number of ribs in molluscs or trilobites.

reached. As Coope suggested in the case of Pleistocene beetles⁵, strong selection for habitat tracking together with major climatic fluctuations may keep gene pools well stirred, inhibiting speciation and promoting stasis. As a corollary, speciation rates should be highest in the narrowly fluctuating tropics.

In quieter, less dynamic environments species need not be so “generalist” in this sense, and finely tuned, less time-averaged adaptations will have longer-term value. Nevertheless, these lineages would be more sensitive to minor environmental nudges. The nudges themselves would be hard to detect in the geological record, and the inverse of that French saying will appear to be true. Perturbations exceeding rather narrow limits of speed and extent might make such lineages prone to cladogenesis or extinction. Irrespective of probable differences in speciation rates, the model predicts a tendency for more continuous phyletic evolution offshore, and in the tropics generally, and for more stasis in shallow waters and temperate zones. There will, of course, be many exceptions. Plankton, such as planktonic foraminiferans, often show gradualism despite wide climatic oscillations. Presumably these lineages can track (remain within) a narrowly fluctuating environment by simply passive oceanic drifting.

The finding of gradualism in relatively complete stratigraphic sequences and apparent punctuations in less complete ones is normally regarded as an artefact of preservation. But the depositional conditions that affect stratigraphic completeness might themselves sometimes induce such evolutionary patterns.

There may be a correlation between *K*-strategists and phyletic gradualism, and *r*-strategists and stasis⁵. On ecological timescales, *r*-strategists are associated with relatively variable and unpredictable environments. But an ecologist's “unpredictable environment” could be highly predictable over geological timescales.

These hypotheses remain to be tested; we are not yet able to assess accurately the relative frequency of particular evolutionary patterns and the domain of their expected settings⁶. Bridging the gap between the neontological and palaeontological scales of observation may unearth many more evolutionary tales of the unexpected.

PETER R. SHELDON

Department of Geology,
University of Wales, PO Box 914,
Cardiff CF1 3YE, UK

1. Sheldon, P.R. *Nature* **330**, 561–563 (1987).
2. Eldredge, N. & Gould, S.J. *Nature* **332**, 211–212 (1988).
3. Maynard Smith, J. *Nature* **332**, 311–312 (1988).
4. Coope, G.R. *Rev. ecol. Syst.* **10**, 247–267 (1979).
5. Sheldon, P.R. *Geol. Soc. Am. Abstr. w. Progr.* **21**(6), A253 (1989).
6. Sheldon, P.R. in *Palaeobiology — a Synthesis* (eds Briggs, D.E.G. & Crowther, P.R.) 106–110 (Blackwell, Oxford, 1990).