

There are dangers on the path to stability. Probably the most serious are delays in receiving, or distortion in communicating, environmental signals⁷. Ecologists have long recognized that the global stability of an animal population is increased by subdividing it into a set of self-sufficient local groups. For humans this would mean national self-sufficiency in essential foods. At the moment, imported food is stimulating population growth in some countries and thereby concealing and increasing a latent overshoot, which will one day be expressed. Despite such problems, the current crop of economists maintain the growth ethic and the notion that only price and the market should determine production and distribution. Perhaps it is time to subsume their discipline into ecology.

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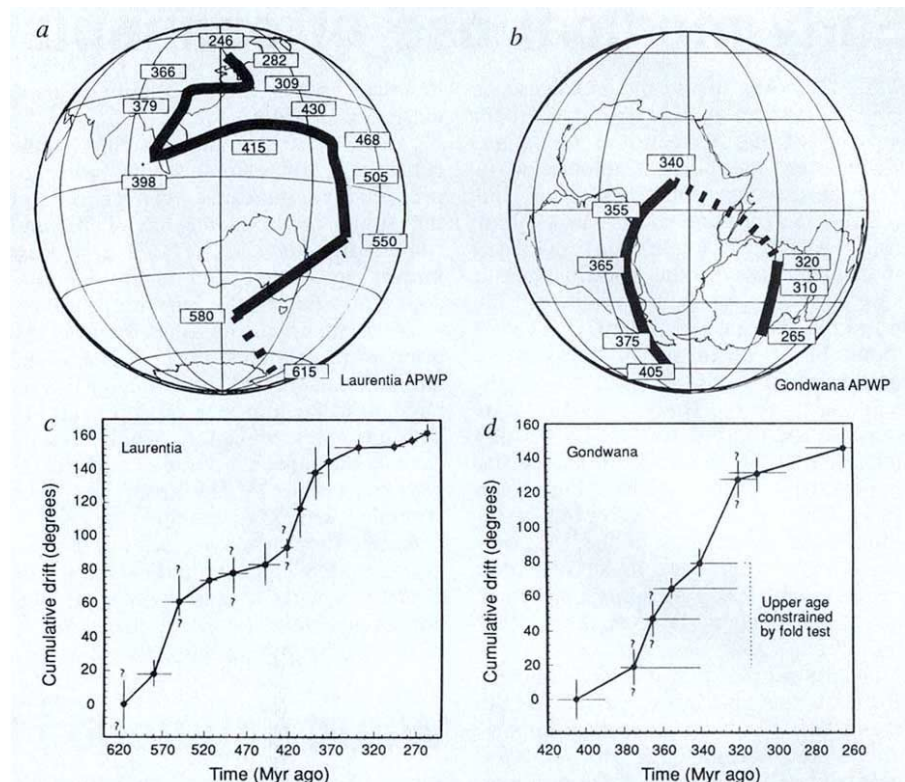
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1. Tuckwell, H. C. & Kozlowski, J. A. *Nature* **359**, 200 (1992).
2. Lotka, A. *Elements of Physical Biology* (Williams & Wilkins, Baltimore, 1925).
3. Boughey, A. S. *Man and the Environment* (Macmillan, New York, 1971).
4. *World Population Prospects* (United Nations, New York, 1988).
5. Wang, J. & Hull, T. H. *Population and Development Planning in China* (Allen & Unwin, Sydney, 1991).
6. Weeks, J. R. *Population* (Wadsworth, Belmont, California, 1989).
7. Meadows, D. H., Meadows, D. L. & Randers, J. *Beyond the Limits* (Earthscan, London, 1992).

A plate-tectonic speed limit?

SIR — Estimates of the minimum velocities of lithospheric plates before the age of the oldest sea floor can be made using paths of apparent polar wander^{1,2}. Today, plates containing a significant amount of continental crust² ($> 2 \times 10^7$ km²) are known to move at speeds approaching those of oceanic plates (6–10 cm yr⁻¹). This contrasts with a suggestion by Forsyth and Uyeda³ that because of excess asthenospheric drag on continental plates, plate velocity should vary inversely with the amount of continental material.

A recent attempt⁴ to balance plate driving forces with observed plate velocities found that a best fit to the models occurs when 'continental drag' is eliminated; however, other models⁵ still call for a significant amount of asthenospheric drag on continental blocks. Klootwijk *et al.*⁶ inferred from sea-floor magnetic anomalies and palaeomagnetic data that India, as part of a mostly oceanic plate, moved at 19 cm yr⁻¹ from 80 to 50 million years (Myr) ago; more recently, Tarduno *et al.*⁷ and Gordon⁸ have suggested that the oceanic plate 'speed limit' could reach 30 cm yr⁻¹ — faster than speeds so far reported for



a, APWP for Laurentia (North Poles). Dates given are Myr ago. The path for Laurentia reflects new data from the Catocin formation (570 Myr, pole at 43° S 128° E), the Callander complex (577 Myr, pole at 44° S 134° E). The preliminary role for the Manitou Islands complex (570 Myr) falls at 40° S 115° E supporting this portion of the path. The portion of the Laurentian APWP from 580–615 Myr is based on a single dyke dated at 615 Myr (pole at 69° S 170° E)¹³. This segment of the path is dashed to reflect the uncertainty. The 550 Myr portion is based on data from the Buckingham flows (pole at 16° S 165° E) and from the Long-Range dykes dated at 553 Myr (pole at 11° S 164° E). The remaining portion of the Laurentian APWP is based on path in ref. 14. **b**, APWP for Gondwana (South Poles) based on the analysis in refs 11, 12. The new Australian data have excellent fossil control with magnetic ages constrained by fold tests to within 60 Myr of deposition. **c**, Cumulative latitudinal drift curve for Laurentia. Drift rates can be calculated from the slope of the curve for any time segment. (Error bars indicate $\alpha 95$ about the mean poles and error in age; ?, error bar calculated from the $\alpha 95$ brackets for 1 or 2 poles only). **d**, Cumulative latitudinal drift curve for Gondwana.

large continental plates. We point out here that new palaeomagnetic data for Laurentia and Gondwana^{9–13} indicate that in the past large continental plates have travelled faster than 16 cm yr⁻¹, approaching the speed of small oceanic plates.

Previously published apparent polar wander paths (APWP) for Laurentia in the Cambrian period form a diffuse swathe prior to a well-constrained Late Cambrian (505 Myr old) pole⁹. New palaeomagnetic results from the Callander complex (Canada)¹⁰, Manitou Islands complex (Canada) (D. T. A. S., unpublished observations), and Catocin Formation (United States)⁹ were combined with earlier results from the Sept-Isles complex and Long-Range dykes in Canada. The new APWP indicates that Laurentia occupied polar latitudes during the interval 615–580 Myr ago followed by rapid drift to the equator during Vendian–Early Cambrian time (*a* in the figure). The figure (*c*) also shows the cumulative drift versus time curve for Laurentia 615–245 Myr ago. The

graph indicates two intervals of fast plate motion. Both intervals (580–550 and 415–379 Myr ago) give minimum peak rates of 16 cm yr⁻¹.

Chen *et al.*^{11,12} recently completed palaeomagnetic investigations of Late Devonian–Early Carboniferous rocks from the Amadeus and Ngalia basins (Australia). These results, combined with a re-evaluation of previous results for Gondwana 405–260 Myr ago lead to a revised APWP with the 375–340-Myr-old segment well represented by sequential poles (*b* in the figure). The 340–320-Myr-old portion of the path is constrained by a key pole 340 Myr ago and the mean of a group of poles 320 Myr ago. The figure (*d*) shows the cumulative drift curve for Gondwana 405–260 Myr ago, with drift rates in excess of 18 cm yr⁻¹ 375–355 and 340–320 Myr ago. Both the Laurentian and Gondwanan drift rates are minimum estimates because we have not included any longitudinal motion.

Do these palaeomagnetic data indicate that a fundamental change is needed in

our understanding of geodynamic forces that drive the plates? The suggestions^{3,5} that continental lithosphere has a greater resistance to motion and hence moves more slowly than oceanic lithosphere owing to asthenospheric drag are not supported by our data. The suggestion³ that the velocity of a plate is controlled by the length of subduction zones 'pulling' the plate cannot yet be tested, as we have no indication of the length of subduction zones bordering the Laurentia and Gondwana plates during their intervals of rapid motion.

We have yet to find an explanation for these periods of fast motion, but note that the duration of rapid drift for each of our examples does not exceed 50 Myr. There could have been intervals of faster motion, especially since we cannot determine longitudinal motion. Forsyth and Uyeda³ analysed only the most recent few million years of plate motions, perhaps giving rates biased by a period of mantle quiescence. Long-term fluctuations in mantle dynamics (for example superplume activity) could alter the balance of forces driving plate motions and allow continental plates to move at rates comparable to the fastest oceanic plates. Finally, true polar wander can always be invoked to explain the fast rates calculated for Laurentia and Gondwana. However, true polar wander is not significant for the past 80 Myr and, because there are currently no compelling data to indicate amounts of true polar wander for earlier times, we conclude that our rates closely approximate true minima.

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- Ullrich, L. & Van der Voo, R. *Tectonophysics* **74**, 17–29 (1981).
- Gordon, R. G., McWilliams, M. O. & Cox, A. J. *geophys. Res.* **84**, 5480–5486 (1979).
- Forsyth, D. W. & Uyeda, S. *Geophys. J. R. astr. Soc.* **43**, 163–200 (1975).
- Harper, J. F. *Geophys. J. Int.* **100**, 423–433 (1990).
- Ricard, Y. & Wuming, B. *Geophys. J. Int.* **105**, 561–573 (1991).
- Klootwijk, C. T. *et al.* *Geology* **20**, 395–398 (1992).
- Tarduno, J. A., McWilliams, M. O. & Sleep, N. *J. geophys. Res.* **95**, 15503–15527 (1990).
- Gordon, R. G. *Nature* **349**, 16–17 (1991).
- Meert, J. G., Van der Voo, R. & Payne, T. *J. geophys. Res.* (submitted).
- Symons, D. T. A. & Chiasson, A. D. *Can. J. Earth Sci.* **28**, 355–363 (1991).
- Chen, Z. *et al.* *Geophys. J. Int.* (in the press).
- Chen, Z., Li, Z.-X., Powell, C. McA. & Balme, B. E. *J. geophys. Res.* (submitted).
- Murthy, G., Gower, C., Tubrett, M. & Patzgold, R. *Can. J. Earth Sci.* **24**, 1431–1438 (1992).
- Van der Voo, R. *Rev. Geophys.* **28**, 167–206 (1990).

Fluctuating asymmetry

SIR — Sullivan *et al.* suggested in Scientific Correspondence¹ that the use of fluctuating asymmetry as an indicator of selective pressures on ornamental characters in animals is statistically flawed (see refs 2–5). The use of relative asymmetry, calculated as the absolute difference in the lengths of paired morphological characters divided by the mean length of the character, rather than absolute asymmetry dates back to 1986 (ref. 6). Relative asymmetry allows comparison of the asymmetry of the same trait in different species, such as the leg of a mouse and an elephant, or different traits in the same species, such as a leg and a tooth. Without controlling for the size of a trait, comparison between species will be uninformative; the elephant or the leg will always have larger asymmetry. Relativization should be with respect to the allometric relationship between characters, and that need not be linear. We used a linear relativization because the allometric relationship demonstrated isometry⁵. Regression of relative asymmetry on character size has only been used once⁴, and the conclusions of this analysis did not differ from those based on regression of absolute asymmetry on character size.

Sullivan *et al.*¹ suggest that a negative relationship between asymmetry and mean size of a character can arise simply because of consistent measurement errors. But this explanation does not apply to our previous results^{2–5}, because measurements of asymmetries were highly repeatable and measurement errors therefore relatively small. If Sullivan *et al.*¹ were correct, a spurious negative correlation between relative asymmetry and character size should arise more frequently in characters with relatively large measurement errors. However, the negative relationship between absolute asymmetry and mean character size is more often negative for secondary sexual characters with large asymmetries and relatively small measurement errors than for ordinary morphological characters with relatively large errors^{2–5}. This result invalidates the explanation of Sullivan *et al.*

Sullivan *et al.* also suggest that differences in character length may be due to unfinished growth, injury or damage, and that this effect may affect estimates of asymmetry. They suggest that the only rigorous approach is to use maximum rather than mean length of characters as the independent variable in statistical analyses. A more rigorous and straightforward approach is directly to

examine specimens for growth, injury or damage rather than basing the approach on untested assumptions. Exclusion of individuals with unfinished growth (birds with feather quills) or damaged characters (broken and worn feathers) has routinely been adopted in previous studies^{2,4,5}. The conclusions drawn from such studies are therefore less biased than would be the case if the approach of Sullivan *et al.*, with its untested assumptions about growth, damage and wear, had been adopted.

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SIR — Sullivan *et al.*¹ rightly point to the dangers of statistical regression analysis where “the same measurement . . . occurs as a component of both the dependent and independent variables, which can lead to spurious correlations”. They claim that measurement error incorporated into the measurement in question can produce a correlation when none exists. They then go on to recommend a procedure where the absolute difference between two measurements is regressed on the larger of the two measurements. They have fallen into their own trap.

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SIR — Fluctuating asymmetry describes the symmetrical distribution of random deviations from the population mean of a bilaterally symmetrical trait, presumed to arise from failure of homeostatic mechanisms in the face of developmental stress^{7–10}. As individuals vary in their ability to resist disruption of symmetrical growth, the relationship between trait asymmetry and trait length can give valuable insights into how selection acts on trait length¹⁰. Traits under stabilizing selection often show U-shaped relationships between asymmetry and mean trait length¹⁰, with extreme individuals poorly adapted to prevailing conditions. It is thus significant that recent studies indicate that many secondary sexual characters show negative relationships between asymmetry and size^{2,4,5,10–12}, indicating that sexual selection is directional and that individuals with large display traits are of ‘high quality’ (better adapted to prevailing conditions)¹⁰. Sullivan *et al.*¹ cast doubt on this evidence by suggesting two reasons for such negative correlations being artefacts. Their first criticism, of the use of relative asymmetry,