scientific correspondence

- Stone, R. A., Lin, T., Desai, D. & Capehart, C. Vision Res. 35, 1195–1202 (1995).
- Raviola, E. & Wiesel, T. N. N. Engl. J. Med. 312, 1609–1615 (1985).
- Larsen, J. S. Acta Ophthalmol. (Copenh.) 49, 873–886 (1971).
- Robinson, J., Bayliss, S. C. & Fielder, A. R. Vision Res. 31, 1837–1840 (1991).
- Hansen, R. M. & Fulton, A. B. in *Early Visual Development*, Normal and Abnormal (ed. Simons, K.) 130–142 (Oxford Univ. Press, New York, 1993).

10. Daw, N. J. Arch. Ophthalmol. 116, 502-505 (1998).

Superconductors under stress

Locquet *et al.*¹ reported a doubling of the critical temperature (T_c) of the superconductor La_{1.9}Sr_{0.1}CuO₄, from 25 to 49 K, in compressively strained thin films on a SrLaAlO₄ substrate. This led to speculation that values of T_c close to or even beyond 200 K could be obtained without excessive external pressure, starting from an unstrained cuprate with high T_c (>100 K). The stress would be applied to the *ab* (CuO₂) plane of this system of tetragonal symmetry. Such expectations are theoretically unrealistic.

To understand the phenomenon they observed, Locquet *et al.* cited data on uniaxial pressure gradients of T_c on the same compound^{2,3}. In particular, they inferred from the negative sign of the quantity $dT_c/d\epsilon_c$, where ϵ_c is the strain (minus the relative change in distances along the *c*-axis), that elongation (negative strain) of the *c*-axis increases the critical temperature, if atomic coordinates in the *ab* plane are kept constant.

Without questioning the validity of their experimental results, we disagree with Locquet *et al.* on two points. First, the higher the critical temperature in the unstrained state, the closer is the system with respect to optimum density in coordinate space, or to the optimum level of the Fermi energy. Quenching will then lead to a much weaker effect than at low T_c , and may even lower the critical temperature. This conclusion reflects *a priori* on results selecting the Hg-cuprate with the present record T_c of 134 K (three CuO₂ layers per molecular unit).

Second, the cuprates $La_{2-x}M_xCuO_4$ (where M is Sr or Ba) are unsuited as a reliable source of microscopic information via stress–strain relations because of observed structural distortions, phase transitions, non-rigid tilting of CuO_6 octahedra, and so on³, under external parameters and doping. As a result, conventional stress–strain relations, which are macroscopic and phenomenological, are not applicable to these systems on an atomic scale. This implies that the usual equalities (all derivatives are partial), $dT_c/d\epsilon_i = \sum_i (dT_c/dP_i)C_{ip}$ where ϵ_i is the strain along the *i*th axis and C_{ji} are elastic moduli, cannot provide the information desired. With *i* denoting the *c*-axis direction, the right-hand side is large and negative^{3,4} for La_{2-x}Sr_xCuO₄, but its indicated relation to a quantity which presupposes that all coordinates except those along the *c*-axis remain unchanged does not hold.

Locquet *et al.* incorrectly conclude that these negative values imply an increase of T_c brought about solely by enlarging the *c*-axis. In particular, their criticism of the interlayer tunnelling model proposed by Anderson *et al.*⁴ is irrelevant, although this model has been criticized on other grounds⁵.

Laurens Jansen*, Ruud Block†

*c/o Institute of Theoretical Physics, ETH-Hönggerberg HPZ 8093, Zürich, Switzerland e-mail: jansen@itp.phys.ethz.ch †J. H. van't Hoff Institute, University of Amsterdam, 1018 WV Amsterdam, The Netherlands

- 1. Locquet, J.-P. et al. Nature **394**, 453–456 (1998).
- Gugenberger, F. et al. Phys. Rev. B 49, 13137–13142 (1994).
 Nohara, M. et al. Phys. Rev. B 52, 570–580 (1995).
- Kohara, M. et al. Phys. Rev. B 52, 570–560 (1995).
 Chakravarty, S., Sudbø, A., Anderson, P. W. & Strong, S. Science
- **261,** 337–340 (1993).
- 5. Tsvetkov, A. A. et al. Nature 395, 360–362 (1998).

Polar gigantism dictated by oxygen availability

The tendency of some animals to be larger at higher latitudes ('polar gigantism') has not been explained, although it has often been attributed to low temperature and metabolism¹. Investigation of gigantism requires widely distributed taxa with extensive species representation at many wellstudied sites. We have analysed length data for 1,853 species of benthic amphipod crustaceans from 12 sites worldwide, from polar to tropical and marine (continental shelf) to freshwater environments. We find that maximum potential size (MPS) is limited by oxygen availability.

Size spectra are right-skewed at all sites, but skewedness increases as temperature decreases (Fig. 1). Analysing gigantism needs emphasis on right-hand extremes of distributions. However, potential sampling bias at some sites precludes using absolute maximum size, so we used the threshold size separating the smallest 95% of species from the largest 5% (which we refer to as TS_{95/5}). For marine sites, TS_{95/5} increases as water temperature decreases. Sites with low salinity, such as Lake Baikal (0 practical salinity units, p.s.u.), Caspian (13 p.s.u.) and the Black Sea (17 p.s.u.) lie above the marine relationship, and the discrepancy increases as salinity decreases (Fig. 2a), with the Lake Baikal TS_{95/5}, for example, being 1.8 times the marine value at the same tem-

🛸 © 1999 Macmillan Magazines Ltd



Figure 1 Amphipod size spectra for the two sites (Madagascar⁸, top; Lake Baikal⁹, bottom) for which the maximum and minimum $\text{TS}_{\scriptscriptstyle 95/5}$ values, indicated by bars, were obtained. In total, data were obtained from 12 sites worldwide: Madagascar, mean annual water temperature (7)=25 °C, TS_{95/5}=8.3, number of species at each site (n)=314; Mediterranean Sea, T=19 °C, TS_{95/5}=12.6, n=350; Black Sea, T=16.5 °C, TS_{95/5}=20.3, n=93; Caspian Sea, T=15 °C, TS_{95/5}=25.4, n=69; British Isles, T=11 °C, TS_{95/5}=23.2, n=172; Magellanic region, T=9.75 °C, TS_{95/5}=23.4, n=164; subantarctic islands, T=9.5 °C, $TS_{95/5} = 21.9$, n = 181; Lake Baikal, T = 6 °C, TS_{95/5}=54.4, n=226; Barents Sea, T=4 °C. TS_{95/5}=35.4, n=134; South Georgia, T=1.5 °C, TS_{95/5}=40.5, n=150; West Antarctica, T=0.75 °C, TS_{95/5}=41.5, n=297; East Antarctica, T=0.0 °C, TS_{95/5}=43.6, n = 195). Analyses were restricted to a depth of 250 m (continental shelf depth), except for Antarctica, which included species to 500 m because of continental shelf depression by the Antarctic icecap. Sites that had fewer than 50 species described were not analysed.

perature. But oxygen solubility increases as salinity decreases, and replotting $TS_{95/5}$ against water-dissolved oxygen content removes this discrepancy and produces a linear relation: $TS_{95/5} = -42.6 + 0.252 \text{ O}_2$ (n = 12; $r^2 = 0.98$; F = 51.69; P < 0.0001) (Fig. 2b).

Thus, oxygen availability controls $TS_{95/5}$. The fit of regressions (not shown) relating lower threshold size values (such as $TS_{90/10}$ and $TS_{50/50}$) with oxygen improves with increasing threshold size value, indicating that oxygen becomes more important relative to other ecological factors as size increases. Furthermore, the relation between $TS_{95/5}$ and temperature for marine sites is curvilinear (Fig. 2a), reflecting the nonlinear relation between seawater oxygen content and temperature.

TS_{95/5} reaches zero when mean environmental oxygen is 183 μ mol per kg of water. This should indicate an environmental limit for amphipods. A variety of hot and/or highly saline conditions would produce 183 μ mol O₂ per kg, but these areas are inhabited by brine shrimp and ostra-

scientific correspondence

cods, and not by amphipods (S. Ruffo, personal communication).

Minimum size does not vary significantly with environmental oxygen (Pearson correlation coefficient = 0.402, P = 0.195). Thus, MPS increases dramatically with oxygen, modal size increases less, and minimum size does not increase at all. The overall effect widens the size spectrum, indicating that oxygen availability is not the same selective pressure for all species, but rather sets upper limits to MPS.

In ectotherms, metabolic rate increases with temperature, increasing tissue maintenance $costs^2$. Although MPS decreases with increased temperature for marine sites, the largest amphipods were not found in the coldest sites (high Antarctic, 0 °C), but in Lake Baikal (+6 °C). Temperature-dependent tissue synthesis and catabolism tradeoffs do not limit MPS, as the observed increases in MPS at freshwater sites, despite greater osmoregulatory costs, would require unfeasibly large increases in resource acquisition.

Oxygen enters amphipod blood through a low-efficiency gill³ and is transported both as dissolved oxygen and bound to haemocyanins. Marine amphipod haemolymph contains $10-20 \text{ mg ml}^{-1}$ haemo-



Figure 2 Effects of temperature and oxygen availability on amphipod MPS. Data are for nine marine (orange circles) and three reduced-salinity sites (blue circles). **a**, TS_{95/5} plotted against mean annual water temperature (inverted scale). **b**, TS_{95/5} plotted against calculated dissolved oxygen content at saturation (µmol per kg), based on surface water mean temperature and salinity. Not every habitat will experience permanent high oxygen saturation, but the 100% value represents optimal conditions for attaining large size.

cyanin⁴, which is low for crustaceans. Polar amphipods are thought to be similar to the Antarctic giant isopod Glyptonotus antarcticus, which also has relatively little haemocvanin⁵ and carries 60-70% of its circulating oxygen in solution. The amount of oxygen carried in solution is thought to be 30-40% in tropical amphipods and 60-70% in Lake Baikal species, and differs because marine amphipod haemolymph is isotonic with seawater (950-1,150 mosM), whereas freshwater species are hypertonic (340-360 mosM) (I. Zerbst-Boroffka, personal communication). Amphipod haemocyanins may also be more important for osmoregulation than oxygen transport⁶.

The amount of oxygen dissolved in saturated haemolymph in amphipods from Lake Baikal at 6 °C is similar to that of marine species at 0 °C, and species from Lake Baikal and the Antarctic should be similar sizes. TS_{95/5} is 54.4 mm for Baikal amphipods and 43.6 mm for Antarctic species. This suggests that saturation levels of dissolved oxygen in the haemolymph increase from tropical to polar environments, and from marine to freshwater environments, with gill efficiency being the critical factor determining MPS.

The difference in partial pressure between the external medium and circulating haemolymph determines oxygen uptake across the gills, according to Fick's law. For similar external partial pressure and efficiency, more oxygen enters the blood at sites with low temperature and salinity because the absolute oxygen concentration is higher. The saturation level and absolute oxygen concentration in the blood are also higher, allowing increased size because a greater oxygen mass will increase the possible path length of the circulatory system.

We obtained strong relations between external oxygen concentration and length, not body mass. However, amphipods, like several groups exhibiting low-temperature gigantism (such as pycnogonids and nemerteans), have restricted circulatory systems with few lateral branches. In other groups, stronger relations with body mass would be expected. Whether the MPS is reached will depend on several factors. In environments with many species, selection pressures will drive niche exploitation and a range of sizes will be represented.

Oxygen supply may also have led to insect gigantism in the Carboniferous period, because atmospheric oxygen was 30–35% (ref. 7). The demise of these insects when oxygen content fell indicates that large species may be susceptible to such change. Giant amphipods may therefore be among the first species to disappear if global temperatures are increased or global oxygen levels decline. Being close to the critical MPS limit may be seen as a specialization

that makes giant species more prone to extinction over geological time. Gauthier Chapelle*, Lloyd S. Peck†

*Institut Royal des Sciences Naturelles de Bruxelles, Rue Vautier 29, B-1000 Bruxelles, Belgium †British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK e-mail: l.peck@bas.ac.uk

 Atkinson, D. & Sibly, R. M. Trends Ecol. Evol. 12, 235–239 (1997).

- 2. Ivleva, I. V. Int. Rev. Ges. Hydrobiol. 65, 1-47 (1980).
- Wolvekamp, H. P. & Waterman, T. H. in *The Physiology of Crustacea* Vol. 1 (ed. Waterman, T. H.) 35–100 (Academic, New York, 1960).
- 4. Spicer, J. I. Mar. Behav. Physiol. 24, 123-136 (1993).
- Whiteley, N. M., Taylor, E. W., Clarke, A. & El Haj, A. J. Polar Biol. 18, 10–15 (1997).
- Hagerman, L., Sandberg, E. & Vismann, B. Mar. Biol. 130, 209–212 (1997).
- Graham, J. B., Dudley, R., Aguilar, N. M. & Gans, C. Nature 375, 117–120 (1995).
- Ledoyer, M. Faune de Madagascar. Crustaces Amphipodes Gammariens (CNRS, Paris, 1982–1986).
- Bazikalova, A. Y. Lake Baikal Amphipods. Proc. Baikal. Limnol. Stn Acad. Sci. USSR 11, 1–440 (1945).

No role for colour in symmetry perception

Bilateral colour symmetry, such as that evident in a Siberian tiger's face (Fig. 1a), is relevant to many animals^{1,2}, including humans^{3,4}. We examined the role of colour in symmetry perception by asking observers to detect colour symmetry in regular grids of coloured squares (a colour-symmetrical image has regions of the same colour located equidistantly from a vertical axis). Our results suggest, unexpectedly, that the mechanisms of symmetry perception are inherently colour-blind: although observers can verify colour symmetry, they do so only by shifting attention from one colour to the next and assessing the symmetry of regions of that colour.

Observers were shown displays that either exhibited complete colour symmetry about the vertical midline (Fig. 1b), or contained one pair of squares that were mismatched in colour. Subjects pressed a button to indicate whether the pattern was colour-symmetrical, and response times and errors were assessed. The displays were constructed with either two colours (crimson and scarlet) or four colours (green, yellow, blue and red). Colours were chosen such that every pair of colours in the fourcolour displays was more easily discriminated than the pair used in the two-colour displays.

The most obvious hypothesis about colour symmetry perception, called colour matching, involves the colours of corresponding points or regions on different sides of an axis being compared at the same time. Colour symmetry is registered when