

mantle, and would also provide the large shear strains necessary for interconnection and thus percolation of metallic melts in a solid silicate matrix.

Our experimental results show that, in a dynamic environment, melt can be efficiently interconnected even if dihedral angles are large enough to cause the melt to be isolated under hydrostatic conditions. Hence, the requirement of a magma ocean as a critical step in the formation of planetary cores cannot be solely based on the argument that percolation of metal sulphide melt is impossible in a solid silicate mantle. □

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1. Minarik, W. G., Ryerson, F. J. & Watson, E. B. Textural entrapment of core-forming melts. *Science* **272**, 530–533 (1996).
2. Ballhaus, C. & Ellis, D. J. Mobility of core melts during Earth's accretion. *Earth Planet. Sci. Lett.* **143**, 137–145 (1996).
3. Shannon, M. C. & Agee, C. B. High-pressure constraints on percolative core-formation. *Geophys. Res. Lett.* **23**, 2717–2720 (1996).
4. Stevenson, D. J. in *Origin of the Earth* (eds Newsom, H. E. & Jones, J. H.) 231–249 (Oxford Univ. Press, 1990).
5. Karato, S. & Murthy, V. R. Core formation and chemical equilibrium in the Earth – I. Physical considerations. *Phys. Earth Planet. Inter.* **100**, 61–79 (1997).
6. Elsasser, W. M. in *Earth Science and Meteorites* (eds Geiss, J. & Goldberg, E.) 1–30 (North Holland, Amsterdam, 1963).
7. Brett, R. Chemical equilibration of the Earth's core and upper mantle. *Geochim. Cosmochim. Acta* **48**, 1183–1188 (1984).
8. Von Bargen, N. & Waff, H. S. Permeabilities, interfacial areas and curvatures of partially molten systems: Results of numerical computations of equilibrium microstructures. *J. Geophys. Res.* **91**, 9261–9276 (1986).
9. Jurewicz, S. R. & Jones, J. H. Preliminary results of olivine/metal wetting experiments and the direct measurement of metal phase interconnectivity. *Proc. Lunar Planet. Sci. Conf.* **26**, 709–710 (1995).
10. O'Neill, H. St. C. & Palme, H. in *The Earth's Mantle* (ed. Jackson, I.) 3–123 (Cambridge Univ. Press, 1998).
11. Zhang, S. & Karato, S. Lattice-preferred orientation of olivine aggregates deformed in simple shear. *Nature* **375**, 774–777 (1995).
12. Karato, S., Zhang, S., Zimmerman, M. E., Daines, M. J. & Kohlstedt, D. L. Experimental studies of shear deformation of mantle materials; towards structural geology of the mantle. *Pure Appl. Geophys.* **151**, 589–603 (1998).
13. Zimmerman, M. E., Zhang, S., Kohlstedt, D. L. & Karato, S. Melt distribution in mantle rocks deformed in shear. *Geophys. Res. Lett.* **26**, 1505–1508 (1999).
14. Daines, M. J. & Kohlstedt, D. L. Influence of deformation on melt topology in peridotites. *J. Geophys. Res.* **107**, 10257–10271 (1997).
15. Arculus, R. J., Holmes, R. D., Powell, R. & Righter, K. in *Origin of the Earth* (ed. Newsom, H. E. & Jones, J. H.) 251–272 (Oxford Univ. Press, 1990).
16. Walter, M. At the magma ocean floor. *Nature* **381**, 646 (1996).
17. Stevenson, D. J. in *Workshop on the Early Earth: The Interval from Accretion to the Older Archean* (eds Burke, K. & Ashwal, L. D.) 76–78 (LPI Tech. Rep. 85-01, Lunar and Planetary Institute, Houston, 1985).
18. Ringwood, A. E. in *Origin of the Earth* (eds Newsom, H. E. & Jones, J. H.) 101–134 (Oxford Univ. Press, 1990).
19. Li, J. & Agee, C. B. Geochemistry of mantle-core formation at high pressure. *Nature* **381**, 686–689 (1996).
20. Righter, K. & Drake, M. J. Effect of water on metal-silicate partitioning of siderophile elements: a high pressure and temperature terrestrial magma ocean and core formation. *Earth Planet. Sci. Lett.* **171**, 383–399 (1999).
21. Murthy, V. R. Early differentiation of the Earth and the problem of mantle siderophile elements: A new approach. *Science* **253**, 303–306 (1991).
22. Benz, W. & Cameron, A. G. W. in *Origin of the Earth* (eds Newsom, H. E. & Jones, J. H.) 61–67 (Oxford Univ. Press, 1990).
23. Agee, C. B. & Longhi, J. (eds) *Workshop on the Physics and Chemistry of Magma Oceans from 1 bar to 4 Mbar* (LPI Tech. Rep. 92–03, Lunar and Planetary Institute, Houston, 1992).
24. Wetherill, G. W. Formation of the Earth. *Annu. Rev. Earth Planet. Sci.* **18**, 205–256 (1990).
25. Hanks, T. C. & Anderson, D. L. The early thermal history of the Earth. *Phys. Earth Planet. Inter.* **2**, 19–29 (1969).
26. Gaetani, G. A. & Grove, T. L. Partitioning of moderately siderophile elements among olivine, silicate melt, and sulphide melt: Constraints on core formation in the Earth and Mars. *Geochim. Cosmochim. Acta* **61**, 1829–1846 (1997).
27. Connerney, J. E. P. et al. Magnetic lineations in the ancient crust of Mars. *Science* **284**, 794–798 (1999).

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Rapid evolution of reproductive barriers driven by sexual conflict

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A growing amount of experimental data indicates extremely rapid evolution of traits and proteins related to fertilization in many diverging taxa^{1–3}. These data come from studies of sperm or pollen competition between closely related species^{3–6}, and from molecular studies of fertilization proteins^{2,7–10}. The positive selection for evolutionary novelty that appears to be acting on fertilization systems seems paradoxical because successful reproduction requires the close matching of female and male traits. It has been suggested^{11–13} that perpetual coevolution between the sexes can result from sexual conflict in mating. Sexual conflict occurs when characteristics that enhance the reproductive success of one sex reduce the fitness of the other sex¹⁴. Numerous examples of sexual conflict resulting from sensory exploitation, polyspermy and the cost of mating have been discussed in detail^{1–3,14,15}. The potential for coevolution due to such conflict has been evaluated experimentally^{15,16}. Here I develop a simple mathematical model describing coevolutionary dynamics of male and female traits involved in reproduction. The model shows that continual change in such traits at a constant speed is expected whenever females (or eggs) experience fitness loss from having too many compatible males (or sperms). The plausibility of runaway coevolution increases with increasing population size. Rapid evolution of reproductive barriers driven by sexual conflict may explain increased speciation rates after colonization of new habitats ('adaptive radiation') and high species richness in resource-rich environments.

An important population characteristic that can be used to incorporate different forms of sexual conflict into the modelling framework is the proportion of the individuals (or gametes) of the other sex that can mate with an individual (or gamete) of a given type. An implicit assumption of classical population genetic models (which did not consider sexual conflicts) is that individual fitness maximizes when this proportion is one. Here I study the coevolutionary dynamics of male and female traits when sexual conflict over mating rate results in an optimal proportion of compatible males for females being smaller than one.

I will say that two individuals (or gametes) are 'compatible' if mating and fertilization are not prevented by isolating mechanisms. Let the degree of 'compatibility' of males and females (or their gametes) be controlled by two independent sex-limited quantitative traits: a male (or sperm) trait y and a female (or egg) trait x . This independence assumption is justified at least for gamete recognition systems². Let $f(x)$ and $g(y)$ be the distributions of x and y in the population with means \bar{x} and \bar{y} and variances V_x and V_y . I assume that compatibility of sexes requires a matching of the corresponding traits. The simplest choice for a corresponding function defining the probability $\Psi(x, y)$ that trait x is compatible with trait y is a quadratic function:

$$\Psi(x, y) = 1 - \alpha(x - y)^2$$

where α is a positive parameter controlling the tolerance of matching¹⁷. The proportion of the males compatible with female trait x is

$$P(x) = \int \Psi(x, y)g(y)dy = 1 - \alpha[V_y + (x - \bar{y})^2]$$

The overall fitness $W_f(x)$ of females (or eggs) having trait x depends

on $P(x)$. This fitness should be an increasing function at small values of $P(x)$ (the more compatible males the higher the probability of fertilization), but should decrease at larger values of $P(x)$ (as a result of polyspermy, predation, sensory exploitation, different costs of mating, seminal fluid toxicity and other forms of sexual conflict; see ref. 18 for a meta-analysis of relevant insect data). The simplest form of a function having these properties is a quadratic function with a maximum at P_{opt} :

$$W_f(x) = 1 - S[P(x) - P_{opt}]^2 \quad (1)$$

where S is a positive parameter. Instead of parameters S and P_{opt} it is more illuminating to use parameters s and θ , which are defined by the equalities $P_{opt} = 1 - \theta$ and $S = s/\theta^2$. That is, parameter θ is the amount by which the optimal proportion of compatible males is smaller than 1, and parameter s is the fitness reduction of a female trait that is compatible with all males (for which $P(x) = 1$). Note that choosing a negative or zero value for θ would describe a situation in which female fitness always increases with $P(x)$ (no sexual conflict). The probability that a male (or sperm) y has offspring from mating a female (or egg) x is a product of the probability $\Psi(x, y)$ that traits x and y are compatible and the probability $F(x)$ that fertilization does take place and result in viable offspring. If there are too many males compatible with female trait x , the chance to be the one who fertilizes a given female decreases. Moreover, even if fertilization does take place, interference from other males (for example, through polyspermy, seminal fluid toxicity, physical harm to females, costs of mating) can prevent successful development of offspring^{11,12}. Therefore, probability F should be a decreasing function of the overall proportion $P(x)$ of males that are compatible with female trait x . The simplest form of a function having this property is a linear function: $F = 1 - BP$, where $0 < B < 1$. To find the male fitness $W_m(y)$ one sums over all females:

$$W_m(y) = \int \Psi(x, y)F(x)f(x)dx \quad (2)$$

Note that both male and female trait fitnesses (defined by equations (1) and (2), respectively) are frequency dependent.

I will assume that $\alpha \ll \theta$, $s \ll 1$. These assumptions imply that selection is weak and linkage disequilibrium can be neglected. I will allow the term $\alpha(\bar{x} - \bar{y})^2$ to have the same order of magnitude as θ and s . Under the above assumptions, the per generation changes in the means are approximately

$$\Delta\bar{x} = 2\alpha V_x \frac{s}{\theta} \left[1 - \frac{\alpha(\bar{x} - \bar{y})^2}{\theta} \right] (\bar{x} - \bar{y}) \quad (3a)$$

$$\Delta\bar{y} = \alpha V_y (\bar{x} - \bar{y}) \quad (3b)$$

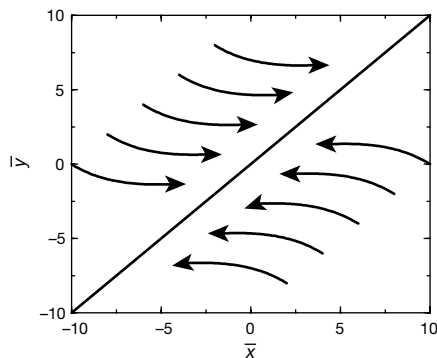


Figure 1 Evolution towards a stable line of equilibria $\bar{y} = \bar{x}$. Parameter values used are $\alpha = 0.01$, $V_x = V_y = 1$, $s = 0.01$, $\theta = 0.15$. The line of equilibria and a set of ten trajectories (corresponding to 100 generations each) starting from different initial states are shown. The direction of change is indicated by arrows.

Equation (3b) shows that if no female trait evolution is allowed (that is, if \bar{x} is fixed, say, because there is no genetic variation, $V_x = 0$, or by some experimental manipulation¹⁵) the mean male trait evolves to a value matching \bar{x} . One can say that for the male trait the optimal strategy is to match the mean female trait. When female *D. melanogaster* are experimentally prevented from coevolving with males, males rapidly adapt to the static female phenotype, and this male adaptation leads to a reduction in female survival¹⁵. Alternatively, if no male trait evolution is allowed (that, is if \bar{y} is fixed) equation (3a) shows that the mean female trait will evolve to a value that differs from \bar{y} by $\pm(\theta/\alpha)^{1/2}$. One can say that this value represents a displacement of the male and female traits that is optimal for females. The difference between the displacements that are optimal for males and females is a result of the sexual conflict over mating rate.

To analyse the dynamics when both male and female traits are allowed to evolve, let us first make a standard assumption that genetic variances V_x and V_y are constant (for example, see refs 17, 19, 20). Then there are two possible dynamical regimes. In the first regime, the system evolves to an equilibrium state at which the mean trait values match: $\bar{y} - \bar{x} \rightarrow 0$ (Fig. 1). One can say that in this case males win the sexual conflict. The dynamical system (3) has a stable line of equilibria similar to those arising in models of sexual selection¹⁷. Changes in the trait values along the line $\bar{y} = \bar{x}$ are neutral, and different allopatric populations can diverge along this line by random genetic drift (see ref. 17). The rate of such a divergence will increase with decreasing the population size. This regime takes place if

$$1 < \frac{1}{2} \frac{V_y \theta}{V_x s} \quad (4)$$

The ratio of the variances in the righthand side of equation (4) characterizes the relative ability of male and female traits to evolve. The second ratio characterizes the strength of the sexual conflict: the smaller the fitness loss s is at a given value θ , the less intense the sexual conflict. Thus, the first regime is promoted if the genetic variation in males is higher than in females, or if the fitness loss of females from having too many compatible males is small.

If inequality (4) is reversed, the difference in the means approaches asymptotically a constant value displaced from zero: $\bar{y} - \bar{x} \rightarrow \pm \delta$, where

$$\delta = \sqrt{\frac{\theta}{\alpha} \left(1 - \frac{1}{2} \frac{V_y \theta}{V_x s} \right)} \quad (5)$$

The value of the displacement δ is intermediate between those that are optimal for males (zero displacement) and females (displacement

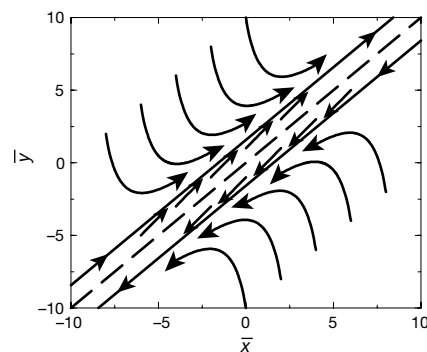


Figure 2 Runaway dynamics along lines $\bar{y} = \bar{x} \pm \delta$. Parameter values used are $\alpha = 0.01$, $V_x = V_y = 1$, $s = 0.1$, $\theta = 0.15$. A line of unstable equilibria $\bar{y} = \bar{x}$ (dashed line), the lines of runaway coevolution $\bar{y} = \bar{x} + \delta$ and $\bar{y} = \bar{x} - \delta$ and a set of 20 trajectories (corresponding to 100 generations each) starting from different initial states are shown. The direction of change is indicated by arrows.

at a value of $(\theta/\alpha)^{1/2}$. Thus, neither sex wins the sexual conflict but rather there is a coevolutionary compromise. This compromise is dynamic—neither male nor female traits settle to an equilibrium but both keep simultaneously increasing (or decreasing) along a line at which the displacement is constant. In sharp contrast to the models in which runaway coevolution occurs at a geometrically increasing rate^{17,20} or is cyclic^{19,20}, here the rate R of morphological changes (that is the change in the means per generation $R = \Delta\bar{x} = \Delta\bar{y}$) is constant:

$$R = \alpha V_y \delta \tag{6}$$

The resulting dynamics are illustrated in Fig. 2.

In both regimes, the characteristic time for approaching a line $\bar{y} - \bar{x} = \text{const}$ is about $1/[\alpha(2V_x(s/\theta) - V_y)]$ generations. For example, let $\alpha = 0.01$, $V_x = V_y = 1$, $s = 0.1$, $\theta = 0.15$. Then depending on the initial conditions, the system approaches one of the two lines: $\bar{y} = \bar{x} + \delta$, or $\bar{y} = \bar{x} - \delta$, where $\delta \approx 1.58$. The characteristic approach time is about 300 generations. The rate of runaway coevolution along the line is $R = 0.0158$. That is, it takes about 63 generations for a shift of the order of one standard deviation. Thus, a few hundred generations will be sufficient for a significant change in the mean trait values.

The ratio of the variances V_y and V_x in inequality (4) is a crucial parameter affecting the qualitative behaviour of the system. On a short time interval this ratio can be treated as a constant (numerically) close to its initial value. On larger time scales, however, genetic variances can change because they are affected by both selection and mutation. Although modelling the dynamics of genetic variances is notoriously difficult^{21,22}, some progress can be made. Let mutation increase genetic variances V_x and V_y by μ_x and μ_y per generation, respectively. Using the method that is consistent with the derivation of equation (3) results in a prediction that at a mutation–selection balance equilibrium

$$V_y^* = \sqrt{\mu_y/\alpha}, \tag{7a}$$

$$V_x^* = \frac{3}{8} V_y^* \frac{\theta}{s} \left(1 + \sqrt{1 + \frac{16\mu_x s}{9\mu_y \theta}} \right) \tag{7b}$$

At this equilibrium, inequality (4) is never true. Thus, mutation and selection are expected to modify genetic variances in such a way that the system always enters the regime in which the means evolve in a runaway fashion. The characteristic time for reaching a mutation–selection balance state is on the order of $1/(\mu\alpha)^{1/2}$ generations. With $\mu_x = \mu_y = 0.01$ and with the same values of α , s and θ as above, the levels of genetic variation maintained are relatively high: $V_x = 1.39$, $V_y = 1$. Studies of gamete recognition proteins indicate that such genes can be highly polymorphic within species². The characteristic time for approaching a mutation–selection balance state is about 100 generations. The above parameter values result in $\delta = 2.15$ and $R = 0.0215$.

A main conclusion of the model studied here is that sexual conflict naturally leads to perpetual changes in traits responsible for reproductive isolation. The sexes get locked in coevolutionary chase in which females continuously evolve to decrease the mating rate while males continuously evolve to increase it. This theoretical conclusion supports previous verbal arguments^{11–13}. What was not expected is the generality of conditions under which coevolutionary chase is expected to occur: continual change in traits responsible for reproductive barriers at a constant speed is expected whenever females (or eggs) experience fitness loss from having too many compatible males (or sperms). Allopatric populations can evolve in the opposite directions or in the same direction but at different rates. In either case, the expected outcome will be rapid genetic divergence and eventual reproductive incompatibility of individuals (or gametes) from different populations. This conclusion is sup-

ported by data²³ that indicate a striking increase in the rate of speciation in groups in which post-mating sexual conflict is intense as compared with related groups in which it is absent.

In earlier models of allopatric speciation driven by genetic drift along a line of equilibria arising under sexual selection¹⁷, or by the accumulation of chromosome rearrangements²⁴, or by mutation and drift on holey adaptive landscapes^{25,26}, the rate of evolution of reproductive barriers is the fastest in small populations. In contrast, because sexual conflict induces direct selection on traits involved in reproduction, large populations will be more responsive to such selection. There is an additional effect of population size on the evolutionary dynamics driven by sexual conflict. Increasing the overall population sizes should intensify sexual conflict (see ref. 27 for relevant examples on water striders). In terms of this model, this translates into the optimum proportion of compatible males becoming smaller than one (θ becomes positive) and an increasing fitness loss of females from having too many compatible males (s becomes bigger). Both these effects will make runaway coevolution of sexes more plausible. Thus, increasing the sizes of geographically isolated populations should make evolution of reproductive barriers between them more plausible. In large populations, significant changes in traits that are involved in reproduction may occur on the timescale of a few hundred to a few thousand generations.

Two explanations of increased speciation rates ('adaptive radiation') after colonization of new resource-rich environments free of competitors and/or predators have been intensively discussed²⁸. One is strong divergent natural selection that causes rapid phenotypic differentiation and, as a by-product, reproductive isolation. Another is increased persistence of local populations that increases the chance that they avoid extinction long enough to evolve reproductive isolation. Our model provides a third possibility: increased speciation rates may be caused by sexual conflict that intensifies after increasing the size of local populations. Founding several isolated populations that quickly increase in size should result in rapid divergence of these populations in traits involved in reproduction. The same argument can be used to explain high species richness that is observed in geographic areas with high productivity²⁹. With sexual conflict, high local population densities that can be maintained in such areas should promote the evolution of reproductive barriers and high species numbers. One way to test this is by comparing the degree of reproductive isolation between natural or laboratory populations that have been maintained for some time at different densities. The hypothesis that rapid speciation is driven by sexual conflict predicts that reproductive barriers will be stronger between populations with high densities than between populations with low densities. Another prediction is that the number of species in a clade should positively correlate with species abundance. It remains to be seen whether these hypotheses are supported by data. □

Methods

Let $p(z)$ be the distribution of a quantitative trait z in the population with the mean \bar{z} and central moments $M_i (= \int (z - \bar{z})^i p(z) dz)$. The mean \bar{z}' and the variance M_2' of the trait after selection specified by fitness function $w(z)$ are

$$\bar{z}' = \frac{\int zw(z)p(z)dz}{\bar{w}} \tag{8a}$$

$$M_2' = \frac{\int z^2 w(z)p(z)dz}{\bar{w}} - (\bar{z}')^2, \tag{8b}$$

where $\bar{w} = \int w(z)p(z)dz$ is the mean fitness. Let the fitness function be represented as a polynomial in $z - \bar{z}$

$$w(z) = a_0 + \sum_{i=1}^k a_i (z - \bar{z})^i, \tag{9}$$

where coefficients a_i are allowed to depend on the moments of $p(z)$ but not on z . Then the within generation changes in the mean and variance are

$$\Delta \bar{z} = \frac{\sum_{i=1}^k a_i M_{i+1}}{a_0 + \sum_{i=2}^k a_i M_i} \quad (10a)$$

$$\Delta M_2 = \frac{\sum_{i=1}^k a_i (M_{i+2} - M_i M_2)}{a_0 + \sum_{i=2}^k a_i M_i} - (\Delta \bar{z})^2 \quad (10b)$$

(compare refs 19–21). These equations are exact. If trait z is additive and linkage disequilibrium can be neglected, segregation and recombination will not change \bar{z} and M_2 . Thus, equations (10) will give the changes in \bar{z} and M_2 between two subsequent generations. For traits with sex-limited expression (such as those considered here) the changes in \bar{z} and M_2 between two subsequent generations will be equal to one-half of the values predicted by equations (10). The fitness functions for male and female traits defined in the main body of the paper belong to a class of polynomial fitness functions (9) with $k = 4$ and $k = 2$, respectively. Resulting equations for the means are given in the main body of the paper whereas the per generation changes in genetic variances are

$$\Delta V_x = 2\alpha V_x^2 \frac{s}{\theta} \left[1 - 3 \frac{\alpha(\bar{y} - \bar{x})^2}{\theta} \right] + \mu_x \quad (11a)$$

$$\Delta V_y = -\alpha V_y^2 + \mu_y \quad (11b)$$

where μ_x and μ_y are genetic variances introduced by mutation. To derive these equations (see Supplementary Information for details) one identifies coefficients a_i of the polynomial expansion (9), then plugs them into equations (10), and simplifies the resulting expressions by assuming that $\alpha \ll \theta$, $s \ll 1$, and allowing the term $\alpha(\bar{x} - \bar{y})^2$ to have the same order of magnitude as θ and s . In addition, to derive the equations for changes in the means, I neglected the third moments; and to derive the equations for the variances, I neglected the third moments and assumed that $M_4 - 3M_2^2 = 0$ (zero kurtosis). Numerical results for a case of stabilizing selection with moving optimum³⁰ suggest that this is a satisfactory approximation. The dynamic equations (3) and (11) can be analysed by standard methods.

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1. Rice, W. R. in *Endless Forms. Species and Speciation* (eds Howard, D. J. & Berlocher, S. H.) 261–270 (Oxford Univ. Press, New York, 1998).
2. Palumbi, S. R. in *Endless Forms. Species and Speciation* (eds Howard, D. J. & Berlocher, S. H.) 271–278 (Oxford Univ. Press, New York, 1998).
3. Howard, D. J., Reece, M., Gregory, P. G., Chu, J. & Cain, M. L. in *Endless Forms. Species and Speciation* (eds Howard, D. J. & Berlocher, S. H.) 279–288 (Oxford Univ. Press, New York, 1998).
4. Arnold, M. L., Hamrick, J. L. & Bennett, B. D. Interspecific pollen competition and reproductive isolation in *Iris*. *J. Hered.* **84**, 13–16 (1993).
5. Wade, M. J., Patterson, H., Chang, N. W. & Johnson, N. A. Postcopulatory, prezygotic isolation in flour beetles. *Heredity* **72**, 163–167 (1994).
6. Rieseberg, L. H., Desrochers, A. M. & Youn, S. J. Interspecific pollen competition as a reproductive barrier between sympatric species of *Helianthus* (Asteraceae). *Am. J. Bot.* **82**, 515–519 (1995).
7. Aguade, M., Miyashita, N. & Langley, C. H. Polymorphism and divergence of the mst 355 male accessory gland region. *Genetics* **132**, 755–770 (1992).
8. Palumbi, S. R. Marine speciation on a small planet. *Trends Ecol. Evol.* **7**, 114–117 (1992).
9. Vacquire, V. D. & Lee, Y.-H. Abalone sperm lysin: unusual mode of evolution of a gamete recognition protein. *Zygote* **1**, 181–196 (1993).
10. Metz, E. C. & Palumbi, S. R. Positive selection and sequence rearrangements generate extensive polymorphism in the gamete recognition protein bindin. *Mol. Biol. Evol.* **13**, 397–406 (1996).
11. Rice, W. R. & Holland, B. The enemies within: intergenomic conflict, interlocus contest evolution (ICE) and the intraspecific red queen. *Behav. Ecol. Sociobiol.* **41**, 1–10 (1997).
12. Holland, B. & Rice, W. R. Chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* **52**, 1–7 (1998).
13. Parker, G. A. & Partridge, L. Sexual conflict and speciation. *Phil. Trans. R. Soc. Lond. B* **353**, 261–274 (1998).
14. Stockley, P. Sexual conflict resulting from adaptations to sperm competition. *Trends Ecol. Evol.* **12**, 154–159 (1997).
15. Rice, W. R. Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* **381**, 232–234 (1996).
16. Holland, B. & Rice, W. R. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl Acad. Sci. USA* **96**, 5083–5088.
17. Lande, R. Models of speciation by sexual selection on polygenic characters. *Proc. Natl Acad. Sci. USA* **78**, 3721–3725 (1981).
18. Arnqvist, G. & Nilson, T. The evolution of polyandry: multiple mating and female fitness in insects. *Anim. Behav.* (submitted).
19. Iwasa, I. & Pomiankowski, A. Continual change in mate preferences. *Nature* **377**, 420–422 (1995).
20. Gavrillets, S. Coevolutionary chase in exploiter–victim systems with polygenic characters. *J. Theor. Biol.* **186**, 527–534 (1997).
21. Barton, N. H. & Turelli, M. Natural and sexual selection on many loci. *Genetics* **127**, 229–255 (1991).
22. Gavrillets, S. & Hastings, A. Dynamics of polygenic variability under stabilizing selection, recombination and drift. *Genet. Res.* **65**, 63–74 (1995).
23. Arnqvist, G., Edvardsson, M., Friberg, U. & Nilsson, T. Sexual conflict promotes speciation in insects. *Proc. R. Soc. Lond. B* (submitted).
24. Walsh, J. B. Rate of accumulation of reproductive isolation by chromosome rearrangements. *Am. Nat.* **120**, 510–532 (1982).
25. Gavrillets, S. Evolution and speciation on holey adaptive landscapes. *Trends Ecol. Evol.* **12**, 307–312 (1997).
26. Gavrillets, S. A dynamical theory of speciation on holey adaptive landscapes. *Am. Nat.* **154**, 1–22 (1999).

27. Arnqvist, G. in *The Evolution of Mating Systems in Insects and Arachnids* (eds Choe, J. C. & Crespi, B. J.) 146–163 (Cambridge Univ. Press, Cambridge, Massachusetts, 1997).
28. Schluter, D. in *Endless Forms. Species and Speciation* (eds Howard, D. J. & Berlocher, S. H.) 114–129 (Oxford Univ. Press, New York, 1998).
29. Rosenzweig, M. L. *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, Massachusetts, 1995).
30. Bürger, R. & Lynch, M. Evolution and extinction in a changing environment—a quantitative genetic analysis. *Evolution* **49**, 151–163.

Supplementary information is available on Nature's World-Wide Web Site (<http://www.nature.com>) or as paper copy from the London editorial offices of Nature.

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Thermal stimulation of taste

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The first electrophysiological recordings from animal¹ and human² taste nerves gave clear evidence of thermal sensitivity, and studies have shown that as many as half of the neurons in mammalian taste pathways respond to temperature^{3–6}. Because temperature has never been shown to induce sensations of taste, it has been assumed that thermal stimulation in the gustatory system is somehow nulled⁶. Here we show that heating or cooling small areas of the tongue can in fact cause sensations of taste: warming the anterior edge of the tongue (chorda tympani nerve) from a cold temperature can evoke sweetness, whereas cooling can evoke sourness and/or saltiness. Thermal taste also occurs on the rear of the tongue (glossopharyngeal nerve), but the relationship between temperature and taste is different there than on the front of the tongue. These observations indicate the human gustatory system contains several different types of thermally sensitive neurons that normally contribute to the sensory code for taste.

Research into thermal effects on taste has focused on modulation of sensitivity to the flavours of chemicals (see, for example, refs 7–9) rather than on the possibility that temperature itself might stimulate taste. Our attention was drawn to this possibility during preliminary experiments on the thermal sensitivity of the tongue. We noticed that warming the tongue tip from 20 to 35 °C caused a transient sensation of sweetness, and that cooling it to ≤20 °C induced a sour taste that for one of us turned to saltiness at temperatures below 10 °C. A screening test for thermal taste conducted on 24 naive subjects yielded 21 individuals who reported at least one taste quality and 19 (5 males and 14 females) who reliably reported two or more tastes at one or more sites along the anterior edge of the tongue. Tastes were generally described as weak but expressions of surprise at their clarity and strength were not uncommon. The subjects who reported two or more taste qualities were enrolled in a study of the psychophysical properties of thermal taste.

We began by exploring the relationship between temperature and taste quality. Figure 1a shows that warming the tongue tip from 20 °C induced sweetness but not other significant tastes in 16 subjects (repeated measures analysis of variance (ANOVA) (temperature × taste quality × replicate), main effect of quality; $F(3, 45) = 40.18$, $P < 0.05$). Sweetness intensified between tem-