*J. Clim.* **14,** 1055–1068 (2001).

24. Plattner, G.-K., Joos, F., Stocker, T. F. & Marchal, O. Feedback mechanisms and sensitivities of ocean carbon uptake under global warming. *Tellus B* **53,** 564–592 (2001).

25. Joos, F. *et al.* Global warming feedbacks on terrestrial carbon uptake under the IPCC emission scenarios. *Glob. Biogeochem. Cycles* **15,** 891–907 (2001).

26. Kattenberg, A. *et al.* in *IPCC Second Scientific Assessment of Climate Change* (eds Houghton, J. T. *et al.*) 285–357 (Cambridge Univ. Press, Cambridge, 1996).

27. Crowley, T. J. Causes of climate change over the past 1000 years. *Science* **289,** 270–277 (2000).

28. Boucher, O. & Haywood, J. On summing the components of radiative forcing of climate change. *Clim. Dyn.* **18,** 297–302 (2001).

29. Knutti, R., Stocker, T. F. & Wright, D. G. The effects of subgrid-scale parameterizations in a zonally averaged ocean model. *J. Phys. Oceanogr.* **30,** 2738–2752 (2000).

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The authors declare that they have no competing financial interests.

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# Origins and estimates of uncertainty in predictions of twenty-first century temperature rise

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**Predictions of temperature rise over the twenty-first century are necessarily uncertain, both because the sensitivity of the climate system to changing atmospheric greenhouse-gas concentrations, as well as the rate of ocean heat uptake, is poorly quantified[1,2] and because future influences on climate—of anthropogenic as well as natural origin—are difficult to predict[3]. Past observations have been used to help constrain the range of uncertainties in future warming rates, but under the assumption of a particular scenario of future emissions[4]. Here we investigate the relative importance of the uncertainty in climate response to a particular emissions scenario versus the uncertainty caused by the differences between future emissions scenarios for our estimates of future change. We present probabilistic forecasts of global-mean temperatures for four representative scenarios for future emissions[5], obtained with a comprehensive climate model. We find that, in the absence of policies to mitigate climate change, global-mean temperature rise is insensitive to the differences in the emissions scenarios over the next four decades. We also show that in the future, as the signal of climate change emerges further, the predictions will become better constrained.**

An estimate of the uncertainty in a climate-model-based prediction of twenty-first century global-mean temperature rise is a potentially valuable tool for policy makers and planners[3,6,7]. Large and difficult-to-quantify uncertainties surround predictions of future demographic changes, economic development and technological change, which will determine future anthropogenic emissions of greenhouse gases and other pollutants. Even with perfect knowledge of emissions, uncertainties in the representation of atmospheric and oceanic processes by climate models limit the accuracy of any estimate of the climate response. Natural variability, generated both internally and from external forcings such as changes in solar output and explosive volcanic eruptions, also contributes to the uncertainty in climate forecasts.

Recently a technique has been developed to quantify uncertainty in predictions by comparing simulations of past temperature changes with observations[4]. Under this approach, based on those developed for the detection and attribution of climate change[8,9], we estimate the factors (with associated uncertainties) by which the model's simulated response to various external forcings over the twentieth century can be scaled up or down while remaining in agreement with the observations. The most important external forcings are well-mixed greenhouse gases, other anthropogenic pollutants such as sulphate aerosols (which are produced by oxidation of sulphur dioxide), changes in tropospheric ozone (which is controlled by photochemical reactions), stratospheric ozone depletion, and natural external forcings such as variations in solar irradiance and stratospheric aerosol from volcanic eruptions.

Temperatures will fluctuate about their mean climatic state owing to natural internal variability. We include decadal variability in our uncertainty analysis, but we do not consider sub-decadal variations that would be additional to the uncertainty in decadal temperatures presented here. We also consider fluctuations due to potential future changes in solar output and volcanic eruptions. As it is not possible to predict deterministically changes in natural forcings, we estimate natural external variability from simulations of the past 140 years that include these natural forcings.

The IPCC, in their Special Report on Emissions Scenarios (SRES[5]), has developed a wide range of future emissions scenarios, based on a variety of narrative 'storylines', each describing a possible future development of population, economies and energy sources. The range of scenarios includes interventions leading to reductions in sulphur emissions and introduction of new energy technologies, but does not include additional initiatives to mitigate climate change. Any estimate of socio-economic trends over the course of the twenty-first century is necessarily very uncertain and highly subjective. Our interest here lies in determining the range of likely future climates consistent with current observations under a representative range of emissions scenarios, and investigating how this uncertainty range will change as the signal of climate change becomes stronger.

We can address these questions with predictions of a coupled atmosphere–ocean general circulation model (AOGCM) using a representative subset of emissions scenarios which span most of the total SRES range, without assigning relative probabilities to the different emissions scenarios. On the assumption that a model that over- or under-estimates the climate response by a certain fraction now will continue to over- or under-estimate it by a similar fraction in the future, we can use a comparison between simulated and observed changes over the past 100 years to calculate the uncertainty in a prediction (according to a particular emissions scenario) over the next 100 years. This assumption appears to be justified for global-mean temperature by the AOGCM runs currently available, all of which evolve similarly over time in response to a given forcing despite differences in sensitivity and thus response amplitude[10]. Even though climate sensitivity is not well constrained by the observed temperature record[4,11], perturbation analysis of simple[4] and intermediate-complexity[11] models indicates that there is a generally linear relationship between past and future global temperature change as we vary the sensitivity of a climate model that continues to hold for unmitigated forcing until the end of the century[12], provided the climate sensitivity and sulphate aerosol forcing are not outside the likely range estimated by the IPCC

Third Assessment Report[13]. This relationship depends on the absence of such possible feedbacks as a shutdown of the thermohaline circulation[14] or the land biosphere switching from being a weak sink for carbon to a strong source[15], and is therefore more likely to hold early on in the century when forcing changes are smallest.

For scenarios in which forcing increases are not sustained, such as stabilization scenarios, an alternative is to calculate probability density functions (PDFs) of key properties of the climate system by varying uncertain model properties and forcings in a simplified climate model[1,2]. This complementary approach produces observational constraints on climate sensitivity and net aerosol forcing but relies on an idealized model.

The model we use in this analysis is HadCM3[16,17], an AOGCM that does not use flux adjustment. To constrain the effects of model uncertainty on future predictions, we have made three ensembles, each of four simulations, of the period 1860–2000. All four simulations in each ensemble are identical except for their initial conditions, which were taken from model states 100 years apart in a 1,820-year control run of HadCM3 in which external forcings have no year-to-year variations. The simulations in the first ensemble incorporate changes in individual well-mixed greenhouse gases including carbon dioxide and methane. Simulations in the second ensemble include, in addition to changes in well-mixed greenhouse gases, changes in tropospheric and stratospheric ozone, and changes in sulphur emissions. The direct effect of sulphate aerosols on planetary albedo is simulated using a fully interactive sulphur cycle scheme that models the emission, transport, oxidation and removal of sulphur species. The indirect effect of tropospheric aerosol, by way of cloud reflectivity[18], is also represented in the model. The simulations in the third ensemble include only natural forcings due to changes in the amount of stratospheric aerosols following volcanic eruptions[19] and spectrally resolved changes in solar irradiance[20].

We have also made a series of model predictions for the twenty-first century[21]. For these predictions, we have chosen four representative SRES marker scenarios (A1FI, A2, B1 and B2), one each from the four SRES storylines and scenario families, and each of which assumes a distinctly different direction for future developments[5]. For each marker scenario we have made two sets of runs starting in 1989. In the first, all anthropogenic forcings are included, whereas the second includes only well-mixed greenhouse gases. As the climate response to greenhouse gases is subject to

different sources of uncertainty from those due to sulphate aerosols, we have included the two effects separately in our analysis to reflect the fact that they may be subject to different errors. We have available three predictions, including all anthropogenic forcings according to the A2 scenario, which we average, and two simulations according to the B2 scenario, which we also average. For the other two scenarios we have only a single simulation including all anthropogenic forcings, and for each of the four scenarios we have a single simulation which includes changes in greenhouse gases only.

Uncertainty ranges of global-mean temperature rise for our four representative emissions scenarios are shown in Fig. 1. (Further details of the methodology are given in the Methods section.) In the first three decades of the twenty-first century, they overlap considerably and indicate that the 5 to 95 percentiles of the forecast temperature distribution are 0.9 to 1.9 K relative to pre-industrial (control) climate by the 2020–30 decade. Only after 2050 is the best estimate of the scenario prediction that warms the greatest over the century (the fossil fuel intensive scenario A1FI) outside the 90% confidence interval of the prediction that warms the least, B1. In the latter half of the century, all SRES scenarios have much reduced $SO_2$ emissions increasing the uncertainty range consistent with past observations[4]. By the end of the century temperatures are predicted to rise from pre-industrial values by 1.9 to 4.0 K according to the B1 scenarios and by 3.6 to 7.5 K according to the A1FI scenario.

Expressed relative to 1990–2000 (Fig. 2), temperatures are predicted to rise between 0.3 and 1.3 K (5–95%) by 2020–30 whichever scenario we take, and by the end of the century by 1.2 to 3.3 K according to the B1 scenario and by 3.0 and 6.9 K according to the A1FI scenario. The upper uncertainty limits for temperature change by 2100 of less than 5 K (1.7–4.9 K, ref. 6; 1.1–4.5 K, ref. 7) depend on assigning a low probability to the A1FI scenario in the absence of climate mitigation policies. The relative contributions to the total forecast uncertainty from externally generated natural variability are greatest early in the century. If we consider anthropogenic warming alone[4], temperatures are predicted to rise from their 1990–2000 values between 0.4 and 1.2 K by 2020–30. The dominant contributor to uncertainty in this decade is that due to response uncertainty.

As the signal of climate change becomes stronger, future predictions of climate change become better constrained. We estimate that by 2020, uncertainties in late twenty-first century global warming
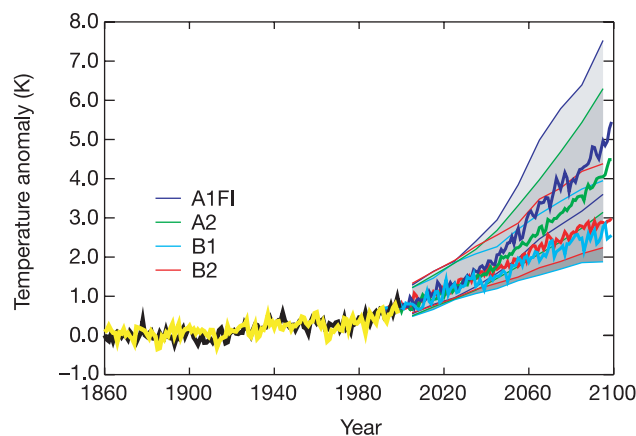


**Figure 1** Uncertainty in predicted global-mean near-surface temperatures. Shown are predictions according to the SRES A1FI (blue), A2 (green), B1 (light blue) and B2 (red) scenarios, with their uncertainties (5 to 95 percentiles) shown as grey regions bounded by lines of the appropriate colour. Also shown are the observed temperatures in black, and a

HadCM3 simulation including both anthropogenic (greenhouse gases, sulphate aerosols and tropospheric and stratospheric ozone) and natural (solar and volcanic) forcings in yellow.

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could potentially reduce to half their values today (Fig. 2). By taking a prediction that follows the B2 scenario to represent a possible future world over the next 20 years and using temperature change observed over the 1920–2019 period to constrain predictions from 2020, we find that global-mean temperatures would be predicted to rise by the end of the century by 2.3 to 3.3 K (5–95%) according to the B1 scenario and by 4.5 to 6.3 K according to the A1FI scenario, relative to pre-industrial values. This calculation assumes a perfect knowledge, to within natural internal variability, of the climatic effects of external forcings from 2000 to 2019, which provides an optimistic estimate of the potential reduction in uncertainty, although diagnostics other than surface temperature might help to reduce uncertainty more rapidly. Also, the spread between the PDFs is likely to change as more information becomes available over the next 20 years about the likely range of emissions paths over the remainder of the twenty-first century.

Our global-mean temperature forecasts, with their associated uncertainty ranges, are based on an objective comparison of the model's simulation of past temperatures with observations and do not depend on a subjective estimate of the model's climate sensitivity based on "expert elicitation"[6]. They are also based on a comprehensive climate model that accurately simulates multi-decadal variations in global-mean near-surface temperatures over the twentieth century when it includes the most important anthropogenic and natural forcings[22]. They show that by the 2020–30 decade, global-mean near-surface temperatures are likely to be 0.3 to 1.3 K warmer than they were three decades earlier, regardless of whether $CO_2$ emissions increase only by $1\,\mathrm{Gt\,C\,yr^{-1}}$ from their 1990 levels, as the B1 scenario predicts, or by $8\,\mathrm{Gt\,C\,yr^{-1}}$ as A1FI predicts[13]. This lack of sensitivity to increases in $CO_2$ emissions arises partly because the climate system's inertia dictates that much of the rise is already committed by pre-2000 emissions, and partly because differences in $CO_2$ emissions are offset to some extent in most scenarios by differences in $SO_2$ emissions.

In our analysis, we account for errors in the magnitude of forecast patterns of temperature change but do not account for errors in the patterns themselves; consequently our approach may not be valid for regional or non-temperature indicators of climate change. To explore fully the influence of model error requires a systematic

evaluation of the sensitivity of coupled AOGCM predictions to varying the many model parameters across their ranges of plausible values[23]. Until such an experiment is performed, a linear analysis represents the most objective approach available for predicting future global-mean temperatures using comprehensive models.

In the first four decades of this century, Fig. 1 shows that predictions for a representative ranges of SRES scenarios differ remarkably little. Until 2040, uncertainty is dominated not by uncertainties in emissions scenarios but by uncertainties in climate response. Later in the century, the effect of different emissions matter much more, although even at the end of the century climate response uncertainty remains as great as emissions uncertainty. Relatively modest increases in global temperature by 2100 are possible under some emissions scenarios, but extremely rapid warming rates over the century cannot be excluded under fossil fuel intensive scenarios.  □

## Methods

The method we use to determine the uncertainty range for each forecast scenario is as follows. First we compare the observed evolution of the surface temperature over the twentieth century with the modelled response to greenhouse gases, sulphate aerosols and natural forcing. This generates a distribution of factors by which the model response to each forcing can be scaled up or down while still matching the observations. Second, we account for uncertainty in the model forecasts, which would be present even if we were certain about the past response to forcing. Third, we combine the distributions of the scaling factors with the distributions of the model forecast to generate a distribution of the forecast temperature response to the combined forcing. Each of these stages is outlined below.

### Calculation of scaling factors

To compare model simulations with observations and calculate the scaling factors to be applied to model predictions of temperature changes due to greenhouse gases and other anthropogenic forcings, we follow the procedure of ref. 24. Decadal-mean data from models and observations are smoothed spatially to retain only scales greater than 5,000 km (ref. 25). Scaling factors on the greenhouse gases, and other anthropogenic and natural contributions are estimated using standard optimal fingerprinting[26], modified to take account of sampling noise in model-simulated signals[27]. Intra-ensemble differences are used to define the optimization space, and a 1,820-year control run of HadCM3 is used for uncertainty analysis. The optimal fingerprinting gives a distribution of scaling factors for the forced response. The uncertainty implied by the distributions results from interdecadal internal variability, which prevents us determining with certainty how much of twentieth-century temperature variation was externally forced and how much can be accounted for by internal variability.

### Uncertainty in model forecasts

Even if there was no uncertainty in the past response of the climate system to external forcing, there are sources of uncertainty in the forecast made by a model. The first source of uncertainty is due to uncertainty in future natural forcing. Here we take this into account by assuming there is no deterministic knowledge of natural forcings over future decades. We calculate the variance in global-mean temperatures due to changes in solar output and volcanic eruptions from the natural ensemble of four simulations described earlier, adjusting the variance to take account of the finite ensemble size by subtracting one-quarter of the variance due to internal variability of the control run. A distribution of possible forecasts of natural climate change is then generated by selecting random members of a normal distribution whose variance is that of this estimate of natural externally forced variability. Note that the use of a normal distribution will probably underestimate the contribution of low-probability, high-impact natural events, but we are focusing here on the central 5–95% uncertainty ranges.

The second source of uncertainty in the model forecast results from internal variability and from having only a small number of predictions from forecast ensembles. We take account of this uncertainty by selecting random perturbations from a normal distribution and adding these to the anthropogenic predictions. The variance of the normally distributed perturbations is calculated from the control run, and adjusted to account for the size of the forecast ensemble.

### Combination of scaling factors with model forecasts

Having obtained distributions of future anthropogenic and naturally forced responses, we combine these with the distribution of factors by which the modelled response must be scaled to match observations of 1900–2000 and additionally include a sample of the internal variability on the top of the forced response. The result is a probability distribution of forecast temperature for each scenario, from which the median temperature forecast and confidence intervals can be determined. In the calculation of temperature changes relative to 1990–2000, we additionally take account of the extra uncertainty arising from taking the difference between two uncertainly known decadal-mean temperatures by doubling the variance due to internal variability about the mean state.

Our uncertainty limits depend on model-based estimates of both internally generated and externally generated natural variability. Reconstructions of past temperature change based on palaeodata indicate that coupled models' internal variability is generally
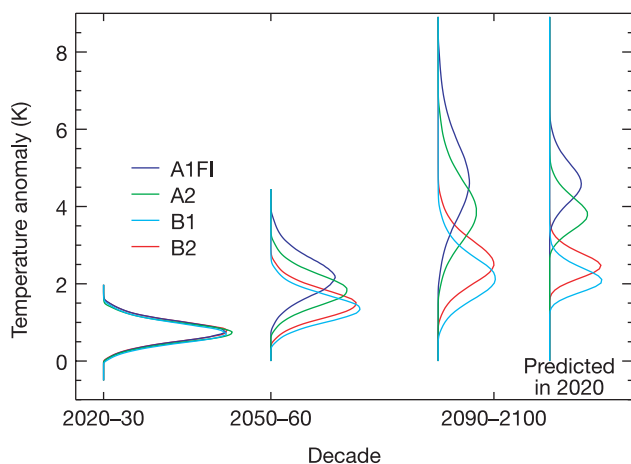


**Figure 2** Probability density functions (PDFs) of temperature change. Shown are PDFs for four SRES scenarios (A1FI, A2, B1 and B2) for 2020–30, 2050–2060 and 2090–2100 decades relative to the 1990–2000 decade, calculated by constraining HadCM3 simulations to the observed temperature change over the 1900–99 period. The PDFs at the far right are for the 2090–2100 decade calculated by constraining HadCM3 simulations to be consistent with the observed temperature change over the 1920–2019 period, where the observations are assumed to follow a B2 scenario prediction after 1999.

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consistent with that observed[28], and HadCM3, when it includes both anthropogenic and natural forcings, simulates many features of observed twentieth-century temperature change[22], indicating some success in incorporating external forcings including those due to solar changes and volcanic aerosol. Nevertheless, the current dependence on model-based rather than observationally based estimates of natural variability needs to be tested further against observational evidence. We do not include the effect of observational error in our analysis. The effect of observational sampling error on detection and attribution results has been shown to be small[29], but we do not as yet have an estimate of the effects of systematic instrumental errors, such as changes in measurement practices or urbanization.

1. Forest, C. E., Stone, P. H., Sokolov, A. P., Allen, M. R. & Webster, M. Quantifying uncertainties in climate system properties using recent climate observations. *Science* **295**, 113–117 (2002).
2. Knutti, R., Stocker, T. F., Joos, F. & Plattner, G.-K. Constraints on radiative forcing and future climate change from observations and climate model ensembles. *Nature* **416**, 719–723 (2002).
3. Allen, M. R., Raper, S. C. B. & Mitchell, J. F. B. Uncertainty in the IPCC's third assessment report. *Science* **293**, 430–433 (2001).
4. Allen, M. R., Stott, P. A., Mitchell, J. F. B., Schnur, R. & Delworth, T. L. Uncertainty in forecasts of anthropogenic climate change. *Nature* **407**, 617–620 (2000).
5. Nakicenovic, N. & Swart, R. *Special Report on Emission Scenarios* (Cambridge Univ. Press, Cambridge, 2000).
6. Wigley, T. M. L. & Raper, S. C. B. Interpretation of high projections for global-mean warming. *Science* **293**, 451–454 (2001).
7. Reilly, J. *et al.* Uncertainty and climate change assessments. *Science* **293**, 430–433 (2001).
8. Allen, M. R. & Tett, S. F. B. Checking for model consistency in optimal fingerprinting. *Clim. Dyn.* **15**, 419–434 (1999).
9. Tett, S. F. B., Stott, P. A., Allen, M. R., Ingram, W. J. & Mitchell, J. F. B. Causes of twentieth century temperature change near the Earth's surface. *Nature* **399**, 569–572 (1999).
10. Cubasch, U. *et al.* in *Climate Change 2001: The Scientific Basis* Ch. 9 (eds Houghton, J. T. *et al.*) 525–582 (Cambridge Univ. Press, Cambridge, 2001).
11. Forest, C. E., Allen, M. R., Stone, P. H. & Sokolov, A. P. Constraining uncertainties in climate models using climate change detection techniques. *Geophys. Res. Lett.* **27**, 569–572 (2000).
12. Booth, B. B. B., Allen, M. R. & Kettleborough, J. A. *Exploring the Linearity of the Climate Response to External Forcing* (Tech. Report RAL-TR2002-005, Rutherford Appleton Laboratory, Chilton, UK, 2002).
13. Houghton, J. T. *et al.* (eds) *Climate Change 2001: The Scientific Basis* (Cambridge Univ. Press, Cambridge, 2001).
14. Stocker, T. F. & Schmittner, A. Influence of CO$_2$ emission rates on the stability of the thermohaline circulation. *Nature* **388**, 862–865 (1997).
15. Cox, P. N., Betts, R. A., Jones, C. D., Spall, S. A. & Totterdell, I. J. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184–187 (2000).
16. Gordon, C. *et al.* The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Clim. Dyn.* **16**, 147–168 (2000).
17. Pope, V. D., Gallani, M. L., Rowntree, P. R. & Stratton, R. A. The impact of new physical parametrizations in the Hadley Centre climate model—HadAM3. *Clim. Dyn.* **16**, 123–146 (2000).
18. Twomey, S. A. Pollution and the planetary albedo. *Atmos. Environ.* **8**, 1251–1256 (1974).
19. Sato, M., Hansen, J. E., McCormick, M. P. & Pollack, J. B. Stratospheric aerosol optical depths (1850–1990). *J. Geophys. Res.* **98**, 22987–22994 (1993).
20. Lean, J., Beer, J. & Bradley, R. Reconstruction of solar irradiance since 1610: implications for climate change. *Geophys. Res. Lett.* **22**, 3195–3198 (1995).
21. Johns, T. C. *et al. Anthropogenic Climate Change for 1860 to 2100 Simulated with the HadCM3 Model under Updated Emissions Scenarios* (Tech. Note 22, Hadley Centre for Climate Prediction and Research, Bracknell, UK, 2001).
22. Stott, P. A. *et al.* External control of 20th century temperature by natural and anthropogenic forcings. *Science* **290**, 2133–2137 (2000).
23. Allen, M. R. Do-it-yourself climate prediction. *Nature* **401**, 642 (1999).
24. Stott, P. A. *et al.* Attribution of twentieth century temperature change to natural and anthropogenic causes. *Clim. Dyn.* **17**, 1–21 (2001).
25. Stott, P. A. & Tett, S. F. B. Scale-dependent detection of climate change. *J. Clim.* **11**, 32892–3294 (1998).
26. Hasselmann, K. Multi-pattern fingerprint method for detection and attribution of climate change. *Clim. Dyn.* **13**, 601–611 (1997).
27. Allen, M. R. & Stott, P. A. Estimating signal amplitudes in optimal fingerprinting. Part I: theory. *Clim. Dyn.* (submitted).
28. Crowley, T. J. Causes of climate change over the past 1000 years. *Science* **289**, 270–277 (2000).
29. Hegerl, G. C., Jones, P. D. & Barnett, T. P. Effect of observational sampling error on the detection and attribution of anthropogenic climate change. *J. Clim.* **14**, 198–207 (2001).

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# Using the fossil record to estimate the age of the last common ancestor of extant primates

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**Divergence times estimated from molecular data often considerably predate the earliest known fossil representatives of the groups studied. For the order Primates, molecular data calibrated with various external fossil dates uniformly suggest a mid-Cretaceous divergence from other placental mammals, some 90 million years (Myr) ago[1–9], whereas the oldest known fossil primates are from the basal Eocene epoch (54–55 Myr ago). The common ancestor of primates should be earlier than the oldest known fossils[10,11], but adequate quantification is needed to interpret possible discrepancies between molecular and palaeontological estimates. Here we present a new statistical method, based on an estimate of species preservation derived from a model of the diversification pattern, that suggests a Cretaceous last common ancestor of primates, approximately 81.5 Myr ago, close to the initial divergence time inferred from molecular data. It also suggests that no more than 7% of all primate species that have ever existed are known from fossils. The approach unites all the available palaeontological methods of timing evolutionary events: the fossil record, extant species and clade diversification models.**

Although several molecular studies indicate that the lineage leading to primates diverged from other eutherian mammals about 90 Myr ago, diagnostic morphological features of primates possibly emerged later, potentially explaining why recognizable

**Table 1 Relative sampling intensities for the primate fossil record**

| Epoch | $k$ | $T_k$ | Observed number of species, $D_k$ | Relative sampling intensity, $p_k$ | |
|---|---|---|---|---|---|
| | | | | Scheme 1 | Scheme 2 |
| Late Pleistocene | 1 | 0.15 | 19 | 1.0 | 1.0 |
| Middle Pleistocene | 2 | 0.9 | 28 | 1.0 | 1.0 |
| Early Pleistocene | 3 | 1.8 | 22 | 1.0 | 1.0 |
| Late Pliocene | 4 | 3.6 | 47 | 1.0 | 1.0 |
| Early Pliocene | 5 | 5.3 | 11 | 1.0 | 0.5 |
| Late Miocene | 6 | 11.2 | 38 | 1.0 | 0.5 |
| Middle Miocene | 7 | 16.4 | 46 | 1.0 | 1.0 |
| Early Miocene | 8 | 23.8 | 36 | 1.0 | 0.5 |
| Late Oligocene | 9 | 28.5 | 4 | 1.0 | 0.1 |
| Early Oligocene | 10 | 33.7 | 20 | 1.0 | 0.5 |
| Late Eocene | 11 | 37.0 | 32 | 1.0 | 1.0 |
| Middle Eocene | 12 | 49.0 | 103 | 1.0 | 1.0 |
| Early Eocene | 13 | 54.8 | 68 | 1.0 | 1.0 |
| Pre-Eocene | 14 | | 0 | 0.1 | 0.1 |

Data are shown for a total of 235 modern species. References for the data can be found in the Supplementary Information.

assembled with various bilins as described[15]. Spectra were obtained after saturating red (660 nm) and far-red (740 nm) irradiations. *In vitro* kinase assays for the active *Br*BphPs were performed as described[5].

### Construction of *BrbphP* and *ppsR* mutant strains

To create *Brbph* and *ppsR* null mutants, the *lacZ-kan*[r] cassette[19] was inserted respectively in the *Xho*I site of *BrbphP* and the *Bgl*II site of *ppsR*. The constructions were introduced in the pJQ200 suicide vector[22] and delivered by conjugation into the ORS278 strain as previously described[8]. Double recombinants were selected on sucrose and confirmed by PCR.

1. Quail, P. H. *et al.* Phytochromes: photosensory perception and signal transduction. *Science* **268**, 675–680 (1995).
2. Smith, H. Phytochromes and light signal perception by plants—an emerging synthesis. *Nature* **407**, 585–591 (2000).
3. Kehoe, D. M. & Grossman, A. R. Similarity of a chromatic adaptation sensor to phytochrome and ethylene receptors. *Science* **273**, 1409–1412 (1996).
4. Hughes, J. *et al.* A prokaryotic phytochrome. *Nature* **386**, 663 (1997).
5. Jiang, Z.-Y. *et al.* Bacterial photoreceptor with similarity to photoactive yellow protein and plant phytochromes. *Science* **285**, 406–409 (1999).
6. Davis, S. J., Vener, A. V. & Vierstra, R. D. Bacteriophytochromes: phytochrome-like photoreceptors from nonphotosynthetic eubacteria. *Science* **286**, 2517–2520 (1999).
7. Schmitz, O., Katayama, M., Williams, S. B., Kondo, T. & Golden, S. S. CikA, a bacteriophytochrome that resets the cyanobacterial circadian clock. *Science* **289**, 765–768 (2000).
8. Giraud, E., Hannibal, L., Fardoux, J., Verméglio, A. & Dreyfus, B. Effect of *Bradyrhizobium* photosynthesis on stem nodulation of *Aeschynomene sensitiva*. *Proc. Natl Acad. Sci. USA* **97**, 14795–14800 (2000).
9. Muratomo, T., Kohchi, T., Yokota, A., Hwang, I. & Goodman, H. M. The *Arabidopsis* photomorphogenesis mutant *hy1* is deficient in phytochrome chromophore biosynthesis as a result of a mutation in a plastid heme oxygenase. *Plant Cell* **11**, 335–347 (1999).
10. Parkinson, J. S. & Kofoid, E. C. Communications modules in bacterial signalling proteins. *Annu. Rev. Genet.* **26**, 71–112 (1992).
11. Zhulin, I. B., Taylor, B. L. & Dixon, R. PAS domain S-boxes in Archaea, Bacteria and sensors for oxygen and redox. *Trends Biochem. Sci.* **22**, 331–337 (1997).
12. Taylor, B. L. & Zhulin, I. B. PAS domains: Internal sensors of oxygen, redox potential, and light. *Microbiol. Mol. Biol. Rev.* **63**, 479–506 (1999).
13. Ponnampalam, S. N., Buggy, J. J. & Bauer, C. E. Characterization of an aerobic repressor that coordinately regulates bacteriochlorophyll, carotenoid, and light harvesting-II expression in *Rhodobacter capsulatus. J. Bacteriol.* **177**, 2990–2997 (1995).
14. Gomelsky, M. & Kaplan, S. Molecular genetic analysis suggesting interaction between AppA and PpsR in regulation of photosynthesis gene expression in *Rhodobacter sphaeroides. J. Bacteriol.* **179**, 128–134 (1997).
15. Li, L. & Lagarias, J. C. Phytochrome assembly. *J. Biol. Chem.* **267**, 19204–19210 (1992).
16. Bhoo, S.-H., Davis, S. J., Walker, J., Karniol, B. & Vierstra, R. D. Bacteriophytochromes are photochromic histidine kinases using a biliverdin chromophore. *Nature* **414**, 776–779 (2001).
17. Fleischman, D. & Kramer, D. Photosynthetic rhizobia. *Biochim. Biophys. Acta* **1364**, 17–36 (1998).
18. Clayton, R. K. The induced synthesis of catalase in *Rhodopseudomonas sphaeroides. Biochim. Biophys. Acta* **37**, 503–512 (1960).
19. Kokotek, W. & Lotz, W. Construction of a *lacZ*-kanamycine–resistance cassette, useful for site-directed mutagenesis and as a promoter probe. *Gene* **84**, 467–471 (1989).
20. Boivin, C., Camut, S., Malpica, C. A., Truchet, G. & Rosenberg, C. *Rhizobium meliloti* genes encoding catabolism of trigonelline are induced under symbiotic conditions. *Plant Cell.* **2**, 1157–1170 (1990).
21. Yurkov, V., Schoepp, B. & Verméglio, A. Photoinduced electron transfer and cytochrome content in obligate aerobic phototrophic bacteria from genera *Erythromicrobium, Sandaracinobacter, Erythromonas, Roseococcus* and *Erythrobacter. Photosynth. Res.* **57**, 117–128 (1998).
22. Quandt, J. & Hynes, M. F. Versatile suicide vectors which allow direct selection for gene replacement in gram-negative bacteria. *Gene* **127**, 15–21 (1993).

### Competing interests statement

organization of *Rps. palustris* was deduced from the genome database at http://spider.jgi-psf.org/JGI-microbial/html/.

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## corrigendum

# Nuclear translocation and transcription regulation by the membrane-associated guanylate kinase CASK/LIN-2

**Yi-Ping Hsueh, Ting-Fang Wang, Fu-Chia Yang & Morgan Sheng**

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In this Letter, we numbered some nucleotides for the upstream region of the *reelin* gene incorrectly. The Reelin-luc construct contains an upstream region of the *reelin* gene corresponding to nucleotides 157700–158620 of human BAC clone AC002067, instead of nucleotides 3700–4620. This does not affect any of the results or conclusions of the paper. We thank A. M. Goffinet, D. Grayson, K. Mendra and T. Curran for alerting us to this mistake. □

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## erratum

# Origins and estimates of uncertainty in predictions of twenty-first century temperature rise

**Peter A. Stott & J. A. Kettleborough**

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On page 725 of this Letter, the words 'predicts[13] fThur lglk al seasitevier' were corrupted. They should read 'predicts[13]. This lack of sensitivity'. □