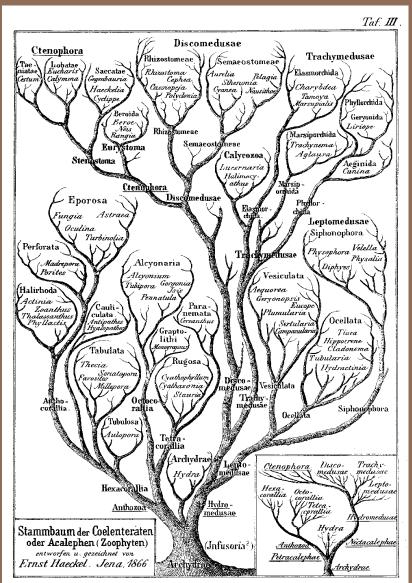
# 基因水平转移

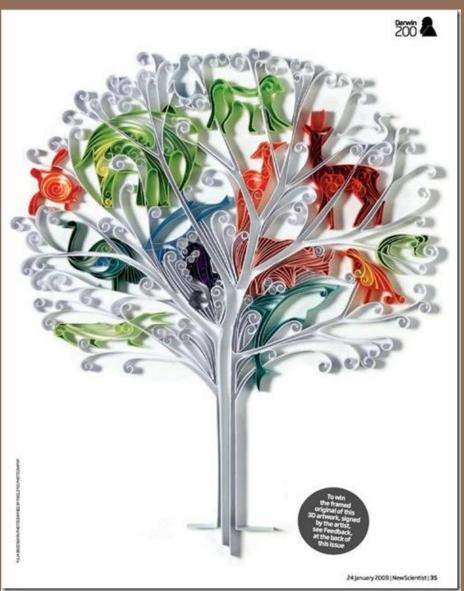
## 系统发育预测与实验验证

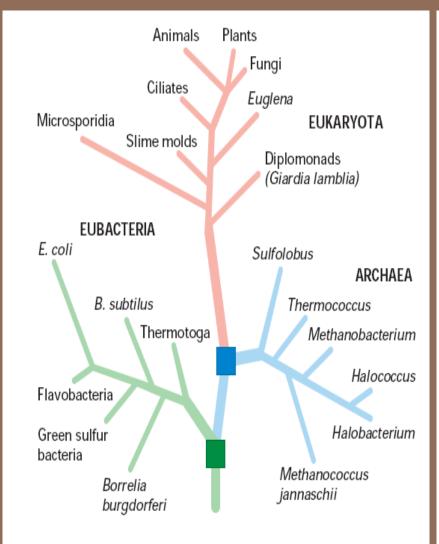
钟 扬

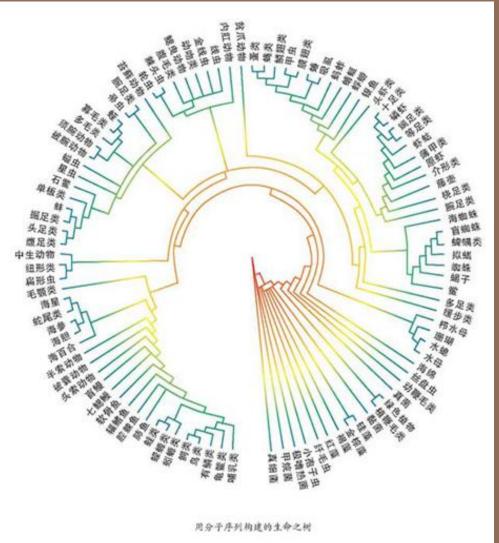
(西藏大学/复旦大学)

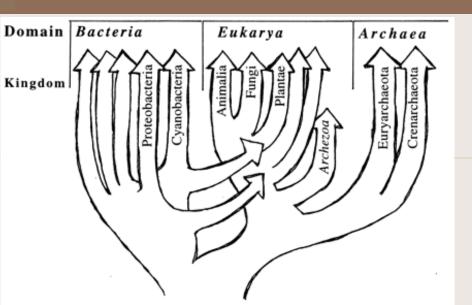
# Tree of Life (生命之树)



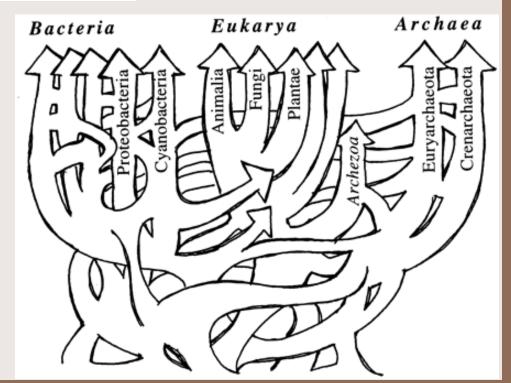






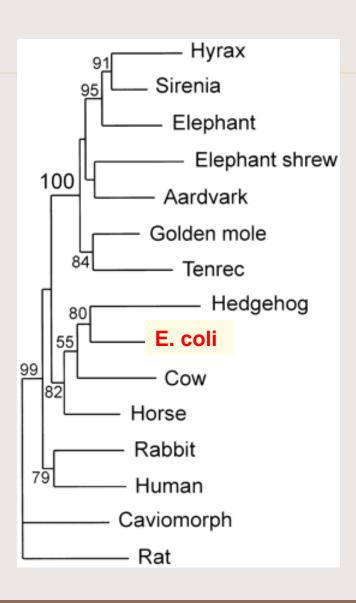


### 细菌与生命之树

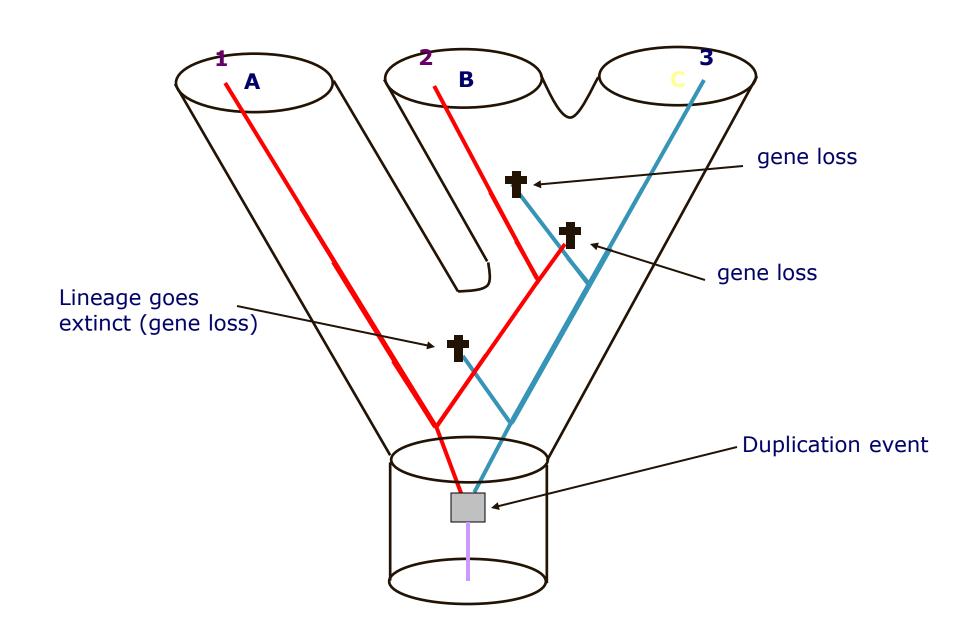


网状树

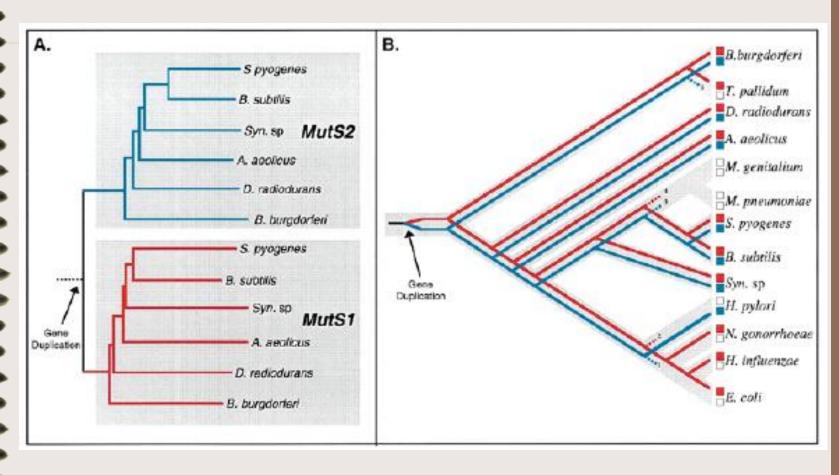
### 基因水平转移(Horizontal gene transfer)?



## 备择假设:基因丧失



## 利用系统发育树了解基因重复和丧失



- A. 基因树
- B. 将基因树叠加在物种树上来鉴定基因重复和丧失

#### articles

# Initial sequencing and analysis of the human genome

International Human Genome Sequencing Consortium<sup>\*</sup>

\* A partial list of authors appears on the opposite page. Affiliations are listed at the end of the paper.

The human genome holds an extraordinary trove of information about human development, physiology, medicine and evolution. Here we report the results of an international collaboration to produce and make freely available a draft sequence of the human genome. We also present an initial analysis of the data, describing some of the insights that can be gleaned from the sequence.

Genome Sequencing Centres (Listed in order of total genomic sequence contributed, with a partial list of personnel. A full list of contributors at each centre is available as Supplementary

Whithhead Institute for Blomedical Research, Center for Genome Research: Fici. S. Lander', Lauren M. Luthon, 'Bruce Birren', 'Chad Nushaum', 'Michael C. Zody', 'Jennifer Badvain', Kari Bevon', Ken Oevera', Michael Doyle', William Fizikuph', Roof Funke', Diane Gage', 'Kathrin Harris', 'Andrew Heafrod', John Howland', 'Lie Sam', Jessica Leboczky, 'Rossie LeVine', 'Paul McYan', 'Kevin McKornan', James McKrim', Jill P. Mesirov', 'Paul McYan', 'William Morris', Jerone Haylor', 'Christin Raymond', Mark Rosetti', Rajah Sanbs', 'Andrew Sherdan', 'Carris Gugore', 'Nocide Stange-Thomann', 'Nikola Stojanovic', 'Aravind Subramarian'

The Sanger Centre: Jane Rogers<sup>2</sup>, John Sulston<sup>2</sup>,
Rachael Airscouph, Stephan Beck, David Bentiey<sup>2</sup>, John Burtor<sup>2</sup>,
Christopher Clee<sup>2</sup>, Nigel Carter<sup>2</sup>, Alan Coulson<sup>2</sup>,
Rebecco Bedman<sup>2</sup>, Parus Deloukar<sup>2</sup>, Andrew Dunham<sup>2</sup>,
Ian Dunham<sup>2</sup>, Richard Durbin<sup>2</sup>, Lisa French<sup>2</sup>, Darren Grafham<sup>2</sup>,
Simon Gregory, Tim Hubbard<sup>2</sup>, Saen Humphray<sup>2</sup>, Adrienne Hunt<sup>2</sup>,
Matthew Jones<sup>2</sup>, Christine Lloyd<sup>2</sup>, Amanda McMurray<sup>2</sup>,
Lucy Matthews<sup>2</sup>, Simon Mercer<sup>2</sup>, Sarah Milm<sup>2</sup>, Janes C. Mulliahr<sup>2</sup>,
Andrew Mungali<sup>2</sup>, Robert Plumb<sup>2</sup>, Mark Ross<sup>2</sup>, Ratna Shownkeen<sup>2</sup>
& Sarah Simo<sup>2</sup>.

& Sarah Simo<sup>2</sup>.

Washington University Genome Sequencing Center: Robert II. Waters both, Richard K. Wilson, \*Labeana W. Hillier<sup>3</sup>\*, John D. McPherson, \*Marco A. Marra<sup>3</sup>, Eshiae R. Mardis<sup>3</sup>, Lucinda A. Futorin, \*Set T. Chimsyalia<sup>3</sup>\*, Kymbrein R. Hepin<sup>3</sup>, Warren R. Gist<sup>3</sup>, \*Stephanie L. Chisson<sup>3</sup>, Michael C. Wendf<sup>3</sup>, Kim D. Gelebaumty<sup>3</sup>, Yazie L. Bimar<sup>3</sup>, Andrew Delbaumty<sup>3</sup>, Jason B. Kramer<sup>3</sup>, Lisa L. Cook<sup>3</sup>, Robert S. Futbon<sup>3</sup>, Douglas L. Johnson<sup>5</sup>, \*Patrick J. Minr<sup>2</sup> & Sandra W. Ciliton<sup>3</sup>

US DOE Joint Genome Institute: Trevor Hawkins\*, Elbert Branscomb\*, Paul Predix\*, Paul Richardson\*, Srarh Wenning\*, Tom Skezak\*, Norman Doggetf, Jan-Fang Cheng\*, Anne Olsen\*, Susan Lucas\*, Christopher Blan\*, Edward Uberscher\* & Marnin Frazier\*

Baylor College of Medicine Human Genome Sequencing Center: Richard A. Gibbs\*\*, Donna M. Muzny\*, Saven E. Scherer\*, John B. Bouck\*, Ficha J. Sodgerer, Kim C. Worley\*, Catherine M. Rives\*, James H. Gorrell\*, Michael L. Metzker\*, Susan L. Naylor\*, Raju S. Kucherlapaly\*, David L. Welson, 8, George M. Weinstock\*

RIKEN Genomic Sciences Center: Yoshiyuki Sakaki<sup>a</sup>, Asao Fujiyama<sup>a</sup>, Masahira Hattori<sup>a</sup>, Te'sushi Yada<sup>a</sup>, Atsushi Toyoda<sup>a</sup>, Takehiko Itoh<sup>a</sup>, Chiharu Kawagoe<sup>a</sup>, Hidemi Watanabe<sup>a</sup>, Yasushi Toblai<sup>a</sup> & Todd Taylor<sup>a</sup>

Genoscope and CNRS UMR-8030: Jean Weissenbach<sup>10</sup>, Roland Heilig<sup>10</sup>, William Saurin<sup>10</sup>, Francois Artiguenave<sup>10</sup>, Philippe Brottier<sup>10</sup>, Thomas Bruls<sup>10</sup>, Eric Pelletier<sup>10</sup>, Catherine Robert<sup>10</sup> & Patrick Wincker<sup>10</sup>

GTC Sequencing Center: Douglas R. Smith<sup>11</sup>, Lynn Doucatte-Stamm<sup>11</sup>, Marc Ruberfield<sup>11</sup>, Keith Weinstock<sup>11</sup>, Hong Mei Lee<sup>11</sup> & JoAnn Dubois<sup>11</sup>

Department of Genome Analysis, Institute of Molecular

Biotechnology: André Rosenthal<sup>12</sup>, Matthias Platzer<sup>12</sup>, Gerald Nyakatura<sup>12</sup>, Stefan Taudien<sup>12</sup> & Andreas Rump<sup>12</sup>

Belling Genomics Institute/Human Genome Center: Huanming Yang<sup>13</sup>, Jun Yu<sup>13</sup>, Jian Wang<sup>13</sup>, Guyang Huang<sup>14</sup> & Jun Gu<sup>15</sup>

Multimegabase Sequencing Center, The Institute for Systems Biology: Leroy Hood<sup>16</sup>, Lee Rowen<sup>16</sup>, Anup Madan<sup>16</sup> & Shizen Qin<sup>16</sup>

Stanford Genome Technology Center: Ronald W. Davis<sup>17</sup>, Nancy A. Federspiel<sup>17</sup>, A. Pia Abola<sup>17</sup> & Michael J. Proctor<sup>17</sup>

Stanford Human Genome Center: Richard M. Myers<sup>18</sup> Jeremy Schmutz<sup>18</sup>, Mark Dickson<sup>18</sup>, Jane Grimwood<sup>18</sup> & David R. Cox<sup>18</sup>

University of Washington Genome Center: Maynard V. Olson<sup>19</sup>, Rajinder Kaul<sup>19</sup> & Christopher Raymond<sup>19</sup>

Department of Molecular Biology, Kelo University School of Medicine: Nobuyoshi Shimizu<sup>20</sup>, Kazuhiko K*a*wasaki<sup>20</sup> & Shinsei Minoshima<sup>20</sup>

University of Texas Southwestern Medical Center at Dallas: Glen A. Evans<sup>21†</sup>, Maria Athanasiou<sup>21</sup> & Roger Schultz<sup>21</sup>

University of Oldahoma's Advanced Center for Genome Technology: Bruce A. Roe<sup>22</sup>, Feng Chen<sup>22</sup> & Huaqin Par<sup>22</sup>

Max Planck Institute for Molecular Genetics: Juliane Ramser<sup>23</sup>, Hans Lehrach<sup>23</sup> & Richard Reinhardt<sup>23</sup>

Cold Spring Harbor Laboratory, Lita Annenberg Hazen Genome Center: W. Richard McCombie<sup>24</sup>, Melissa de la Bastide<sup>24</sup> & Neitav Dechia<sup>24</sup>

GBF—German Research Centre for Biotechnology: Helmut Blöcker<sup>25</sup>, Klaus Hornischer<sup>25</sup> & Gabriele Nordsiek<sup>25</sup>

Genome Analysis Group (Hebot in alphabetical order, also Intodos Individuals Holds under of the headings): Richa Agarwala", L. Azavind", Jeffrey A. Bailey", Alex Batmarri, Serafin Batzoloui, Evan Birnya", Per Botz, P

Scientific management: National Human Genome Research Institute, US National Institutes of Health Francis Collins<sup>60</sup>\*, Mark S. Guyer<sup>61</sup>, Jane Peterson<sup>60</sup>, Adam Felsenfeld<sup>60</sup> & Kris A. Wetterstrand<sup>61</sup>, Office of Science, US Department of Energy, Aristides Patrinos<sup>67</sup>; The Wellcome Trust: Michael J. Morzan<sup>68</sup> Hundreds of genes appear to have resulted from horizontal gene transfer from bacteria...

2001 409:860-921 Nature

#### Genomics

## Genes lost during evolution

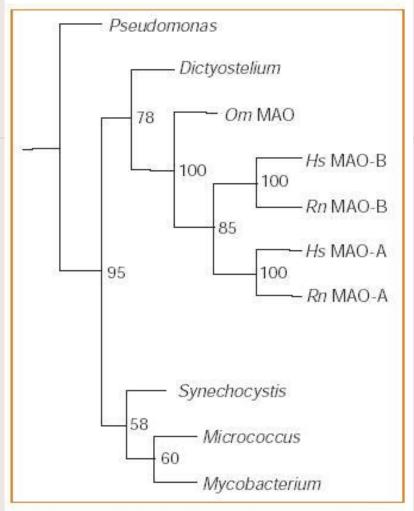
by the International Human Genome Sequencing Consortium is that "hundreds of genes appear to have resulted from horizontal gene transfer from bacteria at some point in the vertebrate lineage". We noticed that a significant proportion of these human genes have closely related orthologues in the primitive eukaryote Dictyostelium. This observation supports independent gene loss in multiple lineages (worm, fly, yeast, plants) rather than hori-

zontal gene transfer from bacteria.

The human genome sequence revealed 113 genes that share a high degree of identity with bacterial genes, but are absent in the completely sequenced genomes Caenorhabditis elegans, Drosophila melanogaster, Saccharomyces cerevisiae and Arabidopsis thaliana<sup>1</sup>. Do these genes represent examples of horizontal gene transfer from bacteria to the vertebrate lineage, or were they present in both prokaryotes and early eukaryotes, but subsequently lost from all non-vertebrate eukaryotic lineages? Although this latter possibility may seem unlikely, we recently identified a gene in *Dictyostelium* that is clearly an orthologue of the gene that encodes soluble

2001 411:1013-1014 Nature

We used all 113 listed human genes to screen for homologous sequences in *Dictyostelium* (27 February 2001; see supplementary information). A TBLASTN screen of the *Dictyostelium* database yielded 36 sequences with expectation values of less than 10<sup>-10</sup>. BLASTX analysis with the obtained *Dictyostelium* DNA sequences against GenBank identified 11 genes that represent clear *Dictyostelium* orthologues of human genes: the human sequences share a higher degree of identity with *Dictyostelium* than with bacterial sequences, and the bacterial sequences score more highly with respect to *Dictyostelium* than they do to humans (on the basis of BLAST expectation values). A further 17 *Dictyostelium* sequences share a high degree of identity with the human sequence, but are not obvious inter-We used all 113 listed human genes to human sequence, but are not obvious intermediates between the bacterial and vertebrate orthologues (see supplementary information). Thus, in at least 11 cases, the Dictyostelium and human genes have a common ancestor, eliminating the need to invoke horizontal gene transfer from bacteria.



**Figure 1** Phylogenetic analysis of monoamine oxidase (MAO). Numbers indicate values of bootstrap analysis (*n* = 100). Hs, *Homo sapiens*; Rn, *Rattus norvegicus* (rat); Om, *Oncorhynchus mykiss* (rainbow trout).





#### Image: Dr. Fleut H. Dear and MRC Visual Aids Unit, Laboratory of Molecular Biology

# 盘基网柄菌(Dictyostelium discoideum)——真核生物中最简洁的基因组之一

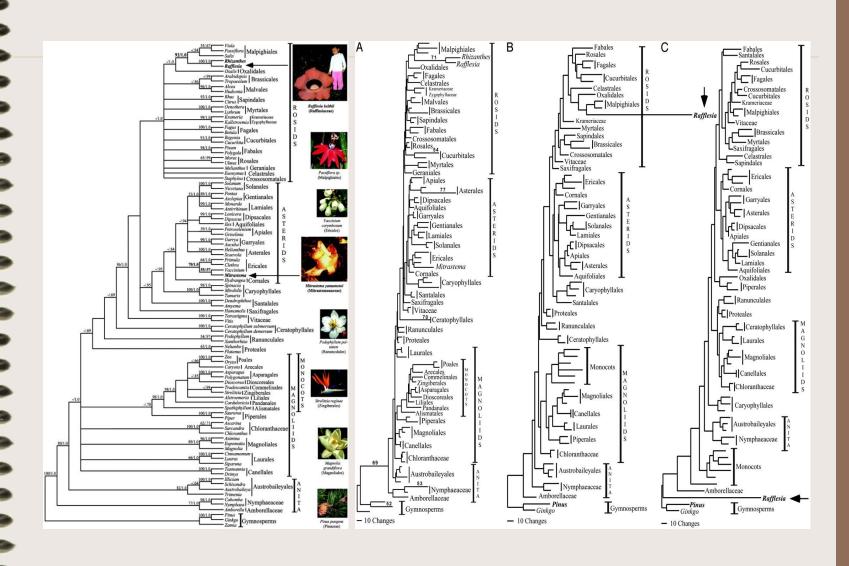
Within the group of 113 genes proposed to have entered the human genome by horizontal gene transfer from bacteria, we have identified at least 11 that probably arose through normal evolution with gene loss in several lineages, suggesting that gene loss is not a rare event. With several ongoing genomic sequencing projects for lower eukaryotes, it will be interesting to see how many genes have truly undergone horizontal transfer.





大花草属 (Rafflesia)

## 全寄生植物大花草的系统发育位置



### 基因水平转移: 从早期陆地植物到被子植物的基出类群

# Massive horizontal transfer of mitochondrial genes from diverse land plant donors to the basal angiosperm Amborella

Ulfar Bergthorsson<sup>†</sup>, Aaron O. Richardson, Gregory J. Young, Leslie R. Goertzen<sup>‡</sup>, and Jeffrey D. Palmer<sup>§</sup>

Department of Biology, Indiana University, Bloomington, IN 47405-3700

Contributed by Jeffrey D. Palmer, November 9, 2004

Several plants are known to have acquired a single mitochondrial gene by hortzontal gene transfer (HGT), but whether these or any other plants have acquired many foreign genes is entirely unclear. To address this question, we focused on Amborella trichopoda, because it was already known to possess one horizontally acquired gene and because it was found in preliminary analyses to contain several more. We comprehensively sequenced the mitochondrial protein gene set of Amborella, sequenced a variable number of mitochondrial genes from 28 other diverse land plants, and conducted phylogenetic analyses of these sequences plus those already available, including the five sequenced mitochondrial genomes of angiosperms. Results indicate that Amborella has acquired one or more copies of 20 of its 31 known mitochondrial protein genes from other land plants, for a total of 26 foreign genes, whereas no evidence for HGT was found in the five sequenced genomes. Most of the Amborelia transfers are from other angiosperms (especially eudicots), whereas others are from nonangiosperms, including six striking cases of transfer from (at least three different) moss donors. Most of the transferred genes are intact, consistent with functionality and/or recency of transfer. Amborella mtDNA has sustained proportionately more HGT than any other eukaryotic, or perhaps even prokaryotic, genome yet

#### Materials and Methods

We used primers for conserved regions of angiosperm mitochondrial genes in an attempt to PCR-amplify and sequence all mitochondrial protein genes from A. trichopoda (primer sequences available on request). Many Amborella reactions produced multiple bands, heterogeneous sequence, or unreadable sequence; these were cloned, and multiple (usually eight) clones were sequenced. This process yielded portions of 27 genes. We then used PCR to amplify and sequence as many of these 27 genes as possible, plus the four genes already sequenced from Amborella mtDNA, from 13 other angiosperms (see Fig. 5, which is published as supporting information on the PNAS web site, for taxa and sources) and three gymnosperms. For each of these plants, we carried out 80 PCRs with conserved mitochondrial primers. Selected genes were amplified and sequenced from 12 additional nonangiosperms. PCR was performed under the following conditions: 95°C for 2 min, 35 cycles of 95°C for 30 s, 55° or 52°C for 30 s, 72°C for 2 min, and 72°C for 5 min. PCR products were cleaned by using 2 µl of ExoSAP-IT (United States Biochemical). Sequences were generated by using an ABI 3730 (Applied Biosystems). Sequence traces were assembled and trimmed by using CODONCODE ALIGNER 1.3.2.

Sequences were aligned by using either BIOEDIT or SE-AL

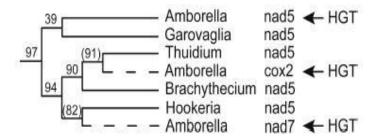


Fig. 2. Amborella acquired three genes from different moss donors. The solid parts of the cladogram and nonparenthetical bootstrap values are from the nad5 intron phylogeny of Fig. 6. The dashed lines and other bootstrap values indicate the relationship to the indicated mosses of the moss-derived cox2 and nad7 genes of Amborella, as per the cox2 gene tree of Fig. 1 and the nad7 intron tree of Fig. 6.

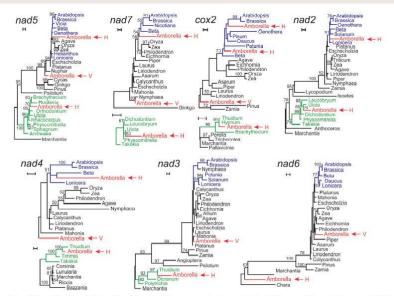


Fig. 1. Phylogenetic evidence for horizontal acquisition of genes from moses and angiosperms in Amborella. Shown are Mt trees. Bootstrap values (100 Mt replicates)—50% are shown. Hand'l undicate Amborella genes of putatively horizontal and vertical transmission, respecie, Amborella genes are in cell core eudicot genes are in blue (basal eudicots commonly included are Platanus, Eschscholzia, and Mahonia), and moss genes are in green. Note that for nad7, cox2, and nad8, seed and nonseed plants were analyzed separately. Scale bars correspond to 0.01 substitutions per site.



Fig. 4. A. trichopoda leaf from a cloud forest at Massif de l'Aoupinié (Province Nord in New Caledonia) at 801 m altitude. Note the greenish bryophyte (liverwort) growth covering the leaf tip, and the small spots of lichens and other epiphytes elsewhere on the leaf. Photograph courtesy of Sean Graham, Centre for Plant Research, University of British Columbia, Vancouver.

### 高等植物间的基因水平转移: 从菟丝子到番茄

#### Plant genetics

#### Gene transfer from parasitic to host plants

lant mitochondrial genes are transmitted horizontally across mating barriers with surprising frequency, but the mechanism of transfer is unclear<sup>1,2</sup>. Here we describe two new cases of horizontal gene transfer, from parasitic flowering plants to their host flowering plants, and present phylogenetic and biogeographic evidence that this occurred as a result of direct physical contact between the two. Our findings complement the discovery that genes can be transferred in the opposite direction, from host to parasite plant<sup>3</sup>.



Figure 2 A parasitic dodder (Cuscuta californica) in flower, with its haustoria penetrating a host tomato plant.

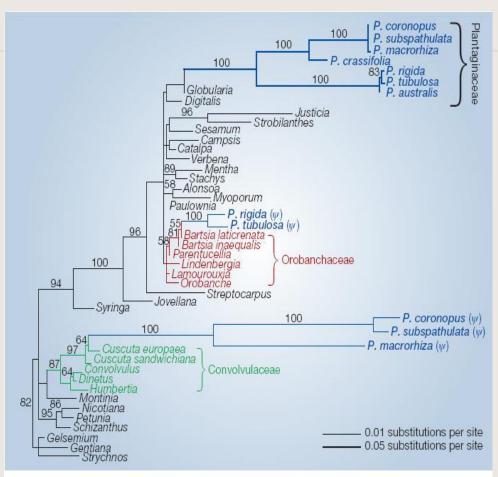


Figure 1 Phylogenetic evidence for two horizontal transfer events of the gene atp1 into Plantago (blue). Seven Plantago atp1 genes at the top of the maximum-likelihood tree are intact, vertically transmitted, and rapidly evolving (scale reduced by 80%). The other two sets of Plantago atp1 genes are pseudogenes (\(\psi\)) acquired from parasitic plants in the Orobanchaceae (red) and Convolvulaceae (green). Bootstrap values of over 50% are shown. For methods, see supplementary information.

## 综述: 植物间的基因水平转移

Journal of Experimental Botany, Vol. 58, No. 1, pp. 1–9, 2007 Intracellular Compartmentation: Biogenesis and Function Special Issue doi:10.1093/ixb/erl148 Advance Access publication 9 October, 2006



#### SPECIAL ISSUE PAPER

#### Horizontal gene transfer in plants

Aaron O. Richardson and Jeffrey D. Palmer\*

Department of Biology, Indiana University, 1001 East Third Street, Bloomington, IN 47405, USA

Received 31 March 2006; Accepted 8 August 2006

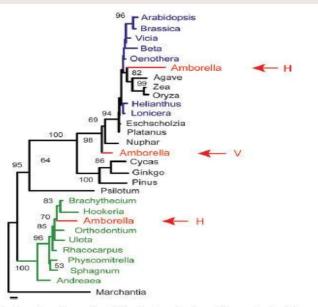


Fig. 3. Two transfers of nad5 to Amborella from disparate plant donors. Maximum likelihood tree of nad5 exons [reproduced from Bergthorsson et al. (2004), Copyright 2004 National Academy of Sciences, USA]. Amborella genes are shown in red, core eudicots genes in blue, and moss genes in green. Bootstrap values (100 ML replicates) >50% are shown. H, horizontally acquired gene; V, vertically inherited gene. The scale bar represents 0.01 nucleotide substitutions per site. The number of nucleotides in the alignment varies across genes as not all exons amplified for all sequences; vertically transmitted copy, 1238 nucleotides; angiosperm-derived copy, 601 nucleotides; moss-derived copy, 1062 nucleotides.

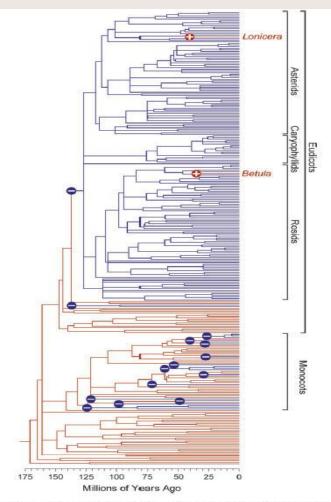


Fig. 1. Distribution of mitochondrial rps11 among 280 flowering plants. Red and blue branches indicate the presence and absence, respectively, of rps11 in the mitochondrial genome. Blue circles with minus signs indicate gene losses as inferred by parsimony; red circles with plus signs indicate putative recaptures of rps11 by mtDNA. Modified from Bergthorsson et al. (2003). See Adams et al. (2002) for names of all 280 angiosperms represented by the tree.

# Horizontal gene transfer of the algal nuclear gene psbO to the photosynthetic sea slug Elysia chlorotica

Mary E. Rumpho<sup>a,1</sup>, Jared M. Worful<sup>a</sup>, Jungho Lee<sup>b</sup>, Krishna Kannan<sup>a</sup>, Mary S. Tyler<sup>c</sup>, Debashish Bhattacharya<sup>d</sup>, Ahmed Moustafa<sup>d</sup>, and James R. Manhart<sup>a</sup>

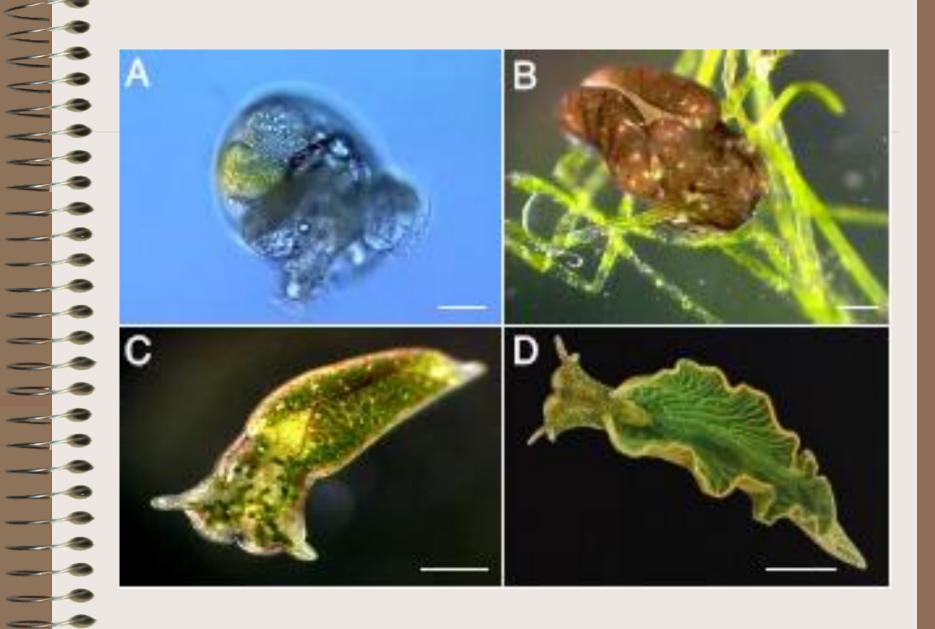
<sup>a</sup>Department of Biochemistry, Microbiology, and Molecular Biology, University of Maine, Orono, ME 04469; <sup>b</sup>Green Plant Institute, Seoul National University, Gwonseon, Suwon, Gyeonggi 441-853, Korea; <sup>c</sup>School of Biology and Ecology, University of Maine, Orono, ME 04469; <sup>d</sup>Department of Biological Sciences and the Roy J. Carver Center for Comparative Genomics, Interdisciplinary Program in Genetics, University of Iowa, Iowa City, IA 52242-1324; and <sup>a</sup>Department of Biology, Texas A&M University, College Station, TX 77843

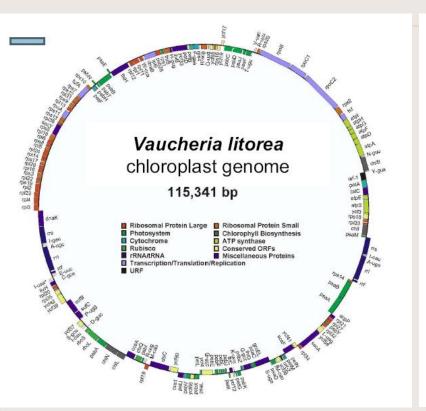
Edited by Lynn Margulls, University of Massachusetts, Amherst, MA, and approved September 17, 2008 (received for review June 9, 2008)

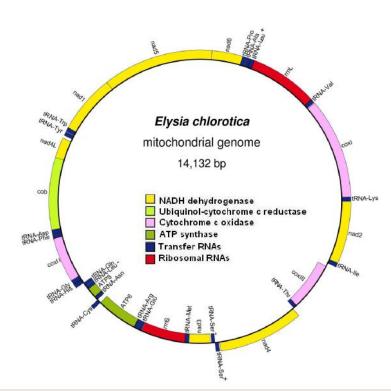
The sea slug Elysia chlorotica acquires plastids by ingestion of its algal food source Vaucheria litorea. Organelles are sequestered in the molluse's digestive epithelium, where they photosynthesize for months in the absence of algal nucleocytoplasm. This is perplexing because plastid metabolism depends on the nuclear genome for > 90% of the needed proteins. Two possible explanations for the persistence of photosynthesis in the sea slug are (i) the ability of V. litorea plastids to retain genetic autonomy and/or (ii) more likely, the mollusc provides the essential plastid proteins. Under the latter scenario, genes supporting photosynthesis have been acquired by the animal via horizontal gene transfer and the encoded proteins are retargeted to the plastid. We sequenced the plastid genome and confirmed that it lacks the full complement of genes required for photosynthesis. In support of the second scenario, we demonstrated that a nuclear gene of oxygenic photosynthesis, psbO, is expressed in the sea slug and has integrated into the germline. The source of psbO in the sea slug is V. litorea because this sequence is identical from the predator and prey genomes. Evidence that the transferred gene has integrated into sea slug nuclear DNA comes from the finding of a highly diverged psbO 3' flanking sequence in the algal and mollusc nuclear homologues and gene absence from the mitochondrial genome of E. chlorotica. We demonstrate that foreign organelle retention generates metabolic novelty ("green animals") and is explained by anastomosis of distinct branches of the tree of life driven by predation and horizontal gene transfer.

20). Most of these latter examples are associated with parasitism or phagotrophy, including the elegant studies of HGT from the  $\alpha$ -proteobacteria Wolbachia to insects and nematodes (16–18), and the finding of rhizobial-like genes in plant parasitic nematodes (19, 20). The exchange of genetic material between two eukaryotes is extremely rare, or at least not well documented to date. The best-studied cases include the transfer of mitochondrial DNA from achlorophyllous or epiphytic plants to the mitochondrial genome (mtDNA) of their closely related photosynthetic hosts (21), the exchange of transposons between two animal (22) or two plant (23) species, and the presence of plant genes in plant parasitic nematodes (in addition to the rhizobial genes discussed previously), which are hypothesized to be "defense" genes whose products protect the parasite from host detection (20).

The sacoglossan mollusc (sea slug) Elysia chlorotica represents a unique model system to study the potential for interdomain HGT between two multicellular eukaryotes—in this case, from a filamentous secondary (heterokont) alga (Vaucheria litorea) to a mollusc. This emerald green sea slug owes its coloring and photosynthetic ability to plastids acquired during herbivorous feeding (24–29). The plastids do not undergo division in the sea slug and are sequestered intracellularly in cells lining the finely divided digestive diverticula. The plastids continue to carry out photosynthesis, providing the sea slug with energy and carbon during its approximately 10-month life span (27, 28). Long-term plastid activity continues despite the absence of algal nuclei (27, 29), and hence a source of nuclear-encoded plastid-targeted







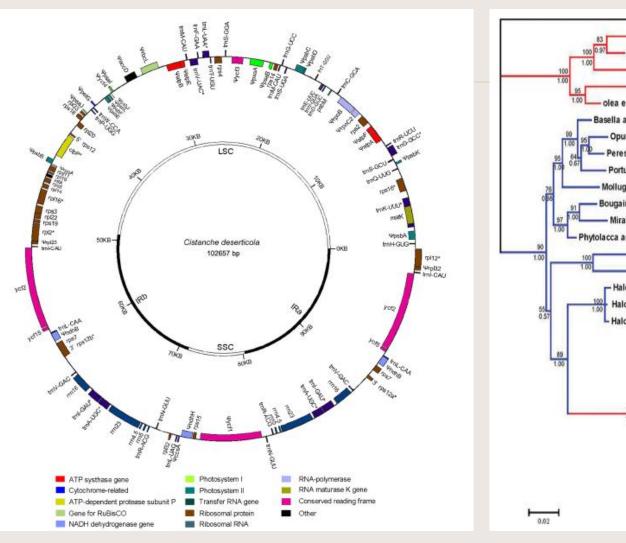


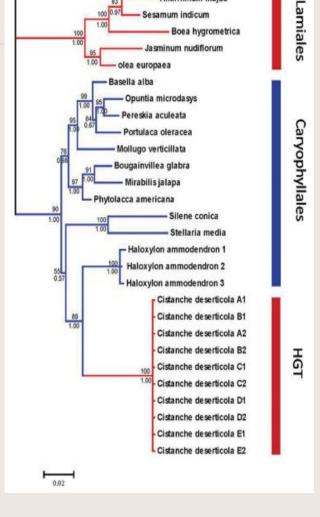


# 肉苁蓉?



### 肉苁蓉与梭梭间的基因水平转移证据





Oryza nivara

Antirrhinum majus

Boea hygrometrica

Sesamum indicum

叶绿体基因组结构与rpoC2基因水平转移



### Complete Chloroplast Genome Sequence of Holoparasite Cistanche deserticola (Orobanchaceae) Reveals Gene Loss and Horizontal Gene Transfer from Its Host Haloxylon ammodendron (Chenopodiaceae)

Xi Li<sup>1,9</sup>, Ti-Cao Zhang<sup>1,9</sup>, Qin Qiao<sup>1</sup>, Zhumei Ren<sup>2</sup>, Jiayuan Zhao<sup>1</sup>, Takahiro Yonezawa<sup>1</sup>, Masami Hasegawa<sup>1</sup>, M. James C Crabbe<sup>3</sup>, Jianqiang Li<sup>4</sup>\*, Yang Zhong<sup>1,5</sup>\*

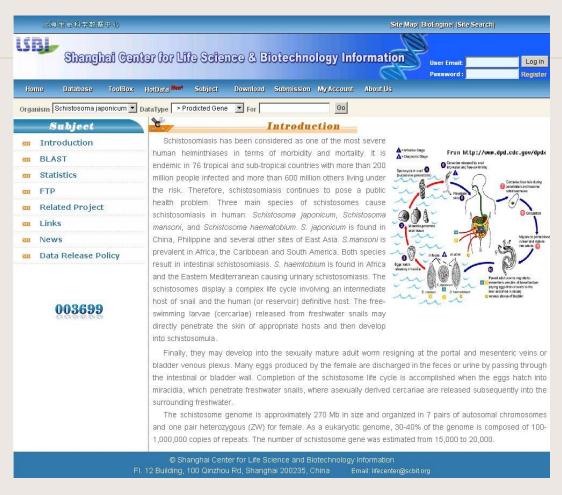
1 Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, School of Life Sciences, Fudan University, Shanghai, China, 2 College of Life Science and Technology, Shanxi University, Taiyuan, China, 3 Faculty of Creative Arts, Technologies and Science, Institute of Biomedical, Environmental Science and Technology, University of Bedfordshire, Luton, United Kingdom, 4 Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, China, 5 Institute of Biodiversity Science and Geobiology, Tibet University, Lhasa, China

#### Abstract

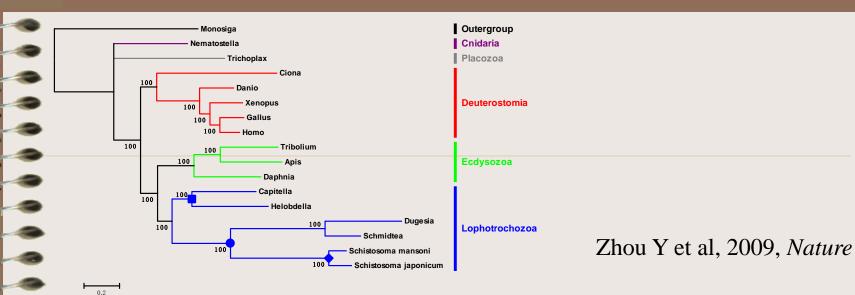
**Background:** The central function of chloroplasts is to carry out photosynthesis, and its gene content and structure are highly conserved across land plants. Parasitic plants, which have reduced photosynthetic ability, suffer gene losses from the chloroplast (cp) genome accompanied by the relaxation of selective constraints. Compared with the rapid rise in the number of cp genome sequences of photosynthetic organisms, there are limited data sets from parasitic plants.

**Principal Findings/Significance:** Here we report the complete sequence of the cp genome of *Cistanche deserticola*, a holoparasitic desert species belonging to the family Orobanchaceae. The cp genome of *C. deserticola* is greatly reduced both in size (102,657 bp) and in gene content, indicating that all genes required for photosynthesis suffer from gene loss and pseudogenization, except for *psbM*. The striking difference from other holoparasitic plants is that it retains almost a full set of tRNA genes, and it has lower *dN/dS* for most genes than another close holoparasitic plant, *E. virginiana*, suggesting that *Cistanche deserticola* has undergone fewer losses, either due to a reduced level of holoparasitism, or to a recent switch to this life history. We also found that the *rpo*C2 gene was present in two copies within *C. deserticola*. Its own copy has much shortened and turned out to be a pseudogene. Another copy, which was not located in its cp genome, was a homolog of the host plant, *Haloxylon ammodendron* (Chenopodiaceae), suggesting that it was acquired from its host via a horizontal gene transfer.

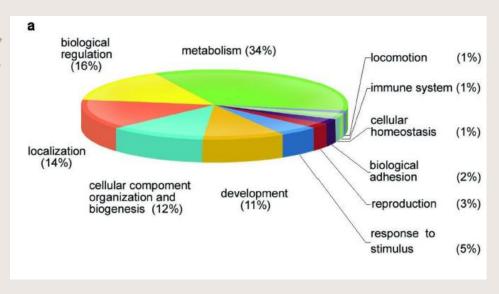
## 血吸虫?

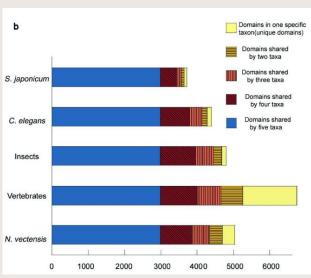


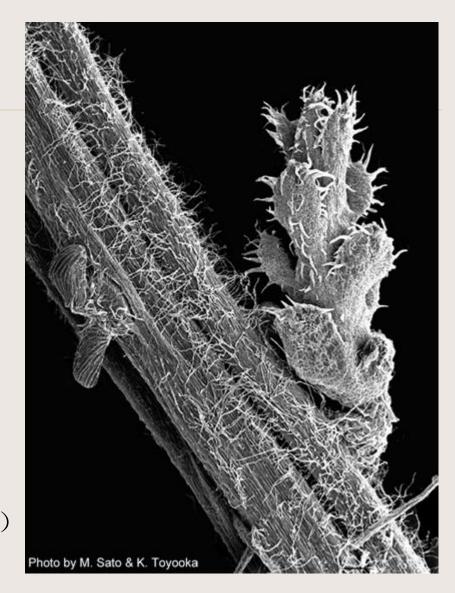
Genome data of *Schistosoma* at Shanghai Center for Bioinformation Technology (http://www.scbit.org/)



#### Phylogenomics of metazoan (>300,000 bp)







黄玄大 黄独脚金(<u>Striga hermonthica</u>)

# Horizontal Gene Transfer by the Parasitic Plant *Striga hermonthica*

Satoko Yoshida, 1 Shinichiro Maruyama, 2 Hisayoshi Nozaki, 2 Ken Shirasu1\*

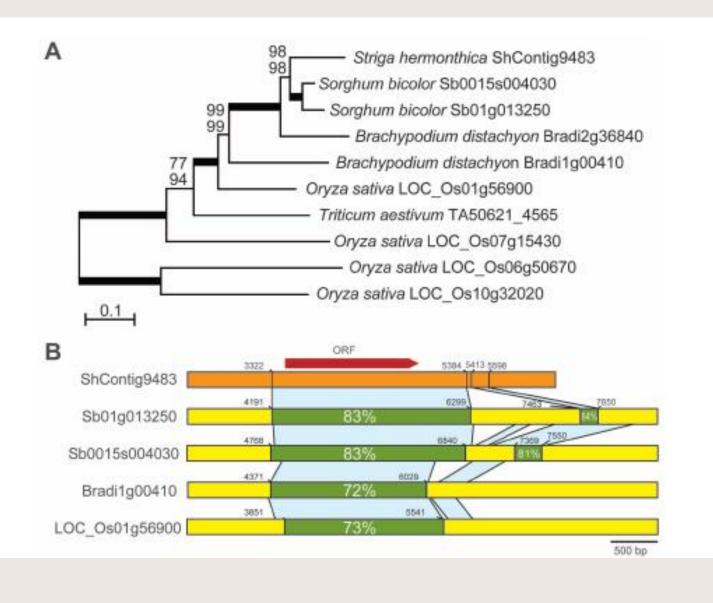
orizontal gene transfer (HGT) plays an important role in genome evolution (1). In plants, the majority of reported cases of HGT have been limited to exchanges between plants and microbes, mitochondrial transfer, or the translocation of mobile elements among related species (1). Parasitic plants are known to be vectors of mitochondrial HGT, but it has been unclear whether they also mediate nuclear HGT (1, 2).

Striga hermonthica (Del.) Benth. is a devastating parasitic plant that infests members of the grass family (Poaceae), including major crops such as sorghum (Sorghum bicolor) and rice (Oryza sativa). S. hermonthica belongs to the eudicot Orobanchaceae family of the order Lamiales (fig. S1) (3) and only infects monocot plants. Thus, we reasoned that we may be able to detect nuclear HGT, if it occurs, by identifying monocot-specific genes in the S. hermonthica genome. From a large-scale expressed sequence tag analysis of S. hermonthica (4), we found one gene, designated ShContig9483, which shows high similarity to genes in sorghum and rice but has no

homologs in eudicots (fig. S2A and table S1) (5). Southern blot analysis revealed *ShContig9483* cross-hybridization signals from sorghum, and rice to a lesser extent, reflecting its lower similarity, whereas no signals were detected from other closely related plants in Orobanchaceae nor from any nonparasitic eudicots (fig. S2B). This indicates that *ShContig9483* most likely originated in the monocots before its transfer to *S. hermonthica*.

ShContig9483 encodes a 448-amino acid protein with unknown function. Phylogenetic analysis of ShContig9483 and related protein-coding sequences clusters S. hermonthica with sorghum (Fig. 1A). This tree conflicts with the phylogenetic position of Striga (3), suggesting that S. hermonthica acquired ShContig9483 from sorghum or a related grass species. The S. hermonthica genomic region containing ShContig9483 resides near a nuclear gene encoding a putative cis-prenyltransferase (fig. S3A). In contrast to ShContig9483, this putative cis-prenyltransferase gene from S. hermonthica clusters with genes from other eudicot species (fig. S3B).

The genomic sequences of the sorghum homologs show similarities to the ShContig9483 locus from about 150 base pairs (bp) up- and 800 bp downstream of the putative open reading frame (ORF), except for several insertions and deletions (Fig. 1B and fig. S4). The similarity to homologs from Brachypodium and rice covers a shorter region with lower identities (Fig. 1B). The high conservation of sequence between S. hermonthica and sorghum outside the ORF suggest that transfer was a relatively recent event. Indeed, a sequence highly similar to ShContig9483 was found in S. gesnerioides but not in Orobanche minor, which is from a closely related genus (figs. S2B and S5). These data suggest that incorporation of the ShContig9483 fragment occurred before speciation of S. hermonthica and S. gesnerioides but after differentiation of the genera Striga and Orobanche. Parasitic plants form an invasive organ called a haustorium, which interconnects their vasculature with that of their hosts to allow transfer of nutrients, water, and even mRNAs (2). Thus, one possibility is that ShContig9483 was originally captured by S. hermonthica as mRNA or cDNA. Interestingly, we found 13 consecutive adenine (A) nucleotides at the 3' end of the ShContig9483 genomic region (fig. S4). This sequence may be indicative of a poly-A tail added to a transcriptional unit of the originally transferred gene. In any case, our comparative genomics analysis of a eudicot parasite and its monocot hosts presents a clear case for nuclear HGT. Because the method used in this study is limited to the



## 五倍子: 一个植物与动物间的水平转移案例?!





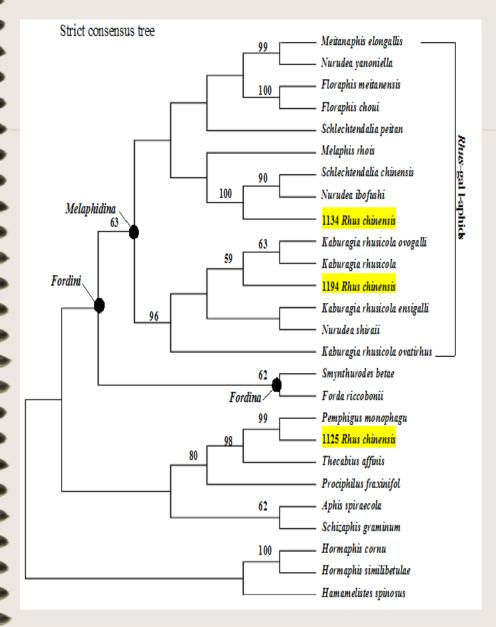


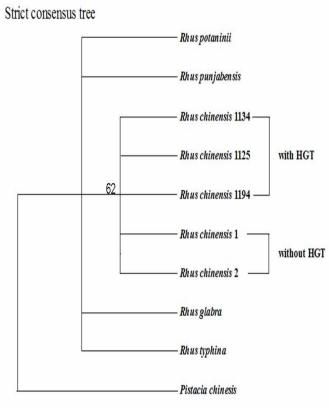


倍蚜/盐肤木/ 提灯藓/五倍子



	1	11 2	1 31	41	51	
Nurudea_shiraii Schlechtendalia_chinensis Rhus_chinensis1194_HGT Rhus_chinensis1194			TCT	AATACATCTT  TCACGC.T		T
Nurudea_shiraii Schlechtendalia_chinensis Rhus_chinensis1194_HGT Rhus_chinensis1194	GGAGACCCTA TA.	c	ACATTTATTT	TGATTTTTTG	.тА С	
Nurudea_shiraii Schlechtendalia_chinensis Rhus_chinensis1194_HGT Rhus_chinensis1194	TTAATTTTAC	CAGGATTCGG	GTT T	1 161 САТАТТАТТА ТТСС.GG	.A	T
Nurudea_shiraii Schlechtendalia_chinensis Rhus_chinensis1194_HGT Rhus_chinensis1194	GAAACATTCG	GAAATATCAG	TT	1 221     GCAATATTAA   GGTAGCGGC	T	
Nurudea_shiraii Schlechtendalia_chinensis Rhus_chinensis1194_HGT Rhus_chinensis1194	ATTGTATGAG	   СССАТСАТАТ  С		1 281 	.TT	
Nurudea_shiraii Schlechtendalia_chinensis Rhus_chinensis1194_HGT Rhus_chinensis1194	ACATCTGCTA	Г СААТААТТАТ .Т		ACCGGAATTA	T	GA
Nurudea_shiraii Schlechtendalia_chinensis Rhus_chinensis1194_HGT Rhus_chinensis1194	ACTATTTATG	GATCAAAAAT	T.AC	   CCATCTACTA  CA.T	TA.	T





## 从猜测到验证

- 污染? 重复/对照
- 群体? 统计比例
- •遗传?种子检测
- 定位? 两端序列

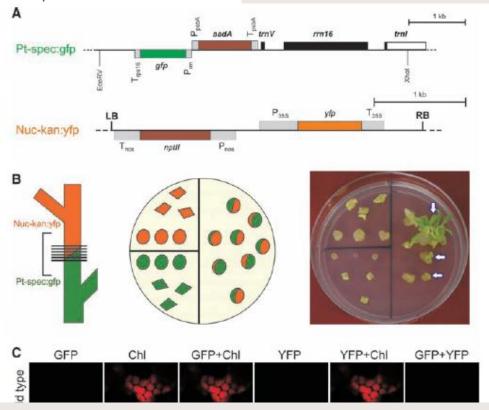
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# Exchange of Genetic Material Between Cells in Plant Tissue Grafts

Sandra Stegemann and Ralph Bock\*

Tissue grafting includes applications ranging from plant breeding to animal organ transplantation. Donor and recipient are generally believed to maintain their genetic integrity, in that the grafted tissues are joined but their genetic materials do not mix. We grafted tobacco plants from two transgenic lines carrying different marker and reporter genes in different cellular compartments, the nucleus and the plastid. Analysis of the graft sites revealed the frequent occurrence of cells harboring both antibiotic resistances and both fluorescent reporters. Our data demonstrate that

Fig. 1. Genetic screen for intercellular gene transfer. (A) Maps of the plastid genome in Pt-spec:gfp plants and the transgenic locus in Nuc-kan:yfp plants. PpsbA and TpsbA, promoter and terminator from the plastid psbA gene; Prrv promoter from the plastid rRNA operon; Trps16, terminator from the plastid rps16 gene; Pnos and Tnos, promoter and terminator from the nopaline synthase gene from Agrobacterium tumefaciens; Pass and Tass, promoter and terminator from the cauliflower mosaic virus 355 transcript, LB and RB, left and right borders of the T-DNA region; Eco RV and Xho I, restriction sites used for restriction fragment length polymorphism analysis (fig. 53). (B) Selection experiments. The grafted stem region was either sectioned (horizontal lines) or directly exposed to selection (bracket). The middle panel shows the arrangement of tissue explants, the right panel a selection plate (right half, stem sections from the graft site; upper left quarter, three stem sections and three leaf explants from Nuc-kan:yfp; lower left quarter, the corresponding explants from Pt-spec:gfp). After 4 weeks on medium with spectinomycin and kanamycin, some explants from the graft site developed growing callus tissue or regenerating shoots (arrows). (C) Expression and subcellular localization of the fluorescent reporters. The wild type, the two grafting partners, and a YG line were assayed for GFP, chlorophyll (Chl), and YFP fluorescence.





#### 复旦大学进化生物学研究中心





