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Abstract
Our recent review included a timeline showing 30 significant events in the history of Neurospora (Davis and Perkins 2002, Nature Reviews Genetics 3:397-403). Many important contributions could not be included in that brief chronology because of space limitations. We present here a somewhat more complete and better documented list of noteworthy developments.

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NEUROSPORA CHRONOLOGY - 1843-2002

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Our recent review included a timeline showing 30 significant events in the history of Neurospora (Davis and Perkins 2002, Nature Reviews Genetics 3: 397-403). Many important contributions could not be included in that brief chronology because of space limitations. We present here a somewhat more complete and better documented list of noteworthy developments. Publications are cited here only by author and date. Complete references will be found in the books and reviews given at the end of the list.

1843. The first published account of Neurospora (commissioned by the Minister of War) describes material from contaminated bakeries in Paris. Orange pigment is shown to be induced by light. (Payen 1843)
1901. F.A.F.C. Went reports the use of Neurospora (called Monilia sitophila) as a component of edible ontjam cakes in Java. He uses the orange fungus to examine the effect of substrates on various enzymes. (Went 1901)
1909. Neurospora is used in a study of oxidases. (Pringsheim 1909)
1913. Neurospora is used in studies of chemical toxicity. (Kunkel 1913, 1914)
1923. Luxuriant growth of Neurospora is seen following the 1923 earthquake and great fire in Tokyo. Perithecia with eight-spored asci are found in the bark of burned trees and are produced on artificial medium. (Kitasima 1924, Kitazima 1925)
1924. The orange pigment is identified as a carotenoid. (Tokugawa and Emoto 1924)
1927. The genus is named, species are described, and B. O. Dodge initiates genetic and cytological studies. Shot ascii are used to show 4:4 segregation of mating type genes. Ascospores are shown to be activated by heat. (Shear and Dodge 1927)
1928. Carl Lindegren selects the California Institute of Technology. (See Lindegren 1973)
1929. The pigment is used in a study of oxidases. (Pringsheim 1909)
1935. N. intermedia is described as a new species. (Tai 1935)
1935. Ascospore activation is examined physiologically. (Goddard 1935, 1939)
1936. The first genetic map is published, consisting of six loci. (Lindegren 1936)
1939. Neurospora is used as a textbook example showing first and second division segregation in the linear ascus, with crossing over at the four-chromatid stage. (Sturtevant and Beadle 1939; Sinnott and Dunn 1939, Waddington 1939)
1941. Beadle and Tatum use Neurospora to obtain the first biochemical mutants. (Beadle and Tatum 1941)
1943. 'Race tubes' are used to measure linear growth rate on agar media and to determine optimal conditions for growth. (Ryan et al. 1943)
1943, 1946. Conditional biochemical mutants are identified. (Stokes et al. 1943, Mitchell and Houlanhan 1946)
1944. Mutants are identified that affect different steps in the same biosynthetic pathway. (Srb and Horowitz 1944)
1944. Heterokaryons are studied systematically using mutant markers. (Beadle and Coonradt 1944)
1944-45. Strains of opposite mating type are shown to be heterokaryon-incompatible. (Beadle and Coonradt 1944, Sansome 1945)
1945. Barbara McClintock identifies the seven chromosomes, describes meiosis and postmeiotic mitoses, and identifies a translocation. (McClintock 1945)
1947. The first suppressor of a biochemical mutation is discovered. (Houlanhan and Mitchell 1947)
1947. A synthetic medium is devised for making crosses. (Westergaard and Mitchell 1947)
1948. Ascospores are shown to be activated by furfural. (M. B. Emerson 1948)
1948. Enzyme activity is shown to be absent in cell-free extracts of a trp-3 mutant. (Mitchell and Lein 1948)
1948. Sorbose is used to obtain colonial growth. (Tatum et al. 1948)
1948, 53. Chromosome cytology and behavior in the ascus are described and documented in detail. (Singleton 1948, 1953)
1948, 53, 67. Genetic linkage groups are assigned to cytologically defined chromosomes. (Singleton 1948, St. Lawrence 1953, Barry 1967)
1949. Linkage data are presented that establish six linkage groups. (Houlanhan et al. 1949)
1949-54. Accumulated evidence makes it increasingly clear that genes specifying different steps in the same biosynthetic pathway are not clustered. (Houlanhan et al. 1949, Barratt et al. 1954)
1950. Temperature sensitive mutants are cited in support of the one gene-one enzyme hypothesis. (Horowitz and Leupold 1951)
1950. A simplified method for preserving cultures by lyophilization is described. (Barratt and Tatum 1950)
1951. Neurospora is found growing in large patches in areas devastated by a volcanic eruption in New Guinea. (Burges and Chalmers 1952)
1952-53. The first maternally transmitted nonmendelian mutants are described. (M. B. and H. K. Mitchell 1952; M. B. Mitchell et al. 1953)

1953. Individual heterokaryon-incompatibility (het) genes are identified, that block heterokaryon formation when alleles are different. (Garnjost 1953)

1953. Heterokaryons are used to recover recessive lethal mutations. (Atwood and Mukai 1953)

1953. Different alleles are shown to produce forms of an enzyme with qualitatively different properties. (Horowitz and Fling 1953)

1953-54. A filtration-enrichment method is used to obtain mutants. (V. Woodward 1953, Catcheside 1954)

1954. Genetic maps are constructed for all seven linkage groups and data are compiled for all the known markers. Genetic nomenclature is adopted using Drosophila as a model. (Barratt et al. 1954)

1955. Cross-reacting material related to the wild-type enzyme is demonstrated immunologically in an auxotrophic mutant. (Suskind et al. 1955)

1955. Mary Mitchell uses ascus analysis to provide the first definitive proof of gene conversion. (Mitchell 1955)

1956. A formula is devised that allows minimal medium to be made up and stored conveniently in 50x strength solution. (Vogel 1956)

1957-59. Complementation between allelic mutations is shown, first for heterokaryons, then for protein products in vitro. (Fincham and Pateman 1957, Giles et al. 1957, D. Woodward 1959)

1957-59. Insertional translocations are identified and shown to generate partial-diploid progeny that are duplicated for the displaced segment. (de Serres 1957, St. Lawrence 1959)

1959. Rhythmic conidiation is shown to be under circadian control. (Pittendrigh et al. 1959)

1959. Enrichment for new mutants is accomplished by the method of ‘inositol-less death’: When an inositol-requiring single-mutant strain is incubated in minimal medium, unbalanced growth results in rapid death unless a new, second mutation has occurred. (Lester and Gross 1959)

1960. Ejected groups of eight ascospores are used extensively for unordered tetrad analysis. (Strickland 1960)

1960. Microconidia are used to determine a haploid DNA content of ~45 megabases. (Horowitz and Macleod 1960)

1960. The Fungal Genetics Stock Center is established, directed by Raymond Barratt.

1961. Intragenic recombination is shown to be polarized. (Murray 1961, 1963)


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1962. Meiotic crossing over and interference in a multiply marked Neurospora chromosome is shown to resemble that of Drosophila and maize. (Perkins 1962)


1962. Methods are developed for studying forward and reverse mutation in the ad-3 region, and heterokaryons are used to recover recessive mutations. (de Serres and Osterbind 1962)

1962. Drug-resistant mutants are characterized and mapped. (Hsu 1962, 1963, Howe and Terry 1962)

1962. A method is described for preserving cultures in suspended animation on anhydrous silica gel. (Perkins 1962).

1962-69. Heterokaryons are used to recover recessive lethal mutations. (Atwood and Mukai 1953)

1962-69. Homothallic Neurospora species are described. (Gochenaur and Backus 1962, Frederick et al. 1969)

1964. Mitochondrial DNA is isolated and characterized. (Luck and Reich 1964)

1964. 'rec' genes are shown to control meiotic recombination differently in local regions. (Catcheside et al. 1964)

1965. Coordinate control of unlinked genes in the same biosynthetic pathway is described. (Gross 1965)

1965. Cross-pathway ('general') control of amino acid synthesis is discovered. (Carsiotis and Lacy 1965)

1966. 'genes are identified, that block heterokaryon formation when alleles are different. (Yanofsky 1956)

1966-74. Patterns of ascospore abortion in unordered asci are used to detect and characterize chromosome rearrangements. Insertional and terminal rearrangements are used to map genes by duplication coverage. (Perkins 1966, 1974)

1967. Metabolic cross-suppression is described between intermediates in arginine and pyrimidine synthesis. (Davis 1967, Reissig et al. 1967)

1967. A terminal pericentric inversion is identified and used to show that unstable partial diploid progeny are generated; these are inhibited because they are heterozygous for the heterokaryon-incompatible mating type genes mat A and mat a. (Newmeyer and Taylor 1967)

1967. Resetting the circadian clock is shown to be mediated by a blue-light photoreceptor. (Sargent and Briggs 1967)

1967. Positive control is demonstrated in the regulation of sulfur metabolism. (Marzluf and Metzenberg 1968)


1968. Radiation-sensitive mutations are obtained, including some that impair meiotic recombination. (Schroeder 1970)

1969. Microelectrode techniques indicate existence of a proton pump in the cell membrane. (Slayman and Slayman 1970)

1970. The tol mutation is discovered and shown to suppress mating type-associated heterokaryon incompatibility in N. crassa. (Newmeyer 1970)

1970. A compilation is published of genetic and microbiological methods. (Davis and de Serres 1970)

1971. Enzymes specific to different biosynthetic pathways are shown to be channelled in separate pools. (Williams et al. 1971)
N. intermedia

1975. Allozymes are used to show that genetic polymorphisms are abundant in natural populations of N. intermedia. (Spieth 1975)

1976-79. The synaptonemal complex karyotype is reconstructed from thin sections and the distribution of recombination nodules is described. (Gillies 1972, 1979)

1973. Mutants are isolated that alter the period length of circadian conidiation. (Feldman and Hoyle 1973).

1973. Compartmentation within the cell is demonstrated for the enzymes and intermediates of arginine metabolism. (Weiss and Davis 1973, Weiss 1973)

1973. DNA-induced changes are reported that are attributed to transformation. (Mishra and Tatum 1973)

1975. A complete 452-residue amino acid sequence is obtained for NADP-specific glutamate dehydrogenase, specified by the am gene (Holder et al. 1975)

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1975-76. The expression of heterokaryon incompatibility differences in partial diploids enables known het loci to be defined and mapped and reveals the presence of previously unrecognized het loci in nature. het genes are shown to be polymorphic in a wild population. (Perkins 1975, Mylyk 1975, 1976).

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Neurospora species and to test validity of the biological species concept. (Nativ et al. 1987, Taylor and Nativ 1989; see Spuksi et al. 1997)

1988. Mating type genes are cloned, sequenced, and shown to be present as single copies. Because mat A and mat a are nonhomologous, they are called idiomorphs rather than alleles. (Glass et al. 1988)

1988. Pulsed field gel electrophoresis is used to separate whole-chromosome DNAs and provide an elecrophoretic karyotype. (Orbach et al. 1988)

1989. The Tad retrotransposon is discovered in a strain from Africa. (Kinsey and Helber 1989)

1989. The first clock-controlled genes are identified. (Loros et al. 1989)

1989. Scanning EM is used to study conidiation in the wild type and in mutants. (Springer and Yanofsky 1989)

1989. Mitochondrial plasmids are shown to be transferred horizontally. (May and Taylor 1989)

1989-93. Premiotic changes in the number of ribosomal DNA repeats are shown to occur in the nucleolus organizer region. (Butler and Metzenberg 1989, 1990, 1993)

1990. Serial reconstruction from electron micrographs of thin sections reveals the occurrence of synaptic adjustment at pachytene in the pairing loops of inversion heterozygotes. (Bojko 1990)

1990. The Tad retrotransposon is shown to be transmitted from one nucleus to another in heterokaryons. (Kinsey 1990).


1992. Wild type N. tetrasperma, which normally exists as a mat A + mat a heterokaryon, is shown to carry a nonfunctional allele of the tol gene. (Jacobson 1992)

1994. The life history of N. intermedia is studied in a natural setting. (Pandit and Maheshwari 1996)

1995. A novel Neurospora kinesin (N-kinesin) is discovered. (Steinberg and Schliwa 1995)

1996. Genes in unpaired DNA segments are shown to be inactivated during meiosis. (Aramayo and Metzenberg 1996).

1996. The mat A idiomorph is shown to consist of three genes, while mat a is a single gene. (Ferreira et al. 1996)

1996 Alleles of the vegetative incompatibility gene het-c are cloned and sequenced (Saupe et al. 1996)

1997-99. Quelling-deficient mutants are obtained and used to show that vegetative-phase gene silencing requires an RNA-dependent RNA polymerase. (Cogoni and Macino 1997, 1999)

1997-2000. Expressed sequences (ESTs) from different developmental stages are used to identify cDNAs (Nelson et al. 1997, Dolan et al. 2000)

1998. Genome sequencing of Linkage Groups II and V (>1/3 of the genome) is initiated in Germany. (http://www.mips.biochem.mpg.de/proj/Neurospora)

1998. Mutants deficient in DNA-methylation are obtained. (Foss et al. 1998)

1999. A gene is identified that encodes an archaeal-like rhodopsin. (Bieszke et al. 1999).

2000. The book Neurospora: Contributions of a Model Organism describes 60 years of research. (Davis 2000)

2000. The Whitehead Institute receives a National Science Foundation grant of $5.25 million to sequence the entire Neurospora genome. (NSF News Release, September 26).

2000-01. Neurospora is found growing under the bark of fire-killed trees at many sites in western North America, and as far north as Fairbanks, Alaska. (Jacobson et al. 2001)

2001. The Neurospora Compendium: Chromosomal Loci is published, with genetic maps and a description of ~1000 loci. (Perkins et al. 2001)


2001. Silencing of unpaired genes during meiosis is shown to require a gene that specifies an RNA-dependent RNA polymerase. (Shiu et al. 2001)

2001. DNA methylation is shown to depend on the presence of a functional histone H3 methyltransferase. (Tamaru and Selker 2001)

2001. Methodology is described for obtaining good expression of Green Fluorescent Protein in Neurospora. (Freitag et al. 2001)

2002. Inactivation of genes by RIP is shown to require a DNA methyltransferase-like protein. (Freitag et al. 2002).

2002. New versions of the genome sequencing projects are released in Germany and the United States, reporting progress with assembly
and annotation:
http://www-encode.wi.mit.edu/annotation/fungi/Neurospora/
http://www.mips.biochem.mpg.de/proj/Neurospora/
http://pedant.gsf.de/cgi-bin/wwwfly.pl?Set=Neurospora_crassa&Page=index