# Basins of Attraction

Helena E. Nusse* and James A. Yorke

**Many remarkable properties related to chaos have been found in the dynamics of nonlinear physical systems. These properties are often seen in detailed computer studies, but it is almost always impossible to establish these properties rigorously for specific physical systems. This article presents some strange properties about basins of attraction. In particular, a basin of attraction is a "Wada basin" if every point on the common boundary of that basin and another basin is also on the boundary of a third basin. The occurrence of this strange property can be established precisely because of the concept of a basin cell.**

If we look at a map of the world, we see a division into regions (countries and states). Typically, a point on the border of one country is on the border of only two. Three countries can have at most two points where all three meet if each country is corrected (that is, it consists of a single piece) (Fig. 1A). Imagine trying to draw a picture of three nonoverlapping regions in the plane, each connected, which have the property that every border point of each region is a border point of all three regions. Surprisingly, such regions occur naturally in dynamics (Fig. 1B), the study of how processes change with time.

## Discrete-Time Processes

The processes described in this article are two dimensional. For example, as a pendulum swings, the angle between the pendulum arm and the rest position varies, as does its angular velocity. The state of the pendulum at a given moment is its angle and angular velocity at that time. In 1976, astronomer Michel Hénon gave the following mathematical rule for how a particular nonphysical, two-dimensional process evolves with time. Two numbers $a$ and $b$ are selected with constant values, for example $a = -0.45$ and $b = 0.8$. The state of the process is a pair of numbers $(x, y)$, each of which change with time. Hénon's rule is that if $(x, y)$ is the state of the process at time $t$, then at $t + 1$, the state will be the pair of numbers $(a - x^2 - by, x)$. Hence, for $a = -0.45$ and $b = 0.8$, the state (0.2, 0.3) at $t$ becomes (−0.73, 0.2) at $t + 1$.

Given any state of the process $(x, y)$ at $t$, one may want to know the state at $t - 1$. In the Hénon process, there is exactly one state $(x', y')$ at $t - 1$ that results in the current state $(x, y)$ at $t$ (provided that $b \neq 0$). We say $(x, y)$ comes from $(x', y')$. This process is called time-reversible. If the process is time-reversible, then the process resulting when time is reversed is called the time-reversed process.

Notice that Hénon's rule tells us where the state is at integral times but does not tell us where it is at intermediate times like 1.5. Such processes are called discrete-time processes. Discrete-time processes are simple models for how processes evolve with time. The discrete-time processes we study mirror aspects expected in many physical experiments.

The Hénon process is a prototype for the study of much more complicated processes, such as the dynamics of a pendulum. It does not tell us anything about the actual motion of a pendulum, but these systems have phenomena in common. Similar phenomena can be observed in biology, chemistry, and economics. The Hénon process is to the mathematician or physicist what the laboratory rat is to the physician: it is of interest only because of what it suggests about real problems.

## Basic Notions in Dynamics

Chaos theory (*1*) began with a particular study of a two-dimensional process. In 1887, King Oscar II of Sweden and Norway offered a prize of 2500 crowns to whomever could determine if the other planets in our solar system could resonate with the Earth to make it collide with another planet (Mars, for example) or run off into the empty interstellar wastes. Poincaré tackled the problem and won King Oscar's award for his work in 1889. By studying a special case, Poincaré reduced the problem to the study of a process in a plane.

To discuss Poincaré's idea, we need to describe more of the elements of dynamics. If a particular state $(x, y)$ does not change when the process being studied is applied, then this state is called an equilibrium of the process. In the Hénon process, the point $(x^*, y^*) = (-0.3, -0.3)$ is an equilibrium. The trajectory of a state $(x, y)$ is the collection of all states passed through as the process is applied repeatedly. An equilibrium $(x^*, y^*)$ is an equilibrium attractor if the trajectory of any initial condition near $(x^*, y^*)$ approaches $(x^*, y^*)$. For an equilibrium attractor $A = (x^*, y^*)$, the collection of points whose trajectories go to A forms the basin of attraction of A (Fig. 2, A and B).

An equilibrium $(x^*, y^*)$ is a saddle point S if there are points whose trajectories approach $(x^*, y^*)$ as time increases and if there are other points whose trajectories approach the equilibrium $(x^*, y^*)$ for the time-reversed process. The collection of all points whose trajectories approach S when the process is applied repeatedly is a curve called the stable curve of the saddle; similarly, the collection of all points whose trajectories approach S when the time-reversed process is applied repeatedly is called the unstable curve of the saddle (Fig. 2C). For the Hénon process with $a = -0.45$ and $b = 0.8$, the point (−1.5, −1.5) is an equilibrium point and a saddle point. The stable curve of this saddle is on the boundary of the basin of the equilibrium attractor

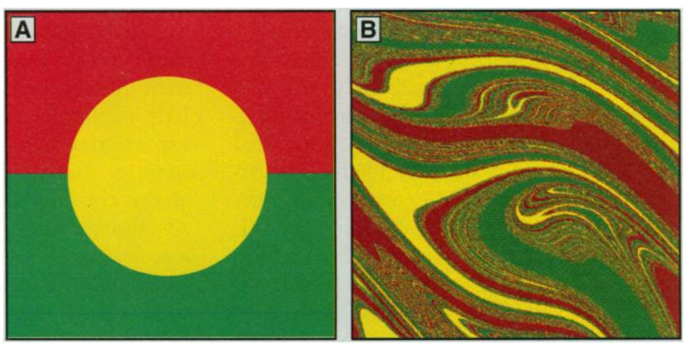


**Fig. 1.** (**A**) Three connected regions. There are only two points that lie on the border of all three regions. (**B**) Three convoluted regions. Every border point of each region is on the border of all three regions. If you draw a line in the picture with one end point in the yellow region and one end point in the red region, then the line enters and leaves the yellow region infinitely many times. In fact, the line enters each of the three regions infinitely many times. Such boundaries are called fractal.

The authors are with the Institute for Physical Science and Technology, University of Maryland, College Park, MD 20742, USA.

*Permanent address: University of Groningen, Econometrics, Post Office Box 800, NL-9700 AV Groningen, Netherlands.

$A = (-0.3, -0.3)$. The stable and unstable curves of a saddle point are invariant; that is, if a point is on the (un)stable curve of a saddle point, then its entire trajectory lies on this (un)stable curve when applying either the process or the corresponding time-reversed process.

One of the important ideas in the study of dynamics attributed to Poincaré is the fact that the stable and unstable curves of a saddle point may cross at points other than the saddle; these crossing points are called homoclinic points (Fig. 2D) (the saddle itself is not a homoclinic point). The key point of Poincaré's analysis of the three-body problem (studied as a discrete-time process in a plane) was to show that homoclinic points exist. However, the stable and unstable curves of a saddle point do not always cross. For any process in a plane, the dynamic behavior near the homoclinic points is incredibly complicated. In this complexity, points on trajectories that return exactly to their starting position after some time, known as periodic points, play a crucial role. The shortest time needed to return is called the period, and the trajectory of a periodic point is a periodic orbit. For example, if the first and second new states are different from the starting state but the state at $t = 3$ is the original state, then the starting point is a periodic point of period three, or a period-3 point. The trajectory of a period-3 point consists of three points and is a period-3 orbit. In our examples, periodic orbits can be attracting or can be saddles having both stable and unstable curves.

## Fractal Basin Boundaries

The complexity of the behavior near homoclinic points can best be described as follows. If the stable and unstable curves of a saddle point cross at $(p^*, q^*)$, then every small disk centered at $(p^*, q^*)$ includes infinitely many periodic points of different periods. Furthermore, Poincaré showed that if there is one homoclinic point, then there are infinitely many; in fact, there are infinitely many in each of the small disks. In many cases, there is a saddle point (or saddle periodic orbit) on the boundary whose stable and unstable curves cross. This crossing produces infinitely many homoclinic points (all of which lie on the boundary as well), which makes the boundary of the basin extremely complicated. Such boundaries are called fractal boundaries (Fig. 2E). The fact that a basin boundary is fractal has important practical consequences. If the goal is to predict the long-term behavior of an initial point, it is necessary to determine which basin it is in. If the basin boundary is fractal, a large proportion of the initial points may be near the boundary, so we may not be able to discern which basin the point is in.

In physical, biological, and economic models, one frequently encounters forced oscillators. The forced damped pendulum is an example. A grandfather's clock has a pendulum bob that is a forced damped oscillator. It is forced to keep moving by weights in the clock. The forced damped pendulum is similar but can swing through 360°. The angle between the pendulum arm and the rest position and the arm's angular velocity are the two variables that determine the state of the forced damped pendulum. Imagine that an impulse is imparted to the bob once each second so that the bob keeps swinging. If a strobe light flashes once each second, one can see the angle of the pendulum and measure the angular velocity. The flashing strobe light makes this a discrete-time process: we only observe it once each second. This discrete-time process is called a stroboscopic process for the forced damped pendulum. Depending on how hard the pendulum is forced, it can have one equilibrium corresponding to the bob rotating clockwise a full 360° each second. This is an equilibrium for the stroboscopic process because at each flash, it is always in the same position and has the same velocity. Another equilibrium would correspond to counterclockwise rotation. These equilibria could be either attractors or saddles. When the two equilibria are attractors, one can plot the corresponding basins of attraction (Fig. 2B).

Our group and scientists elsewhere have been studying basins with fractal boundaries, and a number of properties have been discovered (2). The most obvious property

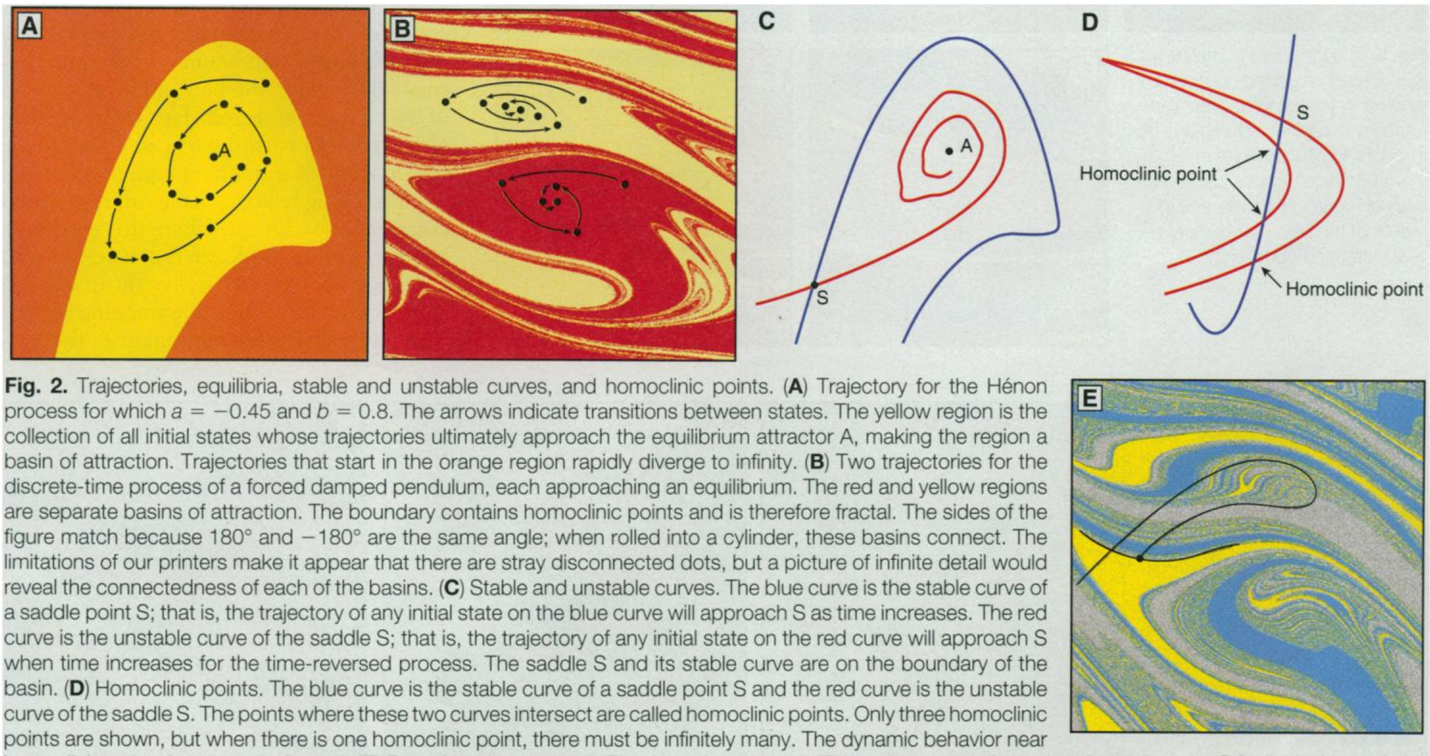


**Fig. 2.** Trajectories, equilibria, stable and unstable curves, and homoclinic points. (**A**) Trajectory for the Hénon process for which $a = -0.45$ and $b = 0.8$. The arrows indicate transitions between states. The yellow region is the collection of all initial states whose trajectories ultimately approach the equilibrium attractor A, making the region a basin of attraction. Trajectories that start in the orange region rapidly diverge to infinity. (**B**) Two trajectories for the discrete-time process of a forced damped pendulum, each approaching an equilibrium. The red and yellow regions are separate basins of attraction. The boundary contains homoclinic points and is therefore fractal. The sides of the figure match because 180° and −180° are the same angle; when rolled into a cylinder, these basins connect. The limitations of our printers make it appear that there are stray disconnected dots, but a picture of infinite detail would reveal the connectedness of each of the basins. (**C**) Stable and unstable curves. The blue curve is the stable curve of a saddle point S; that is, the trajectory of any initial state on the blue curve will approach S as time increases. The red curve is the unstable curve of the saddle S; that is, the trajectory of any initial state on the red curve will approach S when time increases for the time-reversed process. The saddle S and its stable curve are on the boundary of the basin. (**D**) Homoclinic points. The blue curve is the stable curve of a saddle point S and the red curve is the unstable curve of the saddle S. The points where these two curves intersect are called homoclinic points. Only three homoclinic points are shown, but when there is one homoclinic point, there must be infinitely many. The dynamic behavior near homoclinic points is very complicated. (**E**) Fractal basin boundary. There are three basins. The stable curve of a period-3 saddle point S (indicated by a dot) is on the boundary of the yellow basin. The unstable curve of S passes through all three basins and crosses the stable curve of S in a homoclinic point on the boundary. Therefore, the basin boundary is fractal.

is that there is a disk in the basin (centered at the attracting equilibrium). A point is in the basin if its trajectory enters that disk. The second property is much less obvious: the basin of an equilibrium attractor of a time-reversible map is connected in the sense that any two points in the basin have an arc that lies entirely in the basin and extends from one point to the other. The curve may be long and winding and can be chosen in a variety of ways. Sometimes the basins are extremely complicated.

## Strange Boundaries and Wada Basins

Even more complexity can occur in rather simple processes. Let us be more precise. A point is on the boundary of a basin if every disk centered at that point contains points of at least two basins. If a point is on the boundary, then its trajectory is on the boundary. One can imagine situations for which a boundary point of a basin is on the boundary of at least two other basins (Fig. 1A). Examples suggest that there are only finitely many such points. However, in 1910, Brouwer constructed a mathematical example of three regions such that every boundary point is a boundary point of all three regions (3). Independently, Yoneyama gave a similar example in 1917, attributing it to "Mr. Wada"; this example has come to be called "Lakes of Wada" (4). As originally presented, these examples have nothing to do with dynamic systems. It is hard to imagine that such a configuration of three basins could exist for simple dynamic processes. Kennedy and Yorke (5) discovered that such "Wada basins" do occur in some simple processes. It is possible to have three or more basins such that every basin boundary point is on the boundary of at least two other basins. Such a basin is called a Wada basin (6). In other words, no matter how close you zoom in on a boundary point, all three basins would be in the detailed picture. They were unable to prove Wada basins occur except in rather special circumstances, but on the basis of pictures of basins, Kennedy and Yorke suggested that the Wada basins appear to exist even in the forced damped pendulum (5).

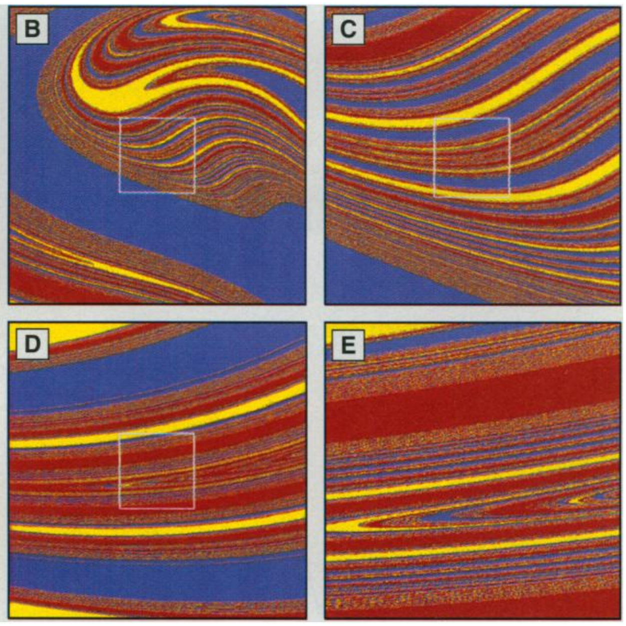


**Fig. 3.** The three Wada basins for the forced damped pendulum (shown in yellow, red, and blue). Each is a connected region. (**A** through **E**) Successive enlargements of the small box in the preceding figure. Further enlargements of the boundary simply reveal increased complexity.

## Basins of Trapping Regions

Recently, by creating the idea of the basin cell, we found an approach to fractal basin boundaries that gives a better understanding of both how basins are structured and when Wada basins occur (6, 7). A succession of enlargements of basins may suggest that they are Wada basins (Fig. 3), but no such sequence is a proof. We must guarantee that the complicated structure of the basins continues no matter how many magnifications are made. If we are only interested in determining that the boundary is fractal, then we only need to look for a saddle in the boundary, a saddle with homoclinic points. Our goal is to present a similar signature of the existence of Wada basins.

Here we limit ourselves to two examples of processes with Wada basins. Such examples are common. Our first example is the Hénon process with $a = 0.71$ and $b = -0.9$, which has three basins of attraction; call them the gray, green, and red basins (Fig. 4). The gray basin is the set of all points whose trajectories diverge when the process is applied repeatedly and is called the basin of infinity; the green basin includes a period-2 attractor; and the red basin includes a period-6 attractor. The gray basin is connected, the green basin consists of two connected regions, and the red basin consists of six connected regions. Our second example concerns the stroboscopic process of the forced damped pendulum. It has three basins—the yellow, the blue, and the red—all of which are connected (Fig. 3). In order to identify Wada basins, we need to introduce the concept of a trapping region.

A trapping region is a region from which points cannot escape when the process is applied. For example, if the image of the boundary of a region is strictly inside the region, then the region is a trapping region. The basin of a trapping region is the col-

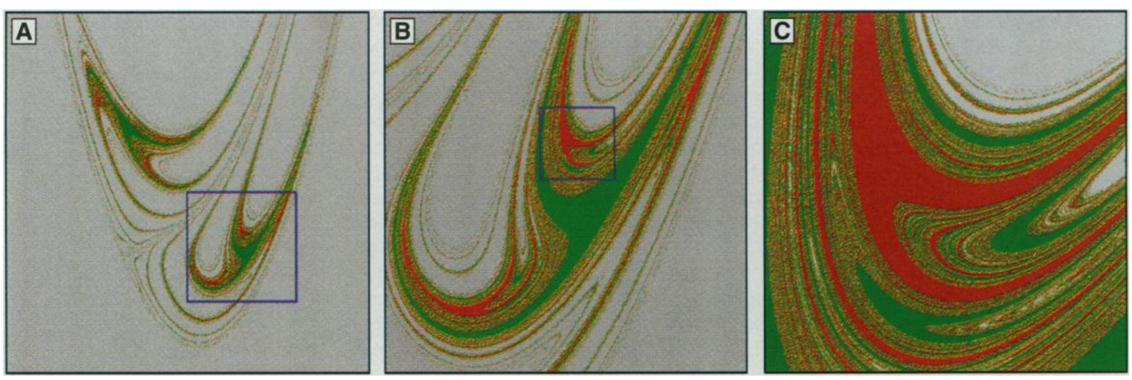


**Fig. 4.** The three Wada basins for the Hénon process. The Hénon process for which $a = 0.71$ and $b = -0.9$ has three basins of attraction, which are colored gray, green, and red. The gray basin is the collection of initial states whose trajectories diverge when time increases. The green basin has a period-2 attractor and consists of two connected regions, whereas the red basin has a period-6 attractor and consists of six connected regions. Successive enlargements (**A** through **C**) show incredible complexity at small scales. Points on the boundary between two basins are in neither basin. A basin is a Wada basin if any point that is on the boundary between two basins is also on the boundary of the third basin.

lection of points whose trajectories ultimately enter the interior of that region. From now on, we say that a basin is the collection of initial conditions whose trajectories eventually enter the interior of some specified trapping region. In our approach to the theory of basins, we examine stable and unstable curves of saddle points (or saddle periodic orbits) and their intersections. We look for trapping regions that are bounded by stable and unstable curves.

## Basin Cells and the Occurrence of Wada Basins

To show that certain basins are Wada basins, we first define a cell to be a connected region (Figs. 5 and 6). The cell's boundary consists alternately of pieces of the stable and unstable curves of some periodic orbit. We say that this periodic orbit generates the cell. Most cells are not trapping regions. When a cell is a trapping region, we call it a basin cell. Examples can be found having two basins, each of whose trapping region is a basin cell. However, the interesting case is when there are three basins. We now state our theorem. Assume there is a basin with a basin cell. If one of the unstable curves of the periodic orbit that generates the basin cell passes through at least two other basins of attraction, then the basin is a Wada basin.

We first turn to the example of the forced damped pendulum. Each of the three basins has a trapping region that is a basin cell (Fig. 5). The basin cell of the yellow basin is a six-sided region and is generated by a period-3 saddle orbit; the two other basin cells are four-sided regions generated by period-2 saddles. The unstable curve of each of the points of the periodic trajectories that generate any of these three basin cells intersects all three basins. Hence, all three basins of the forced damped pendulum are Wada basins; therefore, every point on the boundary of any of the three basins is also on the boundary of the remaining two basins (Fig. 3).

In some cases of the Hénon process, there is a cell that is disjoint from its image at $t = 1$, but its image at $t = 2$ is contained in the cell (this is the case for the green basin). In such cases, we still say the cell is a basin cell even though it is truly a basin cell only for the current process applied a specified number of times. We concentrate on the green and red basins. The green basin is the basin of a basin cell (Fig. 6A). This basin cell is generated by three points of a period-6 orbit. In fact, this cell and its image at $t = 1$ (which is a cell too) are disjoint, but these two cells together constitute a trapping region. If the unstable curve of any point of this periodic orbit intersects all three basins, then by our theorem, the green basin is a Wada basin. Indeed, this is the case. Similarly, there exists a basin cell for the red basin generated by three points of a period-18 orbit (Fig. 6B). In fact, this cell and its images at $t =$ 1, 2, 3, 4, and 5 (each of which is a cell too) are disjoint, but these six cells together form a trapping region. The unstable curve of any point of this period-18 orbit intersects all three basins. Hence, the red basin is also a Wada basin. Furthermore, we can also show that the basin of infinity (the gray region) is a Wada basin. Therefore, all three basins of the Hénon process for which $a = 0.71$ and $b = -0.9$ are Wada basins, so every point on the boundary of any of the three basins is also on the boundary of the remaining two basins; the boundaries of all three basins coincide.

In both examples, each of the three basins is a Wada basin. There are also examples of other processes for which there are three basins, one of which is a Wada basin whereas the other basins are not. Each of the three Wada basins of the pendulum example has a basin cell, and two Wada basins of the Hénon example (the basins that have a periodic attractor) have basin cells.

Basin cells tell us a great deal about the structure of the corresponding basin. For example, the six-sided basin cell of the yellow basin in the pendulum example is generated by a periodic orbit of period 3. This basin can be viewed as a central body (the basin cell) plus three channels that connect to it. These channels are infinitely long and wind in a very complicated pattern without ever crossing each other. The process rotates the basin by one third of a turn. The two remaining basins have a basin cell as the central body from which two channels extend. When the basin cell is generated by a period-2 orbit, the corresponding basin is the four-sided basin cell plus the two channels that emerge from it. The channels vary greatly in thickness but generally get quite thin as they wander back and forth. Yet

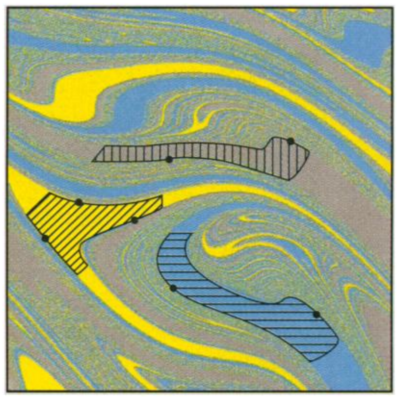

**Fig. 5.** Basin cells for the forced damped pendulum. A trapping region is a region from which a trajectory cannot escape once it has entered that region. Each of the three regions (blue, yellow, and gray) are bounded by parts of the stable and unstable curves of some specially selected periodic points and are trapping regions for the pendulum. Such regions are called basin cells. Basin cells characterize the structure of the corresponding basin. The six-sided basin cell of the yellow basin is generated by a periodic orbit of period 3. Therefore, this basin can be viewed as the basin cell plus the three channels that connect to it. These channels are infinitely long and wind in a very complicated pattern without ever crossing each other. In the figure, the process rotates the basin by one third of a turn. When the basin cell is generated by a period-2 orbit (as with the gray and blue basins), the corresponding basin is the four-sided basin cell plus the two channels that emerge from it. The channels vary greatly in thickness but generally get quite thin as they wander back and forth.

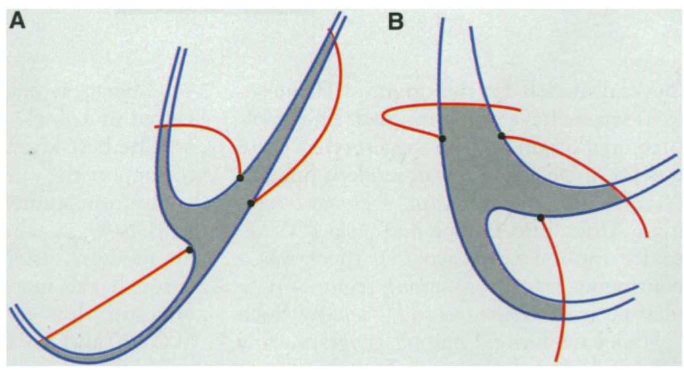


**Fig. 6.** Basin cells for the Hénon process. (**A**) The three dots indicate three periodic points of period 6 of the Hénon process for which $a = 0.71$ and $b = -0.9$. These three points are periodic points of period 3 for the "time-2" Hénon process, that is, the process resulting from two applications of the Hénon process. The shaded region, bounded by parts of the stable and unstable curves of these three points, is a cell. The image of the cell at $t = 1$ is a new cell located outside of the first cell, but the image of the cell at $t = 2$ is contained in the original cell. Hence, once a trajectory enters the cell, it is trapped in this cell when the process is applied twice. Therefore, the cell is a trapping region for the time-2 Hénon process. This basin cell corresponds to the green basin of Fig. 4B. (**B**) The cell is generated by three points of a period-18 orbit. When the Hénon process is applied six times, then these three points are periodic points of period 3; that is, they are period-3 points of the time-6 Hénon process. The images of the cell at times $t = 1, 2, 3, 4$, and 5 are new cells located outside the first cell, but the image of the cell at $t = 6$ is contained in the original cell. Hence, the cell is a trapping region for the time-6 Hénon process. The shaded region bounded by parts of the stable and unstable curves of the three periodic points is a basin cell for the time-6 Hénon process that corresponds to the red basin of Fig. 4C.

another way to view basins such as, for example, the yellow basin of the pendulum example is as if it were a lake (the basin cell) with three rivers draining into the lake.

This intriguing phenomenon of Wada basins can be found in many applications. Many physical, biological, or economic systems can be described by differential equations analogous to those of the pendulum. For various choices of parameter values for the system, there are likely to be several coexisting basins. If the boundaries are fractal, it is likely that basin cells can be found. Here we showed three coexisting basins, but there is no limit to the number of coexisting basins that are Wada basins, all with the same boundary. Such boundaries are uncertain; every boundary point is arbitrarily near every basin. Every boundary point can be perturbed arbitrarily slightly into any of the basins.

### REFERENCES AND NOTES


1. C. Grebogi, E. Ott, J. A. Yorke, *Science* **238**, 632 (1987).
2. E. G. Gwinn and R. M. Westervelt, *Phys. Rev. A* **33**, 4143 (1986); S. W. McDonald, C. Grebogi, E. Ott, J. A. Yorke, *Physica D* **17**, 125 (1985); C. Mira, *C. R. Acad. Sci. Paris A* **288**, 591 (1979); F. C. Moon and G.-X. Li, *Phys. Rev. Lett.* **55**, 1439 (1985); S. Takesue and K. Kaneko, *Prog. Theor. Phys.* **71**, 35 (1984).
3. E. Kasner and J. R. Newman, *Mathematics and the Imagination* (Microsoft Press, Redmond, WA, 1989).
4. J. G. Hocking and G. S. Young, *Topology* (Addison-Wesley, Reading, MA, 1961).
5. J. Kennedy and J. A. Yorke, *Physica D* **51**, 213 (1991).
6. H. E. Nusse and J. A. Yorke, *ibid.*, in press.
7. ______, *Ergodic Theory Dyn. Syst.*, in press.
8. ______, *Dynamics: Numerical Explorations* (Applied Mathematical Sciences 101, Springer-Verlag, New York, 1994).


9. The computer-assisted pictures were made with the program Dynamics (*8*). We thank M. Roberts and J. Tempkin for their comments. This work was supported in part by the Department of Energy (Scientific Computing Staff Office of Energy Research) and the National Science Foundation, and the W. M. Keck Foundation supported our Chaos Visualization Laboratory.


# Global Patterns of Linkage Disequilibrium at the CD4 Locus and Modern Human Origins


S. A. Tishkoff, E. Dietzsch, W. Speed, A. J. Pakstis, J. R. Kidd, K. Cheung, B. Bonné-Tamir, A. S. Santachiara-Benerecetti, P. Moral, M. Krings, S. Pääbo, E. Watson, N. Risch, T. Jenkins, K. K. Kidd



Haplotypes consisting of alleles at a short tandem repeat polymorphism (STRP) and an Alu deletion polymorphism at the CD4 locus on chromosome 12 were analyzed in more than 1600 individuals sampled from 42 geographically dispersed populations (13 African, 2 Middle Eastern, 7 European, 9 Asian, 3 Pacific, and 8 Amerindian). Sub-Saharan African populations had more haplotypes and exhibited more variability in frequencies of haplotypes than the Northeast African or non-African populations. The Alu deletion was nearly always associated with a single STRP allele in non-African and Northeast African populations but was associated with a wide range of STRP alleles in the sub-Saharan African populations. This global pattern of haplotype variation and linkage disequilibrium suggests a common and recent African origin for all non-African human populations.


Several models for the origin of *Homo sapiens sapiens* have been proposed. The "multiregional origin" model suggests that there was no single origin for all modern humans (*1, 2*). After the radiation of *Homo erectus* from Africa into Europe and Asia 800,000 to 1.8 million years ago (*3*), there was a continuous transition among regional populations from *H. erectus* to *H. sapiens*. Such "parallel evolution" among geographically dispersed populations could have been achieved by considerable amounts of gene flow between populations (*1, 2*). By contrast, the "out of Africa" model suggests that all non-African human populations descend from an anatomically modern *H. sapiens* ancestor that evolved in Africa approximately 100,000 to 200,000 years ago and then spread and diversified throughout the rest of the Earth, supplanting any *Homo* populations still present outside of Africa (*1, 4*). Migration out of Africa may have occurred in a single or in multiple waves (*5*).

The best-known genetic evidence used to support the out of Africa hypothesis has come from studies of mitochondrial DNA (mtDNA) in which it was proposed that all modern mtDNA can be traced back through the maternal lineage to a single ancestor that existed in Africa between 100,000 and 300,000 years ago (*6, 7*). The analysis and interpretation of these data have continued to be debated (*8*). Recent mtDNA (*9*) and Y chromosome (*10*) studies support the original findings of a recent origin of all modern humans. We present data from the nuclear autosomal genome that strongly support the out of Africa model of human origins and provide a different and independent estimate, based on linkage disequilibrium, of the recency of the emigration from Africa.

## Genetic Systems Studied

We studied alleles from two tightly linked markers, located ~9.8 kb apart, within noncoding regions of the CD4 gene on the short arm of chromosome 12 (*11–13*) (Fig. 1). These polymorphic markers are of two types that evolve with differing rates. The first is a short tandem repeat polymorphism (STRP). This class of markers consists of tandemly repeated blocks of two to five nucleotides; STRPs often have multiple alleles (defined by the number of repeats) and moderate to high mutation rates (*14*). Many researchers consider them particularly useful as markers for reconstructing recent evolutionary history (*15*). The STRP at the CD4 locus consists of the pentanucleotide sequence TTTTC repeated between 4 and 15 times (*12, 13*); the products (including flanking sequence) of the polymerase chain reaction (PCR) range in size from 80 base pairs (bp) for a 4-repeat allele to 135 bp for a 15-repeat allele (*16*). Most of the 12 alleles seen in humans are found primarily in Africa. Outside of Africa only three alleles (the 85-, 90-, and 110-bp alleles) ever occur at a frequency greater than 10%. Genotype frequencies for all populations are close to predicted Hardy-Weinberg expectations. We have also amplified the CD4 STRP in common chimpanzee ($n$ = 22), pygmy chimpanzee ($n$ = 5), gorilla ($n$ = 5), orangutan ($n$ = 3), and gibbon ($n$ = 4). Most hominoid species are polymorphic, but alleles range only from three to six repeats (75 to 90 bp) (*17*).

The second polymorphism results from the deletion of 256 bp of a 285-bp Alu element (Fig. 1) (*13*). This type of mutation is unlikely to have occurred more than once; DNA sequence analysis of several Alu deletion chromosomes from African and non-African individuals (*18*) revealed that all chromosomes contain the identical deletion, so that common ancestry can be assumed. The Alu deletion allele [Alu(−)] was typed through use of published primers and protocols (*13*); it was found to be rare or