money while the other party does not react to this decision. A similar situation arises with a beggar. The only difference between these two game situations is that the beggar provides nothing other than perhaps a "thanks," whereas the musician provides his or her music. So why can street musicians sometimes earn so much that they are able to take their music on the road and travel around, and why does begging pay enough to support at least some people who beg full time? Is it because many of us are influenced by cultural rules and taboos ("memes") that prompt us to give money (*11*, *12*); or is it because some of us are "bad" players, players of nonadaptive strategies that would disappear rapidly when under strong natural selection?

There is a third possible explanation for this kind of seemingly altruistic behavior, described earlier (*13*, *14*) and now formally proven by Nowak and Sigmund (*1*). This is cooperation by indirect reciprocity. It involves the inclusion of an additional variable to the game—social status. The idea is that being observed giving something to, for example, the street musician increases your social status (see the figure) and that being observed withholding your gift decreases it. Giving something may pay off in the long run if the people you interact with in the future take your social status into account. Giving may not be a real altruistic act—rather, it could be a sophisticated investment into one's own future. Nowak and Sigmund demonstrate that already simple rules about how information on social status is used can lead to cooperation in situations where direct reciprocity is unlikely. They also find that group size is important. For larger groups it is more difficult to establish cooperation, because there are more interactions required to discriminate against defectors. However, cooperation by indirect reciprocity could easily evolve in their models in groups of 20 to 100 individuals, even if the probability of being observed in such interaction varied from 1 to 0.1. This means that if you meet a street musician you are inevitably caught in a game. Whatever you do, it may have an impact on your social status. Even if it is unlikely that none of your future social partners will see or hear about your decision, you can never be sure about this. Moreover, cooperative moves that happened to be observed in apparently anonymous situations are likely to weigh higher on your social status account, but the same may be true for uncooperative moves.

Nowak and Sigmund (*1*) argue that social status is a variable with decisive impact on the evolution of human society, because it binds larger groups of individuals together and makes cooperation on a larger scale possible. Moreover, working on one's own social status and having to deal with the difficulties in continuously readjusting the perceived social status of the many members of a group might have selected for social intelligence and for an ability for abstract thinking in our species. We as human beings have all thought a great deal about the social rules we live under, about right and wrong, and we usually have rather determined opinions. This and our social experience make us intuitive masters of highly sophisticated social games (*9*, *10*). It is funny that we are only now starting to understand the rules that we use in our own games.

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PLANETARY SCIENCE

New Insights on the Kuiper Belt

Alessandro Morbidelli

When Edgeworth and Kuiper first conjectured the existence of a belt of small objects beyond Neptune—now called the Kuiper belt—they were imagining a disk of planetesimals preserving the pristine conditions of the disk of matter that eventually became the planets of the solar system. However, since the first discoveries of Kuiper belt objects, astronomers have realized that it is not pristine: The disk has been affected by a number of processes that altered its original structure that are still not completely understood. On page 2104, Ward and Hahn (*1*) report new results that provide insight into the structure and evolution of this curious planetesimal system.

The known structure of the Kuiper belt, determined on the basis of the discovery of 64 objects (*2*) in the region beyond Neptune, is summarized in the figure (top and middle panels). In the inner belt [semimajor axis smaller than 40 AU (*3*)], all the known objects have large eccentricities. They are associated with first-order mean motion resonances with Neptune, the only dynamically stable regions at large eccentricity (*4*). Actually, all but one of the objects discovered in the inner Kuiper belt are in the 3:2 resonance—like the "planet" Pluto—and are therefore called Plutinos.

Beyond 42 AU (*5*) begins the "classical" belt, where the discovered objects are not specifically related to any mean motion resonance. Although the eccentricities and inclinations are generally smaller than in the inner belt, once again the classical belt does not look like a proto-planetary disk, because the latter should be made of planetesimals on quasi-circular and coplanar orbits. In particular, a few objects have surprisingly high inclinations, despite the observational biases not favoring their discovery (*6*). This allows one to conclude that some process must have excited eccentricities and inclinations not only in the inner belt but also in the classical belt.

In addition to the inner and the classical Kuiper belts, theoretical considerations (*7*) and the discovery of at least one object (*8*) argue for the existence of a third population of bodies, which evolve under the effects of close encounters with Neptune, forming a sort of scattered disk.

According to the statistics of discoveries per unit area of searched sky, about 70,000 objects bigger than 100 km should exist in the Kuiper belt up to 48 AU (*6*), only 10 to 20% of them being in the inner belt (*9*). The estimate of the total mass of the belt up to 48 AU is still uncertain within one order of magnitude, ranging from 0.06 to 0.3

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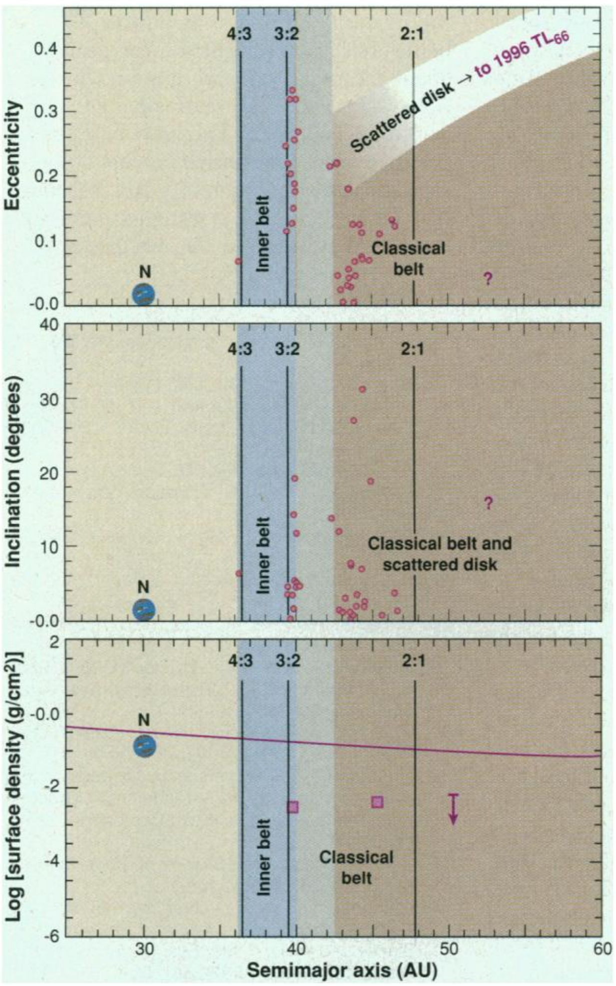

Planetesimal populations. (**Top** and **middle**) The distribution of Kuiper belt objects with well-determined orbits (*1*). The approximate boundaries among the inner belt, classical belt, and scattered disk are indicated. The boundary between the classical belt and scattered disk cannot be defined in the semimajor axis versus inclination plot. The shaded region separating the inner and the classical belts is strongly unstable (*5*). (**Bottom**) Mass distribution in the outer solar system. The solid curve shows the expected primordial surface density. The blue dot denotes the surface density corresponding to the mass of Neptune's solid core distributed over the 25- to 35-AU region. The two squares show the surface density in the 3:2 resonance and in the observed portion of the classical belt [assuming 0.03 M_E in the 39- to 40-AU annulus and 0.25 M_E in the 42- to 48-AU range, in agreement with (*9*)]. The arrow denotes the upper bound of the surface density at 50 AU, as claimed by Ward and Hahn (*1*).

Earth masses (M_E) (6, 9). This is much lower than its estimated (*10*, *11*) primordial mass of about 30 M_E, implying that in the early phases of the solar system some process caused a strong mass depletion. The distribution of the estimated present and primordial masses in the outer solar system is illustrated in the bottom panel of the figure. No direct information exists concerning the present mass of the classical Kuiper belt beyond 48 AU (hereafter called the "deep" belt), but it is believed that this region could have retained the bulk of its primordial mass (*12*).

In this context, the report by Ward and Hahn (*1*) provides two additional constraints on the present structure of the Kuiper belt and its primordial sculpting.

The first constraint is that the present surface density of the deep Kuiper belt beyond 48 AU should not be larger than 0.005 g cm^{-2}—20 times smaller than its estimated primordial value (bottom panel of figure); otherwise the density waves generated by Neptune would have damped the planet's eccentricity below its current 0.009. In the absence of an efficient mass depletion mechanism working beyond 48 AU, this would imply that the usual estimate of the primordial mass in the deep Kuiper belt is in excess by more than one order of magnitude. It is tempting to make the connection between this conclusion and the recent claim (9) that the Kuiper belt "ends" at about 50 AU. However, Ward and Hahn's constraint holds only if the eccentricities and the inclinations of the bodies in the deep belt are smaller than ~0.02 and ~1°, respectively. These values could be exceeded if primordial massive planetesimals evolved on typical scattered disk orbits (*13*) during some 100 million years. In this case, the eccentricity and inclination distribution of the bodies of the deep belt would be similar to those observed in the 42- to 48-AU region. If the typical eccentricities range up to 0.1, the constraint on the present surface density increases to 0.025 g cm^{-2}, reducing the gap from its estimated primordial value.

Similarly, a massive primordial belt with more than 0.1 g cm^{-2} in the 30- to 48-AU region would have damped Neptune's eccentricity below its present value in about 1 million years. Therefore, the second constraint provided by Ward and Hahn's study is that some mechanism exciting Neptune's eccentricity had to persist until the excitation and depletion of the primordial belt.

It is increasingly difficult to design a scenario of formation and primordial evolution of the Kuiper belt that fits all the constraints. At first, the problem seemed to be solved by the sweeping resonances model (*14*). According to this model, by its interaction with small planetesimals, Neptune moved outward, trapping Kuiper belt objects into mean motion resonances. This model successfully explains the existence of a large fraction of bodies in the 3:2 resonance with Neptune and their eccentricity and inclination distributions. However, the eccentricity and inclination excitations later observed in the classical belt, together with the persisting absence of detections of 2:1 resonant bodies, the mass deficiency of the belt, and, last, the second constraint provided by Ward and Hahn's findings, all seem to argue that this scenario is too simplistic, at least in its original version.

The mass depletion of the Kuiper belt could be explained by mutual collisions among the Kuiper belt bodies, provided that most of the primordial mass was carried by small objects (*12*). However, this contrasts with theoretical considerations arguing for the primordial existence of a substantial population of Pluto-sized bodies (*15*).

Alternatively, the primordial existence of massive planetesimals in the scattered disk has been proposed to explain the ejection of a large fraction of the bodies from the stable regions of the Kuiper belt and the eccentricity and inclination excitation of the survivors (*13*).

The absence of a well-defined scenario for the primordial sculpting of the Kuiper belt should not be discouraging. Kuiper belt science is still young and rapidly evolving. A big effort is under way by the astronomical community to acquire more information on its present and past structure, both directly, by telescope observations, and indirectly, by theoretical considerations. The new results will constrain the elaboration of formation scenarios and lead to a better understanding of the early phases of our solar system.

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3. The AU, or astronomical unit, is the mean distance of the Earth from the sun; Neptune is at 30 AU.
4. A body is in a mean motion resonance with Neptune if the ratio of its orbital period to Neptune's is the ratio of small integers *m*:*n*. First-order resonances correspond to $m - n = 1$. The stability of these resonances at large eccentricity is discussed by M. J. Duncan, H. F. Levison, and S. M. Budd [*Astron. J.* **110**, 3073 (1995)]; A. Morbidelli, F. Thomas, and M. Moons [*Icarus* **118**, 322 (1995)]; and R. Malhotra [*Astron. J.* **111**, 504 (1996)].
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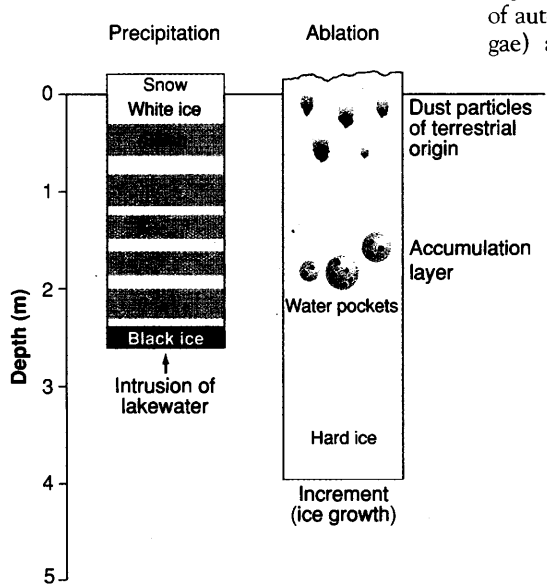
MICROBIAL COMMUNITIES

Life at the Freezing Point

Roland Psenner and Birgit Sattler

What are the chances that one could cultivate bacteria and algae in a deep freezer? The suggestion is not so outrageous, as Priscu and co-workers show on page 2095 of this issue (*1*), with their discovery of living organisms in surroundings that even in summer rarely exceed a chilling –20°C. They describe a thriving microbial assemblage in the thick, hard, and permanent ice layer of lakes in the Antarctic McMurdo Dry Valleys. What at the first glance appears to be a contradiction in terms (being frozen and leading an active life at the same time) turns out to be an exciting example of the adaptation of microorganisms to environmental extremes.

How can there be life in the ice? A closer look at icy ecosystems demonstrates that ice comes in many forms, which are not always what we think of as ice. Sea ice, for instance, has been known for a long time to harbor algae and crustaceans because concentrated brine solutions remain liquid at temperatures well below zero. In contrast, ice layers on freshwater lakes have usually been seen as nothing but physical barriers to light transmission, heat flux, wind-induced turbulence, and gas and particle exchange. The sandwich-like structure of the winter cover on high mountain lakes in the Alps was described in great detail in the early 1950s, but it took a long time to recognize that the slush layers (see figure) host a rich and very productive assemblage of autotrophic and heterotrophic organisms, which we and our co-workers have termed LIMCO (lake ice microbial community) (*2*). Within the winter cover at 0°C, bacterial production was up to an order of magnitude higher than in the pelagic zone of the lake at a "warm" 3° to 4°C. It was Felip, Camarero, and Catalan (*3*) from the University of Barcelona in Spain who showed in a 2-year study that the composition of autotrophic and heterotrophic microbial communities in lake ice clearly differed from that in the lake water, a fact that was also confirmed by Priscu *et al.* (*1*). Researchers from Innsbruck University have demonstrated that the genetic pattern—based on group-specific probes for ribosomal RNA—of communities of ice bacteria differed from that of lake water bacteria and also from that of bacteria found in freshly fallen snow (*4*).



Cold communities. Winter cover of high mountain lakes in the Alps and the Pyrenees (**Left**) and permanent ice cover of Antarctic lakes in the Dry Valleys (**Right**).The alpine lake cover consists of a sandwich-like structure of slush (a mixture of ice and snow crystals with lake water, rainwater, and meltwater) and white ice, covered by snow and separated from lake water by a thin layer of black ice, lasting for about 8 to 10 months. The Antarctic lakes in the Dry Valleys are covered by a permanent layer of hard ice containing pockets of liquid water during summer. These water pockets appear around clusters of terrestrial dust. They form a maximum at 2-m depth, where sinking speed and ice growth are in balance. Both habitats host only microorganisms—with some rare exceptions—and also the active period (the Austral summer in Antarctica and late winter, spring, and early summer in high alpine lakes) is reduced to about 6 to 8 months per year. In alpine lakes, slush has a constant temperature of 0°C; in the water pockets of Antarctic lake ice, temperatures will not exceed 0°C.

A comparison of freshwater ice systems (see figure and table) suggests that the example described by Priscu *et al.* represents the most extreme community one can imagine, both regarding physico-chemical factors and organisms involved; namely, an assemblage of autotrophic cyanobacteria (blue-green algae) and heterotrophic bacteria, encapsulated in the permanent ice cover of lakes. The term "oasis" used by the authors (*1*) refers to the fact that pockets of liquid water form around dust particles and microorganisms blown in from a cold desert, allowing active growth and reproduction of predominantly prokaryotic organisms during the Austral summer. Some ecological properties are similar in high alpine and Dry Valleys lake ice habitats; for example, both systems seem to be closer to the benthic than the pelagic world. However, in the case of the Antarctic lake ice, the sediment derives from the terrestrial catchment, whereas in the alpine lakes the "sediment" consists of ice and snow crystals, surrounded by interstitial water that is a mixture of lake water, rainwater, and snow meltwater. Although Antarctic McMurdo Dry Valleys lakes are permanently ice covered, their microbial communities are active for only about 5 months, which is comparable to the active period of the microbial communities in the transient ice cover of alpine lakes. A major difference concerns the physical structure and the origin of organisms, which in the case of the alpine lakes do not arrive solely from the atmosphere but also from lake water and littoral sediments.

It has been held for some years that bacterial growth and respiratory rates in the ocean are unmeasurably low at 0°C (*5*), but Priscu *et al.*'s and our own findings clearly indicate that in some habitats bacteria may be quite active even at freezing point. Recently, active bacteria and their metabolic products have been found in supercool (around –5°C) cloud droplets collected at altitudes above 3000 m in the Alps (*6*). Thus, our knowledge about the number

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