that led to the stunning realization that all photosystems are basically alike and must have the same evolutionary origin. A more detailed comparison of the two photosystems should soon be possible: we now have Jordan *et al.*'s high-resolution structure[1] of photosystem I, and the structure of cyanobacterial photosystem II, currently at 3.8 Å resolution[6], is being improved and refined. Together, the two structures will provide complete insight into the workings of these fascinating solar-energy converters. ■

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Astronomy

Giants in the asteroid belt

Derek C. Richardson

Models of Solar System formation have always had a hard time explaining the mysterious asteroid belt. By injecting new life into an old myth about the origin of asteroids, astronomers may now have the answer.

The asteroid belt consists of small bodies that orbit the Sun between Mars and Jupiter. On the bicentennial of the discovery of the first and largest asteroid, Ceres, by Italian astronomer Giuseppe Piazzi, it is surprising how little we understand about the history of the asteroid belt. A common misconception is that asteroids are the remains of a large planet that mysteriously exploded long ago. Today there is hardly enough material in the asteroid belt to make a small moon, let alone a planet. So something must have happened either to prevent the formation of a planet between Mars and Jupiter, or to clear out any material that accumulated there.

Typically the blame is cast on Jupiter, our largest and therefore most gravitationally influential neighbour. But exactly how it does this is a matter of some debate, because at the moment Jupiter affects only a few narrow regions of the asteroid belt. In an article in *Meteoritics and Planetary Science*, John Chambers and George Wetherill[1] paint the clearest picture yet of what may have happened. Surprisingly, they find that there may once have been Earth-sized planets in the asteroid belt, but that a combination of complex dynamics and chance events conspired to remove them.

The 'planetesimal hypothesis' of planet formation[2], a modern-day version of theories proposed by Kant and Laplace in the eighteenth century, states that the planets formed when smaller bodies collided and stuck together. These small bodies, called planetesimals, were part of the Solar nebula — a disk of gas and dust swirling around the Sun. In the inner regions of the Solar nebula, only non-volatile material survived to form the rocky Earth-like planets. But in the outer regions, where temperatures were cool enough to allow hydrogen-bearing compounds to solidify, the giant gas planets formed. The present-day masses of all the planets can be explained if the mass per unit area of the Solar nebula decreased smoothly with distance from the Sun — apart from the asteroid belt[3,4], that is, where there is a 1,000-fold drop in the amount of matter. It seems unlikely that this deficit was present at the outset in an otherwise smoothly distributed nebula, so most theories propose that the asteroid belt was cleared later on.

In the Chambers and Wetherill model[1], planets began to form throughout the disk, including the primitive asteroid belt, where a planet-sized body could form within one million years[5]. But the large amount of volatile material around Jupiter meant that Jupiter grew rapidly, eventually perturbing the asteroidal planets. These perturbations are caused by 'resonances' between the orbits of the giant planets and young asteroidal planets. A resonance arises when the orbital periods of two bodies are whole-number ratios of each other.

For example, an object in the asteroid belt, located 3.3 times as far as the Earth from the Sun, orbits the Sun exactly twice for each orbit of Jupiter — it is in a 2:1 resonance with Jupiter. Such an object experiences periodic momentum 'kicks' that gradually elongate its orbit, increasing the risk of it crashing into another body, including a terrestrial planet. It could also end up getting too close to Jupiter or the Sun, and so be ejected permanently from the Solar System because of a 'slingshot' effect (see ref. 6 for a review).

As Jupiter grew in mass, the orbital resonances it created became stronger. Any asteroid unlucky enough to wander into one of these resonances today would be ejected from the Solar System (or crash into the Sun) within one million years[7]. But these zones of instability are much narrower than the existing asteroid belt. Somehow, objects in the primitive asteroid belt were pushed into these zones. Chambers and Wetherill propose that encounters between the embryonic planets in the belt were responsible, at least to begin with. As the belt became depleted, this process slowed until only two or three planet-sized objects remained. It was then a matter of chance whether the stragglers survived or scattered each other into oblivion.

To check their hypothesis, Chambers and Wetherill[1] performed a series of numerical simulations in which they varied the numbers and masses of embryonic planets, and included the effects of an already formed Jupiter. They found that interactions between the embryos and Jupiter caused more than 90% of the mass in the asteroid belt to be cleared in less than a few hundred million years. Moreover, they found that if they started Jupiter (and Saturn in a few cases) in more elongated orbits, the clearing rate increased dramatically, becoming as short as a few million years. This is because the resonance zones become wider and stronger as the orbits of the perturbing planets become elongated.

At the same time, the embryos perturb the orbits of the giant planets by siphoning off energy they need to escape from the asteroid belt, thereby causing the giant orbits to become more circular. This process is analogous to that proposed for clearing objects from the outer Solar System[8,9]. Together these effects imply that the giant planets may have had elongated orbits when they formed. Giant planets with elongated orbits have been observed in other solar systems[10], so perhaps there was insufficient material left over in the nebulae of these systems to make the giant orbits circular.

The Chambers and Wetherill theory also suggests that instability induced by resonances could cause asteroidal embryos rich in volatiles, such as water, to crash into the Earth — a process that may explain the origin of Earth's oceans[11]. Also, in roughly one-third of their simulations, a planet did survive in the outer asteroid belt. This means it was largely a matter of chance whether our asteroid belt would harbour a planet. Although such a planet could have frustrated the beginnings of advanced life on Earth by increasing the rate of impact with planetesimals, it would probably have only delayed our progress for a short while.

Like most theories, there are certain assumptions in the model that may lead to its downfall. Most serious is the need for Jupiter to form slowly enough for planet-sized bodies to form in the asteroid belt before being perturbed[12]. But the elegant way in which the theory extends the standard model for terrestrial planet formation makes it attractive. Until more simulations are performed, or until there are enough data from other planetary systems to favour one model in particular, we must keep all alternatives in mind as we pursue our understanding of planet formation. ■

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Evolutionary biology

Seeing red in speciation

Michael J. Ryan

Mating patterns in sticklebacks have been investigated for over fifty years. The latest studies show how a complex interplay between males, females and the environment can contribute to the formation of new species.

Speciation and sexual selection are central processes in evolution. Speciation occurs when divergence between organisms becomes such that they cannot produce viable offspring, and so constitute different species. Sexual selection results from female preferences for certain male attributes in choosing a mate, and promotes the evolution of extreme male appearance and behaviour during courtship.

How might these processes interact? On page 944 of this issue[1], Janette Boughman describes how she has addressed the question by studying sticklebacks in Canadian lakes. She shows how sexual selection can drive speciation through the complex interplay between ambient light levels in different parts of the lakes, male coloration, and female sensitivity to light in different parts of the spectrum.

Mate preference is important in both speciation and sexual selection[2], but it gained wide recognition only with the appearance of papers by West-Eberhard[3] and Lande[4] some 20 years ago. These papers suggested that sexual selection can cause divergence of mating preferences among populations so that individuals from nearby populations perceive one another as 'different' rather than 'the same'. If so, sexual selection could generate the reproductive isolation that contributes to bringing about new species. When viewed by one another as different, individuals don't reproduce; this is reproductive isolation.

Figure 1 **Courting couple — a male stickleback in red mating livery makes a pass at a female. Inset: a male with black mating coloration.**

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Why would populations come to differ in their mate preferences? One possibility is 'sensory drive'[5], a change in the female perception system that could initially be unrelated to mate choice but could have an effect on it. Although sexual selection generally promotes the evolution of conspicuous male traits, 'conspicuous' is defined by the female's perceptual system and the context in which she perceives it. We know that differences among habitats can influence signal efficacy, one example being the way in which ambient light influences the conspicuousness of visual signals[6].

In the case of the sticklebacks studied by Boughman[1], the signal sent from male to female is throat colour (usually red), which becomes more intense during the mating season. This feature has made sticklebacks the subject of numerous studies in behavioural ecology[7] and evolution[8], ever since Tinbergen[9] observed that their response to red is so strong that a stickleback in an aquarium will swim at red postal trucks driving past on the road outside.

For her study, Boughman predicted the following: first, that male signals are transmitted in a habitat-specific way; in this case the red throat is more conspicuous in some parts of a lake than others because of the ambient light. Second, she predicted that the female's perceptual sensitivity adapts to local conditions, and third, that male signals match female sensitivity. If these three conditions are met, the idea is that mate preferences are then likely to diverge in different populations and that divergence will contribute to the reproductive isolation of those populations.

To test her predictions, Boughman studied six populations of sticklebacks from four lakes in British Columbia. In these populations, male mating coloration varied from red to black (Fig. 1). She found that males appeared redder, at least to her, in habitats with less red light. (This is one of the drawbacks of the study. More quantitative measures of the area and reflectance of red coloration would have allowed direct quantification of its conspicuousness to females; see, for instance, ref. 10. Subjective rankings of colour are based on reflectance as filtered by a human visual system, presumably under very different light conditions to those experienced by sticklebacks.)

To measure the sensitivity of female sticklebacks to wavelength, Boughman used experiments in which the intensity of monochromatic light is varied to determine the threshold at which a fish ceases to follow rotating black and white stripes. She found that females in areas with less red light, such as where the water is 'tea-stained' in colour rather than clear, are more sensitive to red light, and that male signals are matched to female sensitivity. So there is