Ecology

Venus firefly traps

In ancient Roman times, the goddess Venus was revered as the protector of feminine chastity. But times have changed and so, it would seem, have female values. In the 2 September issue of *Proceedings of the National Academy of Sciences*, Thomas Eisner and colleagues present a bloodthirsty tale of 'femmes fatales', who entrap their male victims and devour them whole (*Proc. Natl Acad. Sci. USA* 94, 9723–9728; 1997).

The females in question are fireflies belonging to the genus *Photuris*. During firefly courtship, male fireflies flash their light organs in a characteristic, species-specific manner. After a delay that also varies from species to species, the females flash once in reply.

Eisner *et al.* knew that the cunning *Photuris* female — by faking the flash signal of females from another genus, *Photinus* — can attract a *Photinus* male, which she then traps and eats. But by analysing blood from satiated *Photuris* females (some of which could eat as many as six *Photinus* males over several days), they found that the firefly gains more than a nutritional boost from her prey.

Many species of *Photinus* contain steroidal pyrones which, because of their close relationship to compounds such as bufalin (found in the venom of Chinese toads), are known as lucibufagins. Firefly predators — thrushes and jumping spiders, for example — find these compounds highly unpalatable. Although *Photuris* fireflies do not contain

lucibufagins, the authors found that after feeding upon a *Photinus* male, *Photuris* females were protected from jumping spiders of the genus *Phidippus* — the spiders attacked but they dropped the fireflies soon after contact.

To see whether this protection was due to ingested lucibufagin, Eisner *et al.* gave the compound to unfed *Photuris* females. These fireflies became protected against jumping spiders in the same way as their *Photinus*-fed counterparts, and the more lucibufagin they contained, the more unpalatable they became. But the levels of lucibufagin in all of the *Photuris* females were less than expected. The authors suggest that this could be because the females protect their eggs and, possibly, the emergent larvae, by endowing them with any excess lucibufagin.

When jumping spiders catch unprotected fireflies, they grind them up in their chelicers, suck them dry and then reduce them to a small pellet of solid remains. So by luring and ingesting *Photinus* males, the *Photuris* female acquires a potent defence mechanism. Perhaps Shakespeare put it best in *Twelfth Night*: "Alas! their love may be call'd appetite".

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RNA — the bond between N1 of uracil and C1' of ribose is broken, the plane of the uracil ring is rotated, and a new C5–C1' bond is formed (Fig. 1). Literally, a new angle is generated. Both N1 and N3 in ψ are potentially available for hydrogen bonding, so it is more versatile than uridine in this respect.

The extra hydrogen-bonding capability can, in principle, be used in intramolecular or intermolecular interactions. In several tRNA molecules, ψ occurs in or near the anticodon (where the tRNA pairs with the complementary nucleotides of messenger RNA). Here, through intermolecular interactions, ψ is involved in the regulation of operons for amino-acid biosynthesis in bacteria⁵, and nonsense suppression in yeast⁶. Most interestingly, the ψ modification for nonsense suppression in yeast not only takes place on a precursor tRNA molecule, but it requires an intron in the anticodon arm of the pre-tRNA⁶.

Until recently, ψ has been elusive in the ribosome. Although it is present in rRNA

from all sources examined, it is much more abundant in eukaryotic than in prokaryotic rRNA, with some 95 ψ residues per human ribosome. But, although enzymic-degradation procedures worked well in locating ψ in small molecules such as tRNA⁶, they were much more difficult to apply to large molecules such as rRNA. Progress was made with mammalian 18S (small ribosomal subunit) rRNA⁷, but almost none was made with the bigger, 28S (large ribosomal subunit) rRNA molecule.

The methodological impasse was overcome when Bakin and Ofengand⁸ developed a primer-extension assay for sequence-specific detection of ψ , based on the selective reaction of ψ with bulky chemical reagents that block progress by the enzyme reverse transcriptase. They first showed that several ψ residues in 23S rRNA from *Escherichia coli* are clustered in the peptidyl-transfer region⁸ — the functional centre of the large ribosomal subunit. In their latest study¹, they have phylogenetically mapped the many ψ

residues in the 28S rRNA of several eukaryotes. These findings are spectacular when combined with earlier data for methylation: ψ and ribose methylations are abundantly woven into phylogenetically conserved core regions of rRNA, and especially (although not exclusively) into features that contribute to the peptidyl-transfer region and its neighbourhood.

How does ψ get there, and are there any clues from studies of ribose methylation? In eukaryotic rRNA, ψ formation and ribose methylation both occur in conserved core regions. There are no obvious recurring features in the primary or secondary structure of rRNA that indicate recognition sites for ribose methylation or ψ formation. Moreover, both types of modification take place on pre-rRNA in the nucleolus.

For ribose methylation, a unifying finding explains these facts (see ref. 9 and references therein). Nucleosides that are to be methylated in newly transcribed pre-rRNA are 'targeted' by transient base-pairing with small nucleolar RNAs (snoRNAs). Each so-called 'guide' snoRNA contains a long (≥ 12 -nucleotide) tract next to a CUGA sequence called a D box. The snoRNA tract is complementary to a stretch of rRNA, in the middle of which is the target nucleoside.

Might a comparable process guide the formation of ψ ? This now turns out to be so. Another family of snoRNAs (including most of the remaining known snoRNAs) share conserved elements in their secondary structure, as well as the short sequence ACA, three nucleotides from the 3' end, and an internal single-strand tract called box H (refs 10, 11). At first sight these ACA snoRNAs seemed to lack extensive complementarity to rRNA, so their function remained an enigma. But studies by Ni *et al.*² and Ganot *et al.*³ have now decisively implicated the ACA snoRNAs in the formation of ψ .

At the outset of the work by Ni *et al.*, 20 yeast ACA snoRNAs were known. Seventeen of these had been characterized genetically, and 16 were found to be non-essential for growth. The authors disrupted the snoRNA

Figure 1 Uridine (left) and pseudouridine (ψ ; right), both shown within the polynucleotide backbone. After breakage of the N1–C1' bond, rotation of the uracil ring through 180° would bring C5 into place for making the new bond. Because both N1 and N3 are then potentially available for hydrogen-bonding, ψ is more versatile than uridine, and can be used in intra- and intermolecular interactions.