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Stellar astronomy

Life and death above the plane

Virginia Trimble

MASSIVE, short-lived stars have no business being located hundreds or thousands of parsecs out of the galactic plane, for the giant molecular clouds from which they normally form are confined to a layer with a scale height of 50–70 parsecs, and young stars, as a rule, move slowly. We have, nevertheless, known of a few counterexamples for more than 30 years¹. A fistful of recent papers^{2–10} casts light of varying colours on the phenomenon and forces us to the conclusion that these aberrant objects are not all the same kind of thing. Every hypothesis so far suggested (and perhaps a few yet to be formulated) probably applies somewhere.

The outlaw stars include what appear to be hot (O, B and A), main-sequence (core hydrogen burning) stars with expected lifetimes of 10^6 – 10^7 years and cooler (A–F) supergiant (shell hydrogen or helium burning) stars that are normally descendants of OB main-sequence stars, and so also short-lived. What are we supposed to make of them?

First, the stars might really be old ones, passing through an evolutionary phase that mimics young main-sequence stars and their progeny. Then, the normal increase with age of stellar velocity dispersion and scale height would entitle the stars to their present position. Second, they might be fainter than normal stars of similar colour and surface gravity. Then their distances will have been overestimated and their positions will not be excessively far from the galactic plane. These two can operate together in the case, for instance, of OB subdwarfs which are both much fainter than OB main-sequence stars and much older, being the last pre-white-dwarf gasp of stars with billion-year-plus lifetimes, like our Sun.

Third, something could have greatly delayed the completion of core hydrogen burning. Fourth, the stars might have formed as usual in the galactic plane but acquired anomalous velocities large enough to carry them to their present positions through disruption of binary systems or parent clusters. And, fifth, formation of massive stars may occasionally occur outside the galactic plane.

Consequences

Most of these ideas have observable consequences: sufficiently old stars should be metal poor; velocities are measurable (at least radial velocities); and so, sometimes, are masses. It is along these lines of observational tests that most of the recent progress has occurred. The high latitude A–F supergiants, whose prototype 89

Her has been with us since 1951 (ref. 11), turn out largely to be examples of the first hypothesis. They are systematically metal-deficient^{2–4}, especially in s-process elements like barium, and so almost certainly more than about 10^{10} years old. The most likely evolutionary state for them is the brief proto-planetary-nebula phase, between the termination of helium-shell burning and illumination of a true planetary nebula. Stars of less than 1 solar mass take more than 10^{10} years to get this far.

The high-latitude main-sequence A stars¹², on the other hand, seem to be experiencing prolonged core hydrogen burning. A few such stars occur in open and globular clusters, where they are called blue stragglers because of their location on a graph of luminosity versus colour (Hertzsprung–Russell diagram). It may not seem much progress to have reduced one mysterious phenomenon to a special case of another equally mysterious phenomenon. But the number of blue stragglers released as clusters disperse is, at any rate, sufficient to account for the high-latitude A stars (ref. 10). The main-sequence phase can be lengthened either by mixing fresh hydrogen down into the core of a single star or by bringing in more fuel from a second star in a binary system or collision. There is observational evidence for mixing in the form of enhanced nitrogen in blue stragglers in young associations¹³ and for transfer or mergers in the form of anomalously high masses for the blue stragglers in the globular cluster NGC5466 (ref. 14). Mergers are bound to occur in the crowded conditions of cluster cores¹⁵.

OB stars that are really old, faint subdwarfs often give away the fact by displaying high surface gravities. About 200 such stars have been catalogued¹⁶. For others, we can probe the mass (hence luminosity, using the spectroscopically determined

surface gravities and temperatures) indirectly. Some are probably faint; others almost certainly not.

Ultraviolet spectra of RWT152, for instance¹⁷, reveal a wind whose velocity implies an underlying star of only 0.6 solar masses, and so subdwarf luminosity, despite the apparently normal optical spectrum. On the other hand, PHL346 (ref. 6) and several other high-latitude OBs (ref. 5) display variable brightness and radial velocity of the sort whose prototype is β Cephei. If the variability has been correctly interpreted as non-radial modes, then the periods imply masses near 10 solar masses and lifetimes of 10^7 years. Other stars show such exceedingly normal line ratios for their temperatures and gravities⁷ that it is very hard not to interpret them also as massive main sequence stars. Thus we really do find short-lived objects 1–5 kpc above the galactic plane.

Runaway stars

How did they get there — ejection from the plane (and, if so, how?) or formation *in situ*? Classical runaway stars¹⁸ are OBs whose three-dimensional velocity vectors point back to young associations within which they probably formed. We cannot have this information for stars many kiloparsecs from the galactic plane because their motions in the sky will be immeasurably small. But for the ones at high latitude, motion out of the plane is largely along our line of sight and the measured radial velocities (up to 250 km s^{-1}) are frequently large enough to have carried the stars from plane to present position in the available time^{7,8,19,20}. The ejection mechanism is violent enough to disrupt wide binary systems, because visual binaries are common among OB cluster members, rare among field stars, and non-existent among runaways²¹.

Two candidate accelerators have been suggested — a supernova explosion of a close binary companion or close encounters in the cluster of formation. The former presents several difficulties. Owing to mass-transfer effects, a symmetric explosion leaves the secondary either with the neutron star still bound to it or

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with a velocity of at most 35–40 km s⁻¹ (ref. 22); and most OB runaways do not have neutron star companions²³. Cluster ejection, on the other hand, does seem capable of expelling both single stars and close pairs at the observed speeds⁹.

Finally, there are a few OB stars like PHL346 (refs 6, 23) that appear to be genuinely young and far from the galactic plane and yet to have velocities far too small or even in the wrong direction to get them there. What evidence do we have that they could or could not have formed where we see them? Gas clouds exist up to several kiloparsecs from the plane^{24,25} and collisions between them could plausibly

trigger star formation²⁶. The process must, however, be quite rare and localized, in the sense that the high-latitude clouds presently known to be forming B stars^{27,28} are nearly all within 200 parsecs of the plane. Admittedly the techniques used to find them might not pick out more distant examples. Thus we still cannot be quite certain whether stellar life and death above the galactic plane is preceded by birth there. □

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Genetic code

Modified bases and aminoacylation

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THE discovery of modified bases in the transfer RNAs of all organisms has stimulated much interest in their role¹⁻⁴. Until now, it has been thought that the main role of base modifications in tRNA is in modulation of translational efficiency and/or codon specificity⁵. Base modifications have not been thought to be involved in specificity of aminoacylation, that is, attachment of the correct amino acid to the correct RNA. Now Muramatsu and co-workers report on page 179 of this issue⁶ a striking result in which a particular base modification in an *Escherichia coli* isoleucine tRNA is important for reading the AUA isoleucine codon and for the specificity of its aminoacylation.

The dual effect of a single base modification in specificity of aminoacylation and in codon reading highlights a feature of tRNA research that has generated much recent interest. The ability to mutagenize tRNA genes and to study mutant tRNAs have led to significant advances in understanding the relationship between the structure and function of tRNAs^{6,7}, in particular, identification of sequence elements important for aminoacyl-tRNA synthetase recognition⁸⁻¹³. Such studies have reinforced and extended earlier work which suggested that simple changes in a tRNA can sometimes have striking effects on its properties. Some of these results have generated much excitement in the field and have been the subject of recent commentaries¹⁴⁻¹⁶.

It was already known that modified bases have both subtle and well-defined roles. *E. coli* mutants lacking ribothymidine can grow normally, for example, with only a slight reduction in growth rate of about 4 per cent³. But this deficiency in a tRNA facilitates initiation of protein synthesis without formylation of the initiator tRNA in *Streptococcus faecalis* and in some *E. coli* mutants^{17,18}. The role of modified

bases located in and around the anticodon sequence of tRNA is much clearer; base modifications here increase translational efficiency of the tRNA and fidelity of the translation process³. Mutations in genes encoding some tRNA base-modifying enzymes give rise to effects such as the derepression of amino-acid biosynthetic operons, many of which are regulated by transcriptional attenuation¹⁹.

E. coli contains two isoleucine tRNA species, a main species with GAU as its anticodon, which reads the AUU and AUC codons, and a minor species with LAU as its anticodon, which reads the remaining isoleucine codon AUA. Lysidine (L), a modified base derived from cytosine in which the 2-keto group is replaced by the amino acid lysine, is thought to pair only with A, allowing the tRNA with LAU in the anticodon to read the AUA codon for isoleucine.

Muramatsu *et al.* in their new work⁶ used RNA excision and ligation techniques to replace the anticodon LAU with CAU. They show that the mutant tRNA, with the single change of L to C, is a much poorer substrate for *E. coli* isoleucyl-tRNA synthetase (IleRS). Interestingly, it is now a very good substrate for *E. coli* methionyl-tRNA synthetase (MetRS). These results establish a clear role for a post-transcriptional modification of tRNA in determining aminoacylation specificity and demonstrate the critical role of the anticodon sequence in discrimination between tRNAs by IleRS and by MetRS.

This result supports the earlier conclusion that the most critical requirement for MetRS recognition of a tRNA is the anticodon sequence CAU. Switching of UAC in the anticodon of valine tRNA to CAU has now been shown⁷ to lead to loss of valine acceptance, and to gain of methionine acceptance. Conversely, switching

of the methionine tRNA anticodon from CAU to a valine anticodon, UAC, abolishes methionine acceptance. However, the mutant tRNA is now aminoacylated with valine by ValRS. Taken together^{8,14,16,20}, these results suggest that for MetRS, ValRS, IleRS and some others, the anticodon sequences in the cognate tRNAs constitute the main specificity-determining contacts. The lack of aminoacylation of isoleucine tRNA by MetRS probably results from the base modification L in the anticodon of isoleucine tRNA preventing MetRS from making effective contact with this base, which is critical for recognition.

Replacement of L 34 by C 34 in isoleucine tRNA leads to a substantial reduction in the rate of aminoacylation with isoleucine. This implies that L provides an important contact site for IleRS. Because the main isoleucine tRNA of *E. coli* has a guanosine (G) at this position, IleRS could contact functional group(s) common to both G and L. An alternative possibility, favoured by Muramatsu *et al.*, is that C 34 constitutes a "negative determinant" for IleRS, that is, presence of C 34 somehow interferes with IleRS recognition of this tRNA. These suggestions could be tested by studying the effect of replacing L by U or A on IleRS recognition.

The finding that the presence or absence of a single base modification can have such dramatic effects on properties of a given tRNA does not mean that other base modifications have a similar effect on other tRNAs. Several tRNAs lacking all base modifications have now been prepared using T7 RNA polymerase^{21,22}, and show only small differences in aminoacylation kinetics compared with tRNAs carrying the full complement of base modifications.

Change of L to C affects the coding specificity from AUA (isoleucine) to AUG (methionine) and aminoacylation specificity also, from isoleucine to methionine. (The possibility that the mutant

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