



PERSPECTIVES: ASTRONOMY

Infant Globular Clusters

Kelsey Johnson

The Milky Way is host to remarkable fossils from the early universe. In the halo of our galaxy there are about 150 globular clusters that are nearly as old as the universe itself. And our galaxy is far from unique; globular clusters are ubiquitous around all massive galaxies in the local universe. The clusters are so massive and dense that astronomers have struggled to understand the physical conditions that created them. Observations are now beginning to shed light on the early stages of cluster formation.

According to early theories of globular cluster formation, the clusters collapsed directly out of primordial material in the universe (1). But images obtained with the Hub-

must draw upon our knowledge of the individual massive stars in the clusters.

If the early evolution of globular clusters parallels that of individual massive stars (see the figure on the right), then we expect the youngest globular clusters to be embedded in extremely dense regions of ionized gas. These ionized regions should be surrounded by warm dust cocoons.

To investigate the birth of globular clusters, we therefore need to use long wavelengths that can penetrate the natal cocoons. Powerful radio telescopes, such as the Very Large Array (VLA), are ideal for probing the birth cocoons of globular clusters. The current strategy for finding these ultrayoung clusters is to search for extremely dense regions of ionized gas being powered by very hot young stars. Such regions can be identified by comparing radio observations at different frequencies.

With this method, several ultrayoung clusters have been identified in a handful of galaxies, including Henize 2-10 (see the figure below) and NGC 5253 (3, 4). On the basis of their radio luminosities, these embedded clusters have all the properties that are expected for protoglobular clusters, including the expected masses, radii, and densities.

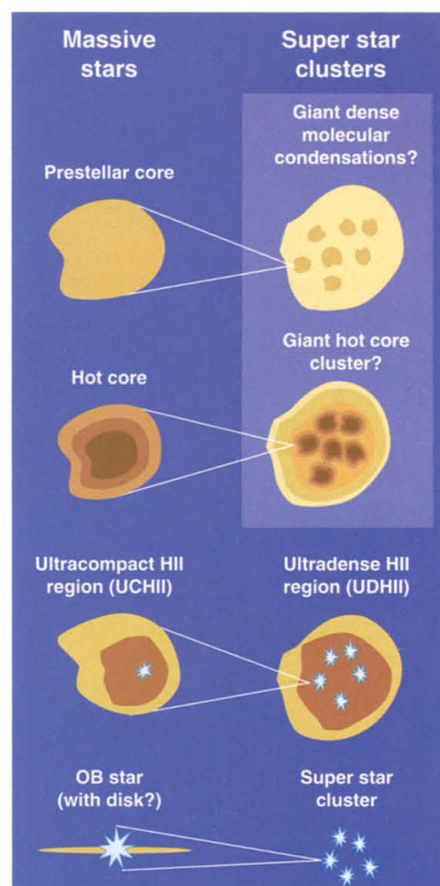
Age estimates of the clusters have relied on "back-of-the-envelope" calculations based on pressure arguments and statistics. These age estimates might be crude, but they all suggest that the embedded clusters are younger than about 1 million years (3, 5).

Observations in the mid-infrared with the Gemini and Keck telescopes confirm that the infant clusters are surrounded by warm dust cocoons. These cocoons are so luminous that they can dominate the infrared emission of the host galaxies (6, 7).

ble Space Telescope showed that this scenario may require drastic revision. High-spatial resolution images of galaxies undergoing tremendous bursts of star formation (so-called starburst galaxies) revealed large numbers of extremely bright, compact, young massive star clusters or "super star clusters" (see the first figure) (2). Could they be adolescent globular clusters? Data assembled over the past decade suggest that the answer is yes.

On a globular cluster time scale, super star clusters are extremely young. However, from a star formation perspective, everything interesting has already happened when these clusters emerge from their birth material to become visible to the Hubble Space Telescope. To gain insights into earlier stages of cluster formation, we

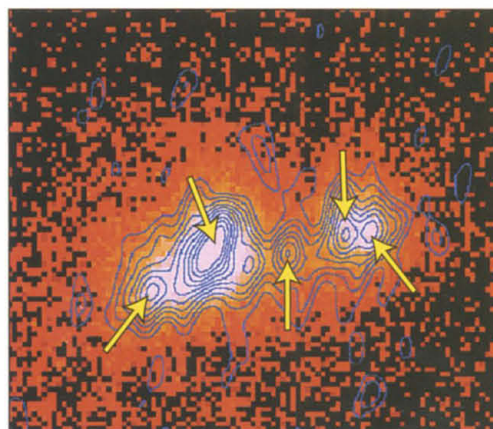
The author is in the Department of Astronomy, University of Wisconsin, Madison, WI 53706, USA and the National Radio Astronomy Observatory, Socorro, NM 87801, USA. E-mail: kjohnson@astro.wisc.edu



Model for the parallel evolution of globular clusters and individual massive stars. The light blue box indicates the stages of extragalactic star cluster evolution that have not yet been identified in observations. [Adapted from (17)]

The clusters appear to have formed with extremely high efficiency, leaving relatively little gas and dust after star formation. Such high star-forming efficiency is critical to a cluster's survival. The violently disruptive effects of massive stars will expel leftover material from the cluster. If a large enough fraction of a cluster's initial mass is in the form of gaseous material, the cluster will become unbound when this material is expelled. If a cluster has any hope of attaining the ripe old age of a globular cluster, it must form with very high efficiency.

Perhaps not surprisingly, the most massive infant clusters were the first to be discovered. However, unless there is a preferred mass for cluster formation,



Clusters in their youth. Mid-infrared image of the inner region of Henize 2-10 (from Gemini) overlaid with 2-cm radio contours (from the VLA) (3, 7). The sources that are luminous in both the radio and mid-infrared regimes but invisible in optical light (arrows) are believed to be the youngest stages of globular cluster evolution observed to date. [Adapted from (7)]

CREDIT: (FIRST FIGURE) FROM (10)

there ought to be a continuum of infant clusters, from individual stars to massive protoglobular clusters. This appears to be the case. A continuum of infant clusters has begun to emerge, and the maximum mass of these clusters appears to correlate with the overall star formation rate of the host galaxies.

This correlation could be statistical (the more clusters are formed, the more likely it is that some of them will be massive), or it could be physical (the most massive clusters form in regions with the highest pressure, and high pressures also result in star formation). Theory might cause us to lean toward the latter; extremely high pressures appear to be required to form massive globular clusters (8, 9).

We can now begin to understand where and how globular clusters formed by examining the formation of star clusters in the local universe. Important insights will come from investigating how the physical environment and properties of star formation scale between individual stars and extremely massive clusters. With the Expanded Very Large Array (EVLA) and Atacama Large Millimeter Array (ALMA) on the horizon, the next decade promises to address these questions with unprecedented sensitivity and resolution.

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PERSPECTIVES: CIRCADIAN RHYTHMS

A White Collar Protein Senses Blue Light

Hartmut Linden

The ability to perceive light is crucial for the survival of most organisms, enabling them to adapt to changing environmental conditions. Consequently, the capacity to sense and respond to light is widespread among bacteria, fungi, plants, and animals. In fungi, light regulates many developmental and

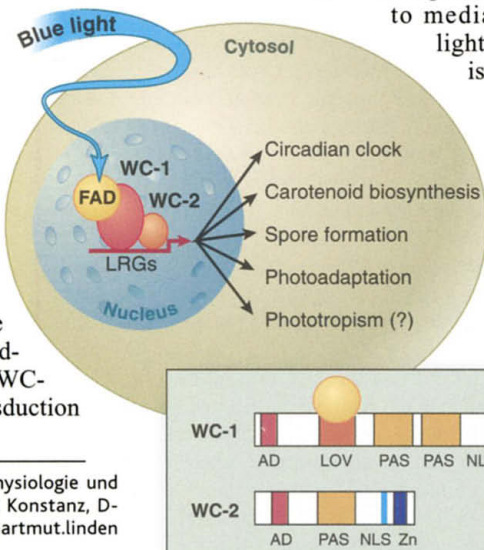
physiological processes. For example, in the fungus *Neurospora crassa* blue light triggers the synthesis of photo-protective pigments (the carotenoids), spore formation, entrainment of the circadian clock, and growth toward a light source (phototropism) (1). *Neurospora* only perceives blue light, and seems to be “blind” to yellow, green, and red light. Exhaustive screening for light-insensitive *Neurospora* mutants only yielded two such mutants. These mutants are unable to synthesize carotenoids in response to light, and so have pigmented spores and white mycelia resulting in the moniker “white collar (*wc*).” Twenty years ago, it was proposed that the two *Neurospora* proteins encoded by the *wc* gene, WC-1 and WC-2, are involved in signal transduction

in response to blue light and that one or both of these proteins might be the long-sought fungal blue-light photoreceptor (2). New studies reported by He *et al.* (3) and Froehlich *et al.* (4) on pages 840 and 815 of this issue, respectively, present convincing evidence that the WC-1 protein of *Neurospora* is indeed the blue-light photoreceptor of fungi.

The WC-1 and WC-2 proteins of *Neurospora* have features characteristic of transcription factors (see the figure) (5, 6). They are found in the nucleus and bind to the promoters of light-regulated genes. The two proteins form heterodimers with each other, and dimerization is independent of the light conditions (7). The WC-1/WC-2 complex, in addition to mediating blue light signaling, is an impor-

tant component of *Neurospora*'s circadian clock (8). Together with the circadian clock protein FREQUENCY (FRQ), the WC-1/WC-2 complex forms an autoregulatory feedback loop that is crucial for operation of the circadian oscillator, the molecular pacemaker that generates physiological rhythms (see the figure).

The WC-1 protein contains a chromophore-binding motif—similar to those identified in the blue-light photoreceptors of ferns and higher plants—called the light, oxygen, and voltage (LOV) domain (9). In their experiments, He *et al.* (3) removed the LOV domain from WC-1 and then expressed this protein in a WC-1-deficient strain of *Neurospora*. They found that light induction of the circadian clock gene *frq* and of another light-regulated gene was abolished in this mutant, suggesting that the LOV domain of WC-1 is important for light entrainment of the fungal circadian clock. Despite this defect in light regulation, the circadian clock could still be entrained according to temperature. He *et al.* also identified a flavin chromophore, flavin adenine dinucleotide (FAD), associated with the purified WC-1/WC-2 complex. The authors concluded that FAD is bound



To see the light, all you need is LOV. Light perception by the transcription factor WC-1 in the fungus *Neurospora*. The light-responsive proteins WC-1 and WC-2 form a heterodimeric complex that is localized to the nucleus of *Neurospora*. Blue light is perceived by a flavin chromophore (FAD) that is bound to the LOV domain of WC-1. Light perception may lead to a conformational change in the WC-1/WC-2 complex resulting in transcriptional activation of light-regulated genes (LRGs). These genes regulate physiological responses to light such as carotenoid biosynthesis, spore formation, and phototropism. The WC proteins have a dimerization (PAS) domain, a putative transcriptional activation (AD) domain, a zinc-finger DNA binding domain (Zn), and a nuclear localization signal (NLS). Only WC-1 contains the LOV domain.