formed with LCs that are remarkably sensitive to the presence of specific biological adsorbates (*9*) and can serve as templates for the synthesis of spherical and nonspherical particles with chemical patches (*10*). These advances are leading to LC-based colloidal systems with functional properties and potential technological impact that go well beyond traditional applications of LCs in displays.

The LCs used in the study by Turiv *et al*. are low–molecular weight organic molecules that can be viewed as structured oils. The long-range orientational ordering of molecules in LCs, which gives rise to anisotropic viscosities and mechanical properties not found in simple isotropic solvents (*11*), is dynamic and patchy; local domains form, consisting of molecules with similar alignment. The alignment can be described theoretically with a director, a vector that represents the local average of the molecular orientations. In the late 1990s, it was shown that colloidal species dispersed in nematic LCs (the simplest type of LC that has no additional positional ordering) could locally strain the director of LCs, as well as introduce so-called topological defects. These defects are nanoscopic regions in which the LC orientational order differs substantially from the bulk (*7*).

The presence of these strains and defects, in combination with the anisotropic viscosities of LCs, were shown to give rise to anisotropic diffusion of colloidal particles in LCs (*12*, *13*). However, in these earlier studies the MSDs followed the classical linear time dependence, and the measurements could be explained by construing the strain in the LC around the colloids as being static. Turiv *et al*. now demonstrate that fluctuations in the orientation of the LC director can influence the transfer of momentum from the LC to a colloid, such that the diffusion of the colloid departs from that predicted using the "static view" of the director (see the figure).

By focusing on a class of LCs with sufficiently slow fluctuations of the director, Turiv *et al*. imaged the displacements of colloids on time scales that lead to diffusive behaviors of the colloids that are faster or slower than classical Brownian motion. The measurements are striking examples of anomalous diffusion arising from purely orientational fluctuations in a solvent, and they define new questions and directions of inquiry. For example, whereas the measurements of anomalous diffusion reported by Turiv *et al*. occur on time scales consistent with the orientational fluctuations of the director in the LC, a detailed description of the dynamic coupling between the colloids and the LC is yet be elucidated. Furthermore, the role of surface chemistry (and, for example, colloid shape) in regulating near-particle fluctuations of the director is yet to be fully understood.

What is clear, however, is that the observations and ideas presented by Turiv *et al*. hint at new principles for manipulating colloidal transport processes. For example, one can envisage the application of time-dependent external fields (electrical, magnetic, or optical) to drive fluctuations in the director on relevant time scales and thus influence the exchange of momentum between colloids and LCs that gives rise to the anomalous diffusion. Alternatively, internally generated fields, such as those that are being explored in the context of designs of active matter (*14*, *15*), might plausibly be harnessed to drive orientational fluctuations in LCs and thus regulate the transport of colloids.

References and Notes

1. A. Ott, J. P. Bouchaud, D. Langevin, W. Urbach, *Phys. Rev. Lett.* **65**, 2201 (1990).
2. D. S. Banks, C. Fradin, *Biophys. J.* **89**, 2960 (2005).
3. F. Höfling, T. Franosch, *Rep. Prog. Phys.* **76**, 046602 (2013).
4. T. Turiv *et al*., *Science* **342**, 1351 (2013).
5. J. Planer, *Ann. Chem. Pharm.* **118**, 25 (1861).
6. M. von Smoluchowski, *Ann. Phys.* **21**, 756 (1906).
7. P. Poulin, H. Stark, T. C. Lubensky, D. A. Weitz, *Science* **275**, 1770 (1997).
8. I. Musevic, M. Skarabot, U. Tkalec, M. Ravnik, S. Zumer, *Science* **313**, 954 (2006).
9. I. H. Lin *et al*., *Science* **332**, 1297 (2011).
10. F. Mondiot, X. Wang, J. J. de Pablo, N. L. Abbott, *J. Am. Chem. Soc.* **135**, 9972 (2013).
11. P. G. de Gennes, J. Prost, *The Physics of Liquid Crystals* (Clarendon, Oxford, ed. 2, 1993).
12. H. Stark, D. Ventzki, *Phys. Rev. E* **64**, 031711 (2001).
13. J. C. Loudet, P. Hanusse, P. Poulin, *Science* **306**, 1525 (2004).
14. T. Sanchez, D. T. N. Chen, S. J. DeCamp, M. Heymann, Z. Dogic, *Nature* **491**, 431 (2012).
15. W. F. Paxton, S. Sundararajan, T. E. Mallouk, A. Sen, *Angew. Chem. Int. Ed.* **45**, 5420 (2006).

Acknowledgments: I thank X. Wang and D. Miller for preparing the figure. Supported by NSF grant DMR-1121288, Army Research Office grant W911NF-10-1-0181, and U.S. Department of Energy grant DE-SC0004025.

10.1126/science.1244987

GENETICS

My Oldest Sister Is a Sea Walnut?

Antonis Rokas

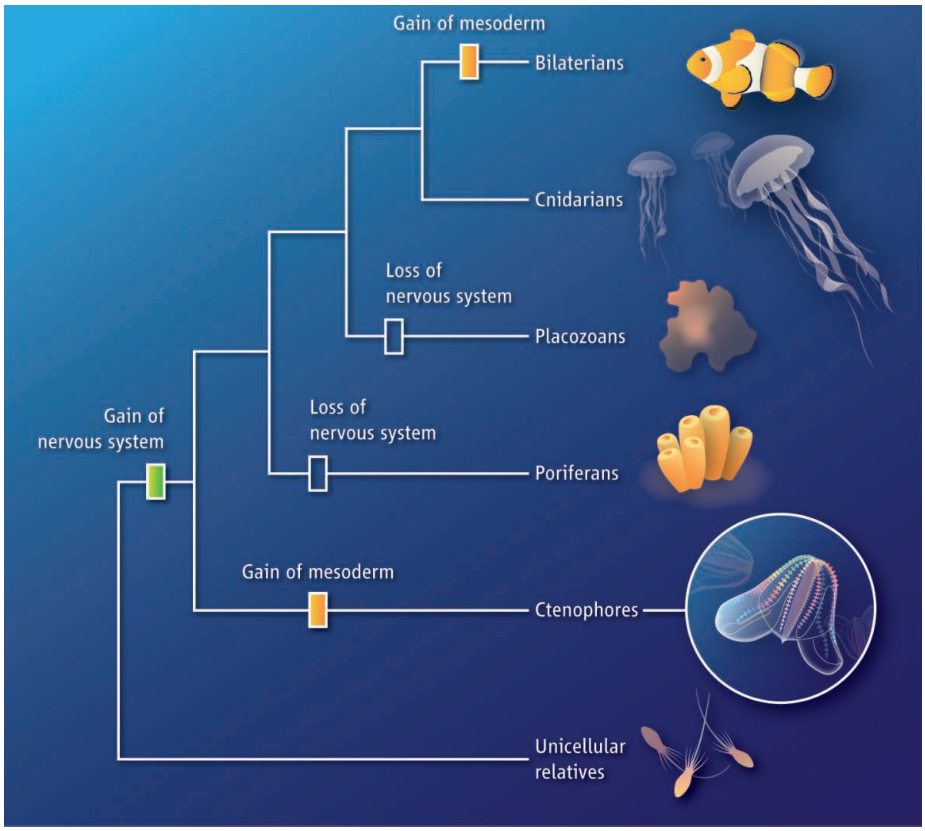
Decoding of the ctenophore genome prompts reevaluation of the complexity of the metazoan ancestor.

With common names such as "sea walnut," "sea gooseberry," and "Venus' girdle" that reflect their morphological diversity, the jelly-like creatures belonging to the phylum Ctenophora that bear distinctive "combs" of cilia are not only breathtakingly beautiful (*1*) but are also key to understanding early animal evolution. On page 1336 of this issue, Ryan *et al*. (*2*) decode the genome of the sea walnut *Mnemiopsis leidyi*, the first member of this phylum to be sequenced, and propose that ctenophores might be the earliest branch of the animal tree and the sister lineage to that of all other animals. This paints a picture of early animal evolution full of cell type complexity, as well as its loss.

The ~200 ctenophore species discovered so far live in a wide variety of marine environments and at all latitudes (*3*). They get their name from the eight rows of linked tiny hairs known as "ctenes" (Greek for combs) that run alongside their body and propel the animals through water. Although superficially similar to jellyfish (cnidarians), ctenophore morphology is quite distinct from that of the other three early-branching animal phyla, the poriferans (sponges), the largely enigmatic placozoans (known solely from organisms belonging to the phylum's single genus, *Trichoplax*), and the cnidarians (jellyfish, sea anemones, and their kin). Unlike the radially symmetrical jellyfish, ctenophores are biradially symmetrical—their main body axis is defined by a mouth at one end and a gravity-sensing apical organ at the other end. Unlike sponges and placozoans, but like jellyfish, ctenophores contain both muscle and nerve cells. The latter are organized as a diffuse net that appears to be centralized at the apical organ (*4*).

With the exception of poriferans, whose bodies lack tissue organization, the tissues of the other three early-branching animal phyla are thought to develop from two distinct embryonic germ layers—the ectoderm (from which the nervous system develops) and the endoderm (the layer that gives rise to the gut). By contrast, the tissues of all bilaterians—

Department of Biological Sciences, Vanderbilt University, Nashville, TN 37235, USA. E-mail: antonis.rokas@vanderbilt.edu



Early branches in the animal tree. Major events of loss and gain in the evolution of early animal tissue complexity are suggested by the analysis of the first representative genome from the ctenophore phylum.

animals such as fruit flies, fish, and humans that have bilateral symmetry—can also be derived from a third germ layer called the mesoderm (the origin of muscle). Although ctenophore bodies are composed of an outer ectodermal layer of skin and nerve cells and an inner endodermal layer of gut cells, the presence of muscle cells and migratory cells in between these two cell layers, both of which originate from mesoderm, has raised the question of whether they share a three-cell-layer architecture with bilaterians (*4*).

The decoding of the ctenophore genome means that at least one genome sequence is now available from each member of the quartet of early-branching metazoan phyla, opening new vistas in both reconstructing early animal evolution and interpreting the somewhat disparate body plans and cell type diversity of ctenophores, cnidarians, poriferans, and placozoans in the context of their phylogeny. Although early embryologists thought ctenophores shared a close affinity with jellyfish, Ryan *et al.*'s phylogenetic analysis of an impressive amount of linear sequence data and gene content from diverse animal proteomes rejects that notion (see the figure). Intriguingly, the analysis also recovers strong support for the placement of ctenophores as the sister group to all other animals (*5*).

Sea walnut (*Mnemiopsis leidyi*) at the New England Aquarium, Boston, MA.

Other recent studies have reached opposite conclusions, most notably grouping ctenophores and jellyfish together and placing poriferans as the earliest-branching lineage, which would mean that the oldest relative to the rest of animals is a sponge, not a sea walnut (*6*). However, this lack of consensus on the relative placement of early-branching phyla (*7*) is hardly surprising. The radiation that eventually gave rise to the body plans of the four early-branching phyla took place in a very narrow window of time more than 550 million years ago (*8*). Because the phylogenetic trees of such radiations have very short internal branches at their base, the historical signal present in gene sequences is often very weak to resolve such short branches and is frequently thwarted by various biases in the ways that genes evolve, muddling efforts to retrace ancient divergences (*9*). Following the lead of Ryan *et al.*, sequencing additional genomes from early-branching animals will be critical for better understanding not only the precise arrangement of the precise sequence of branchings at the base of the animal tree but also the variation in the rate of evolution between lineages over time and the underlying mechanisms that drove these varying rates—the "tempo and mode" of early animal life.

The lack of consensus on the exact branching pattern of the early offshoots of the animal phylogeny notwithstanding, comparison of the ~16,500 genes of the ctenophore genome to those of other early-branching animals, bilaterians, and to animals' closest unicellular relatives, the unicellular and colonial protists known as choanoflagellates (*10*), reveals two remarkable findings that challenge the standard view of early animal evolution. The first surprise is that patterns of coinheritance—the shared presence or shared absence of genes in two or more lineages—of transcription factors, axon guidance genes, and genes thought to be key for nervous system development and function, appear similar in the ctenophore and sponge genomes, even though sponges lack a nervous system. This coinheritance suggests that the genetic machinery required for nervous system development might have been present in the pan-animal ancestor and, more controversially, that this ancestor might have had a not-so-simple nervous system. By contrast, genes involved in mesoderm develop-

CREDITS (TOP TO BOTTOM): H. MCDONALD/*SCIENCE*; S. JOHNSON/WIKIMEDIA

ment in bilaterians lack homologous counterparts in the ctenophore genome (the second surprise), suggesting that the genetic machinery required for ctenophore mesoderm development may have originated independently from that found in bilaterians.

With the findings of Ryan *et al*., we can finally dispense with the teleology-imbued notion that early animal evolution resembled a linear march of evolutionary forms from the "simple" to the "complex." The advent of the ctenophore genome suggests that simplification and loss of genes, pathways, and even cell types, and perhaps also their independent evolution, are an integral part of the fabric of animal origins.

References

1. R. Dawkins, *The Ancestor's Tale: A Pilgrimage to the Dawn of Evolution*. (Houghton Mifflin, Boston, 2004).
2. J. F. Ryan *et al*., *Science* **342**, 1242592 (2013).
3. K. Pang, M. Q. Martindale, *CSH Protocols* **2008**, pdb emo106 (2008); 10.1101/pdb.emo106.
4. M. Q. Martindale, *Nat. Rev. Genet.* **6**, 917 (2005).
5. C. W. Dunn *et al*., *Nature* **452**, 745 (2008).
6. H. Philippe *et al*., *Curr. Biol.* **19**, 706 (2009).
7. M. Dohrmann, G. Wörheide, *Integr. Comp. Biol.* **53**, 503 (2013).
8. A. Rokas, D. Krüger, S. B. Carroll, *Science* **310**, 1933 (2005).
9. L. Salichos, A. Rokas, *Nature* **497**, 327 (2013).
10. N. King *et al*., *Nature* **451**, 783 (2008).

10.1126/science.1248424

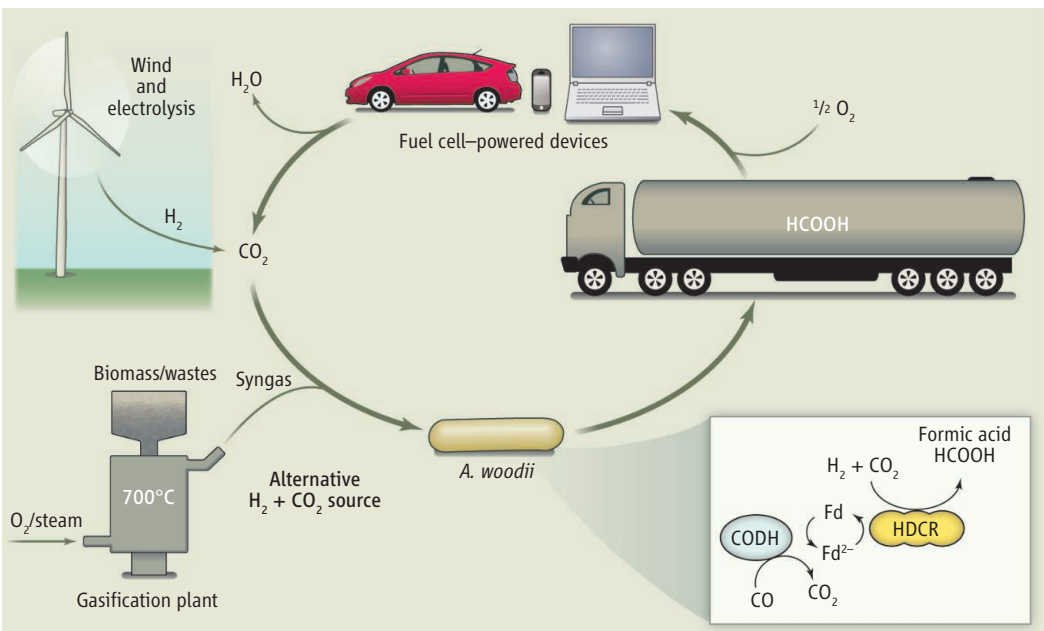
MICROBIOLOGY

An Enzymatic Route to H_2 Storage

An enzyme efficiently hydrogenates carbon dioxide to produce formate, a liquid that has a high energy density and can be safely transported.

Inês A. C. Pereira

Electricity is increasingly produced from renewable sources, but it remains difficult to store electric power at a large scale. Hydrogen is a strong candidate for energy storage, but there is still no safe, economically viable, and reasonably sized solution to store and transport it. The use of a liquid chemical hydrogen carrier with a high H_2 content per unit of mass and a good safety profile may solve this problem (*1*). For example, hydrogen may be safely stored by reducing carbon dioxide (CO_2) to formic acid (*2*), a liquid with a much higher energy density than H_2. Biological systems also use formate as a chemical equivalent of H_2 (*3*, *4*). On page 1382 of this issue, Schuchmann and Müller (*5*) report a single-enzyme system that efficiently hydrogenates CO_2 without the need of cofactors.



Storing hydrogen with enzymes. Schuchmann and Müller show that whole-cell biocatalysis of CO_2 hydrogenation by *A. woodii,* using HDCR, produces formic acid, a storage fuel that is a chemical equivalent of H_2 and can be used directly in fuel cells. Fd, ferredoxin.

Chemical catalysts for the interconversion of CO_2 and formic acid require noble metals and/or extreme conditions that are not economically viable (*2*, *6*, *7*). In biological systems, CO_2 is reversibly reduced to formate by formate dehydrogenases (*4*). These enzymes are abundant in anaerobic microbes that grow by reduction of CO_2 with H_2—acetogens (which produce acetate) and methanogens (which produce methane). Both groups are thought to descend from some of the earliest life forms on Earth (*8*). In acetogens, the first step of energy metabolism is the conversion of CO_2 to formate with H_2 as the physiological reductant. The best known formate dehydrogenases from acetogens are NADPH (reduced nicotinamide adenine dinucleotide phosphate)–dependent enzymes, which require the presence of additional proteins to produce this reduced cofactor.

The enzyme described by Schuchmann and Müller, a hydrogen-dependent carbon dioxide reductase (HDCR), was isolated from the model acetogen *Acetobacterium woodii* and is strikingly simple. It contains only two catalytic subunits—a hydrogenase and a formate dehydrogenase—and two electron transfer subunits. It directly reduces CO_2 with H_2 to produce formate, without the need for NADPH or additional proteins, making it a very attractive target for practical applications. The activity is fully reversible and is controlled only by the substrate concentrations. Most important, its independence of other proteins or cofactors means that it can be decoupled from bacterial growth.

Schuchmann and Müller elegantly exploit the latter property to turn *A. woodii* into a whole-cell catalyst for CO_2 hydrogenation by inhibiting CO_2 consumption for energy metabolism either through the use of ionophores or by omitting Na^+ ions. This is an ingenious way to redirect the metabolic

Bacterial Energy Metabolism Laboratory, ITQB António Xavier, Universidade Nova de Lisboa, Av. da Republica, 2780-157 Oeiras, Portugal. E-mail: ipereira@itqb.unl.pt