

association. Although symbiosis is a fundamental biological relationship, it was a disputed concept until the late 1800s, and the term was only first used in 1878. Its role in ecology and evolutionary theory is still developing.

Biologists recognize several variations of symbiotic association. *Obligate symbiosis*, such as the tropical reef relationship between Zooxanthellae algae and the coral they inhabit, is necessary for the survival of one or more partners. *Facultative symbionts* are optional; in tidepools, some sea anemones have green flecks of algae growing inside them, while neighboring anemones do not. *Endosymbiosis* occurs when one species lives inside another, as cellulose-digesting bacteria inhabit the gut of herbivores. *Ectosymbiosis*, which does not involve internalization, occurs when, for example, birds or fish clean larger species. Finally, there is a range of interactive impacts. In *mutualism*, both species benefit; all the above and what is perhaps the first-described case, the algae-fungus association that forms lichens, are examples of mutualism. *Commensalism* involves advantage to one species and neutral impact on another. *Parasitic symbiosis* benefits one species at a cost to another. Some biologists use the term symbiosis only for mutualistic associations, although scholarly literature and popular textbooks are ambiguous on this point.

Symbiosis was catapulted to prominence in evolutionary theory by the notion that mitochondria and chloroplasts (internal organelles within cells) originated through the endosymbiotic internalization of simpler prokaryotic cells. This theory has been championed by Lynn Margulis, who developed the *serial endosymbiosis theory*, which attempts to account for the successive development of all eukaryotic cells (cells with nuclei), through a sequence of unions between various prokaryotic bacteria (non-nucleated cells). While some details of serial endosymbiosis theory are still debated, the endosymbiotic origin of eukaryotes is found in virtually all textbooks.

Symbiosis theory has been extended in several profound but controversial ways. The notion of *symbiogenesis* suggests that symbiosis contributes significantly to the origin of novel traits and new species. Traditional Darwinian theory argues that speciation occurs by natural selection operating on random genetic mutations. Symbiogenesis posits that the symbiotic union of diverse genetic

information is a source of creative novelty on which selection acts. Some symbioses, such as lichens, result in an altogether different kind of organism. Moreover, instead of the win-lose scenarios of competitive individual selection, symbiogenesis may more readily create win-win cooperative scenarios that entail new capabilities and resources. Symbiosis as a major evolutionary mechanism has significant though still debated implications, especially for notions of cooperation and complexity in evolutionary history.

Another provocative extension of symbiosis theory entails the scale at which symbiotic associations are conceived to exist. Traditional examples of symbiosis involve individual organisms in physical association with other individuals: for example, a plant and the nitrogen-fixing fungi in its roots. However, one could think of symbioses as involving groups of organisms, such as oxygen-breathing animals and oxygen-generating plants in a pond community. In principle, this could be extended to communities interacting in an ecosystem, or global ecosystems interacting with each other on a planetary scale. James Lovelock's notion of Gaia holds that the entire living world, or biosphere, interacts to regulate water, atmospheric gasses, pH, and temperature. Margulis and others suggest that this reflects the symbiotic integration of life into a global superorganism.

See also COMPETITION; EVOLUTION, BIOLOGICAL

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## SYMMETRY

In the most general sense, *symmetry* can be defined as a property that an entity has whereby it preserves some of its aspects under certain actual

or possible transformations. A sphere is symmetrical because a rotation about its axis preserves its shape. A crystal structure is symmetrical with respect to certain translations in space. The existence of symmetries in natural phenomena and in human artifacts is pervasive. However, nature also displays important violations of symmetry: Some organic molecules come only or predominantly in left-handed varieties; the bilateral symmetry of most organisms is at best only approximate.

The general concept of symmetry applies not only to objects and their collections, but also to properties of objects, to processes they may undergo, as well as to more abstract entities such as mathematical structures, scientific laws, and symbolic and conceptual systems, including mythology and religion. Symmetry symbols pervade ancient cosmologies. Thus the concept of *axis mundi* (the world axis) is a famous mytho-poetic archetype expressing the idea of centrality in the arrangement of the Cosmos. Whether *axis mundi* is represented as a sacred mountain, tree, or ladder, it invariably signifies a possibility for humans to connect with heaven. The central image of Christianity, the cross, belongs in the same broad category, as far as its symbolic connotations are concerned. The concept of *triadicity* so essential to many religions is closely linked to symmetry considerations.

The abstract notion of symmetry also lies at the very foundation of natural science. The fundamental significance of symmetries for physics came to the fore early in the twentieth century. Prior developments in mathematics contributed to this. Thus, in his Erlangen Program (1872), the German mathematician Felix Klein (1849–1925) proposed interpreting geometry as the study of spatial properties that are invariant under certain groups of transformations (translations, rigid rotations, reflections, scaling, etc.). Emmy Noether (1882–1935) applied Klein's approach to theoretical physics to establish in 1915 a famous theorem relating physical conservation laws (of energy, momentum, and angular momentum) to symmetries of space and time (homogeneity and isotropy). By that time, Albert Einstein's (1879–1955) Theory of Relativity had engendered the notion of *relativistic invariance*, the kind of symmetry all genuine physical laws were expected to possess with respect to a group of coordinate transformations known as the *Lorentz-Poincaré group*. With this came the realization that symmetry (invariance) is a clue to reality: Only

those physical properties that "survive" unchanged under appropriate transformations are real; those that do not are merely *perspectival* manifestations of the underlying reality.

With the development of particle physics the concept of symmetry was extended to internal degrees of freedom (quantum numbers), such as *C* (charge conjugation, the replacement of a particle by its antiparticle) and isospin (initially the quantum number distinguishing the proton from the neutron). Along with *P* (parity, roughly a mirror reflection of particle processes) and *T* (time-reversal operation), these were long believed to be exact symmetries, until the discovery in 1956 of *C*- and *P*-symmetry violations in certain weak interactions, and the discovery in 1964 of the violation of the combined *CP*-symmetry. However, theoretical considerations preclude violation of the more complex *CPT*-symmetry.

The emergence of quantum electrodynamics (QED), the first successful quantum relativistic theory describing the interaction of electrically charged spin-1/2 particles with the electromagnetic field, made the notion of gauge symmetry central to particle physics. The exact form of interaction turns out to be a consequence of imposing a local gauge invariance on a free-particle Lagrangian with respect to a particular group (U(1) in the case of QED) of transformations of its quantum state. Extending this principle to other interactions led to the unification of electromagnetic and weak forces in the Weinberg-Salam-Glashow theory on the basis of the symmetry group  $SU(2) \times U(1)$  and to quantum chromodynamics (a theory of strong quark interactions based on the group  $SU(3)$ ), and eventually paved the way for the ongoing search for a theory unifying all physical forces.

See also LAWS OF NATURE

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