VESTIGIAL ORGANS AND STRUCTURES

Vestigial organs and structures (also called vestigia, rudiments, or remnants) are reduced body parts or organs, often without visible function in the derived bearers, that were fully developed and functioning in earlier members of that phylogenetic lineage. These structures, sometimes described as atrophied or degenerate, are usually small in comparison with their relative size in ancestral generations or in closely related species. Vestigia, etymologically derived from Latin vestigium ("footprint, trace, mark"), played an important role in the founding of evolutionary theory because they represented tangible traces of past generations in recent organisms. Today, anatomical vestigia do not represent a major topic in evolutionary research; their presence in all species is taken as given, although the causal mechanisms responsible for both their reduction and their retention are not fully understood.

Vestigial structures are identified by the comparative method. This means that homology (sameness, identity) of the reduced character with a more fully developed, ancestral counterpart must be established not only on the basis of structural and positional criteria but also with regard to the continuous presence of the structure in the lineage leading from the ancestral to the derived form. The latter criterion represents a critical distinction from features called atavisms, which occur after prolonged periods of complete absence of a character. Whereas atavisms appear only in exceptional cases and in single individuals, a vestigial structure is present in all representatives of a species. Another distinction should be made with regard to the term rudiment. Although often used synonymously with vestigium, a rudiment is properly a developmental primordium or anlage, and it coincides with a vestigium only when a primordium is retained in the adult.

Vestigialization affects structures and organs that have reduced or lost their function as the result of an evolutionary change in lifestyle of the derived forms. Classical examples are eye and limb reductions in cave-dwelling or burying organisms, wing reductions associated with ground dwelling, or dental and intestinal reductions attributable to changes of diet. The affected organs can show different stages of reduction in different members of a clade. Thus, we see different degrees of limb reduction in skinks, pelvic bones of different sizes in certain whales and snakes, and various stages of eye regression
in vertebrate and nonvertebrate cave organisms, or of wing rudiments in flightless birds and insects. In many cases, the vestigia are present only in fossil forms and are completely lost in extant representatives of a lineage. In other cases, the rudiments are present only in the embryo or juvenile and are completely lost in the adult, such as teeth in the embryos of baleen whales. Extensive collections of vestigial structures from many organisms and from a wide range of organ systems can be found in classical treatises of comparative morphology. Wedensheim (1883), for example, provides long lists of cases in human anatomy, including the often cited vermiform appendix, the pineal gland, the vomeronasal organ, the coccygeal bone, muscles of the ear, the third molar teeth, remnants of nephric and genital ducts, and many more. The degree to which vestigial organs are developed in the adult can vary extensively both within and among species. Often the structures are relatively more developed in the embryo than in the adult. When their presence is confined to the embryo, the idea of recapitulation is evoked.

The evolutionary mechanisms of vestigialization are thought to be well understood. It is argued that initial behavioral or environmental changes lead to a partial or complete loss of function of an organ, with consequent selection against that structure, which would have become a burden or hindrance for further evolution. Yet the extent to which vestigialization can be explained in terms of adaptation is debated. Direct selection for vestigialization seems to be rare. Rather, organs often undergo reduction as a byproduct of other adaptive changes, such as limb reduction in association with body elongation or miniaturization. Other explanations invoke indirect selection through energy trade-offs or antagonistic pleiotropy. But nonadaptive scenarios prevail; structures may most often degenerate because of a relaxation of stabilizing selection and the accumulation of selectively neutral mutations.

The specific, developmental realization of vestigialization can be effected by various processes. Mutational changes can affect developmental control, disturb cell division and histological differentiation, or interrupt inductive interactions. Several general modes can be distinguished. Either the entire progression of an embryonic primordium is slowed down or halted, leading to the preservation of a rudiment in the adult; or development of an organ proceeds rather normally up to a certain point at which it is actively destroyed—for example, by hormonal activity, apoptosis, or phagocytosis, as in the tail of anuran tadpoles. A third possibility is that general, heterochronic shifts in larval or embryonic development simply prevent adult structures from forming fully. As a rule of thumb, morphological vestigialization proceeds in the reverse order of the sequence of normal development. For instance, digits of regressing reptilian limbs are deleted in the reverse order of their embryonic formation; eye reduction of cave-dwelling fish and salamanders follows a distal to central progression from cornea, to lens, to bulbous, to nervous components—roughly the opposite order of their formation.

The most interesting question of vestigialization probably concerns not the fact of structural regression itself, but rather the maintenance of remnants that have no obvious function in the derived bearers, or even seem to be under negative selection. An example is the vermiform appendix, which must have caused extensive numbers of prereproductive deaths during hominin evolution. Since it is quite unlikely that structures completely without function would be preserved, certain functions must be assumed to persist. One obvious class of such functions is their intermediate role in development, when a structure that is tightly integrated in developmental interactions cannot be removed without deleterious downstream effects. In other cases, vestigial structures may have acquired new, less obvious functions that differ from the original ones. Hence, a vestigium should not generally be considered without function, or only with respect to its ancestral, adult roles. Finally, vestigia may be maintained because of intact gene networks. Reduction or loss of a phenotypic structure does not necessarily mean that its genetic basis is lost too. Even structural genes that have not been activated for many millions of years, such as those for enamel proteins in birds or lens proteins in moles, are often retained in the genome.

The significance of vestigial structures, these echoes of the past, lies mostly in the illustration of nonadaptive origins of certain features of organismal construction. They are also of taxonomic interest, and a number of morphological phenomena can be understood only if the processes of vestigialization are known. This is the case with atavisms, which are often based on embryonic vestigia, such as the occasional extra toes in horses. Another case is morphological innovation, which can take its origin from retained rudiments of reduced structures. Experimental enhancements of embryonic vestigia can also uncover suppressed developmental interactions. Finally, certain vestigia in humans are of medical significance, as exemplified by parovarian cysts, branchial fistulae, or appendicities. In general, vestigial structures and the processes of their formation shed light on the relationship between development and evolution.

[See also Adaptation; Atavisms; Homology; Recapitulation.]

**BIBLIOGRAPHY**


— Gerd B. Müller

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Mark Pagel
EDITOR IN CHIEF

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