

"The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme" (1979), by Stephen J. Gould and Richard C. Lewontin

"The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme," hereafter called "The Spandrels," is an article written by Stephen J. Gould and Richard C. Lewontin published in the *Proceedings of the Royal Society of London* in 1979. The paper emphasizes issues with what the two authors call adaptationism or the adaptationist programme as a framework to explain how species and traits evolved. The paper is one in a series of works in which Gould emphasized the role of development in evolutionary theories. The article suggests that constraints on how organisms can develop and constraints on how species can evolve from others play a central role in explaining how species and traits evolve. The authors note that organisms from different species develop as embryos through stages similar across species, genera, and higher classes. Gould and Lewontin hypothesize that those stages constrained the possible pathways of evolution and has therefore guided the history of life. Throughout the paper, the authors rely on analogy of some parts of organisms to architectural structures called spandrels, marked in this image as 'a'.

Gould and Lewontin both worked at Harvard University in Cambridge, Massachusetts, from 1967 until 2002 when Gould died of lung cancer. When "The Spandrels" was published in 1979, Gould had already published *Ontogeny and Phylogeny*, which explores the relationship between how organisms develop and how species evolved from other species.

During this time, Lewontin studied how constraints on how organisms can develop (developmental constraints) related to the diversification of species from one another. Gould and Lewontin challenged the use of adaptation stories to explain how all of organisms' traits evolved, and they warned the scientific community against a theory of biological determinism. Proponents of biological determinism, which is the claim that many organisms' traits are determined primarily by their genetic makeup, argued that evolution could explain social behaviors such as altruism and aggression. Theories of biological determinism worried Gould and Lewontin because, in the past, individuals with similar theories had used them to justify violations of civil rights, based on claims that some people in some populations had innate criminality or poor intellect, whereas people in other populations did not. An example was the eugenic movement at the beginning of the twentieth century, when many people were sterilized against their will to prevent those who were seen as weak or feeble minded from reproducing. But in addition to their concerns about biological determinism, Gould and Lewontin noted that biologists continually disregarded non-selective forces like phyletic and developmental constraints when they described the history of life on earth. Gould and Lewontin argued that these forces shaped the diversity of life.

Gould and Lewontin described the adaptationist program as a framework with which researchers described the causes of particular forms and functions in animals, which those researchers conceived as collections of separate parts. According to Gould and Lewontin, the adaptationist program, each part of an organism had a particular shape due to the action of natural selection. Adaptationists created evolutionary stories without collecting any evidence about how traits actually evolved, and Gould and Lewontin described this procedure as making up just-so stories. The authors argued that this explanatory method falters often because it ignores constraints, which limit the number of possible forms into which organisms can develop. Furthermore, the authors claimed that constraint theories often provide better explanations of structure and function than adaptationist theories do.

"The Spandrels" has six sections. The first three sections describe Gould and Lewontin's interpretation of the adaptationist program. The last three sections offer an alternative interpretation of evolutionary processes by pointing to phyletic and developmental constraints as main causes of the evolution of traits.

In the introduction, Gould and Lewontin describe what they call the shortcomings of the adaptationist program using an analogy. The authors describe the spandrels in the church of St. Mark's Cathedral in Venice, Italy. After the cathedral was built, artists painted images in the spandrels. If we investigated the spandrels without that information, we might conclude that the architects designed the cathedral to have spandrels to bear images. Spandrels, then, provide an example of how something that looks intricately designed may lead us to believe that architects purposefully created the spandrels for the decorations themselves. However, Gould and Lewontin note that the spandrels result when builders place a domed ceiling upon a square room that has arched doorways, and although spandrels only exist for structural purposes, they also host artistic decorations. Anytime a building has domed ceiling on a square room with arched doorways, the structure will have spandrels. Lewontin and Gould argue that if we understand the origin of the spandrels, then we can analogously understand the origin of some biological structures. Maybe, Gould and Lewontin hypothesize, developmental constraints are the cause of many traits, as they explain the origin of particular traits better than does adaptation, just as architectural constraints explain the origin of spandrels better than does the intricate artwork inside them.

In sections two and three, Gould and Lewontin claim that adaptationists see natural selection as the only and all-powerful force that can overcome any constraint to species' traits. The authors compare the adaptationists view to the character of Dr. Pangloss, a parody of Gottfried W. von Leibniz in one of Voltaire's 1759 pamphlets. In the story, Dr. Pangloss, a naive optimistic philosopher, claims that our world is the best of all possible worlds. Like Dr. Pangloss, adaptationists are naive according to Gould and Lewontin. They say that adaptationists naively atomize organisms into particular traits and then provide optimality stories about how those parts evolved. If an optimality story proves false, the adaptationists then set another optimality story instead of exploring the different possibilities that do not involve adaptation.

In the fourth section of the article, Gould and Lewontin describe how Charles Darwin's 1859 theory of evolution is similar to their view and not to adaptationists' approaches. The authors note that Darwin consistently showed a pluralistic approach to the causes of evolution, considering several alternatives to natural selection. Gould and Lewontin argue that Darwin did not claim that natural selection was the only important cause of evolution.

In the fifth section of the article, Gould and Lewontin highlight several instances in which adaptation is not the primary cause of the form and function of particular traits. According to the authors, selection does not necessarily result in a trait being adapted to the environment, whereas adaptation cannot occur without selection. The authors point to genetic drift, an evolutionary process due to random mating in finite populations, as a process that requires neither selection nor adaptation. Furthermore, the authors show that selection without adaptation can occur in the hypothetical scenario where a mutation doubles the amount of offspring an organism can birth at once. The mutation would spread throughout the population, but if environmental resources didn't also double, then parents in the evolved population would have no more offspring than parents in the ancestral population, and thus would be no better adapted to their environment. Also, adaptation without selection occurs when the environment itself physically causes adaptive traits. For example, the currents in the ocean physically change sponges and corals. These changes, although not selected, increase the chances of survival of the organisms. Gould and Lewontin highlight the difficulties in distinguishing the origin of a part adapted to its environment, because that part might have been originally adapted for a different function than it later serves, and it might have undergone multiple adaptations for different functions throughout the evolutionary history of the species.

The final section of the article proposes a theory of how species evolve with developmental constraints. The authors stress the importance of integrating developmental constraints with adaptive explanations into evolutionary biology. Additionally, they discuss the concept of body plan or Bauplan, which is analogous to a blue print by which an organism develops. For instance, humans are poorly adapted to walking on two legs, because the majority of the human Bauplan has evolved for

walking on arms and legs, as apes do. Proponents of the Bauplan consider organisms as integrative wholes, not as mere collections of parts.

To support their claim that developmental constraints operate in evolutionary processes, Gould and Lewontin describe Karl Ernst von Baer's 1828 embryological laws. Von Baer's laws state that early developmental stages are highly conserved throughout species, meaning that there are not many changes made early on in the development of organism from across many animal species. Changes made early in development will accumulate and affect all systems in later stages of development so that, if a change occurs at early stages, it can disrupt the further development of the organism. The authors state that this conservation leads to developmental constraints, and they claim that there are a limited number of developmental pathways an organism can follow without dying. Therefore, organisms are constrained to a particular evolutionary pathway.

Gould and Lewontin conclude their article by emphasizing that the adaptationists' theory is not compatible with the theory of organisms as integrative wholes. In early developmental stages, an organism cannot be pulled apart piece by piece into different traits that can then each be described for a specific function. All parts of a system depend upon one another. Small changes to the Bauplan can be explained by adaptation, but adaptation cannot explain the origin of variation between individuals within the same species.

"The Spandrels" prompted Gould and Elisabeth Vrba to publish a further article in 1982, suggesting the term exaptation to describe a trait once adapted for a function but that natural selection has remodeled for a different use.

Sources

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