The Shape of Things to Come
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Source: *Systematic Zoology*, Vol. 22, No. 4 (Dec., 1973), pp. 401-404
Published by: Taylor & Francis, Ltd. for the Society of Systematic Biologists
Stable URL: http://www.jstor.org/stable/2412947
Accessed: 22-04-2015 16:08 UTC

I. C. S. E. B.

BOULDER—AUGUST 1973

SYMPOSIUM

"EVOLUTIONARY DEVELOPMENT OF FORM AND SYMMETRY"

CONVENOR—STEPHEN JAY GOULD

THE SHAPE OF THINGS TO COME

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We celebrate, in this symposium, a quiet renaissance of biology's oldest subject. During the past decade, like a thief in the night, morphology has surreptitiously become interesting again. The descriptive concerns of cataloguers, constrained by their jargon to communication with a few other specialists, are yielding, or at least accommodating, to analytical and explanatory approaches. There are several reasons for this: A panoply of new machinery and techniques have extended the bounds of both perception (the SEM) and analysis (multivariate biometry). But no machine can match the finest computer of them all. Evolutionary theory has been so vigorous of late that it could scarcely avoid a mutual relationship with morphology—by supplying it with ideas to catalyze the advance of explanatory procedures and by drawing insights from it in return. Thus, we find Stanley using the competition theories of ecology to elucidate an old dilemma of morphological diversity (patterns of radiation in "conservative" vs. "dynamic" groups); while, in return, Liem reminds ecologists that the causes of relative diversity are often to be sought not in the favored environmental parameters of stability and diversity of habitat but in differences of morphological adaptation. "Billiard ball" ecology, like the modelling of ideal gases, has its place at a certain level of generality; but it may fail badly in trying to explain both the particular case of explosive diversity in African lake fishes and such general problems as the increase of organic diversity through time—(under billiard ball models, each species is a black box of no unique construction and the causes of increasing diversity through time must be sought in such environmental parameters as increasing endemicity through continental drift rather than in classical, and basically sound, notions of increasing complexity of structure in major groups, *vide* Vermeij and Stebbins). Liem shows elegantly that a small morphological change (the shift in insertion of the fourth *levator externi*) and its functional correlate (the use of pharyngeal jaws for preparation of food and freeing of anterior jaws for gathering alone) has triggered the truly fantastic radiation of African cichlid fishes. I believe, in short, that we are approaching a true "science of form" (Gould, 1970 and 1971)—a claim that has not been made with justification since Cuvier's time (Haeckel had an historical theory, D'Arcy Thompson a functional one: a satisfactory science of morphology must integrate both).

The papers of this symposium were presented on August 7, 1973 at the first ICSEB meeting in Boulder, Colorado. We regret that the limitations of this venerable medium cannot fully convey both the beauty and excitement that films and colored slides added to the presentations.

In organizing the symposium, I avoided "state of the art" and "contemporary problems in . . ." talks as obvious magnets for potboilers, and opted instead for a set of exemplifications—of new techniques, particularly interesting or important case studies, and general evolutionary hypotheses. This leads to a certain incoherence; but this may, itself, be a mark of virility (any rigid portrayal of this unformed renaissance would, in any event, be as gratuitous as *Ichthyostega* discoursing in Devonian times on its future estate). The sequence of presentations is not, however, utterly haphazard. The first papers are case studies using both deductive procedures of physical analysis (Liem, Kokshaysky) and inductive methods of multivariate biometry (Oxnard). They display many of the new techniques alluded to above (Liem on the SEM, electromyography and cineradiography; Oxnard on multivariate morphometrics and experimental stress analysis). They treat particularly interesting or important cases: Oxnard reaches some rather startling conclusions on the morphological uniqueness of australopithecines; Kokshaysky introduces us to the Soviet school of evolutionary morphology in a carefully chosen natural experiment on size-required allometry in the dynamics and morphology of wing slots in four species of herons. Liem considers the most outstanding case of explosive evolution in modern vertebrates. Seilacher's paper is transitional: he finds the same structures as adaptations for burrowing in taxa of several phyla and, noting that the same constructional principles are used to build features of such diverse function as ammonite septa and the "windows" of *Corculum*, he presents a striking hypothesis on the developmental basis of adaptive form. The last three papers present specific hypotheses on the general development of form through time. They are different in approach and even slightly contradictory in methodology. Vermeij and Stebbins trace patterns in diversity to morphological constraints: (Vermeij attributes evolutionary increase in potential versatility to "complexity" as measured by numbers of parameters needed to specify the construction of form; Stebbins traces patterns of diversity in multinucleate organisms to the preadaptive features of unicellular eukaryotes, primarily to polarity, nature of the cell covering, autotrophy vs. heterotrophy, and cell shape and size). Stanley emphasizes ecological constraints in arguing that the exuberant and rapid rates of diversification in mammals vs. bivalves are primarily related to more intense interspecific competition among the mammals.

I have prefaced these papers with the manifesto of an architect (and sensitive naturalist) because Stevens shares D'Arcy Thompson's vision that the biological science of morphology can expand well beyond the confines of our discipline to enlighten and be a part of the wider science of form that applies to all objects. We rarely recognize how our own laws of form regulate the properties of buildings, machines and planets as well. To choose a simple-minded example: medieval churches are excellent exemplars of the laws of form in correlations between size and shape—for they were built in an enormous range of sizes to serve fairly similar purposes before technological inventions (from steel girders to electric lighting to air conditioning) allowed architects to circumvent many constraints imposed by increasing size. The law of surfaces and volumes regulates much of the external and internal structure of large organisms: a remarkable array of features can be explained functionally by the need to increase surface allometrically in order to allow something (food, oxygen, light) to penetrate into the interior of large organisms. Churches are subject to the same constraints. Light must penetrate through windows of the periphery and illuminate the entire internal area (candles do have their limitations). Periphery increases as L, area of floor plan as L^2; large

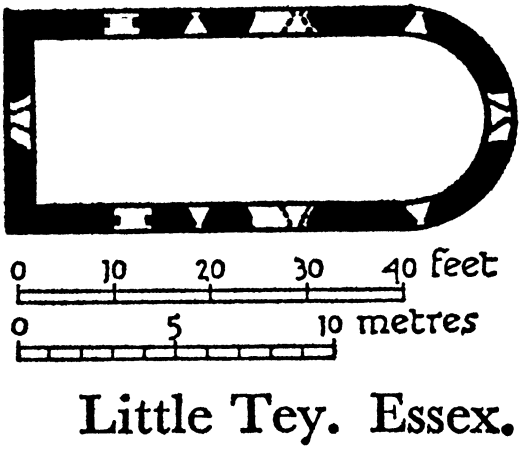

FIG. 1.—Ground plan of the parish church of Little Tey, Essex. From Clapham, 1934.

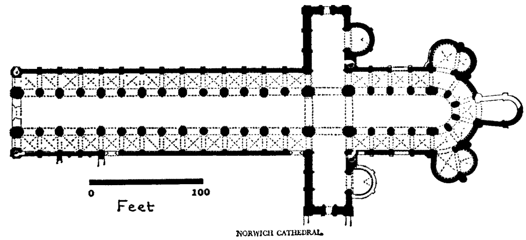

FIG. 2.—Ground plan of Norwich Cathedral. From Clapham, 1934.

churches cannot maintain the same shape as small ones and receive sufficient illumination. This is especially true for Romanesque churches with their massive masonry and limited possibilities for windows; (the invention of the flying buttress reduced the need for massive outer walls and permitted the remarkable increase in window area and "lightening" that characterizes later Gothic architecture). In order to maintain sufficient periphery, large churches had to be built as more elongated rectangles and had to introduce "outpouchings" in the form of transepts and chapels (the form of the cross may have dictated the shape and position of transepts, but laws of size required their presence). Enlarge the tiny parish church of Little Tey (Fig. 1) to the size of Norwich Cathedral (Fig. 2) and the interior would have been darker than the deeds of Herod; reduce Norwich to the size of Little Tey and the Christ child himself could scarcely have squeezed into the apsidal chapels. A plot of square root of area vs. periphery for all floor plans of post-conquest Romanesque churches of Britain depicted in Clapham (1934) illustrates the positive allometry of periphery. The isometric line of slope 1, drawn through an average small church, misses all intermediate and large churches by a wide margin.

The log correlation of .995 astounded me—I would have thought that the vagaries of human will would have imposed more scatter than the centrifugal adaptation of organisms. Medieval builders had their rules of thumb, but there is no evidence that they knew anything of these laws of form.

I can only end, therefore, by repeating D'Arcy Thompson's hope (1942, p. 1026) that biology might form the central core for a truly general science of form: "Our own study of organic form, which we call by Goethe's name of Morphology, is but a portion of that wider Science of Form which deals with the forms assumed by matter under all aspects and conditions,

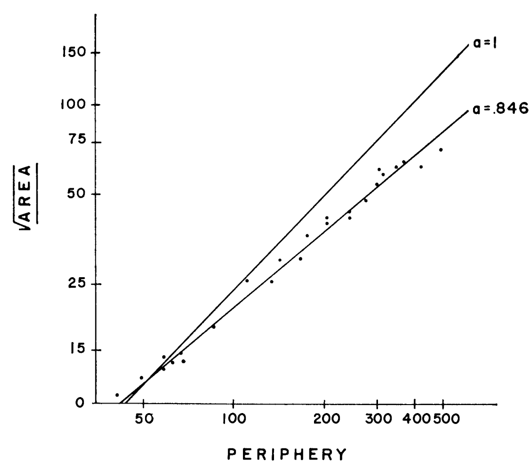

FIG. 3.—Plot, on logarithmic scales, of square root of area vs. periphery for all ground plans of post-conquest Romanesque churches in Britain given in Clapham, 1934. Data compiled by author using map reader and polar planimeter directly from scaled drawings of Clapham.

and, in a still wider sense, with forms which are theoretically imaginable."

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