8 Size, Shape and Evolution
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INTRODUCTION

Given the enormous scope of Julian Huxley's research interests, most modern biologists are bound to acknowledge some kind of intellectual debt to his contributions. When it comes to the question of size relationships in organisms, however, a double debt to Huxley must be recognised. In a very general context, there is of course Huxley's pervasive influence in the sphere of evolutionary biology, which constitutes the overall framework within which biological size relationships can be interpreted. To take just one example, he provided a timely and valuable discussion of the concept of 'grade' with respect to evolutionary processes and taxonomy (Huxley, 1958). As it happens, the grade concept has also proved to be of particular relevance with respect to adjustments to body size in the evolution of organisms (see below). More specifically, studies of the relationships between the size of individual bodily components and overall body size (scaling biology) can be said to owe much of their origin to Huxley's seminal treatise Problems of Relative Growth (1932). When it first appeared, this book provoked a flurry of discussion and active practical application that lasted for about two decades. Thereafter, interest subsided quite markedly as if a once promising mine had eventually been exhausted; but - following a steady resurgence - interest in scaling biology has peaked again in recent years and studies in this area have now become something of a 'growth industry'.

Scaling studies have been particularly emphasised in comparative vertebrate physiology for some time and Schmidt-Nielsen (1984) has recently provided a very effective review of some of the most striking and successful applications in this field. Following a very early start with respect to the study of relative brain size (Snell, 1891; Dubois, 1897; for a review see Jerison, 1973) the central importance of scaling effects has been slowly but progressively acknowledged in the field of
comparative morphology. To take one example, a recent edited volume has brought together a variety of specific applications in morphological aspects of primate evolutionary biology (Jungers, 1985). In recent years, scaling studies have also been extended into essentially new areas, such as comparative ecology (Peters, 1983) and the analysis of life history parameters (Calder, 1984). Huxley would undoubtedly have been pleased to see the extension of scaling studies from his original context of developmental biology into the realms of behavior and ecology, which later figured so prominently in his research. Special mention should also be made of the entertaining and instructive book by McMahon and Bonner (1983), which neatly demonstrates the generality of scaling effects in biology and graphically shows that the topic is both thriving and productive.

One important point that must be made at once is that it is necessary to distinguish clearly between interspecific and intraspecific scaling. Huxley’s concern with scaling biology was essentially confined to the developmental processes involved in the growth of individuals and in his influential book (1932) he was hence primarily interested in intraspecific scaling (hence the title ‘relative growth’). Only one chapter of the book was devoted to the implications of scaling in phylogenetic, rather than ontogenetic, terms. By contrast, in the modern resurgence of scaling biology, interspecific aspects have been dominant and this may explain the curious hiatus in the history of this subject. The temporary decline in interest in scaling as a topic for research may be attributed to the fact that its immediate contribution to the understanding of individual development within species was somewhat limited, while it was only gradually realised that it had an absolutely fundamental part to play in the understanding of phylogenetic relationships between species.

It should also be noted that nonlinear scaling of individual bodily components to body size is now generally referred to as allometry (Huxley and Teissier, 1936; Reeve and Huxley, 1945). Initially, Huxley (1932) did not use the word allometry at all and employed instead (following Pézard, 1918) the term heterogony. This term was subsequently rejected by Huxley and Teissier (1936), in a brief paper devoted to the terminology of relative growth, because ‘heterogony’ had also been employed to refer to a particular kind of life cycle. This joint publication of Huxley and Teissier is of special interest for two reasons. In the first place, it provided a valuable early definition of many of the basic terms and concepts of allometric analysis. In addition, however, it rightly associated Teissier’s name with a crucial