1.2.1 Homology and homologous points

D'Arcy Thompson (1961: 274–275) introduces the study of form-comparisons in this way:

...The morphologist, when comparing one organism with another, describes the differences between them point by point, and ‘character’ by ‘character.’ If he is from time to time constrained to admit the existence of ‘correlation’ between characters ..., yet all the while he recognizes this factor of correlation somewhat vaguely, as a phenomenon due to causes which, except in rare instances, he can hardly hope to trace; and he falls readily into the habit of thinking and talking of evolution as though it had proceeded on the lines of his own descriptions, point by point, and character by character.

...But when the morphologist compares one animal with another, point by point or character by character, these are too often the mere outcome of artificial dissection and analysis. Rather is the living body one integral and indivisible whole, in which we cannot find, when we come to look for it, any strict dividing line even between the head and the body, the muscle and the tendon, the sinew and the bone. Characters which we have differentiated insist on integrating themselves again; and aspects of the organism are seen to be conjoined which only our mental analysis had put asunder. The coordinate diagram throws into relief the integral solidarity of the organism, and enables us to see how simple a certain kind of correlation is which had been apt to seem a subtle and a complex thing.

But if, on the other hand, diverse and dissimilar fishes can be referred as a whole to identical functions of very different co-ordinate systems, this fact will of itself constitute a proof that variation has proceeded on definite and orderly lines, that a comprehensive ‘law of growth’ has pervaded the whole structure in its integrity, and that some more or less simple and recognisable system of forces has been in control.

In this manner Thompson explicitly identifies the object under discussion, namely the relationship between biological forms, with a latent variable: an abstraction designed to explain diverse comparative findings distributed over the organism. His identification of this latent variable with a “system of forces” reflects the biomechanical understanding typical of his era, now obsolete; what remains, the idea of a “simple and recognisable” geometrical pattern of explanation (Fig. 1.2.1), has fascinated mathematical biologists and morphologists from Thompson’s day to the present.

The endurance of Thompson’s insight owes to its felicitous blending of two previously unrelated descriptive traditions. The latent variable of which he speaks had hitherto been studied in biology and in mathematics separately, where it went by two different names. The biologist knew it as homology, the rules by which parts of different organisms were understood to correspond, whereas the mathematician knew it as the pointwise deformation, or “Cartesian transformation,” acting to distort a picture or other specifically geometric representation of form.

In saying that deformation is a mathematical model for homology, as Thompson did in the quotation above, we mean that the quantitative statistical analysis of
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The homology function is a mathematical model of homology as a smooth deformation. One way of displaying the correspondence of homologous points (a) is by a Cartesian grid transformation (b). Example after Thompson (1961).

*Argyropelecus*  
*Sternoptyx*

**Figure 1.2.1** The homology function. The homology function is a mathematical model of homology as a smooth deformation. One way of displaying the correspondence of homologous points (a) is by a Cartesian grid transformation (b). Example after Thompson (1961).

deformation, according to the methods set forth here, provides geometrical summaries of differences that will eventually be “explained” biologically. Whenever we find systematic aspects of deformation that correspond to trends or contrasts of biological interest, we assume that the biological interpretation of these findings will crucially involve phylogenetic or ontogenetic aspects of homology (Chapter 5).

Biological homology refers to the rules by which definable structures or “parts” correspond: we speak of the homology of the reptilian quadrate and the mammalian incus. It is not the purpose of this manuscript to discuss the rules—spatial, ontogenetic or phylogenetic—by which these correspondences are founded. We will, however, extend the traditional use of homology to include the correspondence of points and boundaries as well as parts. For example, we will consider the origin of the spinous dorsal fin in two centarchid fishes to be a homologous point. Likewise, the segment of the boundary between the origin of the spinous dorsal and the origin of the soft dorsal
will be considered homologous in those two forms. (For the computation of homology in this sense, see Section 3.3.2.) The definition and verification of such homologies are identical to those of their more traditional counterparts. We will refer to points whose comparisons are consistent with the rules of homology and that have reliable anatomical definitions as landmarks.

Because we are interested in comparisons of forms rather than their separate definitions, we introduce here the concept of the homology function or homology map (Woodger, 1945; Jardine, 1967, 1969; Bookstein, 1978a:120–123), a geometric tool for describing the correspondence between two or more forms. Specifically, a homology function is a mathematical model that starts with the landmarks and smooth boundary curves of one form and describes how to map these onto the homologous curves and points of a second form. This mapping is modeled as smooth: points nearby in one form correspond to points relatively nearby in all other forms, and short segments nearly straight in one form do not manifest large kinks in other forms.

The homology function associates different kinds of points—landmark and non-landmark—among geometric forms. (By geometric form (Fig. 1.2.2) we mean the landmark points and curving arcs between them that constitute a sketch of the organ or organism under discussion.) We will refer to computed-homology as the relationship among points (one on each geometric form) that are interpolated between appropriate landmarks. Included in this definition will be all interior points not located by reason of their anatomical definition, as well as specific points along the boundary—for example, the point halfway between the origins of the spinous and soft dorsal fins. In accordance with this distinction we will speak of two types of correspondence: homologues, which are defined by the conventional rules of biological homology and which drive the mapping function, and computed-homologues, which are defined by the mapping function.

The biological aspect of this homology function, as it associates points or curves, varies from example to example. When we study a fish scale or a mollusk shell with growth rings, for instance, the approximate history of the organ and its homologous points and curves may be explicit in its image at any moment. Sometimes, instead, homologues are analogous by position: the sutures separating a particular pair of bones should be homologous as curves from form to form of a skull series. Intersections of sutures often serve to characterize homologous points.

Computation of a homology function from data representing two forms begins with a sample of the correspondence: landmark sets, which must be located reliably in all the forms of a series. The computed-homologues for all the other points—the non-landmarks—of a form are interpolated among the locations of the homologous landmarks.

Landmarks must satisfy several constraints imposed by the deformation model. Although landmarks may later be assigned coordinate values, a good landmark needs to have an operational definition in terms of the anatomy and/or ontogenetic history in its vicinity. It is not sufficient to choose as landmarks points having extreme values relative to a particular coordinate system. For example, the designation of highest or
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Figure 1.2.2 The geometric form. The geometric form represents a biological specimen by the set of landmarks and curving arcs between them. Landmarks are indicated by arrows on the drawing and by dots on the geometric form. In this example we have excluded the fins.

The lowest points of the form in Figure 1.2.3 as supposed homologues is arbitrarily dependent on the orientation of the form relative to the coordinate axis, here the line from premaxilla to center of hypural plate. When a coordinate system is defined by reference to landmarks, it is inappropriate to subsequently define landmarks in terms of their coordinates, because inconsistency in positioning the forms can cause dramatic shifts in the location of these supposedly homologous points. Other ways of defining one landmark in terms of another (i.e., endpoints of minimum or maximum diameters) may also lead to violations of homology. For example, points constructed as nearest to or farthest from other landmarks, and geometric combinations of landmarks at a distance, are not proper landmarks. These criteria proscribe intersections of lines or "axes," points at extreme distance from landmarks defined earlier, and so forth. "The base of the dorsal fin" will be definitive on many fishes; "the highest point of the back" will not. Points on a projected drawing or radiograph representing the abutment of three structures in space are often helpful selections; points where two curves cross in projection but not in space are not as useful.

The homology function, anchored at the landmarks, specifies a computed correspondence along the outline arcs and within the interiors of the forms. This requires that the landmarks be selected not individually but as a set, over all forms, to
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![Figure 1.2.3](image)

Figure 1.2.3 Landmarks must be characterized locally. As we change the form of the fish, the spatial relationships of “the highest point of the back” alter excessively. Here “height” is distance above a segment from the premaxilla to the center of the hypural plate.

eensure that the correspondence as computed is sensible (see Sec. 5.1). In practice, certain landmarks with a clear anatomic definition may have to be excluded from a morphometric analysis by this criterion. For instance, landmarks very close together in some forms should not be far apart in others; and landmarks found within a region defined by other landmarks in one form should not be outside of that region in another form. While such landmarks may be appropriate in multivariate analyses of morphometric distances, they are unsuitable for morphometric modeling of shape-change as a deformation.

Landmarks not only anchor the homology maps but also guide the construction of data sets for samples of geometric forms. For this purpose, landmarks may be assigned coordinates in any convenient coordinate system (Cartesian, polar) registered and oriented howsoever. In place of coordinates, we may record any other system of quantities that permits the complete reconstruction of the landmark configuration, such as the box truss of interpoint distances (Sec. 3.2). Note that the archive of coordinate data contains no derived variables: no angles, ratios, diameters, functions of azimuth, or other complex constructs.

Arcs of the outline between landmarks may be recorded by sequences of points (i.e., coordinate pairs) along them or instead may be abstracted into curves represented by formula—arcs of circles, ellipses, and so forth (see Sec. 3.3). Whether such a representation, or any particular selection of landmarks and connections, is satisfactory depends entirely on the empirical context of the research and the comparisons that are to be investigated. For certain comparisons information on boundary arcs may be discarded, whereupon the outline is represented by the straight lines connecting the landmarks around the form.