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Three Dimensional Mammalian Skull Morphology

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This thesis deals with archiving morphological data utilizing a three dimensional coordinate system. Morphological reference points are archived via rectangular position coordinates, rectangular position vectors, and spherical position vectors. The concepts of translation trajectories, translation vectors, and relative position vectors are developed. Analysis of three dimensional coordinate data utilizing translation trajectories and translation vectors is described. In order to test the methodolgy developed, the method is applied to an analysis

of harbor porpoise, *Phocoena phocoena* L., skull morphology.
(Key words: morphology, ontogenetic trajectories, allometry, position coordinates, position vectors, translation trajectories, translation vectors, relative position vectors, and harbor porpoise).

THREE DIMENSIONAL
MAMMALIAN SKULL MORPHOLOGY

by

SUZANNE LOUISE KRIPPAEHNE

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DEDICATION

My father, William Wonn Krippaehne, once told me that the greatest compliment that could ever be given to a teacher is for a student to eclipse their teacher. This thesis is dedicated in memory of my father with whom I shared this philosophy, to my teachers who have provided me with the opportunity to eclipse them, and to those students of mine who will eclipse me. This thesis is also dedicated to my mother, Marion Carolyn Larsen Krippaehne, for whose love and support I am thankful.

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To the members of my thesis committee, I offer my thanks. In particular, I give a special thanks to Dr. Debbie Duffield for allowing me to pursue this research under her. To all of the people who have contributed to this thesis, I offer my gratitude. To the National Marine Mammal Laboratory of the National Marine Fisheries Service, I extend my appreciation for allowing me access to the harbor porpoise research collection.

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BACKGROUND

As evidenced by innumerable artworks and publications, biological form has long intrigued both artists and scientists. Three individuals stand out for their contributions to the study of biological form. The first person is D'Arcy Wentworth Thompson who wrote On Growth and Form, a book first published in 1917 with an expanded edition published in 1942. This classical work describes organic growth and form in relation to physical and mathematical laws utilizing the idea of force to interpret cellular, tissue, plant and animal morphology. The second individual is Sir Julian S. Huxley who published his first edition of Problems of Relative Growth in 1932. The major contribution of this text is the development of an equation which describes the relation of relative size with absolute size. This equation has come to be known as the allometric equation. The last person is Stephen Jay Gould who has contributed much to the literature on evolutionary biology over the past few decades. Included in his list of publications is Ontogeny and Phylogeny which was recognized as a classical work at the time it was published in 1977. Among the ideas presented in this book, Gould develops a clock model of heterochrony. In the clock model of heterochrony, Gould dissociates the three component processes of growth (which include size, shape and age) in order to analyze evolutionary changes in form between ancestors and descendants.

MORPHOLOGY

Morphology, a term coined by Johann Wolfgang von Goethe (Thompson, 1917, 1961; Gifford and Foster, 1989), is literally the "science (or study) of form" (Hildebrand, 1982; Minkoff, 1983; Gifford and Foster) or the study of organic form (Thompson, 1917, 1961). Webster's New Universal Unabridged Dictionary (1983, p. 1170) defines morphology as "the branch of biology that deals with the form and structure of animals and plants, without regard to function." In the field of biology, definitions of morphology emphasize either the study of structure (Walker, 1987) or the study of relating and interpreting structure (Bold, 1973; Hildebrand, 1982; Gifford and Foster, 1989). Liem and Wake (1985, p. 366) clearly take the definition of morphology beyond the science of structure when they describe "the task of the morphologist" which is "to analyze and explain the diversity of structure and function exhibited by organisms."

Morphological studies are utilized to describe, analyze, relate or interpret (Thompson, 1917, 1961; Oxnard, 1978; Pimentel, 1979; Liem and Wake, 1985), and predict (Vogel, 1988; Jackson, 1989) organic structure and function. These studies use characters or suites of characters to address issues involving either systematics or ecology (Corvello, 1970). Radinsky (1987, p. 5), states that "systematics is the special discipline in biology that studies the evolutionary relationships among organisms." Therefore, systematic investigations include both intraspecific (i. e., within species) and interspecific (i. e., between species) analysis and interpretation. Topics of interest include: empirical species descriptions, intraspecific variation, populational or racial differences, sexual dimorphism, anatomy, physiology, pathology or disease, genetics, ontogeny, taxonomy, palaeontology, phylogeny, and evolution. Other applications of systematic studies include: the assignment of unknown specimens to a taxon, the determination of an unknown sex of a specimen, filling in the missing parts of damaged or incomplete specimens, and extrapolating data from known species to theorize about past and future species or trends. Minkoff (1983, p. 150) describes "ecology as a science is simply the study of the environment and the interactions of various species with their environment, including interactions with each other." Ecological inquiries include the subjects of biomechanics, scaling, biophysics, zooarchaeology, biogeography, geographic variation, clinal variation and coevolution. To reiterate, morphology is an intergral part of (or plays a supplementary role in) the systematic and ecological investigations listed.

Interpretation of form, whether structural or functional, involves qualitative and quantitative investigations. However, Vogel (1988, p. 316) states, "one source of the great explanatory and predictive power of contemporary science is its quantitative character," and that "even outwardly qualitative questions often yield answers in response to investigations that are quantitative at every stage." Quantitative reasoning and methodology involves measurement and calculations or mathematics (Vogel, 1988). Thompson (1961, p. 270) found the laws and methods of mathematics to be "peculiarly fitted to interpret" the phenomena of growth and form. Morphometrics is the measurement of biological form which allows the quantification of descriptive and investigative data. Oxnard (1978, p. 219) defines morphometrics as "the characterization of biologically relevant forms and patterns in ways that allow their quantitative handling." Bookstein (1982, p. 451) regards morphometrics as "the empirical fusion of geometry with biology" where "its methods must explicitly take cognizance of two wholly distinct sources of information - geometric location and biological homology."

In regard to the previous discussion on morphology and morphometrics, an inclusive definition of morphology is the study of biological form for descriptive and investigative inquiries involving the structure and function of organisms whereby descriptive, analytical, interpretive, and predictive studies of structure and function are quantified through the measurement and mathematical analysis of the geometric description of anatomical characteristics. One aspect of a comprehensive investigation involving the morphology of an organism is a developmental study of the organism.

ONTOGENETIC TRAJECTORIES

Ontogeny, a term coined by Ernst Heinrich Haeckel (Minkoff, 1983; Gould, 1988), comes from "onto" meaning "being" and "geny" meaning "development" (Webster, 1983); therefore, ontogeny literally means "the development of being." It then follows that the basic definition of ontogeny is the biological development of an individual (Webster, 1983; Walker, 1987). A narrow definition of ontogeny is the sequence of development of an individual from an egg, through embryonic development, to an adult (Gould, 1977; Hildebrand, 1982; Minkoff, 1983). A broader definition of ontogeny is the life history (or life cycle) of a single organism (Webster, 1983). An all encompassing definition of ontogeny, which is the development of an individual organism throughout its life history, allows for conceptual development of the topic, yet retains the flexibility to encompass specific or narrow ontogenetic investigations.

To conceptualize and quantify ontogeny, Alberch et al. (1979) and Alberch (1980) described the use of ontogenetic trajectories. Ontogenetic trajectories are trajectories in age-size-shape space which trace the path of a developmental event from the time of inception to its mature form. Alberch et al. (1979, p. 300) stated that "the ontogenetic trajectory is an idealization which refers to the growth of a single individual in a population." If a number of individual ontogenetic trajectories, which are representative of a population, are taken collectively, then an ontogenetic trajectory representing the population may be derived. These population ontogenetic trajectories represent the mean ontogenetic trajectory for the population. The ontogenetic variance exhibited within the population may also be represented. Population ontogenetic trajectories may be utilized to study heterochrony in evolution. See Alberch et al. (1979) for a detailed discussion of ontogenetic trajectories; see Alberch (1980) for an excellent account of relating ontogeny to morphology; and see both Fink (1982) and Alberch (1985) for discussions about considerations for and limitations of ontogenetic investigations.

When the term heterochrony was first introduced by Ernst Heinrich Haeckel, the term was used to describe a change in the timing (or unequal acceleration) of the development of one organ relative to other organs in the same individual (Gould, 1988). Gould (1977, pp. 481 - 482) stated that "according to Haeckel, (heterochrony is) the displacement in time of ontogenetic appearance and development of one organ with respect to another, causing a disruption of the true repetition of phylogeny in ontogeny." Later, Gavin R. de Beer retained the notion that heterochrony involves a change in developmental timing, but de Beer used the term to refer to a change in the developmental timing of one feature relative to the same feature in an ancestor (Gould, 1988). Gould (1977, p. 482) stated that de Beer defined "heterochrony as phyletic change in the onset of timing of development, so that the appearance or rate of development of a feature in a descendant ontogeny is either accelerated or retarded relative to the appearance or rate of development of the same feature in an ancestor's ontogeny." In reference to the modern usage of the term heterochrony, Gould (1988, p. 2) stated that heterochrony is regarded "as the definition of evolutionary change in developmental timing" and that the term is used "for the course of a trait relative to the ontogeny of the same trait in an ancestor (or related form)." McKinney (1988, p. 17) expanded Gould's usage of the term heterochrony to include changes in developmental rates, when he stated that "heterochrony is evolution via change in timing (and/or rate) of development." For a historical account of heterochrony, see

Gould (1977); and see Gould (1988) for a brief sketch of heterochrony.

Heterochrony as a process involves perturbations in the developmental control parameters of ontogenetic timing and/or ontogenetic rates which result in alterations in the morphology of descendants relative to ancestors (Alberch et al., 1979). The control parameters of ontogenetic timing are: the onset of growth which occurs at a specific age; and the offset (i. e. cessation) of growth which occurs at a specific age, at a limiting size, or at a limiting shape (Alberch et al., 1979; Alberch, 1980). Conceptually, a pure perturbation in a control parameter involves a change in one control parameter without a concomitant change in any other control parameter. Earlier onset of growth, the heterochronic process known as pre-displacement, results in peramorphosis (Alberch et al., 1979) Peramorphosis, meaning "shapes beyond" (Liem and Wake, 1985), is the morphological process which produces descendants whose form transcends the ancestral form. The resulting morphology is known as a peramorph (Alberch et al., 1979). Therefore, pre-displacement is one of the heterochronic processes which causes peramorphosis. Delayed onset of growth, the heterochronic process known as post-displacement, results in paedomorphosis (Alberch et al., 1979). Paedomorphosis, which means "juvenile shapes" (Liem and Wake, 1985), is the morphological process which produces descendants whose morphology resembles a juvenile stage of an ancestral form. This results in forms known as paedomorphs (Alberch et al., 1979). Hence, one of the heterochronic processes underlying paedomorphosis is post-displacement. When the growth period is truncated by an early signal for offset of growth, which is the heterochronic process known as progenesis, the resulting morphology is a paedomorph. On the other hand, when the growth period is prolonged by a delayed offset signal, which is the heterochronic process known as hypermorphosis, a peramorph results (Alberch et al., 1979). Changes in the control parameters affecting rates include altering the rate of shape change and altering the growth rate involving size (Alberch et al., 1979). If the rate of shape change in form is speeded up, which is the heterochronic process known as acceleration, peramorphosis results (Alberch et al., 1979). If the rate of change in form is retarded, which is the heterochronic process known as neoteny, paedomorphosis results (Alberch et al., 1979). When the growth rate in size is increased, proportional giantism occurs. Yet, when the growth rate in size is decreased, proportional dwarfism occurs (Alberch et al., 1979). The last controlling parameter which will cause a change in the ontogenetic trajectory of a descendant, when compared to the ancestral ontogenetic trajectory, is a change in the initial size at the commencement of growth (Alberch et al., 1979).

If ontogenetic trajectories are to be utilized to study heterochrony in evolution, two conditions must be met in order for appropriate analysis to occur. First, the relationship of the ancestor to the descendant must be known (Fink, 1982). Secondly, complete morphological data must be obtained (or determined), including: the initial size at onset of growth, the age at onset of growth, the age at offset of growth, the rate of change in size, and the rate of change in shape (Alberch et al., 1979). These data, once complete, allow the use of ontogenetic trajectories as a quantitative method for describing and analyzing ontogeny. Ontogenetic trajectories are trajectories which trace developmental events through age-size-shape space (Alberch et al., 1979; Alberch, 1980). Graphically, ontogenetic trajectories [$X(t)$] are obtained by plotting the dependent variables of size (S) and shape (σ) against the independent variable of age (a) utilizing points [$X(t)=(a,S,\sigma)$] along a path from the age at onset of growth (α) to the age at cessation of growth (β) (Alberch et al., 1979). As presented in Alberch et al. (1979) and Alberch (1980), age (a) is plotted on the x-axis, size (S) is plotted on the y-axis, and shape (σ) is plotted on the z-axis. Alberch et al. (1979) formalized the mathematical description of an ontogenetic trajectory as $X(t)=[a(t),S(t),\sigma(t)]$, where $X(t)$ equals the ontogenetic trajectory through time, $a(t)$ is age as a function of time, $S(t)$ represents size as a function of time, and $\sigma(t)$ represents shape as a function of time.

When ontogeny is conceptualized through the use of ontogenetic trajectories, it becomes obvious that age, size and shape may be analyzed collectively, or may involve pairwise analysis. The customary studies involving a pairwise analysis are either a study of growth through time using the variables of age and size, or an allometric study involving the variables of size and shape.

ALLOMETRY

A succinct definition of allometry is provided by Gould (1977, p. 238), who stated that "allometry is the study of relationships between size and shape." A slightly expanded version of the definition, which includes the notions of growth and proportion, may be found in Webster's New World Dictionary of the American Language (Guralnik, 1980, p. 37) where allometry is defined as "the study and measurement of relative growth of a part of an organism in comparison with the whole." Sweet (1980), Curruccini (1981), Hildebrand (1982), Jones (1988), McKinney (1988), Tissot (1988), and German and Meyers (1989), limit their discussions involving allometry to the relationships between an organism's size and shape. Not all authors so limit their use of the term allometry; some authors include functional and scaling relationships. Here again, Gould (1966, p. 587) provides a concise definition of allometry when he writes that allometry "is the study of size and its consequences." Jackson (1989, p. 602) confined allometry to biomechanical studies when he stated that "in biology, allometry is the study of the biomechanical relationship between body size and body proportion." Furthermore, Jackson defined the realm of biomechanical studies when he continued to write that "the study of allometry encompasses both how this relationship is modified through growth in an individual organism as well as the nature of intra- and interspecific differences in body proportions predicted by differences in body size." A comprehensive, yet broad, definition of allometry was provided by Gould (1966, p. 629) who wrote: "Allometry is defined as the study of proportion changes correlated with variation in size of either the total organism or the part under consideration. The variates may be morphological, physiological or chemical; the size differences may arise in ontogeny, phylogeny or the static comparison of related forms differing in size; the term is not confined to any one form of mathematical expression, such as the power function." This thesis uses the term allometry to mean the description of the relationship between size and shape, of a part in relation to the whole, of an individual organism or the part of an organism under consideration, whether the comparisons are ontogenetic, intraspecific, or interspecific in nature.

In morphological studies, allometric data is often used to describe ontogeny, to analyze structures for phylogenetic relationships, and to analyze features for functional significance. Form involves both size and shape (cf. Thompson, 1917, 1961), and the study of ontogeny involves the study of form (cf. Gould, 1977). Therefore, allometry is an important aspect of ontogenetic investigations. Natural selection operates on the morphology of organisms via genetic and epigenetic phenomena (cf. Alberch, 1980). Morphological evolution occurs through novel morphologies and heterochrony (Gould, 1977). Since inquiries of heterochrony include size and shape relations (Alberch et al., 1979), and heterochrony is an important part of evolutionary studies involving phylogenetic relationships (Gould, 1977), it follows that allometry is a prominent feature of phylogenetic analysis. Functional morphology is interpreted through structural description and functional experimentation (cf. Liem and Wake, 1985). Because a comprehensive description of structure involves characterizing the structure, position, size and shape of the structural elements (Liem and Wake, 1985), allometry is one component of functional analyses.

In On Growth and Form, D'Arcy Thompson (1917, 1961) utilized Cartesian coordinate transformations to qualify and quantify form and growth during ontogeny and phylogeny. In Cartesian coordinate transformations, the shape or form of a reference organism, or part of an organism, is inscribed into a Cartesian coordinate system. Comparisons are made by deforming the reference coordinate system to fit the shape or form of the related organism(s) or the parts under consideration (Thompson, 1917, 1961). Julian Huxley (1932, 1972), in Problems of Relative Growth, presented the equation: $y=bx^k$. This equation is currently referred to as the allometric equation. The allometric equation is a mathematical description of how the growth of one part of an organism (or component part) relates to the growth of the whole organism (or part of the organism). In the equation $y=bx^k$, x is the magnitude of the whole, y is the magnitude of the part, b is the fraction of x that y occupies at unity, and k is the ratio of the growth rate of the part to the growth rate of the whole (Huxley, 1932, 1972). When log transformed, the allometric equation becomes $\log y = \log b + k \log x$ (Huxley, 1932, 1972), which then provides a linear model of allometry (German and Meyers, 1989). For a summary and discussion of linear and nonlinear allometric models, see German and Meyers (1989).

In order to subject allometric data to quantitative analysis, the data collected must be standardized and must be either inherently numerical or possess the capacity to be expressed numerically. In mammalian skull morphology a standardized set of measurements has traditionally been recorded. However, these measurements provide little information about three dimensional morphology. It is then beneficial to develop a standardized method for recording mammalian skull data which can be utilized in three dimensional morphological investigations. It is necessary for that method to retain the capacity to be used for quantitative allometric analysis, to retain the ability to record the information which has traditionally been collected on mammalian skull specimens, and to be applicable to any mammalian species. In order for such a standardized method to be valid across all mammalian species, the method must be applicable to both those species which are characterized by having a "typical" mammalian skull morphology as well as by those species which exhibit an extremely modified morphology.

THESIS GOAL

The goal of this thesis is twofold. The first goal is to develop a methodology to record and analyze three dimensional mammalian skull morphological data. To achieve this goal, this thesis describes archiving morphological characters utilizing three dimensional Cartesian coordinates and position vectors, and describes the use of translation trajectories and translation vectors for allometric analysis. The second goal is to utilize the highly modified skull of the harbor porpoise, *Phocoena phocoena* (L.), to test the method being developed in this thesis.

THREE DIMENSIONAL MAMMALIAN SKULL MORPHOLOGY

In mammalogy, measurements are routinely utilized in taxonomic descriptions and comparisons. For example, when a museum specimen consisting of a study skin and skull is prepared, a standardized set of external measurements are taken prior to preparation. These external measurements, which are usually recorded in millimeters, are: total length, length of the tail, length of the hind foot, and height of the ear (Cockrum, 1962; Hall, 1962; DeBlase and Martin, 1974; Orr, 1982). For a description of the external measurements taken on mammalian study specimens, see Cockrum (1962), Hall (1962), and DeBlase and Martin (1974). The weight of the animal, which is generally recorded in grams, is also taken prior to preparing the specimen (Cockrum, 1962; Hall, 1962; DeBlase and Martin, 1974).

Cranial measurements are used by mammalogists to describe variation in mammalian skulls. DeBlase and Martin (1974) consider several measurements to be more or less standardized and state that the following measurements are taken on most species: condylobasal length, greatest length of the skull, breadth of the braincase, least interorbital breadth, postorbital constriction, zygomatic width, maxillary tooth row length, palatal length, length of the mandible, and mandibular tooth row length. Orr (1982) states that the following measurements of mammalian skulls are the most useful measurements to show intraspecific and interspecific variation: condylobasal length, basilar length, zygomatic breadth, mastoid breadth, palatilar length, interorbital constriction, length of the tooth row, length of the nasal bones, and length of the incisive foramina. For a description of mammalian skull measurements, see Cockrum (1962), DeBlase and Martin (1974), and Orr (1982).

Although many different measurements are used to describe the mammalian skull, only a few measurements are more or less standardized (DeBlase and Martin, 1974). Given the diversity and complexity of the skull, many measurements are tailored for use on the specific taxon under investigation. For example, diastema length is a valuable character in the study of rodent skulls (Orr, 1982). In the study of primates, craniometry is highly developed due to scientific contributions from the fields of medicine, dentistry, and anthropology. For a description of traditional landmarks of the human skull, and commonly used measurements and indices of the human skull, see Steele and Bramblett (1988).

Skull measurements have been used extensively in species descriptions and interspecific comparisons. These measurements, generally taken in a straight line from one landmark to another, are well defined and are easy to obtain (cf. Cockrum, 1962; DeBlase and Martin, 1974; Orr, 1982). An investigator can address a specific taxonomic problem by careful selection of a suite of characteristics which addresses the question. One consideration for selecting a suite of measurements is that the measurements selected should yield meaningful results. For example, diastema length is an important characteristic in rodent taxonomy (Orr, 1982).

The largest limitation to traditional skull measurements stems from the fact that these measurements are not oriented with respect to one another in three dimensional space, and consequently cannot be quantified in relation to one another in space. Therefore, in quantifying measurements of this sort, each measurement must be treated as a separate entity, as a proportionality, or as an index.

ARCHIVING THREE DIMENSIONAL MAMMALIAN SKULL MORPHOLOGY

Mammalian skulls occupy space. Therefore, there exists a theoretical advantage to archive (i. e., to record or to place in public record) mammalian skull morphology in relation to three dimensional space. Reference points, such as landmarks and foramina, may then be utilized in interspecific and intraspecific variation and ontogenetic studies. Lengths may be indirectly derived from three dimensional data and relations between reference points may be determined.

Creel and Preuschoft (1976) conducted an extensive study of lesser ape crania in which tridimensional coordinates of anatomical landmarks were determined and were subsequently utilized to analyze interspecific variation, intraspecific variation, and sexual dimorphism. The three dimensional coordinate system utilized by Creel and Preuschoft was defined as follows: the zero point for the point coordinates (x,y,z) is the intersection of a modified Frankfort plane, the transmeatal frontal plane, and the median sagittal plane (1976). The modified Frankfort plane is defined by the transmeatal axis and the orbital inferior (Creel and Preuschoft, 1976). The transmeatal axis is the line passing through the center of the external auditory meati (Creel and Preuschoft, 1976). Creel and Preuschoft (1976) point out a few advantages to determining three dimensional point coordinates of landmarks when compared with determining the linear measures of distance between anatomical points. One advantage is that coordinates are more efficient (e. g., 496 distance determinations can be made among 32 independent points which are defined by 96 coordinates). Another advantage is that it is easier to visualize points in space relative to one another than it is to visualize the relationship between measurements whose orientation in space is unknown. A further advantage is that the linear distances between points may be determined by calculation if those distances are desired.

Although Creel and Preuschoft (1976) were able to employ three dimensional analysis in the study of primate cranial morphology, the planes utilized in their coordinate system will not work for all mammals. For example, the Myrmecophagidae (anteaters) have incomplete zygoma (Vaughan, 1986) which would make it difficult to find the orbitale inferior; the skulls of the Odontoceti (toothed whales) often have the jugal bones broken off the specimen; and the auditory bullae of the Odontoceti are generally not attached to cleaned skulls. Another drawback of using the modified Frankfort (or Frankfort), transmeatal, and median sagittal planes involves being unable to readily visualize the origin of the coordinate system since it lies in the braincase and is not defined as a specific landmark. The use of the coordinate system defined by Creel and Preuschoft (1976) also makes it difficult to visualize the orientation of the skulls as they would appear in either a living animal or as a part of an articulated skeleton.

The following coordinate system is being proposed by this author as a standardized three dimensional coordinate system to be utilized in archiving and analyzing three dimensional mammalian skull morphology. The origin is the basion which is defined as the midpoint of the anterior margin of the foramen magnum in humans (Garber, 1942; Gray, 1942; Steele and Bramblett, 1988), as the most ventral point on the rim of the foramen magnum in the lesser apes (Creel and Preuschoft, 1976), and as the middle of the ventral margin of the foramen magnum in the dog (Evans and Christensen, 1979). The basion was chosen by this author as the origin because it is a traditional landmark of the skull (Steele and Bramblett, 1988), it is considered an important reference point in making linear measurements (Evans and Christensen, 1979), it appears to be a reasonably stable reference point (in that it is identifiable early in ontogeny and undergoes little change during development), and it tends to remain intact after a necropsy. The median, coronal and transverse planes intersect at the origin (or basion). The median plane is a vertical, longitudinal plane that divides the body into "symmetrical" left and right halves (Gray, 1942; Schaeffer, 1942; Dyce, Sack and Wensing, 1987; Steele and Bramblett, 1988; Pasquini and Spurgeon, 1989). Any plane parallel to the median plane is a sagittal plane (Gray, 1942; Schaeffer, 1942; Jacob and Francone, 1974; Walker, 1986; Dyce, Sack and Wensing, 1987, Steele and Bramblett, 1988; Pasquini and Spurgeon, 1989). The coronal plane passes through the longitudinal axis of the body and is perpendicular to the median plane (Gray, 1942; Schaeffer, 1942; Walker, 1986; Steele and Bramblett, 1988; Pasquini and Spurgeon, 1989). The transverse plane is perpendicular to both the median and coronal planes and is therefore perpendicular to the longitudinal axis of the body (Gray, 1942; Schaeffer, 1942; Walker, 1986; Dyce, Sack and Wensing, 1987; Pasquini and Spurgeon, 1989). Agreement exists in the definitions of the anatomical planes in both human and comparative vertebrate anatomy. However, when the definitions of the coronal and transverse planes are put into practice, a conflict involving the use of the terms exists between human anatomy and comparative vertebrate anatomy. This conflict stems from a difference in anatomical position. In human anatomy, anatomical position is established when the body is erect, with the arms at the sides and the palms forward (Gray, 1942; Schaeffer, 1942; Jacob and Francone, 1974; Steele and Bramblett, 1988). This position lends itself to utilizing the coronal plane to divide the body into front (i. e., anterior or ventral) and back (i. e., posterior or dorsal) parts, and the transverse plane to divide the body into upper (or superior) and lower (or inferior) parts (Schaeffer, 1942; Jacob and Francone, 1974; Walker, 1986; Steele and Bramblett, 1988). In quadruped anatomy, Dyce, Sack and Wensing (1987) describe standard anatomical position as being a position in which the animal is "foursquare and alert". This posture leads to employing the term "coronal plane" to be used to divide the body into dorsal and ventral portions, and the term "transverse plane" to be used to divide the body into cranial (or anterior) and caudal (or posterior) parts (Walker, 1986; Dyce, Sack and Wensing, 1987; Pasquini and Spurgeon, 1989). The definitions of coronal and transverse planes lead to direct conflict with human anatomy if they are used in mammalian skull morphology. Hence, this thesis will not employ either the term "coronal plane" or the term "transverse plane".

In the coordinate system being proposed in this thesis for mammalian skull morphology, the median plane passes through the origin (or basion), and bisects the skull into the "most bilaterally symmetrical" halves possible. Generally, the median plane will pass through the opisthion and the prosthion. The opisthion is the midpoint on the posterior margin of the foramen magnum in humans (Steele and Bramblett, 1988), or the most dorsal point on the rim of the foramen magnum (Creel and Preuschoft, 1976). The prosthion is the rostral end of the interincisive suture located between the roots of the upper central incisor teeth (Evans and Christensen, 1979), or the most anterior point on the exterior of the alveolar arch between the mesial incisors (Creel and Preuschoft, 1976). In this thesis, the median plane is the xz-plane. Therefore, the xz-plane divides the skull into left and right halves (Figure 1). The xy-plane is the plane which divides the skull into ventral and dorsal portions as noted in quadruped anatomical position (Figure 1). The xy-plane is perpendicular to the xz-plane, passes through the origin (or basion), and passes through the point in the median plane along a line connecting the most anterioventral extent of the premaxillae. One reason

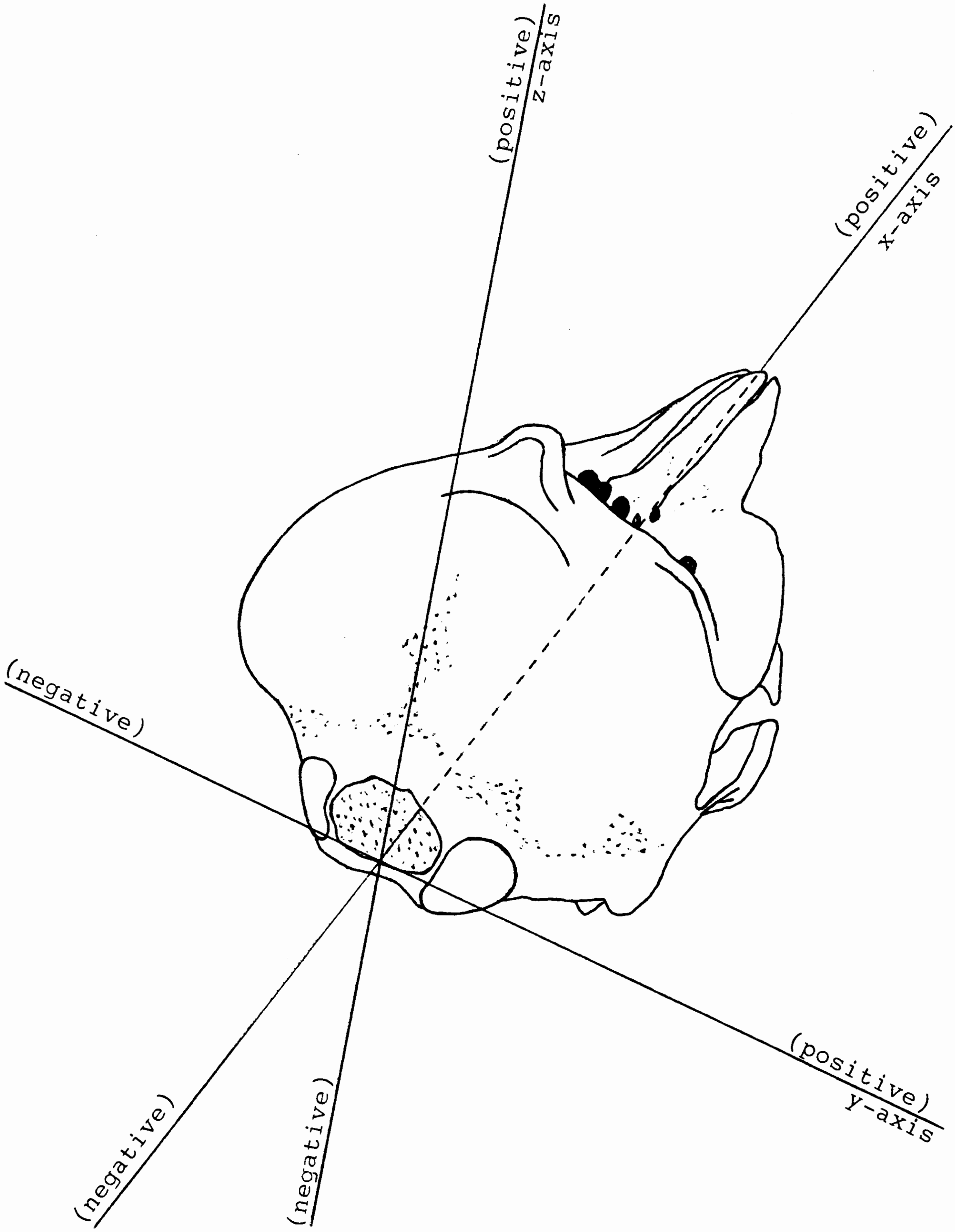


Figure 1. The orientation of the three dimensional coordinate system for a harbor porpoise (Phocoena phocoena) skull.

for recommending this anterior point is that it relates to the cranial measurement of basal length. When present, the prosthion may be a preferred landmark for the anterior point defining the xy-plane. The yz-plane is perpendicular to both the xz-plane and the xy-plane, and passes through the origin (or basion) (Figure 1). The x-axis is a longitudinal axis where the negative values are posterior to the origin and the positive values are anterior to the origin (Figure 1). The x-axis was chosen to be the longitudinal axis since most allometric studies use some form of skull length as the basis for comparing the growth of a part of the skull. For example, facial allometry may be expressed as the proportion of facial length to total skull length. The y-axis is transversely oriented so that the negative values are to the left of the origin and the positive values are to the right of the origin (Figure 1). The z-axis is dorsoventrally oriented such that the negative values are ventral to the origin and the positive values are dorsal to the origin (Figure 1).

Once a three dimensional coordinate system has been established for the mammalian skull, then morphological characteristics may be archived (i. e., recorded) for descriptive and analytical purposes. Basic morphological characteristics to be considered for archiving into such a database include landmarks such as the nasion and the porion, and openings such as the optic canal, the incisive foramen and the external auditory meatus.

In mammalian taxonomy, linear measurements are generally recorded in millimeters (Cockrum, 1962). Therefore, this author recommends that the morphological characteristics archived in the three dimensional coordinate system be recorded in millimeters. The measurements recorded should reflect the degree to which the instrumentation allows (e. g., millimeters or tenths of millimeters). The position of the morphological characteristic may be archived in a rectangular coordinate system as point coordinates or position vectors. The location of a point (P) having rectangular coordinates (x,y,z) in space may be mathematically expressed as P(x,y,z) (Ellis and Gulick, 1982; Edwards and Penney, 1986). This point coordinate will henceforth be known as a position coordinate. Figure 2 is a graphic representation of a position coordinate in a rectangular coordinate system. A point in space may also be expressed by a position vector $v=\langle x,y,z\rangle$ which is determined by a directed line segment ($\overline{OP}$) from the origin (O) to the point (P) (Ellis and Gulick, 1982; Edwards and Penney, 1986). Figure 3 is a graphic representation of a position vector in a rectangular coordinate system. In mammalian skull morphology, this author proposes that the definition of a position vector be limited to describing a vector from the origin to a point in space. Note that this definition is utilized in a more

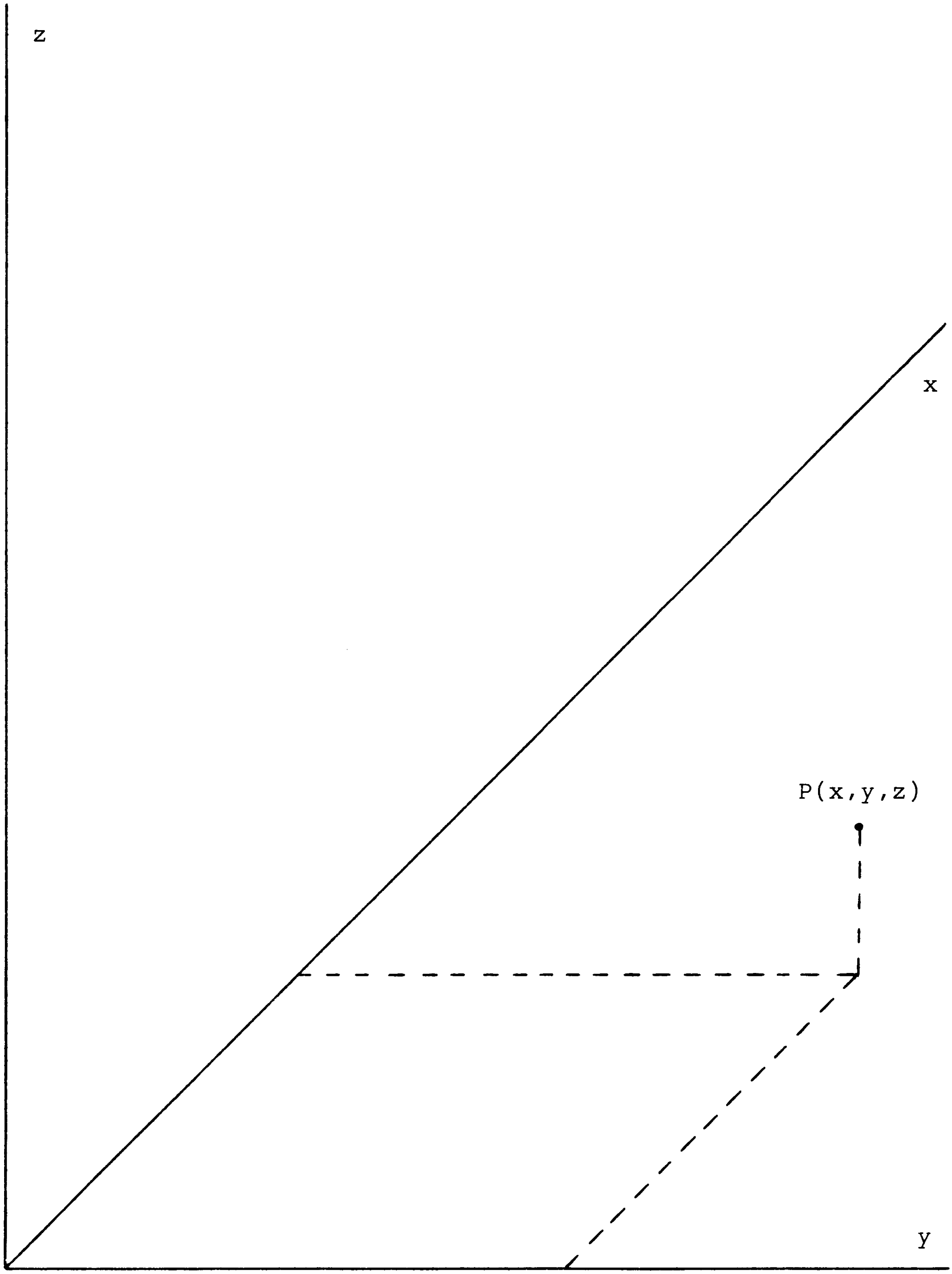


Figure 2. A position coordinate in a rectangular coordinate system.

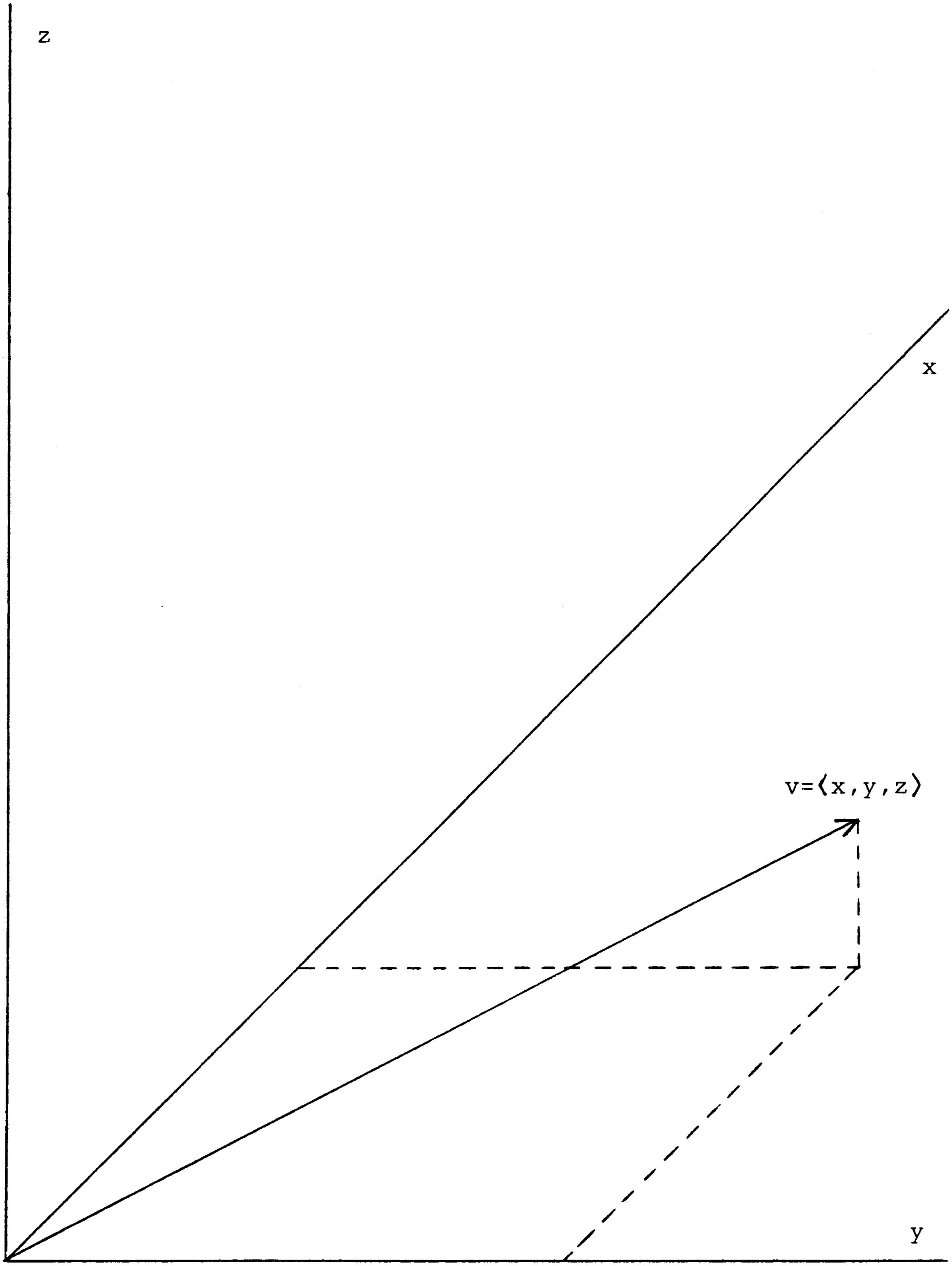


Figure 3. A position vector in a rectangular coordinate system.

restrictive manner than that which is used in calculus where any vector of the same magnitude and direction is considered to be representative of the position vector.

Aside from archiving morphological reference points in rectangular coordinate systems, spherical coordinate systems may also be utilized. In calculus, a point (P) in space may be defined by spherical coordinates $(\rho,\phi\cdot\theta)$ where ρ is the magnitude of the line segment $\overline{OP}$ (therefore $\rho=|\overline{OP}|$), ϕ is the angle between the line segment $\overline{OP}$ and the positive z-axis, and is expressed in radians, and θ is the angular polar coordinate of the projection (Q) of the point (P) into the xy-plane, and is expressed in radians where θ is measured counterclockwise from the x-axis (Ellis and Gulick, 1982; Edwards and Penney, 1986).

In order to utilize the spherical coordinate system to archive three dimensional skull morphology, the following alterations are proposed by this author. The x, y, and z axes are defined as described earlier in the thesis (Figure 1). The first spherical coordinate (m_v) is the magnitude of the position vector (v_s) and is recorded in millimeters (Figure 4). The second spherical coordinate ($\angle_{xy}$) represents the angle between the positive x-axis and the projection of the position vector onto the xy-plane (i. e., the xy-plane projection) (Figure 4). This angle is positive (i. e., $0^\circ<\angle_{xy}\leq 180^\circ$) when the y-coordinate is positive and is negative (i. e., $0^\circ>\angle_{xy}\geq -180^\circ$) when the

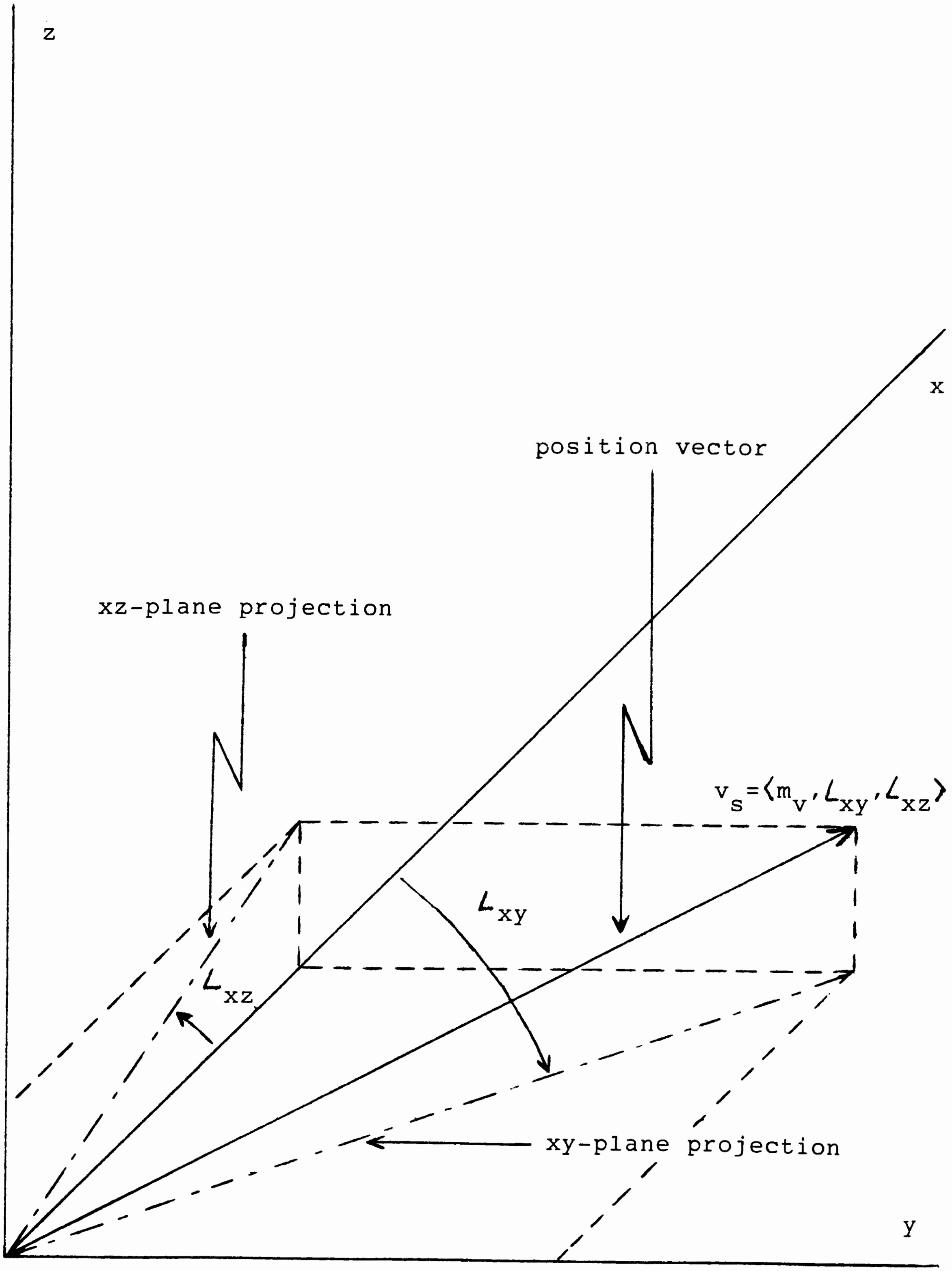


Figure 4. A position vector in a spherical coordinate system.

y-coordinate is negative. The third spherical coordinate ($\angle_{xz}$) is the angle between the positive x-axis and the projection of the position vector onto the xz-plane (i. e., the xz-plane projection) (Figure 4). This angle is positive (i. e., $0^\circ < \angle_{xz} \leq 180^\circ$) when the z-coordinate is positive and is negative (i. e., $0^\circ > \angle_{xz} \geq -180^\circ$) when the z-coordinate is negative. Figure 4 shows a graphic representation of a position vector in a spherical coordinate system.

Position coordinates and position vectors can be utilized as a proxy for shape. This is possible since either the ordered triple of the position coordinates or the x, y, and z components of the position vector may be utilized to describe a volume of space. This space is a rectangular box of known dimension, known location, and known orientation in the coordinate system. The rectangular box has a length x, a width y, and a height (or depth) z. The corner of the rectangular box is at the origin. The orientation of the rectangular box is determined by the values of x, y, and z. The shape of the box may then be described by two proportions. The first proportion comes from the x-component and the y-component of the ordered triple. It is the ratio of the y-component over the x-component (i. e., y/x). The second proportion comes from the x-component and the z-component of the ordered triple. It is the ratio of the z-component over the x-component (i. e., z/x).

Through the previous discussion, it should be evident that morphological reference points may be archived in a three dimensional coordinate system with the aid of position coordinates or position vectors. During ontogeny, the reference points may be translated within the coordinate system to a position described by different coordinates or vectors. Richards and Kavanagh (1945) discussed the use of a three dimensional coordinate system to determine the rate of change of the coordinates of reference points at any instant in time. When plotted on a three dimensional coordinate system, this reference point traces a trajectory which this author will henceforth refer to as a translation trajectory. Although a translation trajectory is biologically continuous, the morphological data will probably be collected at discrete time intervals. Therefore, when the data are plotted onto a coordinate system, the translation trajectory will appear as a series of points. These points may then be connected, in chronological order, by a series of vectors. Each vector thus drawn will be referred to as a translation vector by this author.

The idealization of a translation trajectory is that the trajectory should be derived from data taken periodically from an individual organism. This may be described as an individual translation trajectory. The concept of an individual translation trajectory can be extended to a population translation trajectory. If a series of individual translation trajectories of a given population are plotted onto a three dimensional coordinate system, then the population translation trajectory is represented by a "cloud" of points moving through space. Typically, the data required for individual and population translation trajectories cannot be acquired. This is particularly true of skeletal studies in which the specimens generally consist of prepared (or cleaned) skeletons. However, the idea of a translation trajectory may still be used to study ontogeny in a given species. This is achieved by taking measurements on a group of individual specimens which represent an ontogenetic series (e. g., a series which covers all pertinent age classes or a series which includes the size range encompassed within the species).

Translation vectors may be utilized in comparative studies concerned with sexual dimorphism, intraspecific variation, or interspecific variation. Utilized in this fashion, the translation vectors consist of a series of pairwise comparisons between two individual specimens. In practice, the position coordinates of a specified reference point in one specimen are "transformed" into the position coordinates of the same reference point in the other specimen. Rather than transforming the points within a coordinate system, D'Arcy Thompson (1917; 1961) transformed one species into another by deforming the Cartesian coordinate system. Medawar (1945) pointed out that the transformations may be represented by transforming the coordinate system or by transforming the points within the coordinate system. In regard to this point, Medawar (1945) stated that when the coordinate system is transformed then the space frame of reference is changed, and that when the points are transformed then the frame of reference is fixed and the points change. Medawar considered these two methods to be formally identical. The use of translation vectors in the stated manner falls into Medawar's catagory of maintaining a fixed coordinate system and changing the points.

When a three dimensional coordinate system is utilized to archive a suite of morphological characteristics, then the spatial relationship between the reference points may be derived from the archived database. As stated earlier, this is considered by Creel and Preuschoft (1976) to be one of the advantages of a three dimensional archive. The relative position between one reference point and another may be characterized by a relative position vector. A relative position vector lies between two reference points of the same specimen. The magnitude of the relative position vector is the length (in millimeters) between the reference points. It is the relative position vector magnitude which is customarily measured in mammalian skulls.

ANALYSIS OF THREE DIMENSIONAL MORPHOLOGY

When analyzing three dimensional morphology, the analysis is greatly simplified if two separate two dimensional analyses are performed. An analysis of the data in the xy-plane coupled with an analysis of the data in the xz-plane will achieve the same result that one three dimensional analysis would achieve. However, it should be noted that two dimensional analyses are mathematically easier to conduct than three dimensional analyses. Also, graphic representation of two dimensional analyses are less visually complicated and are easier to interpret than three dimensional analyses.

THEORETICAL EXAMPLES

Suppose that, during ontogeny, the position coordinate of a landmark on a skull is $P_0(4,2)$ at the initial time of measurement. If the position coordinate at a later time is $P_1(8,4)$, then a size change has occurred but no concomitant change in shape has occurred (Figure 5a and 5b). Both the length and the width have doubled in size. The slope of the position vector $v=\langle 4,2\rangle$ and the slope of the position vector $v=\langle 8,4\rangle$ are equal, which indicates that a change in shape has not occurred. Using the initial position coordinate $P_0(4,2)$ and position coordinate $P_1(8,2)$ at a later time, it may be seen that the slope of the corresponding position vector has changed and that the magnitude of the x-component

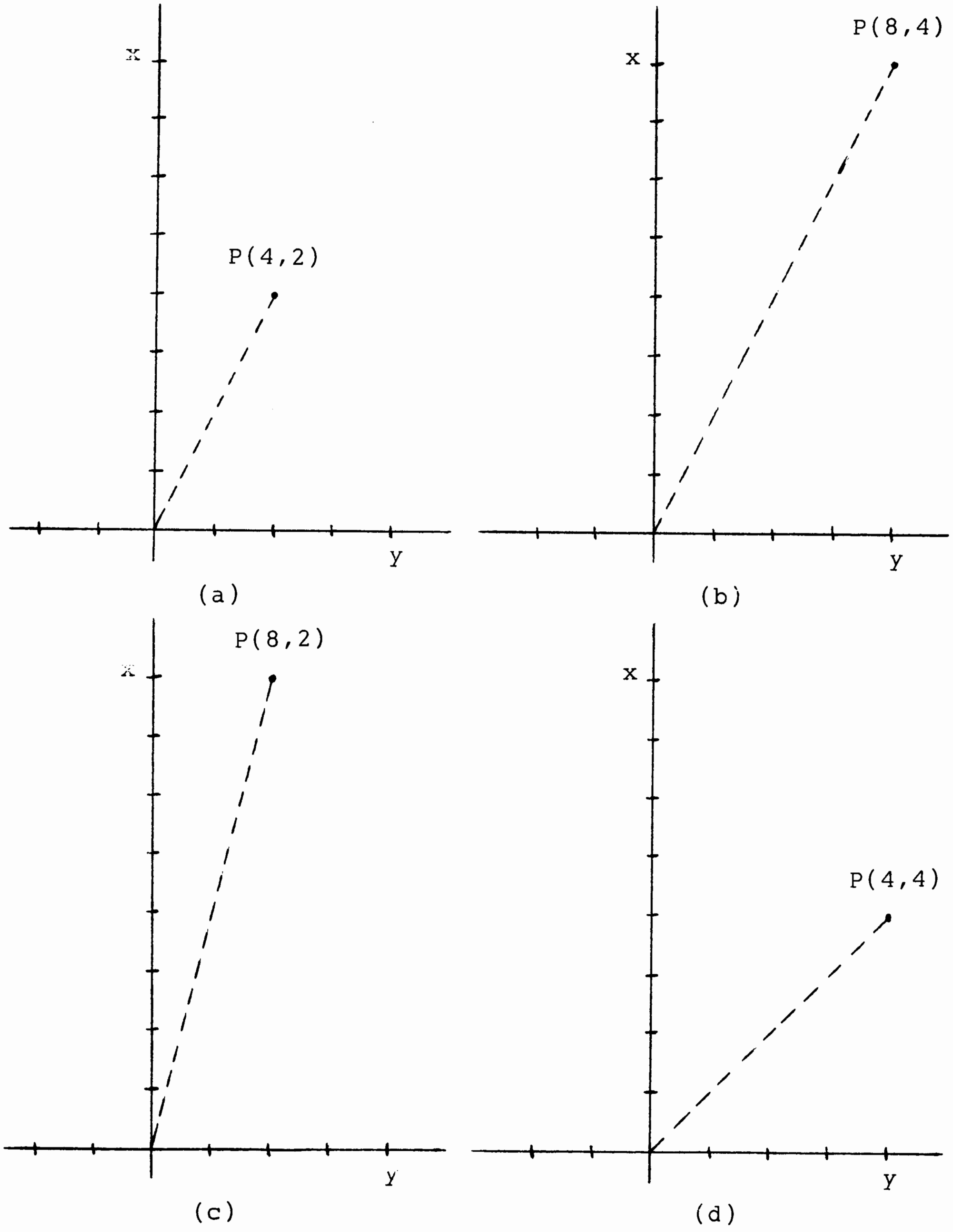
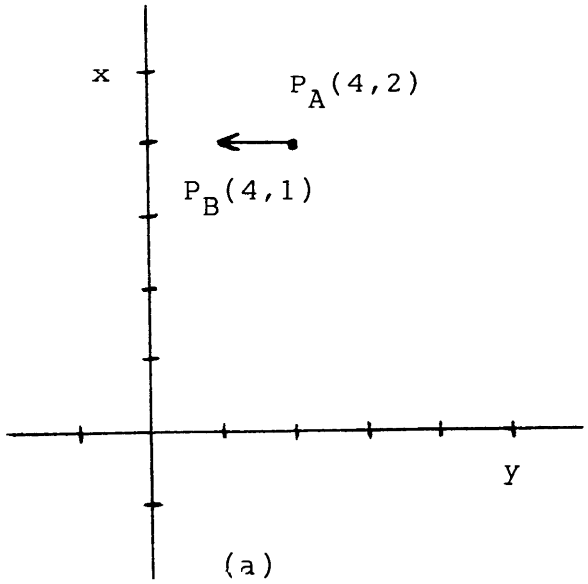


Figure 5. The position coordinates utilized in the theoretical examples involving ontogeny. Position coordinates diagrammed include: (a) P(4,2), (b) P(8,4), (c) P(8,2), and (d) P(4,4).

has changed but that the magnitude of the y-component has not changed (Figure 5a and 5c). The slope change from ½ to ¼ indicates a shape change in which the length has increased proportionally over the width. The magnitude of the x-component has doubled, whereas the magnitude of the y-component has remained unchanged. Finally, if the initial position coordinate is $P_0(4,2)$ and the position coordinate at a later time is $P_1(4,4)$, then both a shape change and a size change have occurred (Figure 5a and 5d). The increase in slope from ½ to 1 indicates a proportional broadening of the skull. In this example, the magnitude of the x-component has remained constant; therefore no increase in length has occurred. The doubling of the magnitude of the y-component indicates a doubling in width at the reference point.

These examples illustrate that position coordinates or position vectors may be employed to describe both size and shape change in ontogenetic studies. A change in size will be indicated by a change in the magnitude of the coordinates (or the position vector components). An increase in magnitude indicates an increase in size, and a decrease in magnitude indicates a decrease in size. A change in shape will be indicated by a change in slope. A decrease in slope indicates a proportional elongation, whereas an increase in slope indicates a proportional broadening if the analysis involves the xy-plane, or a proportional increase in height (or depth) if the xz-plane is being analyzed.

In comparative studies, the use of position coordinates (or position vectors) and translation vectors may be combined to analyze size and shape change, or to transform one morphology into another. For example, if specimen A of one species has a specified reference point at position coordinate $P_A(4,2)$ and specimen B of another species in the same genus or family has the same specified reference point at position coordinate $P_B(4,1)$, then a translation vector (T_{AB}) from the reference point on specimen A to the reference point on specimen B may be described as $T_{AB}=\langle 0,-1\rangle$ (Figure 6a). This translation vector indicates that this reference point has not undergone a translation involving length since the x-component is 0. The translation vector also indicates that the reference point has been translated medially so that, in specimen B, the reference point resides at a position which is ½ the distance in width of the reference point in specimen A. Another example is provided by transforming a reference point in specimen A located at position coordinate $P_A(4,2)$ to the same reference point in specimen B which is located at $P_B(2,2)$ (Figure 6b). The translation vector involved is then $T_{AB}=\langle -2,0\rangle$, which indicates that the reference point in specimen B is at the same width but at half the length when compared with specimen A. It should be noted from the previous two examples that the translation vector is derived from the two



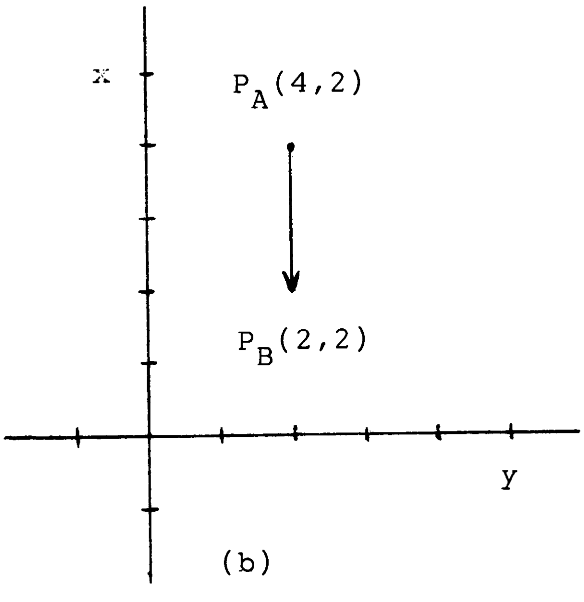


Figure 6. The position coordinates and translation vectors utilized in the interspecific theoretical examples. A translation vector from position coordinate $P_A(4,2)$ of species A to position coordinate $P_B(4,1)$ of species B (a). A translation vector from position coordinate $P_A(4,2)$ of species A to position coordinate $P_B(2,2)$ of species B (b).

position coordinates such that $T_{AB}=\langle x_B-x_A, y_B-y_A\rangle$. Also evident in the examples is the fact that the proportion of a dimension occupied by the transformed coordinate when compared to the untransformed coordinate is the ratio of the transformed coordinate component to the untransformed coordinate component times one hundred. The other quantity which may be derived from the position coordinates and the translation vector is the proportional change in dimension. The proportional change in dimension is derived by taking the ratio of the translation vector component over the untransformed position coordinate component and then multiplying that quantity by one hundred.

In all of the preceding examples, the reference points were located in the first octant of the coordinate system. For reference points located in other octants, analyses may be carried out in a manner similar to the analyses carried out for the reference points located in the first octant. When analyzing data from other octants, the investigator should keep in mind what the mathematical analysis is indicating relative to the planes of orientation. The method of three dimensional analysis should allow the investigator to check, by inspection, both the data and the conclusions drawn from the data.

SKULL MORPHOLOGY AND THE MODEL OF HETEROCHRONY

As discussed in the background section of this thesis, the model of heterochrony utilizes ontogenetic trajectories which are inscribed into age-size-shape space. As previously indicated, position coordinates (and position vectors) may be utilized as a proxy for shape. Therefore, the position coordinates of a given ontogenetic translation trajectory may be used in plotting the shape coordinates in age-size-shape space. This also implies that the same position coordinates may be utilized in allometry studies when the age data is missing.

BIOMETRY IN ALLOMETRY

Graphs of allometric data generally take the form of rectangular coordinates including arithmetic, semilogarithmic, and logarithmic coordinates. These graphs provide visual representation of the numerical data. In allometric analyses, the data are often interpreted by the use of the mathematical expression $y=mx+b$ (where m is the slope and b is the y-intercept). This equation expresses a linear relationship between the x and y components. Linear relationships are easily interpreted since the variables covary directly with one another. If analysis of the data yields an arithmetic linear relationship, an isometric relationship exists between the variables (Simpson, Roe and Lewontin, 1960).

In allometric growth, the arithmetic ratio of the variables changes over time (Simpson, Roe and Lewontin, 1960). Allometric growth may often be modeled by the arithmetic expression $y=ax^b$ (White and Gould, 1965; Walker, 1987), which may be log transformed into the expression $\log y = \log a + b \log x$ (Huxley, 1972; Reeve and Huxley, 1945; Richards and Kavanagh, 1945; Simpson, Roe and Lewontin, 1960: Gould, 1966, 1977; Schmidt-Neilson, 1984; McKinney, 1988; German and Meyers, 1989). The logarithmic transformation of the allometric equation $y=ax^b$ often linearizes allometric data.

In allometric relationships, the two variables under investigation are considered to be random variables which are interdependent. For ststistical analysis of interdependent variables, Sokal and Rohlf (1981, 1987) and Walpole and Myers (1989) consider correlation analysis to be appropriate. In correlation analysis, a correlation coefficient is computed and is utilized to describe the functional strength of the relationship between the two variables (Sokal and Rohlf, 1981, 1987; Walpole and Myers, 1987). Both Sokal and Rohlf (1981, 1987) and Walpole and Myers (1989) consider it to be inappropriate to use regression analysis and regression coefficients when the two variables under investigation cannot be described as a dependent variable covarying with an independent variable. When discussing the proper statistical technique to employ to the allometric equation, Simpson, Roe and Lewontin (1960) stated that the coefficient of correlation gives the intensity of the relationship, while regression gives the quantitative relationship. They state further that a zoologist renders useless the entire procedure of observation if only the intensity of the relation is determined and not its quantitative nature, and that the methods of regression analysis may be applied with perfect confidence. It seems reasonable to employ both regression and correlation analyses to the study of allometry since even Sokal and Rohlf (1981, 1987) stated that a simple mathematical relationship exists between the regression coefficient and the correlation coefficient. For statistical treatment of allometric data, the reader is referred to Simpson, Roe and Lewontin (1960), Creel and Preuschoft (1976), Sokal and Rohlf (1981, 1987), and Walpole and Myers (1989).

THE ARCHIVE: LANDMARKS, OPENINGS AND PSEUDOLANDMARKS

Biologically homologous structures are important in the study of comparative anatomy and morphology. Homologous structures may be topographically or spatially homologous, ontogenetically homologous, or phylogenetically homologous (Bookstein et al., 1985). A correspondence in location or relative position (Woodger, 1945; Jardine, 1969; Hansell, Bookstein and Powell, 1980) may be described as spatial homology. A correspondence in ontogeny may be described as ontogenetic homology (Bookstein et al., 1985). A feature which is directly or indirectly inherited from the same feature in a common ancestor may be described as phylogenetic or evolutionary homology (Woodger, 1945; Jardine, 1969; Gould, 1977; Minkoff, 1983).

Morphological correspondences (Woodger, 1945) or homologous features may be utilized in morphological studies. Generalized landmarks and openings in the skull provide reference points which may be utilized in comparisons across taxons. A landmark is a homologous reference point which may be identified by a feature of local morphology (Bookstein et al., 1985). Openings in the skull include foramina, canals, fissures and passages (Cockrum, 1962; Walker, 1986). Landmarks and openings provide the homologous features needed for archiving morphology. In narrowly focused comparative studies, pseudolandmarks may also be archived into a database. Pseudolandmarks are points which bear a reliable operational definition but are not homologous landmarks (Bookstein et al., 1985). For descriptions of mammalian skull landmarks and openings, see Gray (1942), Schaeffer (1942), Cockrum (1962), DeBlase and Martin (1974), Creel and Preuschoft (1976), Evans and Christensen (1979), Walker (1986), Steele and Bramblett (1988), and Pasquini and Spurgeon (1989). Ultimately then, the three dimensional archive should include homologous landmarks and openings in all morphological studies, and may include pseudolandmarks in specialized investigations.

SUMMARY

A standardized method of archiving three dimensional mammalian skull morphology has been developed in this section of this thesis. The method developed includes a description of the orientation of the three dimensional coordinate system on a mammalian skull, and a description of three distinct ways to mathematically define the position of morphological characteristics within the coordinate system. Methods of analyzing the three dimensional archive are developed for use in allometric, ontogenetic, heterochronic, and comparative studies. The methods developed include the utilization of translation trajectories, translation vectors, and relative position vectors. The use of correlation and regression analyses are briefly discussed, and the conclusion is drawn that both methods of analysis are appropriate in allometric investigations. Also, the general content of the morphological archive is discussed. Therefore, the purpose of this section of this thesis has been to develop a standardized method of archiving and analyzing three dimensional mammalian skull morphology.

HARBOR PORPOISE SKULL MORPHOLOGY

Scientific publications on the harbor porpoise have employed many different names as shown by the lists of synonyms in works by Gaskin et al. (1974) and Hall (1981). The scientific name of a species is a binomen consisting of a generic name and a specific name (DeBlase and Martin, 1974). The specific epithet for the harbor porpoise dates back to 1758 when Carolus Linnaeus applied the binomen *Delphinus phocoena* (Gaskin et al., 1974; Hall, 1981). The generic name (*Phocoena*) was given by George S. Cuvier and dates back to 1816 (Schevill et al., 1969; Hall, 1981). Therefore, the correct name for the harbor porpoise is *Phocoena phocoena* (Linnaeus, 1758) (Schevill et al., 1969; Gaskin et al., 1974; Leatherwood et al., 1976; Rice, 1977; Hall, 1981; Evans, 1987). The harbor porpoise, *Phocoena phocoena* (L.), has been put into either the family Delphinidae (Rice, 1977; Hall, 1981) or the family Phocoenidae (Gaskin et al., 1974; Leatherwood et al., 1976; Barnes, 1985; Evans, 1987). The content and context of the harbor porpoise is: Order Cetacea, Suborder Odontoceti, Superfamily Delphinoidea, Family Phocoenidae, Subfamily Phocoeninae (Schevill et al., 1969; Gaskin et al., 1974; Leatherwood et al., 1976; Barnes, 1985; Evans, 1987). In the genus *Phocoena*, the following four extant species are currently recognized: *Phocoena phocoena*, *Phocoena spinipinnis*, *Phocoena diotrica*, and *Phocoena sinus* (Gaskin et al., 1974; Barnes, 1985). In 1961, the American Society of Mammalogists Committee on Marine Mammals published "Standardized Methods for Measuring and Recording Data on the Smaller Cetaceans" (Norris, 1961). Along with the weight and counts such as the number of teeth and the number of throat grooves, the committee presented a number of standardized external measurements to be recorded on cetaceans (Appendix A). The committee stated that, with the exception of girths, all measurements should be taken in straight lines, and not over the curvature of the body; and that all length measurements from the tip of the snout should be taken parallel to the longitudinal axis of the body. In 1976, Leatherwood et al. added several additional measurements to the standardized list of external measurements of cetacea (Appendix B). Perrin (1975), in his study on the spotted porpoise (*Stenella attenuata*) and the spinner porpoise (*Stenella longirostris*), used 22 of the 36 measurements proposed by Norris (1961). However, Perrin's measurements were made from one anatomical point to another, whereas those proposed by Norris are to be measured parallel to the longitudinal axis of the body. Therefore, the data recorded via these two methods are not directly comparable. Perrin (1975) argues that the point to point method of measurement produces more precise results.

Scheffer and Slipp (1948) reported weights and as many as 18 external measurements of six adult female harbor porpoises. Their paper also provided measurements of weights and lengths of eight fetal specimens (three females, five males) and two juvenile specimens (one female, one male). Mohl-Hansen (1954) provided an extensive table of weight and length data from harbor porpoises including 389 harvested specimens (164 females, 225 males) and 119 fetal specimens (61 females, 58 males). Bryden (1972) analyzed Mohl-Hansen's 1954 data and derived mathematical relationships between length and weight for the harbor porpoise. Bryden stated that for females, $\log \text{length} = 1.606 + 0.329 \log \text{weight}$; and for males, $\log \text{length} = 1.552 + 0.357 \log \text{weight}$. Fisher and Harrison (1970) provided lengths and weights in their descriptions of harbor porpoises which included embryos, fetuses, juveniles, immature females, mature females, immature males, and mature males. Nielsen (1972) correlated growth layers in the dentine of harbor porpoise teeth with the body length of the animal. Nielsen also demonstrated that the teeth in the harbor porpoise exhibit sexual dimorphism. In a comparison involving harbor porpoise length, van Bree (1973) wrote that the females may attain greater length than the males. Stuart and Morejohn (1980) studied three external measurements of the harbor porpoise in relation to dentinal growth layer groups. The authors found a significant correlation between the log of the dentinal growth layer groups and total length, snout to the tip of the dorsal fin length, and flipper length. Stuart and Morejohn described these relationships with separate regression equations for the females and for the males.

Perrin's (1975) detailed investigation of the spotted porpoise (Stenella attenuata) included 119 skeletal measurements and meristics (i. e., number of body parts or segments) which involved 42 measurements and five meristics of the head skeleton, 27 measurements and 28 meristics of the postcranial axial skeleton, and 12 measurements and five meristics of the appendicular skeleton (Appendix C). Many of the cranial and postcranial skeletal measurements and meristics exhibited covariance with the postnatal dentinal layers. Walker (1981) utilized 32 of the cranial measurements and meristics found in Perrin (1975) and added mandibular condyle width in an investigation of the geographic variation of the bottlenose dolphin (Tursiops). Schnell et al. (1985) analyzed 612 adult specimens of the spotted dolphin (Stenella attenuata) for sexual dimorphism. This study included 32 cranial measurements and four cranial meristics. Most characters are represented in Perrin (1975) with three modifications and five additions. Hersh and Duffield (1990) utilized a suite of 32 skull characteristics, all of which may be found in Perrin (1975), to compare coastal and offshore bottlenose dolphins

(*Tursiops*).

In describing *Phocoena sinus* (the Gulf of California harbor porpoise), Norris and McFarland (1958) compared the new species with three other *Phocoena* species including *Phocoena phocoena*. Eleven skull characters and two ratios were utilized in this comparison. Stuart and Morejohn (1980) presented data for 12 cranial measurements taken on 57 harbor porpoise specimens (31 females, 26 males) (Appendix D). Correlation coefficients and regression equations were derived for the cranial measurements in relation to the log of the dentinal growth layer groups (Stuart and Morejohn, 1980). Correlation coefficients and regression equations were provided separately for female and male specimens (Stuart and Morejohn, 1980). Yurick and Gaskin (1987) utilized 16 cranial measurements and meristics to assess populational differences in harbor porpoise populations (Appendix E). Regression coefficients for the cranial measurements were derived for the three populations under investigation by Yurick and Gaskin as well as a few regression equations. Furthermore, Yurick and Gaskin (1988) addressed the issue of asymmetry in harbor porpoise skulls utilizing a few cranial measurements.

It is evident from the preceding papers which utilized craniometrics to study the harbor porpoise that skull morphology has been used to address interspecific variation (Norris and McFarland, 1958), growth (Stuart and Morejohn, 1980), intraspecific variation (Yurick and Gaskin, 1987), and asymmetry (Yurick and Gaskin, 1988). As developed earlier in this thesis, the method of archiving three dimensional mammalian skull morphology may be utilized to investigate intraspecific variation, interspecific variation, and ontogeny. This is achieved through the use of position coordinates or position vectors to locate the position of landmarks and openings in three dimensional space via a standardized coordinate system oriented on each skull. The main advantage of archiving morphological characteristics in a three dimensional coordinate system is that the data recorded retains the ability to be used in traditional investigations such as comparative and developmental studies as well as having the ability to be subjected to three dimensional morphological analysis. In this section of this thesis, harbor porpoise skulls were utilized to test the methodology developed in the section of this thesis entitled "Three Dimensional Mammalian Skull Morphology". Harbor porpoise skulls were employed to test the standardized method of archiving and analyzing three dimensional mammalian skull morphology because the harbor porpoise skulls are highly modified in comparison to "typical" mammalian skulls and therefore provide a good model to test whether or not the standardized method developed in this thesis may be applied to all mammalian species.

MATERIALS AND METHODS

Three female harbor porpoise (Phocoena phocoena) skulls from the National Marine Mammal Laboratory (NMML) Research Collection of the National Marine Fisheries Service (NMFS) at the National Oceanic and Atmospheric Administration (NOAA) in Seattle, Washington were measured. The specimens came from incidental takes (i. e., kills) from the Spike Rock Fishery off the Washington coast. Data provided by the NMFS NMML on each harbor porpoise specimen included: species, date of collection, collection location, circumstance, sex, length, weight and age (Appendix F). The age of the specimen was determined by the number of growth layer groups of teeth extracted from the middle of the lower jaw. The position coordinates for 93 skull landmarks and pseudolandmarks were placed into a three dimensional morphological archive utilizing the three dimensional coordinate system discussed in the section of this thesis entitled "Three Dimensional Mammalian Skull Morphology". The skull landmarks and pseudolandmarks contained in the three dimensional morphological archive for the harbor porpoise are described in Appendix G.

Position coordinates were obtained in the following manner. A T-square was suspended between two lab stands with the broad side of the rule in the vertical plane to avoid sagging. Utilizing an aluminum level, the ends of the T-square were adjusted until the T-square was level. Two plumb lines were attached to the same side of the T-square. Each plumb line consisted of a medium weight sewing needle acting as the plumb bob attached to a lightweight thread which served as the line. The skull was placed under the T-square with the rostrum of the skull placed on a horizontal rod that was vertically adjustable. Utilizing the plumb bobs, the rostrum was moved up or down until the basion and the most anterior inferior point of the most anterior premaxilla were level. This procedure leveled the xy-plane. The plumb lines were adjusted so that the tip of one needle just touched the basion and the tip of the other needle resided at the same level as the anterior inferior point of the premaxillae. The median plane of the skull was aligned with the ruled side of the T-square, which brought the median plane of the skull into alignment with the tips of the plumb bobs. This procedure set the median plane (i. e., the xz-plane) when the skull was in the upright position. When the skull was upside down, the median plane was oriented by adjusting the skull so that the basioccipital crests were level. A second T-square was attached to an aluminum level. A third plumb line was suspended from this T-square on the side with the rule. The guide on the head of this second T-square was abutted against and moved along the top of the suspended T-square. By moving the second T-square and the plumb line suspended from it, the plumb bob was adjusted so that it just touched the landmark or pseudolandmark which was being measured. This process made it possible to simultaneously measure and archive an ordered triple representing the distances from the origin along the x, y, and z axes to each landmark or pseudolandmark. Figure 7 shows the apparatus used to measure the three dimensional coordinates. The anterioposterior component (i. e., the x-component) was measured as the distance between the plumb line suspended at the origin (or basion) along the suspended T-square to either the landmark plumb line or to the edge of the movable T-square which has the landmark plumb line suspended from it. The mediolateral component (i. e., the y-component) was measured as the distance between the edge of the suspended T-square (located at the median plane) and the landmark plumb line suspended from the movable T-square. The dorsoventral component (i. e., the z-component) was measured as the difference between the basion plumb line length and the landmark plumb line length. The distances were measured and recorded to the nearest millimeter (mm). Plus (+) and minus (-) signs were used to indicate the positive and negative directions along the axes. The landmarks or pseudolandmarks which were accessible from the dorsal aspect of the skull were measured with the skull in an upright position. The landmarks which were accessible from the ventral aspect of the skull were measured with the skull upside down.

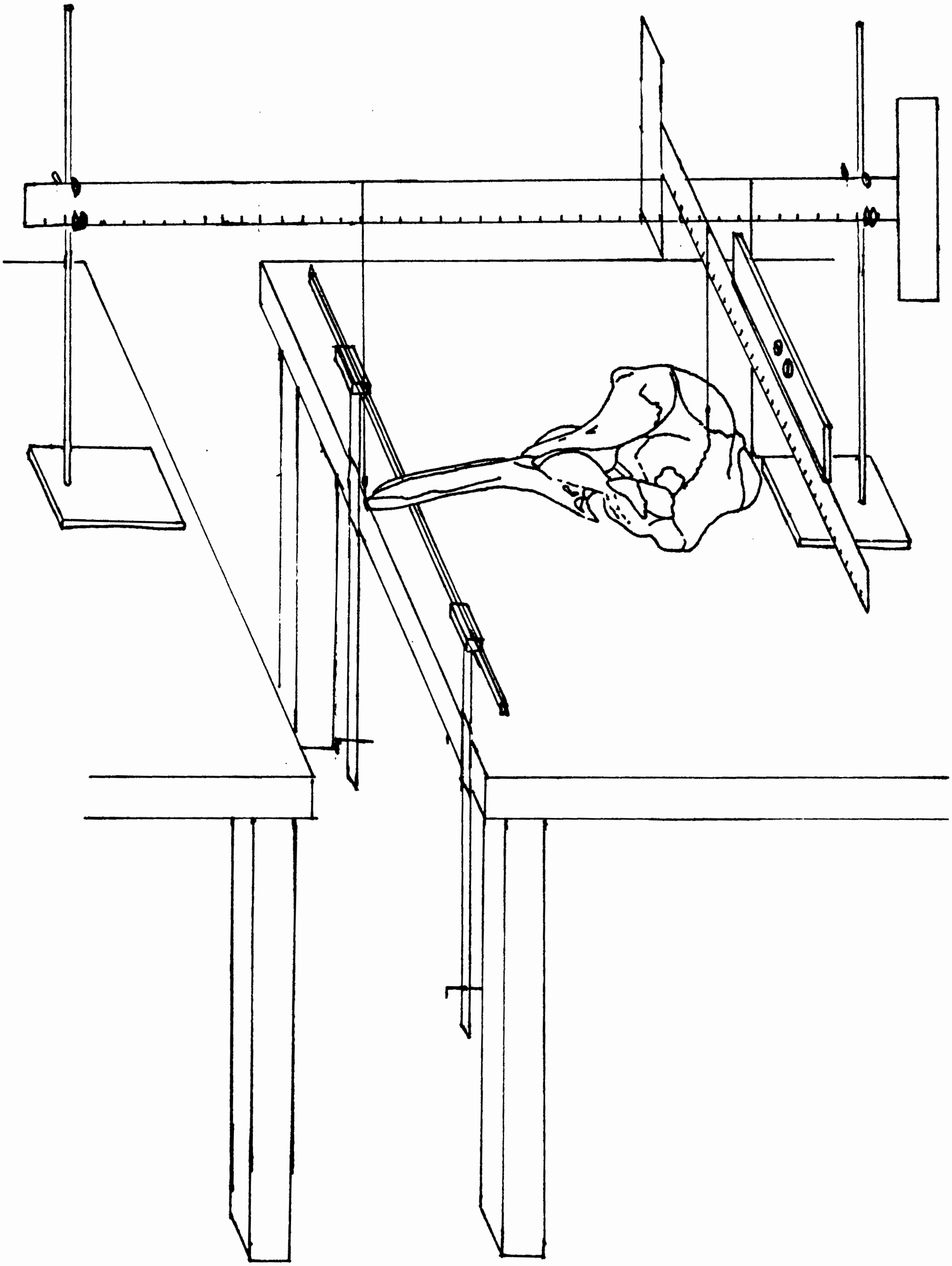


Figure 7. The apparatus used to measure the location of the skull features within the three dimensional coordinate system.

RESULTS

For the three harbor porpoise skulls measured, 93 landmarks, pseudolandmarks, and foramina were archived via position coordinates into a three dimensional skull morphology archive (Appendix H). The archive was inspected to determine the sequence of specimens which comprise a series of specimens in a continuum from the smallest specimen (i. e., the shortest specimen) to the largest specimen (i. e., the longest specimen). The series was determined to be: SK 0002, SK 0001, SK 0003. The archive was then inspected for reference points which might have informative translation trajectories. During this process, reference points were excluded from analysis for several reasons. The foramen magnum inferior (FRMGIF) was omitted from analysis since by definition it is the origin of the coordinate system and is therefore not subject to change. The exoccipital sinistral lateralis (EXOCSNLT) and the exoccipital dextral lateralis (EXOCDXLT) were not spatially homologous between specimens or within a specimen. Other reference points were omitted because the reference points were not correlated by inspection or the reference points had excess variation due to the fact that the reference points were pseudolandmarks. Potentially informative translation trajectories were identified as having reference points which showed a trend in translation in one or more component axes. Translation vectors were derived for the reference points selected. These translation vectors included the translation vector from SK 0002 to SK 0001 (i. e., $T_{2-1}=\langle x,y,z\rangle$) and the translation vector from SK 0001 to SK 0003 (i. e., $T_{1-3}=\langle x,y,z\rangle$) (Table I). The slopes (i. e., the ratio of the y-component to the x-component) of the position vectors were determined for the reference points showing a trend in both the x-component and the y-component (Table II, Figures 8 through 13). In the same manner, the slopes of the position vectors were determined for the reference points showing trends in both the x-component and the z-component (Table III, Figures 14 and 15). The archive was also inspected for reference points showing a trend toward an increased deviation from symmetry. Only one reference point showing this trend was found. A translation vector was derived for this reference point (Table IV). This reference point was also subjected to an analysis to determine the deviation from symmetry in relation to the skull size. This was achieved by determining the ratio and the percent of the y-component of the reference point to the magnitude of the x-component of the relative position vector from the origin to the right anterioventralmost point of the right premaxilla (Table V, Figure 16). An ontogenetic trajectory from the smallest skull to the largest skull was derived for cranial growth in relation to skull growth by combining age, size, and shape data (Table VI, Figure 17). For the ontogenetic trajectory, the growth layer groups of the teeth were used as a proxy for age, the size of the skull was defined as the magnitude of the relative position vector between the origin and the anterioventralmost point of the right premaxilla, and the ratio of the cranial length to the skull length was employed as a shape proportionality.

DISCUSSION

Harbor porpoise skulls were employed to test whether or not the method of archiving three dimensional skull morphology (which as developed in the second section of this thesis) may be utilized in ontogenetic and allometric investigations. The reference points which show a trend in the translation of the reference point in one or more of the coordinate axes (Table I) provide evidence for directional growth and thus illustrate that the archive may be utilized in ontogenetic studies. The reference points which show a trend in the translation of the reference point in two (or three) of the coordinate axes, indicate that the components of those axes covary. Table II and Figures 8 through 13 show covariance in the xy-plane; Table III and Figures 14 and 15 show covariance in the xz-plane. When components covary with one another, then isometry or allometry is exhibited. When the slopes of the position vectors for a given reference point are equal, then isometry for that reference point is indicated (Table II, Figures 10-13). On the other hand, when the slopes of the position vectors for a given reference point change, then allometry is indicated for that reference point (Tables II and III, Figures 8-9 and 14-15). Thus, the reference points which covary with one another illustrate that the archive may be utilized in all metric investigations. The archive may also be utilized to study skull asymmetry as illustrated by the reference point which shows a trend to increase deviation from symmetry (Tables IV and V, Figure 16). An ontogenetic trajectory for the harbor porpoise was developed in order to illustrate that the archive may also be utilized in ontogenetic investigations involving ontogenetic trajectories (Table VI, Figure 17).

Conclusions cannot be drawn regarding the allometry and ontogeny of the harbor porpoise skull with a sample size of three skulls. However, the harbor porpoise has provided a vehicle to test the use of a three dimensional archive in mammalian skull morphology. The methodology employed to demonstrate that the use of a three dimensional archive to detect ontogeny, allometry and asymmetry in harbor porpoise skulls indicates that the three dimensional archive proposed in this thesis may in fact be utilized in morphological investigations of this sort.

TABLE I

TRANSLATION VECTORS FOR THE REFERENCE POINTS WHICH SHOW A TREND IN TRANSLATION IN ONE OR MORE COMPONENT AXES

REFERENCE POINT ABBREVIATION	TRANSLATION VECTOR T_{2-1}=⟨x,y,z⟩	TRANSLATION VECTOR T_{1-3}=⟨x,y,z⟩
01) LTOCCDLSP	⟨-1,1,11⟩	⟨-1,0,-2⟩
02) RTOCCDLSP	⟨0,1,9⟩	⟨-1,6,-6⟩
03) SPOCSP	⟨14,0,18⟩	⟨-1,0,0⟩
04) LTJGPRAPX	⟨4,-14,3⟩	⟨3,-2,-6⟩
05) RTJGPRAPX	⟨2,8,-4⟩	⟨8,3,0⟩
06) ITPRTAPX	⟨10,-3,15⟩	⟨-3,-6,-2⟩
07) LTSQMLMB	⟨2,-14,11⟩	⟨1,0,0⟩
08) RTSQMLMB	⟨2,7,11⟩	⟨5,5,-1⟩
09) LTPTOBAPX	⟨9,-11,-2⟩	⟨7,0,-4⟩
10) LTZYGPR	⟨7,-16,8⟩	⟨12,-1,-8⟩
11) RTZYGPR	⟨4,10,10⟩	⟨14,4,-9⟩
12) ITNSLSTAT	(2,3,11)	⟨1,-4,3⟩
13) ITNSLFTNSL	⟨8,3,9⟩	⟨-2,-4,1⟩
14) LTNSLLT	⟨7,-2,14⟩	⟨5,-3,-10⟩
15) RTNSLLT	⟨7,2,10⟩	⟨3,1,-2⟩
16) LTMXAT	⟨33,2,1⟩	⟨26,2,-4⟩
17) LTMXDRPT	⟨-3,-14,-1⟩	⟨0,-2,-1⟩
18) RTMXAT	⟨33,-2,4⟩	⟨27,1,-5⟩
19) RTMXDRPT	⟨0,4,9⟩	⟨4,6,-2⟩
20) VTITMXSTAT	⟨15,-2,6⟩	⟨24,-1,1⟩
21) VTITMXSTPT	⟨0,-1,5⟩	⟨25,-1,0⟩
22) LTATOBAPX	⟨13,-11,12⟩	⟨8,-4,-1⟩
23) RTATOBAPX	⟨12,7,13⟩	⟨11,2,1⟩
24) LTPTIFOBFR	⟨9,-11,15⟩	⟨4,-4,-4⟩
25) LTATIFOBFR	⟨5,-4,12⟩	⟨20,6,0⟩
26) RTPTIFOBFR	⟨9,2,12⟩	⟨3,2,0⟩
27) RTATIFOBFR	⟨3,4,16⟩	⟨21,-3,-2⟩
28) LTPRMXAT	⟨31,1,4⟩*	⟨27,-2,0⟩
29) LTPRMXDRPT	⟨-3,3,14⟩	⟨4,-9,-1⟩
30) LTPRMXVTPT	⟨16,1,7⟩	⟨20,-2,1⟩
31) RTPRMXAT	⟨30,-1,9⟩*	⟨27,5,-5⟩
32) RTPTMXDRPT	⟨-1,0,12⟩	⟨3,-1,-1⟩
33) LTPRMXFR	⟨11,0,9⟩	⟨8,-7,5⟩
34) RTPRMXFR	⟨8,4,14⟩	⟨5,-4,4⟩
35) VMRAT	⟨24,0,12⟩	⟨28,0,-9⟩
36) VMRDRPT	⟨-1,1,15⟩	⟨3,-4,3⟩

TABLE I

TRANSLATION VECTORS FOR THE REFERENCE POINTS WHICH SHOW A TREND IN TRANSLATION IN ONE OR MORE COMPONENT AXES (continued)

REFERENCE POINT ABBREVIATION	TRANSLATION VECTOR $T_{2-1}=\langle x,y,z\rangle$	TRANSLATION VECTOR $T_{1-3}=\langle x,y,z\rangle$
37) VMRPRC	⟨3,0,1⟩	⟨10,-2,-1⟩
38) LTPTRAT	⟨6,-4,2⟩	⟨11,2,2⟩
39) LTPTRPRCPT	⟨2,-7,-1⟩	⟨9,2,0⟩
40) ITPLTSTAT	⟨-2,-1,2⟩	⟨27,-2,4⟩
41) ITPLTSTPT	⟨9,-1,6⟩	⟨17,-2,4⟩
42) LTPLTAT	⟨11,-8,7⟩	⟨11,5,4⟩
43) LTPLTPT	⟨8,-3,2⟩	⟨9,0,-1⟩
44) RTPLTAT	⟨10,4,9⟩	⟨14,-4,-3⟩
45) RTPLTPT	⟨5,-1,2⟩	⟨11,-4,-1⟩
46) LTLCAT	⟨14,-9,13⟩	⟨10,-5,-2⟩
47) RTLCAT	⟨11,12,14⟩	⟨12,-2,-3⟩
48) LTOBSP	⟨11,-10,13⟩	⟨12,-9,-8⟩
49) RTOBSP	⟨8,15,13⟩	⟨17,-4,-3⟩
50) LTTMPFSSP	⟨-1,-4,14⟩	⟨18,-7,-5⟩
51) RTTMPFSSP	⟨-4,4,12⟩	⟨11,4,0⟩
52) LTEXNRSAT	⟨2,-1,14⟩	⟨9,0,-7⟩
53) LTEXNRSPT	⟨5,-2,9⟩	⟨4,1,0⟩
54) LTEXNRSLT	⟨7,0,14⟩	⟨9,3,0⟩
55) RTEXNRSAT	⟨1,3,10⟩	⟨9,-7,-6⟩
56) RTEXNRSPT	⟨5,0,8⟩	⟨7,0,-3⟩
57) RTEXNRSLT	⟨4,1,11⟩	⟨4,-3,2⟩

* measure suspect

TABLE II

POSITION VECTORS AND SLOPES FOR REFERENCE POINTS SHOWING TRANSLATION TRENDS IN BOTH THE X-COMPONENT AND THE Y-COMPONENT

REFERENCE POINT ABBREVIATION	POSITION VECTOR $V=\langle x,y\rangle$	SLOPE y/x
1) LTZYGPR	$V_2=\langle 81,-63\rangle$	-0.78
	$V_1=\langle 88,-79\rangle$	-0.90
	$V_3=\langle 100,-80\rangle$	-0.80
2) RTZYGPR	$V_2=\langle 82,64\rangle$	0.78
	$V_1=\langle 86,76\rangle$	0.88
	$V_3=\langle 100,80\rangle$	0.80
3) LTNSLLT	$V_2=\langle 83,-21\rangle$	-0.25
	$V_1=\langle 90,-23\rangle$	-0.26
	$V_3=\langle 95,-26\rangle$	-0.27
4) RTNSLLT	$V_2=\langle 82,8\rangle$	0.10
	$V_1=\langle 89,10\rangle$	0.11
	$V_3=\langle 92,11\rangle$	0.12
5) LTATOBAPX	$V_2=\langle 143,-32\rangle$	-0.22
	$V_1=\langle 156,-43\rangle$	-0.28
	$V_3=\langle 164,-47\rangle$	-0.29
6) RTATOBAPX	$V_2=\langle 142,30\rangle$	0.21
	$V_1=\langle 154,37\rangle$	0.24
	$V_3=\langle 165,39\rangle$	0.24

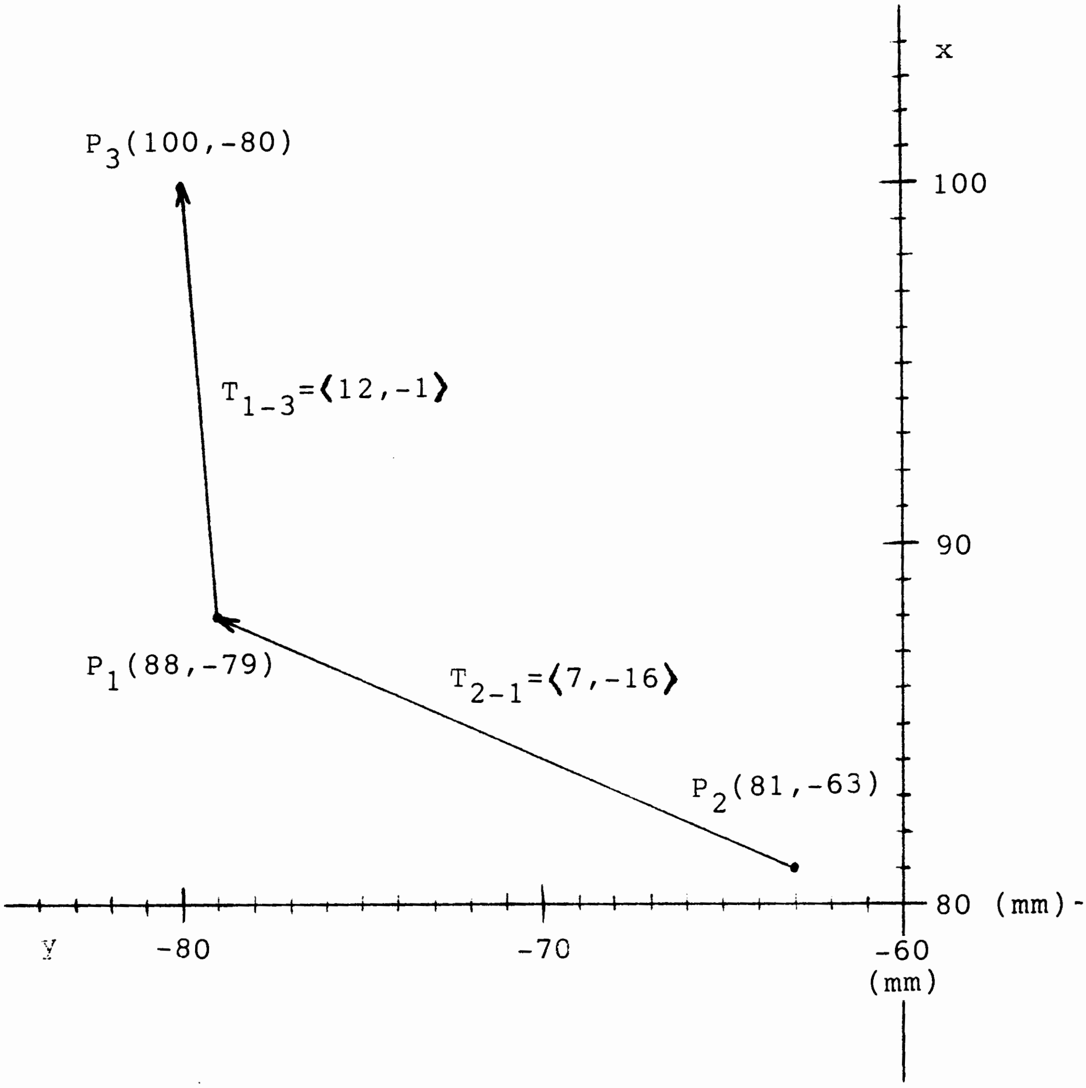


Figure 8. A graphic representation of the xy-translation trajectory for the left temporal zygomatic process distalis (LTZYGPR). The xy-translation trajectory consists of two translation vectors ($T_{2-1}=\langle 7,-16\rangle$ and $T_{1-3}=\langle 12,-1\rangle$) between a series of three position coordinates ($P_2(81,-63)$, $P_1(88,-79)$, and $P_3(100,-80)$).

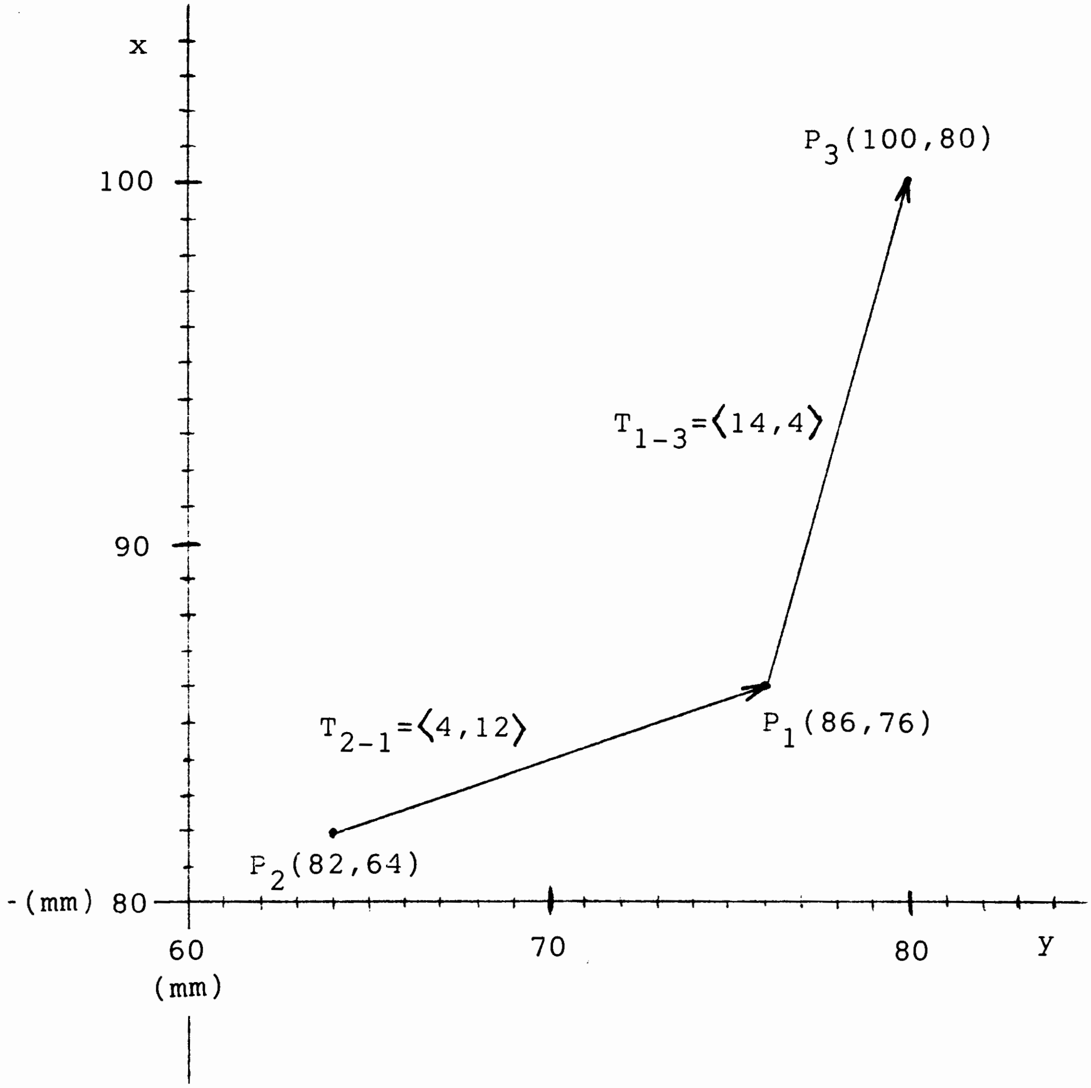


Figure 9. A graphic representation of the xy-translation trajectory for the right temporal zygomatic process distalis (RTZYGPR). The xy-translation trajectory consists of two translation vectors ($T_{2-1}=\langle 4,12\rangle$ and $T_{1-3}=\langle 14,4\rangle$) between a series of three position coordinates ($P_2(82,64)$, $P_1(86,76)$, and $P_3(100,80)$).

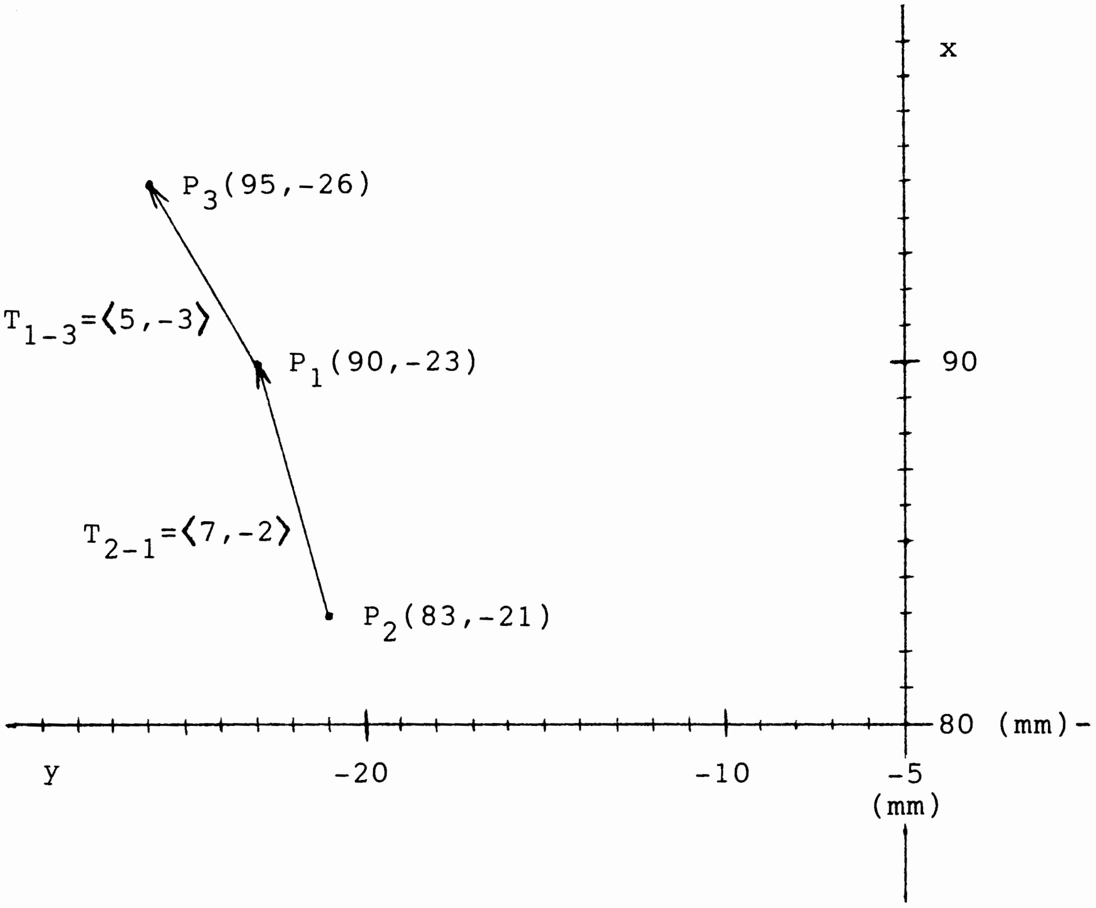


Figure 10. A graphic representation of the xy-translation trajectory for the left nasal lateralis (LTNSLLT). The xy-translation trajectory consists of two translation vectors ($T_{2-1}=\langle 7,-2\rangle$ and $T_{1-3}=\langle 5,-3\rangle$) between a series of three position coordinates ($P_2(83,-21)$, $P_1(90,-23)$, and $P_3(95,-26)$).

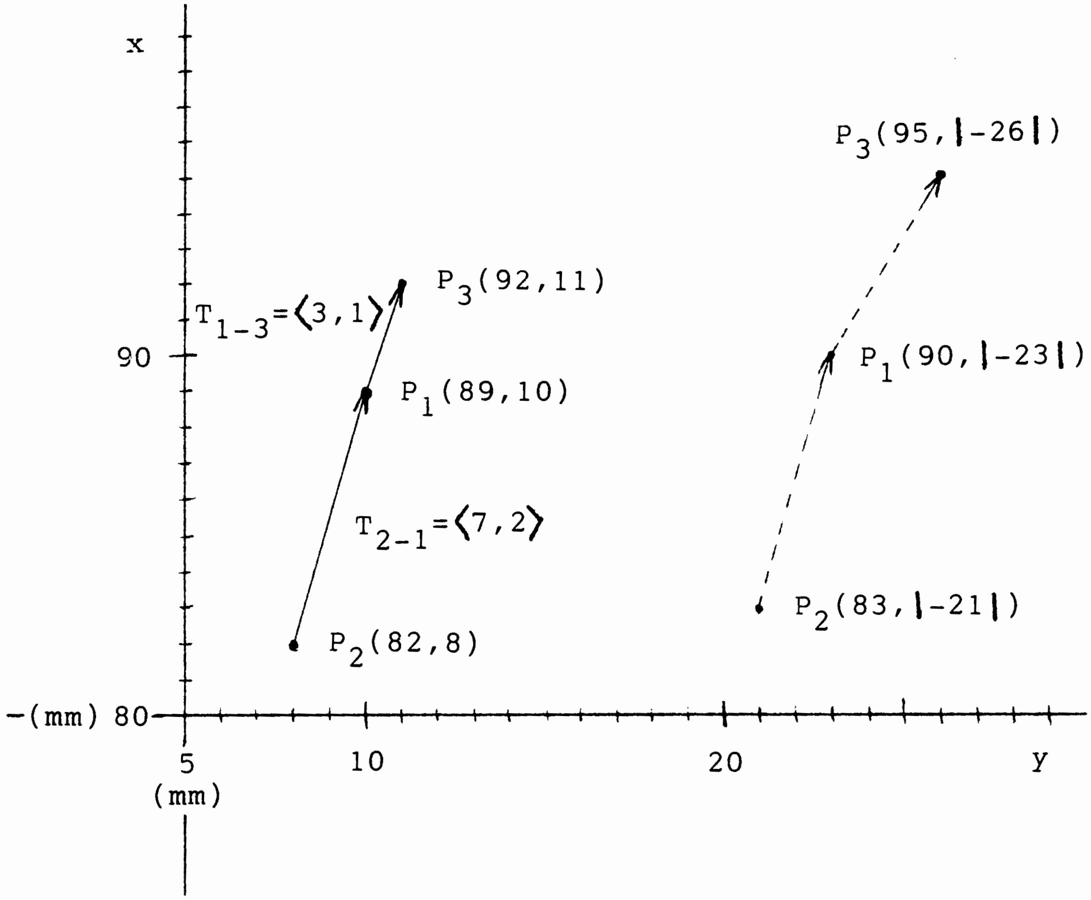


Figure 11. A graphic representation of the xy-translation trajectory for the right nasal lateralis (RTNSLLT). The trajectory consists of two translation vectors ($T_{2-1}=\langle 7,2\rangle$ and $T_{1-3}=\langle 3,1\rangle$) between a series of three position coordinates ($P_2(82,8)$, $P_1(89,10)$, and $P_3(92,11)$). Also represented is the mirror image across the x-axis of the xy-translation trajectory for the left nasal lateralis (LTNSLLT) which is shown by using dashed translation vectors. This was achieved by taking the absolute values of the negative y-components along with the unchanged x-components.

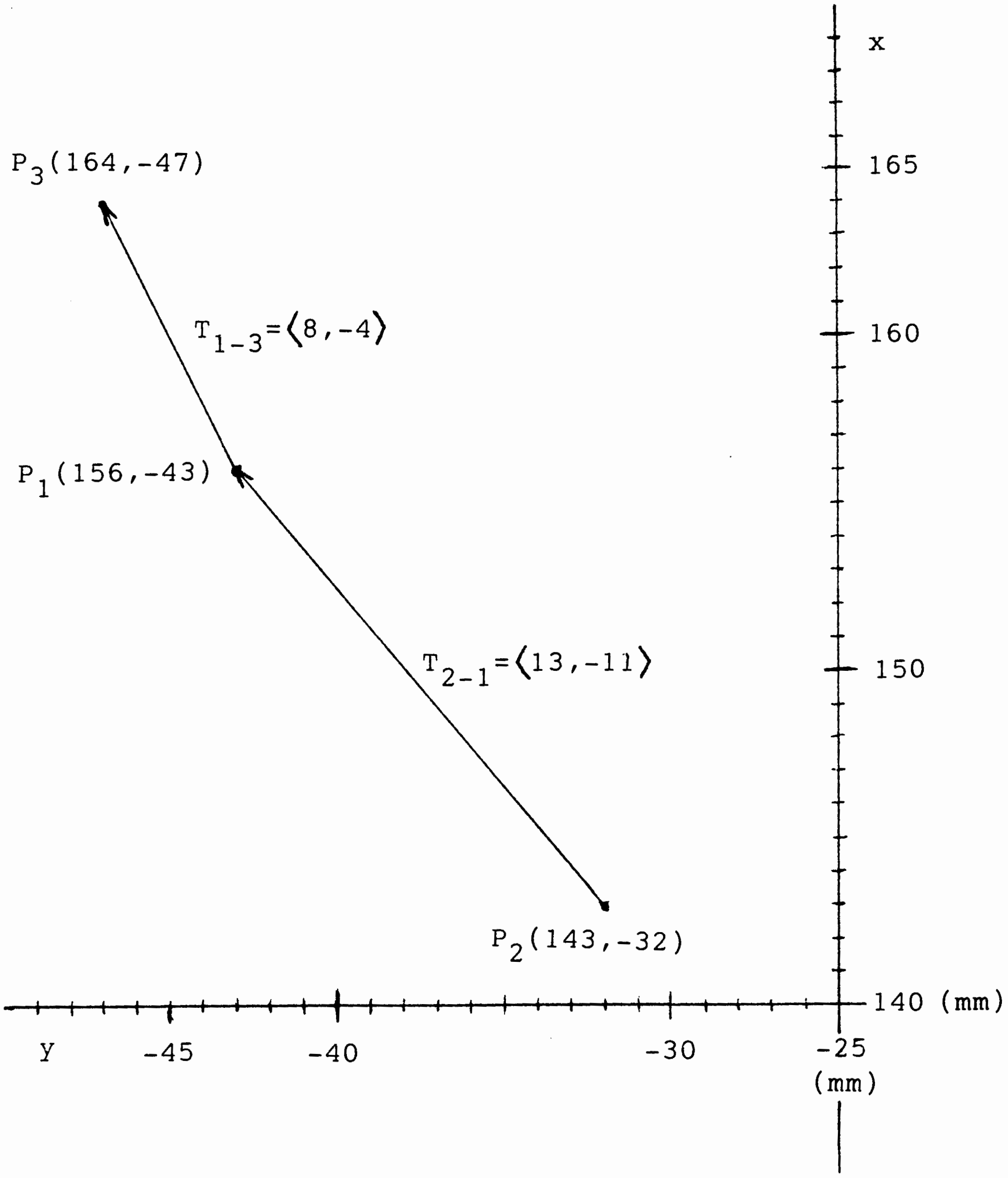


Figure 12. A graphic representation of the xy-translation trajectory for the left anorbital notch apex (LTATOBAPX). The translation trajectory consists of two translation vectors (T_{2-1}=⟨13,-11⟩ and T_{1-3}=⟨8,-4⟩) between a series of three position coordinates (P_2(143,-32), P_1(156,-43), and P_3(164,-47)).

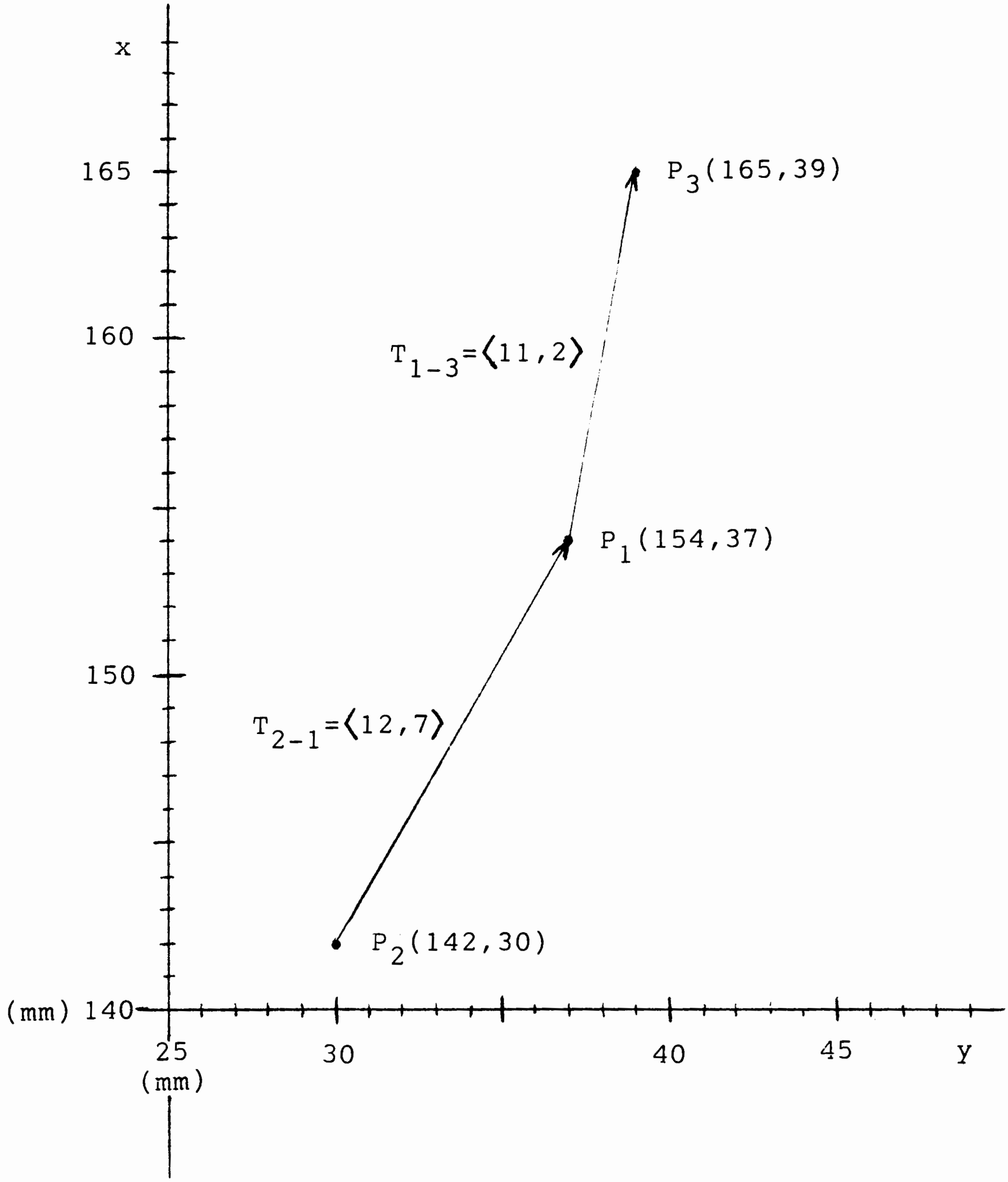


Figure 13. A graphic representation of the xy-translation trajectory for the right antorbital notch apex (RTATOBAPX). The translation trajectory consists of two translation vectors ($T_{2-1}=\langle 12,7\rangle$ and $T_{1-3}=\langle 11,2\rangle$) between a series of three position coordinates ($P_2(142,30)$, $P_1(154,37)$, and $P_3(165,30)$).

TABLE III

POSITION VECTORS AND SLOPES FOR REFERENCE POINTS SHOWING TRANSLATION TRENDS IN BOTH THE X-COMPONENT AND THE Z-COMPONENT

REFERENCE POINT ABBREVIATION	POSITION VECTOR $V=\langle x,z\rangle$	SLOPE z/x
1) ITNSLSTAT	$V_2=\langle 97,53\rangle$	0.55
	$V_1=\langle 99,64\rangle$	0.65
	$V_3=\langle 100,67\rangle$	0.67
2) VTITMXSTAT	$V_2=\langle 175,6\rangle$	0.034
	$V_1=\langle 190,12\rangle$	0.063
	$V_3=\langle 214,13\rangle$	0.061

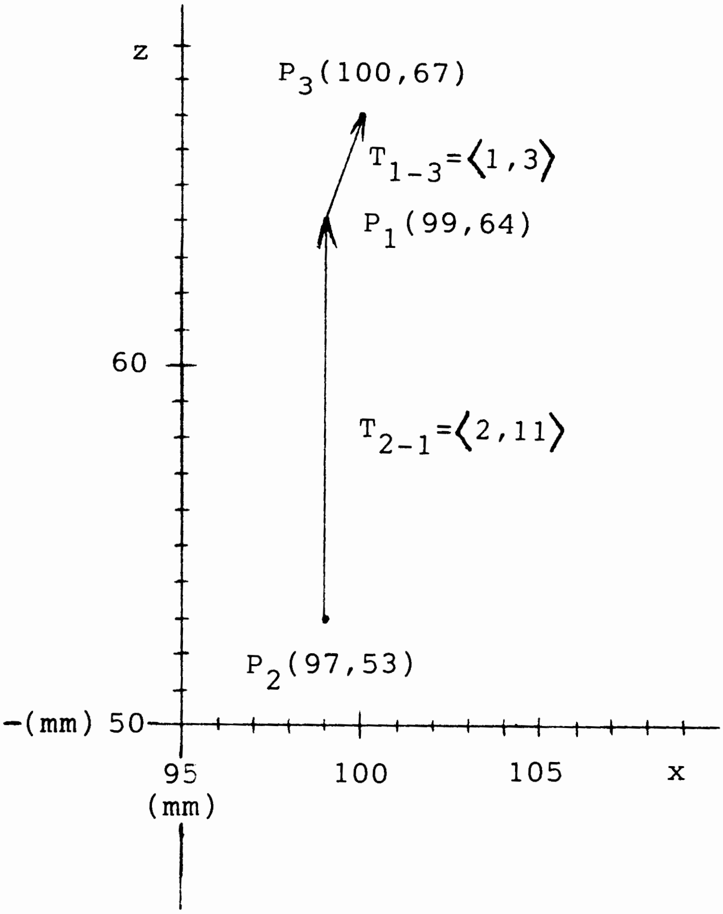


Figure 14. A graphic representation of the xz-translation trajectory for the internasal suture anterior (ITNSLSTAT). The xz-translation trajectory consists of two translation vectors ($T_{2-1}=\langle 2,11\rangle$ and $T_{1-3}=\langle 1,3\rangle$) between a series of three position coordinates ($P_2(97,53)$, $P_1(99,64)$, and $P_3(100,67)$).

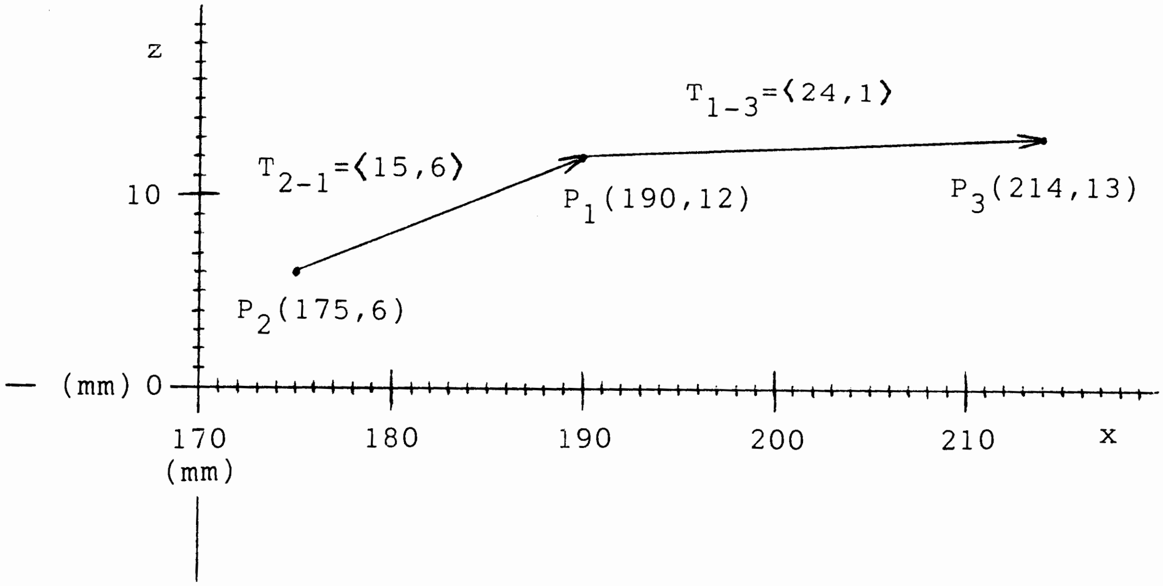


Figure 15. A graphic representation of the xz-translation trajectory for the ventral intermaxillary suture anterior (VTITMXSTAT). The translation trajectory consists of two translation vectors ($T_{2-1}=\langle 15,6\rangle$ and $T_{1-3}=\langle 24,1\rangle$) between a series of three position coordinates ($P_2(175,6)$, $P_1(190,12)$, and $P_3(214,13)$).

TABLE IV

TRANSLATION VECTORS FOR THE REFERENCE POINT SHOWING A TREND TO INCREASE DEVIATION FROM SYMMETRY

REFERENCE POINT ABBREVIATION	TRANSLATION VECTOR $T_{2-1}=\langle x,y,z\rangle$	TRANSLATION VECTOR $T_{1-3}=\langle x,y,z\rangle$
1) ITPRTAPX	$\langle 10,-3,15\rangle$	$\langle -3,-6,2\rangle$

TABLE V

POSITION VECTORS OF THE REFERENCE POINT SHOWING A TREND TO INCREASE DEVIATION IN SYMMETRY AND BOTH THE RATIO AND THE PERCENT OF THE Y-COMPONENT OF THE REFERENCE POINT TO THE MAGNITUDE OF THE X-COMPONENT OF THE RELATIVE POSITION VECTOR FROM THE ORIGIN TO THE ANTERIOVENTRALMOST POINT ON THE RIGHT PREMAXILLA

REFERENCE POINT ABBREVIATION	POSITION VECTOR	RATIO y/x	PERCENT
1) ITPRTAPX	$V_2=\langle 81,-4,76\rangle$	-4/242=-0.017	-1.7
	$V_1=\langle 91,-7,91\rangle$	-7/272=-0.028	-2.8
	$V_3=\langle 88,-13,93\rangle$	-13/299=-0.043	-4.3

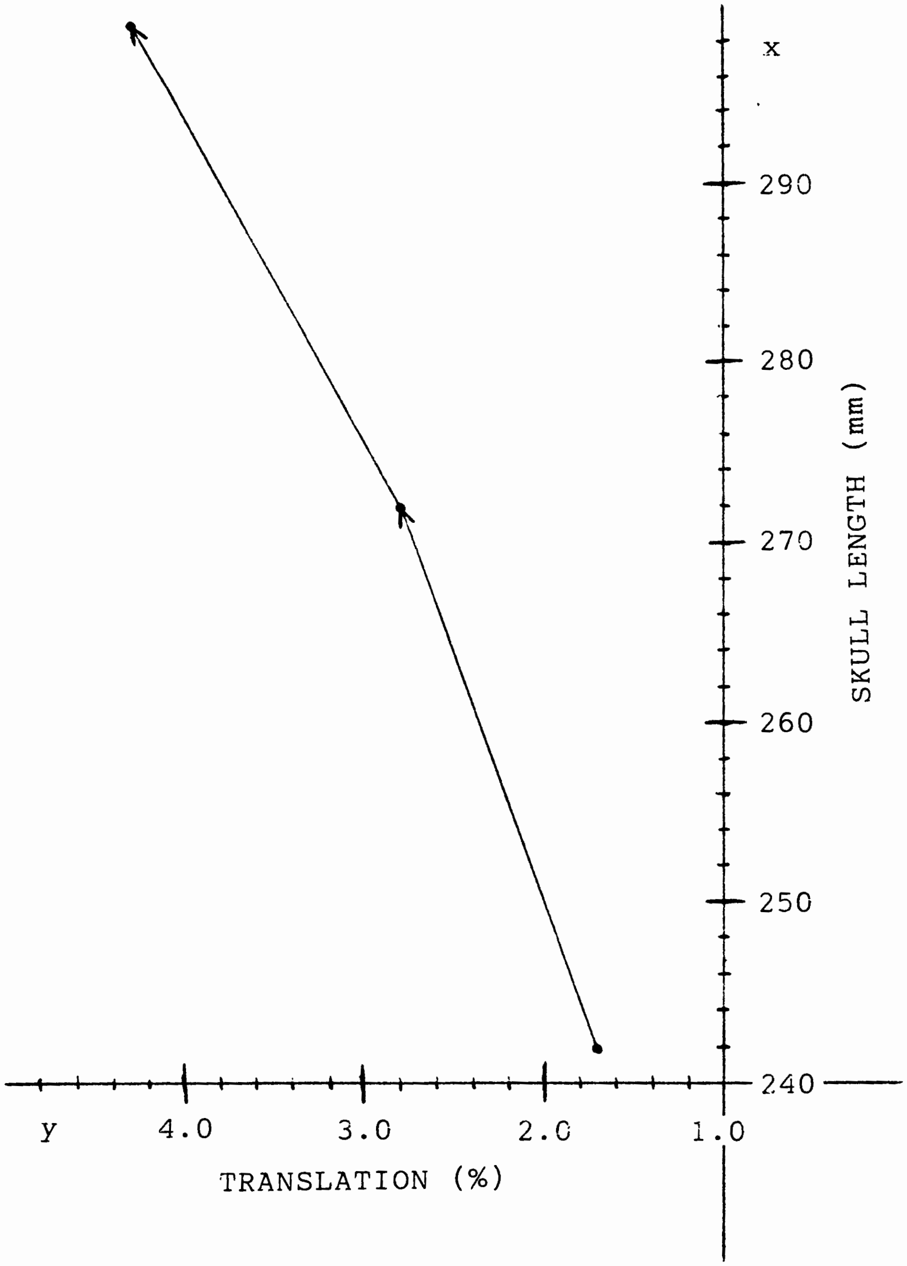


Figure 16. A graphic representation of the percent translation from the median plane for the interparietal apex (ITPRTAPX) in relation to the magnitude of the x-component of the relative position vector from the origin to the anterioventralmost point on the right premaxilla.

TABLE VI

ONTOGENETIC TRAJECTORY DATA INCLUDING AGE, SIZE, AND SHAPE DATA FOR THE HARBOR PORPOISE, *PHOCOENA PHOCOENA* (L.)

SPECIMEN	AGE	SIZE (mm)	SHAPE RATIO	SHAPE PROPORTIONALITY
SK 0002	3	242	0.59	59%
SK 0003	5	299	0.55	55%

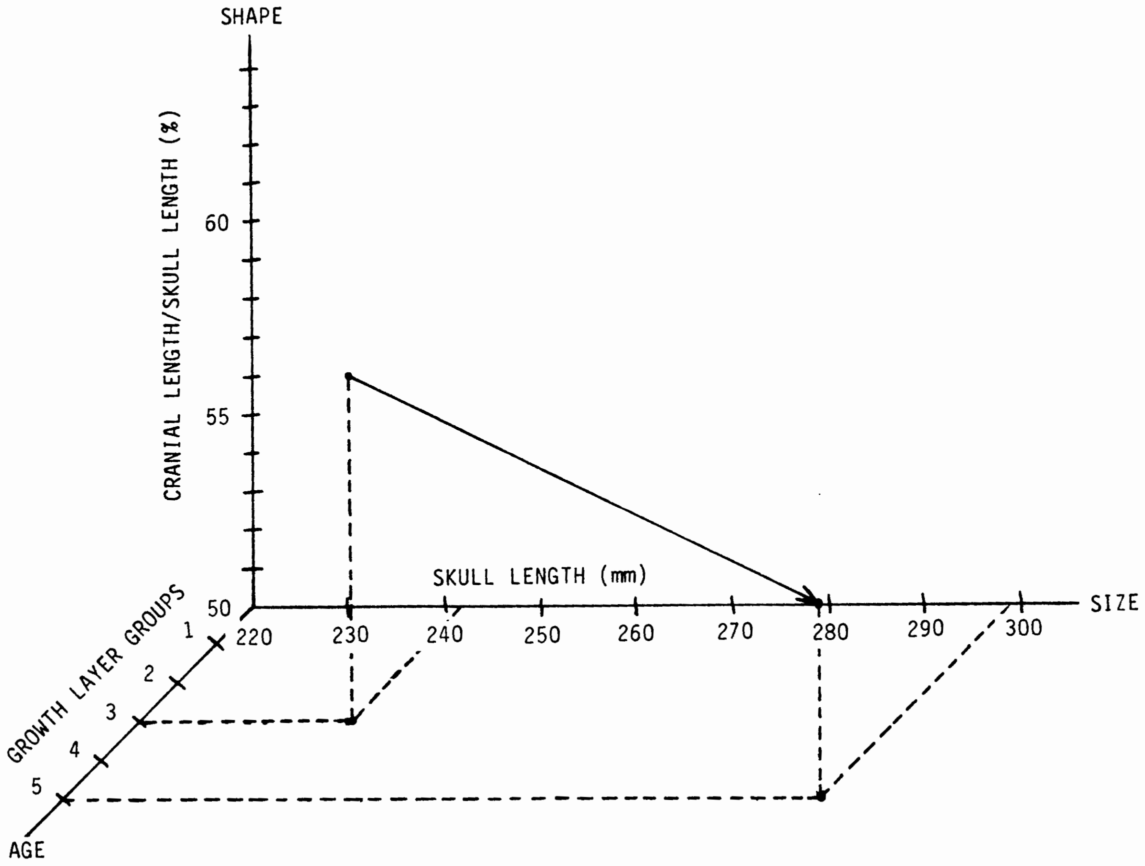


Figure 17. A graphic representation of the ontogenetic trajectory for the cranial growth in relation to the skull growth in the harbor porpoise. The growth layer groups of the teeth are utilized as a proxy for age. The size of the skull (or skull length) is defined as the magnitude of the x-component of the relative position vector from the origin to the anterioventralmost point of the right premaxilla. The shape under consideration is the ratio of the cranial length to the skull length. Cranial length is considered to be the magnitude of the x-component of the relative position vector from the origin to the left antorbital notch apex (LTATOBAPX). The shape proportionality plotted in this diagram is the shape ratio multiplied by 100.

CONCLUSION

The main goal of this thesis was to develop a method of archiving three dimensional mammalian skull morphology. This goal was achieved through the use of position coordinates and position vectors in a standardized coordinate system. In order to facilitate analysis of the morphological data, terminology was developed to describe the translation of reference points within the coordinate system (e. g., translation vectors and translation trajectories) and to describe the relative position of one reference point in relation to another reference point (i. e., via relative position vectors).

The second goal of this thesis was to test the method of archiving three dimensional mammalian skull morphology to determine whether or not the methodology could be employed in ontogenetic and allometric studies. The method developed was intended to be applicable to any mammalian species, and was therefore developed utilizing both typical and highly modified skulls. Since the methodology developed was shown to be useful in detecting ontogeny and allometry in the extremely modified skull of the harbor porpoise, it is expected to be applicable in any other mammalian species.

Although it was not set forth as a research goal, the method of archiving and analyzing three dimensional morphology appears to be useful in investigations involving asymmetry as evidenced by the ability to detect a trend toward asymmetry in the harbor porpoise. Finally, the methodology has been shown to provide the information necessary to construct ontogenetic trajectories and therefore provides evidence for its use in ontogenetic studies of this sort as well as its potential use in investigations involving heterochrony.

In conclusion, the methodology developed in this thesis provides a standardized method for archiving three dimensional mammalian skull morphology and provides both the terminology and methodology necessary for detecting ontogeny and allometry in mammalian skulls.

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APPENDIX A

STANDARDIZED EXTERNAL MEASUREMENTS OF CETACEA
(FROM NORRIS, 1961)

STANDARDIZED EXTERNAL MEASUREMENTS OF CETACEA (FROM NORRIS, 1961)

BODY MEASUREMENTS

01) Length, total (tip of upper jaw to deepest part of notch between flukes, or middle of posterior fluke margin if no notch is present).
02) Length, tip of upper jaw to center of eye.
03) Length, tip of upper jaw to apex of melon.
04) Length of gape (tip of upper jaw to angle of gape).
05) Length, tip of upper jaw to external auditory meatus (direct).
06) Center of eye to external auditory meatus (direct length).
07) Center of eye to angle of gape (direct length).
08) Center of eye to center of blowhole(s) (direct length).
09) Length, tip of upper jaw to blowhole along midline, or to midlength of two blowholes.
10) Length, tip of upper jaw to anterior insertion of flipper.
11) Length, tip of upper jaw to tip of dorsal fin.
12) Length, tip of the upper jaw to midpoint of umbilicus.
13) Length, tip of upper jaw to midpoint of genital aperture.
14) Length, tip of upper jaw to center of anus.
15) Projection of lower jaw beyond upper (if reverse, so state).
16) Length, tip of upper jaw to posterior extremity of throat creases.
17) Thickness of blubber, mid-dorsal at anterior insertion of dorsal fin.
18) Thickness of blubber, mid-lateral at midlength.
19) Thickness of blubber, mid-ventral at midlength.
20) Length, throat creases: maximum, and minimum.
21) Girth, on a transverse plane intersecting axilla.
22) Girth, maximum (describe location as distance from tip of upper jaw).
23) Girth, on a transverse plane intersecting the anus.

APERTURE MEASUREMENTS

24) Dimensions of eye: height, and length.
25) Length, mammary slits: right, and left.
26) Length, genital slit, and anal opening.
27) Dimensions of blowhole(s): width, and length(s).
28) Diameter of external auditory meatus: right, and left, or absent.

APPENDAGE MEASUREMENTS

29) Length, flipper (anterior insertion to tip).
30) Length, flipper (axilla to tip).
31) Width, flipper (maximum).
32) Height, dorsal fin (fin tip to base).
33) Length, dorsal fin base.
34) Width, flukes (tip to tip).
35) Distance from nearest point on anterior border of flukes to notch.
36) Depth of notch between flukes (if none, so state).

APPENDIX B

ADDITIONAL EXTERNAL MEASUREMENTS TO THE LIST OF STANDARDIZED EXTERNAL MEASUREMENTS OF CETACEA (FROM LEATHERWOOD, ET AL., 1976)

ADDITIONAL EXTERNAL MEASUREMENTS TO THE LIST OF STANDARDIZED EXTERNAL MEASUREMENTS OF CETACEA (FROM LEATHERWOOD, ET AL., 1976)

1) Tip of upper jaw to leading edge of dorsal fin.
2) Rostrum - maximum width.
3) Center of eye to center of eye.
4) Fluke width.
5) Notch of flukes to center of anus.
6) Notch of fluke to center of genital aperture.
7) Notch of flukes to umbilicus.
8) Girth at eye.
9) Width of head at post-orbital process of frontals.

APPENDIX C

MEASUREMENTS AND MERISTICS OF THE CETACEAN HEAD SKELETON (FROM PERRIN, 1975)

MEASUREMENTS AND MERISTICS OF THE CETACEAN HEAD SKELETON (FROM PERRIN, 1975)

01) Condylobasal length. From tip of rostrum to hindmost margin of occipital condyles.
02) Length of rostrum. From tip of rostrum to line across hindmost limits of antorbital notches.
03) Width of rostrum at base. Along line across hindmost limits of antorbital notches.
04) Width of rostrum at 60 mm anterior to line across hindmost limits of antorbital notches.
05) Width of rostrum at midlength.
06) Width of premaxillaries at midlength of rostrum.
07) Width of rostrum at 3/4 length, measured from posterior end.
08) Distance from tip of rostrum to external nares (to mesial end of anterior transverse margin of right naris).
09) Distance from tip of rostrum to internal nares (to mesial end of posterior margin of right pterygoid).
10) Greatest preorbital width.
11) Greatest postorbital width.
12) Least supraorbital width.
13) Greatest width of external nares.
14) Greatest width across zygomatic processes of squamosal.
15) Greatest width of premaxillaries.
16) Greatest parietal width, within posttemporal fossae.
17) Vertical external height of braincase from midline of basisphenoid to summit of supraoccipital, but not including supraoccipital crest.
18) Internal length of braincase from hindmost limit of occipital condyles to foremost limit of cranial cavity along midline.
19) Greatest length of left posttemporal fossa, measured to external margin of raised suture.
20) Greatest width of left posttemporal fossa at right angles to greatest length.
21) Major diameter of left temporal fossa proper.
22) Minor diameter of left temporal fossa proper.
23) Projection of premaxillaries beyond maxillaries measured from tip of rostrum to line across foremost tips of maxillaries visible in dorsal view.
24) Distance from foremost end of junction between nasals to hindmost point of margin of supraoccipital crest.
25) Length of left orbit. From apex of preorbital process of frontal to apex of postorbital process.
26) Length of antorbital process of left lacrimal.
27) Greatest width of internal nares.
28) Greatest length of left pterygoid.
29) Greatest width of anterior overhang of supraoccipital crest.
30) Greatest length of bulla of left tympanoperiotic.
31) Greatest length of periotic of left tympanoperiotic.
32) Length of upper tooth row. From hindmost margin of hindmost alveolus to tip of rostrum.
33) Number of teeth. Upper left.
34) Number of teeth. Upper right.
35) Number of teeth. Lower left.
36) Number of teeth. Lower right.
37) Length of lower left tooth row. From hindmost margin of hindmost alveolus to tip of mandible.

MEASUREMENTS AND MERISTICS OF THE CETACEAN HEAD SKELETON (FROM PERRIN, 1975) (continued)

38) Greatest length of left ramus.
39) Greatest height of left ramus at right angles to greatest length.
40) Length of left mandibular fossa, measured to mesial rim of internal surface of condyle.
41) Deviation of skull from symmetry in dorsal view, in degrees.
42) Length of basihyal along midline.
43) Greatest width of basihyal.
44) Greatest width of left thyrohyal proximally.
45) Greatest length of left thyrohyal.
46) Greatest width of left stylohyal.
47) Greatest length of left stylohyal.

APPENDIX D

HARBOR PORPOISE SKULL MEASUREMENTS
(FROM STUART AND MOREJOHN, 1980)

HARBOR PORPOISE SKULL MEASUREMENTS
(FROM STUART AND MOREJOHN, 1980)

01) Cranial length. Distance in the midline of the skull from a line connecting the posterior margins of the most anterior upper alveoli to a line connecting the posteriormost margins of the condyles.

02) Rostral length. Distance in the midline of the skull from a line across the hindmost limits of the antorbital notches to the posterior margins of the most anterior alveoli.

03) Mandibular length (left). Distance from the posteriormost tip of the left mandible to the posterior margin of the anteriormost alveolus taken parallel to the long axis of the mandible.

04) Mandibular height. Greatest height of the left mandible taken as a perpendicular to the ventral margin of the mandible at the coronoid process.

05) Length of mandibular symphysis. Distance parallel to the long axis of the mandible from the posterior of the anteriormost alveolus to the most posterior edge of the mandible at the coronoid process.

06) Length of dental foramen. Distance from the most anterior edge of the left dental foramen to the mesial rim of the internal surface of the condyle.

07) Squamosal width. Greatest width of the skull across the zygomatic processes of the squamosals.

08) Interparietal width. Greatest width of the parietals within posttemporal fossae.

09) Rostral width. Width of the rostrum along a line connecting the hindmost limits of the antorbital notches.

10) Pterygoid length. Greatest length of left pterygoid.

11) Frontal crest to occipital condyle base. Distance from the uppermost point of frontal crest to the farthest point on the left occipital condyle.

12) Height of basioccipital processes. From a midpoint between the most anterior edge of the basioccipital along the midline to the posterior ventral lip of the foramen magnum, a perpendicular is made ventrally from the basioccipital to a transverse line between the most ventrolateral margins of the basioccipital. This region of the basioccipital is usually slightly posterior to the pituitary depression of sella tursica.

APPENDIX E

SKULL MEASUREMENTS OF THE HARBOR PORPOISE (FROM YURICK AND GASKIN, 1987)

SKULL MEASUREMENTS OF THE HARBOR PORPOISE
(FROM YURICK AND GASKIN, 1987)

01) Condylobasal (skull) length.
02) Rostral length.
03) Rostral width at base.
04) Width at nares.
05) Maximum width across zygomatic processes.
06) Maximum width of premaxillaries.
07) Inside width of nares.
08) Maximum width of nasals.
09) Maximum width of occipital condyles.
10) Rostrum junction (antorbital notch) to posterior base of parietal.
11) Frontal crest to occipital condyle base.
12) Mandibular length.
13) Maximum height of mandible, perpendicular to length axis.
14) Height of mandible at subapical swelling.
15) Minimum height of mandible posterior to subapical swelling.
16) Length of tooth row: tip of mandible to hind margin of most posterior alveolus.

APPENDIX F

LIFE HISTORY DATA
FOR THE HARBOR PORPOISE (*PHOCOENA PHOCOENA*) SPECIMENS
PROVIDED BY THE NMFS NMML

LIFE HISTORY DATA FOR THE HARBOR PORPOISE (PHOCOENA PHOCOENA) SPECIMENS PROVIDED BY THE NMFS NMML

archive number	SK 0001	SK 0002	SK 0003
field number	PJG 097	PJG 116	PJG 084
institution number	NMML 1391	NMML 1439	NMML 1359
collection date	880728	890717	880716
collection location	48°16'00" N 124°41'30" E	48°16'00" N 124°41'30" E	48°16'00" N 124°41'30" E
circumstance	incidental take from the Spike Rock fishery	incidental take from the Spike Rock fishery	incidental take from the Spike Rock fishery
sex	female	female	female
length (cm)	157.8	158.4	177.5
weight (kg)	62.0	52.2	86.5
growth layer groups	3	3	5

APPENDIX G

DESCRIPTIONS OF THE LANDMARKS, PSEUDOLANDMARKS AND FORAMINA CONTAINED IN THE THREE DIMENSIONAL SKULL MORPHOLOGY ARCHIVE FOR THE HARBOR PORPOISE, *PHOCOENA PHOCOENA* (L.)

DESCRIPTIONS OF THE LANDMARKS, PSEUDOLANDMARKS AND FORAMINA CONTAINED IN THE THREE DIMENSIONAL SKULL MORPHOLOGY ARCHIVE FOR THE HARBOR PORPOISE, *PHOCOENA PHOCOENA* (L.)

	ABBREVIATION	DESCRIPTION
01)	FRMGIF	Foramen magnum inferior (basion). The midpoint on the ventral border of the foramen magnum.
02)	FRMGSP	Foramen magnum superior (opisthion). The most symmetric midpoint on the dorsal border of the foramen magnum.
03)	FRMGSNLT	Foramen magnum sinistral lateralis. The lateralmost border on the left side of the foramen magnum.
04)	FRMGDXLT	Foramen magnum dextral lateralis. The lateralmost border on the right side of the foramen magnum.
05)	LTOCCDLSP	Left occipital condyle superior. The dorsalmost point on the left occipital condyle.
06)	LTOCCDLIF	Left occipital condyle inferior. The ventralmost point on the left occipital condyle.
07)	LTOCCDLMD	Left occipital condyle medialis. The medialmost point on the left occipital condyle.
08)	LTOCCDLLT	Left occipital condyle lateralis. The lateralmost point on the left occipital condyle.
09)	RTOCCDLSP	Right occipital condyle superior. The dorsalmost point on the right occipital condyle.
10)	RTOCCDLIF	Right occipital condyle inferior. The ventralmost point on the right occipital condyle.
11)	RTOCCDLMD	Right occipital condyle medialis. The medialmost point on the right occipital condyle.
12)	RTOCCDLLT	Right occipital condyle lateralis. The lateralmost point on the right occipital condyle.
13)	LTOCCDLPT	Left occipital condyle posterior. The posteriormost point on the left occipital condyle.
14)	RTOCCDLPT	Right occipital condyle posterior. The posteriormost point on the right occipital condyle.
15)	SPOCSP	Supraoccipital superior. The superiormost point in the median plane of the smooth portion of the supraoccipital just caudal to the nuchal crest.
16)	EXOCSNLT	Exoccipital sinistral lateralis. The lateralmost limit of the left exoccipital.
17)	EXOCDXLT	Exoccipital dextral lateralis. The lateralmost limit of the right exoccipital.
18)	LTJGPRAPX	Left jugular process apex. The distalmost point of the left jugular process on the left exoccipital.
19)	RTJGPRAPX	Right jugular process apex. The distalmost point of the right jugular process on the right exoccipital.
20)	LTJGNTAPX	Left jugular notch apex. The apex of the left jugular notch on the left exoccipital.
21)	RTJGNTAPX	Right jugular notch apex. The apex of the right jugular notch on the right exoccipital.
22)	BSOCAT	Basioccipital anterior. The anterior limit of the basioccipital in the median plane.
23)	ITPRTAPX	Interparietal apex. The anteriodorsal apex of the interparietal

DESCRIPTIONS OF THE LANDMARKS, PSEUDOLANDMARKS AND FORAMINA CONTAINED IN THE THREE DIMENSIONAL SKULL MORPHOLOGY ARCHIVE FOR THE HARBOR PORPOISE, PHOCOENA PHOCOENA (L.) (continued)

	ABBREVIATION	DESCRIPTION
		region of the occipital.
24)	LTSQMLMB	Left squamosal suture and lambdoidal suture intersection. The point of intersection of the left squamosal suture and the lambdoidal suture on the left side of the skull.
25)	RTSQMLMB	Right squamosal suture and lambdoidal suture intersection. The point of intersection of the right squamosal suture and the lambdoidal suture on the right side of the skull.
26)	LTPTOBAPX	Left frontal postorbital process apex. The apex of the left postorbital process on the frontal bone.
27)	RTPTOBAPX	Right frontal postorbital process apex. The apex of the right postorbital process on the frontal bone.
28)	LTZYGPR	Left temporal zygomatic process distalis. The distalmost limit of the zygomatic process of the squamosal region of the temporal bone.
29)	RTZYGPR	Right temporal zygomatic process distalis. The distalmost limit of the zygomatic process of the squamosal region of the temporal bone.
30)	ITNSLSTANT	Internasal suture anterior. The anterior extent of the internasal suture.
31)	ITNSLFTNSL	Internasal suture and frontonasal suture intersection. The point of intersection of the internasal suture and the frontonasal suture.
32)	LTNSLPT	Left nasal posterior. The posterior limit of the left nasal bone.
33)	LTNSLAT	Left nasal anterior. The anterior limit of the left nasal bone.
34)	LTNSLMD	Left nasal medialis. The medial limit of the left nasal bone.
35)	LTNSLLT	Left nasal lateralis. The lateral limit of the right nasal bone.
36)	RTNSLPT	Right nasal posterior. The posterior limit of the right nasal bone.
37)	RTNSLAT	Right nasal anterior. The anterior limit of the right nasal bone.
38)	RTNSLMD	Right nasal medialis. The medial limit of the right nasal bone.
39)	RTNSLLT	Right nasal lateralis. The lateral limit of the right nasal bone.
40)	LTMXAT	Left maxilla anterior. The anterior limit of the left maxilla.
41)	LTMXDRPT	Left maxilla dorsalis posterior. The posterior limit of the left maxilla on the dorsal aspect of the skull.
42)	RTMXAT	Right maxilla anterior. The anterior limit of the right maxilla.
43)	RTMXDRPT	Right maxilla dorsalis posterior. The posterior limit of the right maxilla on the dorsal aspect of the skull.
44)	VTITMXSTAT	Ventralis intermaxillary suture anterior. The anterior limit of the intermaxillary suture on the ventral aspect of the skull and posterior to a portion of the vomer which is visible between the maxillae.
45)	VTITMXSTPT	Ventralis intermaxillary suture posterior. The posterior limit of the intermaxillary suture on the ventral aspect of the skull.
46)	LTATOBAPX	Left antorbital notch apex. The apex of the left antorbital notch.
47)	RTATOBAPX	Right antorbital notch apex. The apex of the right antorbital notch.
48)	LTPTIFOBFR	Left large posteriorly directed infraorbital foramen. The large posteriorly directed infraorbital foramen on the left maxilla.

DESCRIPTIONS OF THE LANDMARKS, PSEUDOLANDMARKS AND FORAMINA CONTAINED IN THE THREE DIMENSIONAL SKULL MORPHOLOGY ARCHIVE FOR THE HARBOR PORPOISE, *PHOCOENA PHOCOENA* (L.)

(continued)

	ABBREVIATION	DESCRIPTION
49)	LTATIFOBFR	Left large anteriorly directed infraorbital foramen. The large anteriorly directed infraorbital foramen on the left maxilla.
50)	RTPTIFOBFR	Right large posteriorly directed infraorbital foramen. The large posteriorly directed infraorbital foramen on the right maxilla.
51)	RTATIFOBFR	Right large anteriorly directed infraorbital foramen. The large anteriorly directed infraorbital foramen on the right maxilla.
52)	LTPRMXAT	Left premaxilla anterior. The anterior limit of the left premaxilla.
53)	LTPRMXDRPT	Left premaxilla dorsalis posterior. The posterior limit of the left premaxilla on the dorsal aspect of the skull.
54)	LTPRMXVTPT	Left premaxilla ventralis posterior. The posterior limit of the left premaxilla on the ventral aspect of the skull.
55)	RTPRMXAT	Right premaxilla anterior. The anterior limit of the right premaxilla.
56)	RTPRMXDRPT	Right premaxilla dorsalis posterior. The posterior limit of the right premaxilla on the dorsal aspect of the skull.
57)	RTPRMXVTPT	Right premaxilla ventralis posterior. The posterior limit of the right premaxilla on the ventral aspect of the skull.
58)	LTPRMXFR	Left premaxillary foramen. The center of the largest foramen in the groove in the left premaxilla.
59)	RTPRMXFR	Right premaxillary foramen. The center of the largest foramen in the groove in the right premaxilla.
60)	VMRTAT	Vomer anterior. The anterior limit of the vomer.
61)	VMRDRPT	Vomer dorsalis posterior. The posteriodorsal limit of the vomer in the median plane on the dorsal aspect of the skull.
62)	VMRVTPT	Vomer ventralis posterior. The posterioventral limit of the vomer in the median plane on the ventral aspect of the skull.
63)	VMRPRC	Vomer hard palate process. The apex of the hard palate process of the vomer.
64)	LTPTRAT	Left pterygoid anterior. The anterior limit of the left pterygoid.
65)	LTPTRPRCPT	Left pterygoid process posterior. The posterior limit of the left pterygoid process.
66)	RTPTRAT	Right pterygoid anterior. The anterior limit of the right pterygoid.
67)	RTPTRPRCPT	Right pterygoid process posterior. The posterior limit of the right pterygoid process.
68)	ITPLTSTPT	Interpalatine suture anterior. The anterior limit of the interpalatine suture.
69)	ITPLTSTPT	Interpalatine suture posterior. The posterior limit of the interpalatine suture.
70)	LTPLTAT	Left palatine anterior. The anterior limit of the left palatine.
71)	LTPLTPT	Left palatine posterior. The posterior limit of the left palatine.
72)	RTPLTAT	Right palatine anterior. The anterior limit of the right palatine.
73)	RTPLTPT	Right palatine posterior. The posterior limit of the right palatine.

DESCRIPTIONS OF THE LANDMARKS, PSEUDOLANDMARKS AND FORAMINA CONTAINED IN THE THREE DIMENSIONAL SKULL MORPHOLOGY ARCHIVE FOR THE HARBOR PORPOISE, PHOCOENA PHOCOENA (L.) (continued)

	ABBREVIATION	DESCRIPTION
74)	LTLCAT	Left lacrimal anterior. The anterior limit of the left lacrimal.
75)	RTLCAT	Right lacrimal anterior. The anterior limit of the right lacrimal.
76)	LTOBSP	Left orbital superior. The dorsalmost point on the rim of the left orbit.
77)	RTOBSP	Right orbital superior. The dorsalmost point on the rim of the right orbit.
78)	LTTMPFSAT	Left temporal fossa anterior. The anterior limit of the left temporal fossa.
79)	LTTMPFSPT	Left temporal fossa posterior. The posterior limit of the left temporal fossa.
80)	LTTMPFSSP	Left temporal fossa superior. The dorsalmost point of the left temporal fossa.
81)	LTTMPFSIF	Left temporal fossa inferior. The ventralmost point of the left temporal fossa.
82)	RTTMPFSAT	Right temporal fossa anterior. The anterior limit of the right temporal fossa.
83)	RTTMPFSPT	Right temporal fossa posterior. The posterior limit of the right temporal fossa.
84)	RTTMPFSSP	Right temporal fossa superior. The dorsalmost point of the right temporal fossa.
85)	RTTMPFSIF	Right temporal fossa inferior. The ventralmost point of the right temporal fossa.
86)	LTEXNRSAT	Left external naris anterior. The anterior extent of the left external naris.
87)	LTEXNRSPT	Left external naris posterior. The posterior extent of the left external naris.
88)	LTEXNRSMD	Left external naris medialis. The medial extent of the left external naris.
89)	LTEXNRSLT	Left enternal naris lateralis. The lateral extent of the left external naris.
90)	RTEXNRSAT	Right external naris anterior. The anterior extent of the right external naris.
91)	RTEXNRSPT	Right external naris posterior. The posterior extent of the right external naris.
92)	RTEXNRSMD	Right external naris medialis. The madial extent of the right external naris.
93)	RTEXNRSLT	Right external naris lateralis. The lateral extent of the right external naris.

APPENDIX H

THREE DIMENSIONAL SKULL MORPHOLOGY ARCHIVE FOR THE HARBOR PORPOISE, *PHOCOENA PHOCOENA* (L.)

THREE DIMENSIONAL SKULL MORPHOLOGY ARCHIVE FOR THE HARBOR PORPOISE, *PHOCOENA PHOCOENA* (L.)[+]

	REFERENCE POINT	SK 0001	SK 0002	SK 0003
01)	FRMGIF	(0,0,0)	(0,0,0)	(0,0,0)
02)	FRMGSP	(8,0,39)	(7,0,13)*	(9,0,32)
03)	FRMGSNLT	(4,-15,32)	(3,-14,20)	(-1,-16,28)
04)	FRMGDXLT	(5,16,34)	(5,11,22)	(-2,17,25)
05)	LTOCCDLSP	(6,-18,35)	(7,-19,24)	(5,-18,33)
06)	LTOCCDLIF	(7,-15,-12)	(8,-8,-15)	(6,-16,-14)
07)	LTOCCDLMD	(-2,-3,-1)	(-2,-3,-7)	(-6,-3,-3)
08)	LTOCCDLLT	(10,-35,19)	(9,-30,15)	(7,-35,17)
09)	RTOCCDLSP	(8,13,36)	(8,12,27)	(7,19,32)
10)	RTOCCDLIF	(7,18,-11)	(6,13,-14)	(5,14,-15)
11)	RTOCCDLMD	(-5,12,7)	(1,6,-9)	(-2,6,-8)
12)	RTOCCDLLT	(12,37,20)	(4,27,5)	(9,35,14)
13)	LTOCCDLPT	(-5,-11,9)	(-4,-13,4)	(-9,-15,12)
14)	RTOCCDLPT	(-5,13,13)	(-3,10,9)	(-8,12,8)
15)	SPOCSP	(71,0,96)	(57,0,78)	(70,0,96)
16)	EXOCSNLT	(42,-68,8)	(37,-61,13)	(50,-70,-11)
17)	EXOCDXLT	(50,67,2)	(46,60,-3)	(56,72,5)
18)	LTJGPRAPX	(35,-56,-35)	(31,-42,-32)	(38,-54,-29)
19)	RTJGPRAPX	(34,55,-35)	(32,47,-31)	(42,58,-35)
20)	LTJGNTAPX	(29,-42,-18)	(23,-30,-18)	(25,-47,-23)
21)	RTJGNTAPX	(26,40,-17)	(23,35,-17)	(28,44,-19)
22)	BSOCAT	(68,0,-2)	(70,0,-2)	(76,0,0)
23)	ITPRTAPX	(91,-7,91)	(81,-4,76)	(88,-13,93)
24)	LTSQMLMB	(43,-69,13)	(41,-55,2)	(44,-69,13)
25)	RTSQMLMB	(40,63,20)	(38,56,9)	(45,68,19)
26)	LTPTOBAPX	(93,-79,6)	(84,-68,8)	(100,-79,2)
27)	RTPTOBAPX	***	(83,64,14)	(101,79,15)
28)	LTZYGPR	(88,-79,11)	(81,-63,3)	(100,-80,3)
29)	RTZYGPR	(86,76,17)	(82,64,7)	(100,80,8)
30)	ITNSLSTAT	(99,-2,64)	(97,-5,53)	(100,-6,67)
31)	ITNSLFTNSL	(92,-4,75)	(84,-7,66)	(90,-8,76)
32)	LTNSLPT	(84,-3,81)	(78,-19,67)	(84,-23,79)
33)	LTNSLAT	(99,-2,64)	(97,-4,52)	(98,-16,58)
34)	LTNSLMD	(99,-2,64)	(97,-4,53)	(99,-9,67)
35)	LTNSLLT	(90,-23,74)	(83,-21,60)	(95,-26,64)
36)	RTNSLPT	(86,6,81)	(78,4,68)	(86,7,82)
37)	RTNSLAT	(99,0,64)	(97,-4,52)	(99,1,57)
38)	RTNSLMD	(90,-1,77)	(84,-6,62)	(90,-8,76)
39)	RTNSLLT	(89,10,73)	(82,8,63)	(92,11,71)
40)	LTMXAT	(270,-5,4)	(237,-7,3)	(296,-7,0)

THREE DIMENSIONAL SKULL MORPHOLOGY ARCHIVE FOR THE HARBOR PORPOISE, *PHOCOENA PHOCOENA* (L.)[+]
(continued)

	REFERENCE POINT	SK 0001	SK 0002	SK 0003
41)	LTMXDRPT	(53,-59,60)	(56,-45,59)	(53,-61,59)
42)	RTMXAT	(270,6,5)	(237,8,1)	(297,7,0)
43)	RTMXDRPT	(54,49,68)	(54,45,59)	(58,55,66)
44)	VTITMXSTAT	(190,-2,12)	(175,0,6)	(214,-3,13)
45)	VTITNXSTPT	(134,-1,7)	(134,0,2)	(159,-2,7)
46)	LTATOBAPX	(156,-43,29)	(143,-32,17)	(164,-47,28)
47)	RTATOBAPX	(154,37,34)	(142,30,21)	(165,39,35)
48)	LTPTIFOBFR	(113,-46,48)	(104,-25,33)	(117,-42,44)
49)	LTATIFOBFR	(138,-23,39)	(133,-19,27)	(158,-17,39)
50)	RTPTIFOBFR	(113,31,51)	(104,29,39)	(116,33,51)
51)	RTATIFOBFR	(136,21,44)	(133,17,28)	(157,18,42)
52)	LTPRMXAT	(272,0,0)	(241,-1,-4*)	(299,-2,0)
53)	LTPRMXDRPT	(104,-15,54)	(107,-18,40)	(108,-24,53)
54)	LTPRMXVTPT	(209,-2,11)	(193,-3,4)	(229,-4,12)
55)	RTPRMXAT	(272,0,5)	(242,1,-4*)	(299,5,0)
56)	RTPRMXDRPT	(106,10,52)	(107,10,40)	(109,9,51)
57)	RTPRMXVTPT	(206,2,11)	(193,2,6)	**
58)	LTPRMXFR	(152,-9,36)	(141,-9,27)	(160,-16,41)
59)	RTPRMXFR	(151,8,40)	(143,4,26)	(156,4,44)
60)	VMRAT	(239,0,16)	(215,0,4)	(267,0,7)
61)	VMRDRPT	(97,-3,66)	(98,-4,51)	(100,-7,69)
62)	VMRVTPT	**	(71,0,-2)	(77,0,-1)
63)	VMRPRC	(104,0,-10)	(101,0,-11)	(114,-2,-11)
64)	LTPTRAT	(132,-20,-1)	(126,-16,-3)	(143,-18,-3)
65)	LTPTRPRCPT	(98,-22,-21)	(96,-15,-20)	(107,-20,-21)
66)	RTPTRAT	**	**	(143,17,2)
67)	RTPTRPRCPT	(96,18,-21)	***	(106,21,-19)
68)	ITPLTSTAT	(132,-1,3)	(134,0,1)	(159,-3,7)
69)	ITPLTSTPT	(114,-1,-4)	(103,0,-10)	(121,0,-8)
70)	LTPLTAT	(153,-26,12)	(142,-18,5)	(164,-21,8)
71)	LTPLTPT	(109,-4,-9)	(101,-1,-11)	(118,-4,-10)
72)	RTPLTAT	(151,23,17)	(141,19,6)	(165,19,14)
73)	RTPLTPT	(107,2,-9)	(102,3,-11)	(118,-2,-10)
74)	LTLCAT	(156,-48,27)	(142,-39,14)	(166,-53,25)
75)	RTLCAT	(153,46,36)	(142,34,22)	(165,44,33)
76)	LTOBSP	(116,-62,32)	(105,-52,19)	(128,-71,24)
77)	RTOBSP	(114,69,39)	(102,54,26)	(131,65,36)
78)	LTTMPFSAT	(95,-72,27)	**	**
79)	LTTMPFSPT	(31,-64,34)	(34,-56,18)	(37,-75,31)

THREE DIMENSIONAL SKULL MORPHOLOGY ARCHIVE FOR THE HARBOR PORPOISE, PHOCOENA PHOCOENA (L.)+
(continued)

	REFERENCE POINT	SK 0001	SK 0002	SK 0003
80)	LTTMPFSSP	(49,-65,47)	(50,-61,33)	(67,-72,42)
81)	LTTMPFSIF	(49,-67,0)	(66,-67,2)	(64,-84,2)
82)	RTTMPFSAT	(91,71,36)	**	**
83)	RTTMPFSPT	(34,64,31)	***	(38,68,36)
84)	RTTMPFSSP	(44,62,50)	(48,58,38)	(55,66,50)
85)	RTTMPFSIF	(51,71,5)	(48,57,3)	(59,72,12)
86)	LTEXNRSAT	(122,-11,53)	(120,-10,39)	(131,-11,46)
87)	LTEXNRSPT	(102,-17,52)	(97,-15,41)	(106,-16,52)
88)	LTEXNRSMD	(112,-2,53)	(115,-2,31)	(117,-6,54)
89)	LTEXNRSLT	(113,-19,53)	(106,-19,39)	(122,-16,53)
90)	RTEXNRSAT	(121,6,51)	(120,3,41)	(130,-1,45)
91)	RTEXNRSPT	(101,4,52)	(96,4,44)	(108,4,49)
92)	RTEXNRSMD	(112,0,54)	(108,-2,41)	(126,-6,52)
93)	RTEXNRSLT	(112,11,50)	(108,10,39)	(116,8,52)

+ position coordinates are given in millimeters (mm)

* measure suspect

** data absent/reference point not accessible

*** reference point missing

APPENDIX I

GLOSSARY

GLOSSARY

Allometry (allos: other; metron: measure): the description of the relationship between size an shape, of a part in relation to the whole, of an individual organism or the part of an organism under consideration, whether the comparisons are ontogenetic, intraspecific, or interspecific.

Archive: to record or place in public record three dimensional morphological data.

Hererochrony (heteros: other, different; chronos: time): evolution via change in timing and/or rate of development (McKinney, 1988).

Meristics: number or arrangement of body parts or segments.

Morphology (morphe: form; logy: science): The study of biological form for descriptive and investigative inquiries involving the structure and function of organisms whereby descriptive, analytical, interpretive, and predictive studies of structure and function are quantified through the measurement and mathematical analysis of the geometric description of anatomical characteristic.

Morphometrics (morphe: form; metron: measure): the measurement of biological form which allows the quantification of descriptive and investigative data.

Ontogenetic trajectory (onto: being; geny: development: trans: across; jacere: to throw): trajectories which trace the path of a developmental event, from the time of inception to its mature form, in age-size-shape space.

Ontogeny (onto: being; geny: development): the development of an individual organism throughout its life history.

Position coordinates: a point P(x,y,z) in a rectangular coordinate system representing the position of a morphological reference point.

Position vector: 1) a vector $v=\langle x,y,z\rangle$ which is determined by the point P (x,y,z) in a rectangular coordinate system where the vector is represented by a directed line segment $\overrightarrow{OP}$ from the origin to the point; this vector defines the position of a morphological reference point; 2) a vector $v_s=\langle m_v,\angle xy,\angle xz\rangle$ in a spherical coordinate system where v_s is the position vector, m_v is the magnitude of the position vector, $\angle xy$ is the angle between the positive x-axis and the projection of the vector onto the xy-plane, and $\angle xz$ is the angle between the positive x-axis and the projection of the vector onto the xz-plane.

Pseudolandmark: reference points which bear a reliable operation definition but are not homologous landmarks (Bookstein, et al., 1985).

Relative position vector: a vector between the position coordinates of two nonhomologous morphological reference points of the same specimen.

Standardized three dimensional coordinate system: for mammalian skulls, a coordinate system with the origin at the basion; the xz-plane divides the skull into left and right halves; the xy-plane divides the skull into ventral and dorsal portions; and the yz-plane divides the skull into posterior and anterior

GLOSSARY
(continued)

portions.

xz-plane: the median plane which passes through the origin and bisects the skull into the "most bilaterally symmetrical" halves possible; this plane divides the skull into left and right halves.

xy-plane: the plane which passes through the origin and the point in the median plane along a line connecting the most anterioventral extent of the premaxillae; this plane divides the skull into ventral and dorsal portions.

yz-plane: the plane which passes through the origin and is perpendicular to both the xz-plane and the xy-plane.

Three dimensional archive: record of an ordered triple representing the distances from the origin along the x, y, and z axes to a reference point.

Translation trajectory: the trajectory (or path) of a morphological reference point translated through three dimensional space during ontogeny.

Translation vector: a vector (or directed line segment) between the position coordinates of two homologous morphologous morphological reference points in which one reference point is translated with respect to the other reference point in three dimensional space.