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Are landmarks analysis adequate to identify fish assemblages in a subtropical ecosystem? Study of case for the Araçá Bay (São Sebastião, Brazil).

Thesis submitted to the Oceanographic Institute of University of São Paulo, in partial fulfilment of the requirement for the degree of Doctor of Science, Program of Oceanography, Biological Oceanography area.

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ABSTRACT

This thesis is part of the project “*Biodiversity and functioning of a subtropical coastal ecosystem: a contribution to integrated management*” funded by FAPESP – São Paulo Research Foundation – Process 2011/50317-5. Known as *Biota Araçá*, this project was performed in order to evaluate the diversity and the functionality of a subtropical tidal flat located at the northern coast of São Paulo State, a high diversity area. Our study, based on landmark analysis of fish body shape and otoliths shape, was conducted at the University of São Paulo in collaboration with researchers from the Institut de Ciències del Mar (Consejo Superior de Investigaciones Científicas, Barcelona, Spain). The thesis was organized in five chapters. In the first one, we present a historical review about the use of morphology as a tool for the Science. Initially this theme was to supply my curiosity about “*how the shape of organisms contributed to the development of biodiversity studies*”. The second chapter shows the dependence of the fish assemblages’ morphological structure according to the samplers utilized. For that, nine fishing gears were used to sample the Araçá fish assemblages and we determined which samplers are more useful to represent the total fish morphological variability of the area. Given the heterogeneity and complexity of habitats of Araçá Bay, we supposed that some habitats have major influence in the morphological diversity. Therefore, the aim of the third chapter was to determine how fish diversity techniques reveal the ichthyofauna of the three main habitats of Araçá Bay: intertidal, inner/outer sublittoral, marginal shallow sublittoral (elected as results of the previous chapter). Here we emphasize the importance of abundance data and morpho-functional approaches to understand fish habitat complexities, and consequently, the ecosystem functioning. Thus, we present the more sensible habitats in case of the Araçá’s environmental degradation. During the development of our study, one question emerged: “*are sagittae landmarks able to describe the fish assemblage biodiversity as well as are fish body shapes?*” To answer this question, in the fourth chapter, the morphological correspondence between fish body shapes and otolith *sagittae* shapes were assessed. We investigated 43 species using different shape descriptors, attempting to habit, diet, swimming type, and hearing capabilities. Other specific questions were answered: 1- which method: shape indices, wavelets or landmarks, better discriminate species classification and, 2- which one shows the ecological significance of otoliths? In the last chapter, considerations are presented

taking in account our initial question “*Are landmarks analysis adequate to identify fish assemblages in a subtropical ecosystem?*” The conclusion is that the method is a useful tool to describe fish body and otolith shapes as well as to define fish assemblages in highly diverse ecosystems.

Keywords: fish body, *sagittae* otoliths, morphofunctional diversity, morphometric geometric, landmark analysis, habitat uses, multiple fishing gears.

RESUMO

Esta tese é parte do projeto “*Biodiversidade e funcionamento de um ecossistema subtropical: uma contribuição ao manejo integrado*” financiado pela FAPESP – Fundação de Amparo a Pesquisa do Estado de São Paulo – Processo 2011/ 50317-5. Conhecido como *Biota Araçá*, este projeto foi desenvolvido com o objetivo de avaliar a diversidade e a funcionalidade de uma planície de maré subtropical localizada no litoral norte do Estado de São Paulo, uma área de alta diversidade. Nosso estudo, baseado na análise de pontos homólogos relacionados à forma dos corpos de peixes e à forma de otólitos, foi conduzido na Universidade de São Paulo com a colaboração de pesquisadores do Institut de Ciències del Mar (Consejo Superior de Investigaciones Científicas, Barcelona, Espanha). A tese está organizada em cinco capítulos. No primeiro, apresentamos uma revisão histórica sobre o uso da morfologia como ferramenta para a Ciência. Inicialmente, este tema surgiu a partir da nossa curiosidade sobre “*como a forma dos organismos contribuiu para o desenvolvimento dos estudos de biodiversidade*”. O segundo capítulo mostra a dependência da estrutura morfológica das assembléias de peixes de acordo com os amostradores utilizados. Para isso, nove artes de pesca foram empregadas para amostrar as assembléias de peixes do Araçá e, foi analisado quais delas foram mais úteis para representar a variabilidade morfológica total das espécies presentes na área. Dada a heterogeneidade e complexidade dos habitats da Baía do Araçá, supusemos que alguns deles apresentariam maior influência na diversidade morfológica da ictiofauna. Assim, o objetivo do terceiro capítulo foi analisar como as técnicas utilizadas na avaliação da diversidade de peixes revelam esta diversidade nos três principais habitats da Baía do Araçá: entremarés, sublitoral interno/externo, sublitoral marginal raso (eleitos a partir dos resultados obtidos no capítulo anterior). Aqui, enfatizamos a importância dos dados de abundância e de abordagens morfofuncionais para entender as complexidades dos habitats para os peixes e, conseqüentemente, o funcionamento do ecossistema. Ainda aqui, apresentamos os habitats mais sensíveis no caso de uma degradação ambiental do Araçá. Durante o desenvolvimento do estudo, uma questão emergiu: “*pontos homólogos em sagittae são capazes de descrever a biodiversidade da assembléia de peixes, assim como o são as formas corporais?*” Para responder esta questão, no quarto capítulo, avaliamos

a correspondência morfológica entre formas corporais de peixes e formas de otólitos *sagittae*. Nós investigamos 43 espécies utilizando diferentes descritores de forma, com vistas aos hábitos, dieta, tipo de natação e capacidades auditivas. Outras questões específicas foram respondidas: 1- qual método: índices de forma, *wavelets* ou *landmarks*, melhor discriminam as espécies para classificação e, 2- qual deles mostra a significância ecológica dos otólitos? No último capítulo, são apresentadas considerações levando em conta nossa pergunta inicial “*A análise de pontos homólogos é adequada para identificar assembléias de peixes em um ecossistema subtropical?*” A conclusão é que o método é uma ferramenta útil para descrever formas de corpos de peixes e otólitos, bem como definir associações de peixes em ecossistemas altamente diversificados.

Palavras-chave: forma de peixes, otólitos *sagittae*, diversidade morfofuncional, morfometria geométrica, análise de pontos homólogos, usos do habitat, múltiplas artes de pesca.

1.

**Shape's diversity towards ecomorphology: a historical
review**

1. Importance of the morphology in biological studies

Form and diversity are the two greatest subjects of natural history (GOULD, 1971; MOTTA et al., 1995). The high diversity of the living nature has been considered product of the evolutionary process, including similarities and differences among organisms, patterns of distribution and behaviours, adaptations and interactions (MAYR, 1966, 1977). According to Begon et al. (2006) the organisms were moulded by past environments and their characteristics (evolutionary baggage) reflects successes and failures of their ancestors. In this sense, the physical forces, which operate indirectly specifying the forms, provide optimal adaptation for animals' subject to their influence (THOMPSON, 1966). As said D'Arcy Thompson, in 1917, "*the organisms are well projected*" (THOMPSON, 1966).

At present and over the evolutionary time, the interaction of morphological with ecological diversities (among organisms) is the central focus of a comparative discipline named *ecological morphology* or *ecomorphology* (WINEMILLER, 1991). The ecomorphology hypothesis supports that morphological attributes of an organism should reflect its ecology and, thus indicate habits or adaptations to different habitats (VAN DER KLAUW, 1948; WINEMILLER, 1991). Bock (1990) explained, "*Ecomorphology is primarily concerned with analyses of the adaptiveness of morphological features and all dependent correlated topics such as the comparisons of adaptations in different organisms, modifications of adaptive features due to competition and other causes, structure of ecological communities, diversity within taxa, etc*". Winkler's (1988) definition is: "*Ecomorphology deals with the covariation of morphology and ecology*".

Morphology has been considered a predictor of the way-of-life (KARR AND JAMES, 1975). The shape of an organism can determine the niche occupied (GATZ, 1979), hence diverse morphologies are indicatives of distinct ecological and adaptive strategies (NORTON et al., 1995). Therefore, the communities are structured by biotic and abiotic processes which ecological niches (habitat use and relationships) and organization can variate in space and time (MOTTA et al., 1995; NORTON et al., 1995). Nowadays, the ecomorphology is an useful tool for biological studies related to: a) structure of communities, share of resources, ecological niche description; b) intra and interspecific interactions (predation,

defence and competition); c) biodiversity; and, d) population dynamics (relative and absolute growth, ontogeny, description and identification of populations) (MOTTA; KORTSCHALL, 1992; MOTTA et al., 1995; RECASENS; LOMARTE; SÁNCHEZ, 2006; LOMBARTE et al., 2012; TUSET et al., 2014; FARRÉ et al., 2013, 2015, 2016a). Moreover, the overall body shapes and common characteristics have been used to define biological groups phylogenetically related through morphometric geometric methods (ZELDITCH et al., 2003; PRICE et al. 2012), widely employed in the biology and palaeontology fields (ELEWA, 2010).

Research's on morphology have not been surveyed by a historical review so this chapter has as objective to scrutinize the ancient literature, showing (1) the contribution of the forms on the biodiversity discovery and (2) on animal sciences' development, according to the different thoughts, (3) presenting the shift from an evolutionary vision to an ecological approach and, in addition, (4) creating the theoretical base for the sequential chapters.

2. Historical survey about measuring the morphological variability

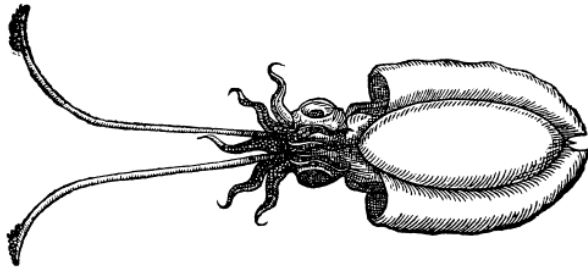
The first classification system based on resemblance of morphological characters (form and structure) in order to establish phylogenetic relationships emerged from the **comparative anatomy** (QUEIROZ, 2005). Due to the high diversity of living organisms, many philosophers were encouraged to study anatomy. Aristotle (384-322 *b.C.* – *before Christ* or 2,402-2,340 *ybp* - *years before present*) was the pioneer concentrating his dissections studies in other vertebrates than humans (MOORE, 1990; SINGER, 1996; CHAGAS, 2001). Aristotle investigated and compared shapes and structures and, besides the morphology, studied growth, physiology, behaviour and ecology of most than 500 mammals, birds, fishes, reptiles, amphibians, insects and cephalopods species (BLITS, 1999; REVERÓN, 2015). However, it cannot be said that Aristotle established an evolutionist principle because he expressed clearly: “...*man produces man, the plant produces the plant, according to the material constituting of everything*”, never thinking about an animal common ancestor (CRIVELLATO; RIBATTI, 2007). Using a comprehensive scope with rigorous and systematic methods, Aristotle wrote several books (as *History of Animals*, *Parts of Animals*, *Generation*

of Animals, Motion of Animals, Progression of Animals, Parva Naturalia and *De Anima*) and was considered “the Zoology’s father” (BLITS, 1999). Nevertheless, he followed the inductive reasoning and his scientific theories were elaborated from observations.

The principle of **inductivism** was substantiated by singular observations generating an equal number of trues and after that, generalized to everything (VIANA, 2007). To discover patterns of resemblance within major groups of animals, Aristotle recognized and used homologous structures and analogous functions (BLITS, 1999). Thus, **homologous structures** presenting the same anatomic pattern and embryonic origin, translate organisms’ adaptations to different environment types and reflecting a divergent evolution, while **analogous structures** differing in anatomic patterns and do not having the same embryonic origin, perform the same function in different living beings (COLE, 1944). Afterward, Richard Owen (1804-1892) defined homology in 1843 as “*the same organ in different animals under every variety of form and function*”. The Owen's concept of homology remains an important concept and helped biology in relation to public understanding (HARRISON, 1993).

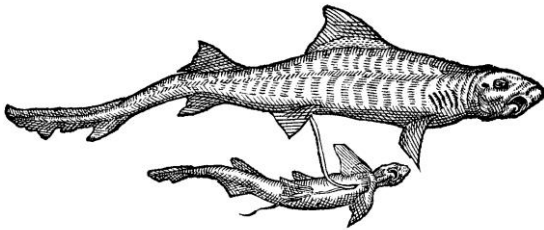
Aristotle’s writings also originated the Ichthyology (from the greek *ikhthus*, meaning fish) science, as he recognized about 115 fish species (MOYLE; CECH, 1988). Around 2,000 years later, in the 16th century, Guillaume Rondelet (1507-1572) summarized all the knowledge about fishes at that moment, and published the first ichthyological text, including drawings based on Aristotle’s’ writings (Figure 1). At the same time, Hippolito Salviani (1514-1572) published the first regional faunal paper and an Italian treatise with 92 fish species, followed by Pierre Belon (1517-1564) with the first modern systematic treatise on fish according anatomical characteristics (MOYLE; CECH, 1988). However, the Ichthyology’s father was Petrus Artedi (1705-1735) through his standard methods for making counts and measurements of anatomical features, which contributed to Carl von Linné (1707-1778) refinement of the principles of taxonomy (MERRIMAN, 1938; BROBERG, 1987).

De Sepia.



CAPUT II.

De Galeo læui.



CAPUT III.

Figure 1. Rondelet's Illustrations based on Aristotle's descriptions of an adult sepia (left side), and a young dogfish (*Mustelus laevis*) still attached by the umbilical cord to its mother (right side) (Modified of BLITS, 1999).

René Descartes (1596-1650), the mathematician who developed the analytical geometry, considered the living organisms as complexes machines whose structures were associated to functions: “...*But in my opinion, all things in nature occur mathematically*”. Thus, he developed an extensive physiological description of animal bodies, in which he explained the functions of life as a purely mechanical way, without appeal to a soul or vital principle (HATFIELD, 1992, 2015). Since these descriptions, the Physiological Science (from the greek *physis*, meaning functioning) was born. In Brazil, the understanding about animals and plants started in 1638 with the arrival of the german naturalist George Marggraf (1610-1644), who published the *Historia Naturalis Brasiliae*, ten years later.

The idea of shape evolution arose for the first time by George-Louis Leclerc (1707-1788), in France. Commonly known as Count de Buffon, he conducted an extensive work on the earth history, and his “*Histoire Naturelle, générale et particulière*” was published in three volumes’ in 1749 with the idea of species changing according to the time (a prerogative of evolution)

(LOVELAND, 2004). Contemporaneous and a critic of Carl von Linné (1707-1778), Buffon believed in a natural classification method defending the principles of continuity and affinity between species, based on anatomical structure comparisons. Linnaeus, on the contrary, was engaged with the nature's diversity, using classification methods based on discontinuity and morphology as main taxonomy aspects (CAMPOS, 2010). In 1761, in the Volume IX of his *Histoire Naturelle*, Buffon described similar species between the Old World (Europe, Africa and Asia) and the New World (Americas), concluding that mammals were originated from a single centre of dispersion located in the Old World, specifically Europe. He believed that species had degenerated, in other words, the Old World species became those found in the Americas. In 1766, in the volume XIV of *Histoire Naturelle*, Buffon published the article *Dégénération des animaux*, dealing with the theory of origin of the American fauna and presenting, perhaps for the first time in history, the theory that the South American continent was in the past attached to the African continent, forming a single super-continent: “*Let us suppose, that the Old and New worlds were formerly but one continent, and that, by a violent earthquake, the ancient Atalantis of Plato was sunk ... The sea would necessarily rush in from all quarters, and form what is now called the Atlantic Ocean.*” (GERBI, 1996).

Meanwhile Buffon was concerned with this theory, Linné (or Linnaeus) attempted to describe all the known natural world, by assigning a name that consisted of two parts, specifying the three kingdoms of nature, the mineral, the vegetable and the animal (NOMURA, 2011). In *Systema Naturae* (LINNÉ, 1758), he expanded the concept of the binomial nomenclature created nearly 200 years before by Johan Bauhin (1541-1613), a Guillaume Rondelet student, publishing in *Historia Plantarum Universalis*, the first international flora, containing 5,226 plants descriptions, an indicative of the great strides done about the knowledge of botany during the 16th century (CINCINNATI HISTORY LIBRARY AND ARCHIVES, 2015). Linné utilized the form of the structures to group the organisms in classes, orders, genders and species (BLUNT, 1982), also replacing previously descriptions as - *physalis amno ramosissime ramis angulosis glabris foliis dentoserratis* – by the concise and familiar names “Gender - Species” – *Physalis angulata* (MOBERG, 2008). Since the binomial

nomenclature was officially adopted in January 1, 1758, when Linné published the 10^o edition of his work, it is in use until the present days. Regarded as an exceptional mind, Linnaeus is the “Taxonomy’s father”, having described 4382 animal species and about 7000 plants (NOMURA, 2011).

During that time, the natural history had as one of its great goals the development of a natural classification system based on hidden laws of the form of organisms, which could reflect the way they were “built”. Completely subordinate to function, Georges Cuvier (1769-1832) was the first to classify the animal kingdom based on a structural and morphological point of view, expanding Linnaeus’s taxonomy by grouping classes into phyla, and arranging both fossils and living species in this taxonomy (RUDWICK, 1997). Cuvier (1818) preserved the natural history descriptive and classificatory rigor from Linnaeus without renouncing the theoretical claims of Buffon (CAPONI, 2004). He was the great promoter of the comparative anatomy. According to him, the classification method should be grounded analysing shapes and understanding how different beings coordinate their different functions (SMITH, 1993; FARIA, 2015).

Until then, all naturalists believed in **creationism** as species origin and, in consequence, in **fixism**. As a defender of fixism, Cuvier realised that fossils were the organic remains of extinct animals, believing that the fossilized species had no connection with those of his time. Thus, he created the catastrophism theory to explain that the geological and biological changes on the planet have never occurred by gradual changes but by sudden and violent ones, stablishing the extinction as a fact (by comparing fossils pieces with actual species) (PALMER, 1999). Unlike fixists, the defenders of the **transformism** believed that species had changed over time in response to certain circumstances, such as the Count de Buffon and Jean-Baptiste Pierre Antoine de Monet, the Chevalier of Lamarck (CAPONI, 2009). Jean-Baptiste Lamarck (1744-1788), the naturalist early proponent of the idea that biological evolution proceeded in accordance with natural laws, and the creator of the “Theory of the progression of animals”, admitted that species undergone changes in a constant progression towards the more complexity and advancement, stating that the transformation of an organ was passed down from generation to generation, changing the species (PACKARD, 1901). For Cuvier the term “analogy” just referred to similarities of

functions while for Étienne Geoffroy Saint-Hillaire (1772-1844), a naturalist with formalistic conception, the analogy was based on structural correspondence between distinct organisms, which all vertebrates were modifications of a common archetype. The debate of Cuvier and Geoffroy theoretical views was named “controversy of analogues” (APPEL, 1987).

The morphological school at the time, called **functionalism**, compared organisms owning certain features with others of the same type, and types with resemblance belonged to the same species. The “**type concept**” was an attempt to explain the true forms of organic bodies (STEINER, 1984). For Cuvier, an organism was compounded by a functional system, where each component acquired its specific position according to its function. For Johann Wolfgang von Goethe (1749-1832), the poet philosopher who accepted both the holistic nature of an organism as the functionality of its parts, the bodies were in continuous transformation, another way to see the “type” (RADL, 1988). Goethe’ typologism played a paradigmatic role in the science of biological form and the name gave to this new manner of research was “**morphology**”, published in 1796 (STEINER, 1984; LEVIT; REINHOLD; HOßFELD, 2015).

Later, Goethe in the 1817 *Zur Morphologie* defined it as “the theory of form, formation and transformation of organic bodies” (STEIGERWALD, 2002; OPITZ, 2004). To compare differences and similarities between various organic structures, two basic and different methodologies were employed: **idealistic** (constructionist, structuralistic) and **evolutionary** (historical) (LEVIT; REINHOLD; HOßFELD, 2015). The structuralist method, commonly outlined in works of Goethe, Cuvier and Geoffroy, presupposed that two characters of two different taxa are homologous, since they are located in a similar structural position, expressing a similar structural concept. On the other side, the evolutionary morphology used morphological data of all sorts in an evolutionary context (historical, often phylogenetic) and was connected mainly with the names of the anatomist Carl Gegenbaur (1826-1903) and Ernst Haeckel (1834-1919) (LEVIT; REINHOLD; HOßFELD, 2015).

It was common to explain such homologies by supposing that the Creator (God) used a certain pattern, which he modified in different ways. Despite Goethe’s theory had been developed on these lines, he sometimes argued that

the Creator modified the pattern by direct influence of the environment. Goethe used the word “metamorphosis” (meaning, in this context, transmutation of species) in the sense of “evolution of species” as a valuable but dangerous idea, since it “leads to formlessness” as said by himself (WELLS, 1967). Goethe was certainly not thinking in evolution of species, however he inspired both Darwinian and Lamarckian evolutionism as well as ‘counter-revolutionary’ idealistic morphology (LEVIT; REINHOLD; HOßFELD, 2015).

Erasmus Darwin (1731-1802), the Charles Darwin’s paternal grandfather, was the founder of the modern evolutionism and proposed the **transmutations of species** including the laws of organic life (artificial, natural and sexual selections). Unfortunately, his book *Zoonomia: the laws of organic life* published in 1792 was not well understood at that time (SALGADO-NETO, 2009). Indeed, the first well understood theory about organic evolution was presented by Jean Baptiste Lamarck (BURKHARDT, 1977, 2013). In the 1809 *Phylosophic Zoologique*, Lamarck presented his explanation about the species origin, called “**Theory of inheritance of acquired characters**” based on: the use and disuse of organs; and the inheritance of acquired traits (MAYR, 1972; CORSI, 1988). According to him two intrinsic abilities allowed the animals to vary and the evolution to take place: the first was the “*Le pouvoir de vie*” - the force that led to increasing complexity and was responsible for the evolution of the major life forms (hence **homologous structures**); the second was the “*L'influence des circonstances*” - the adaptive force responsible for the animals’ adaptation to their environment (hence **analogous structures**) (MAYR; PROVINE, 1980). Lamarck claimed that the organs form, structure and functioning were affected by environmental effects according to the use or disuse of a characteristic which lead to its progressive inheritance or loss. In turn, that implied in the inheritance of acquired characteristics albeit did not exist a clear mechanism related to these acquisitions (BARD, 2011). Continuous and extra use of particular organs make them more efficient while the continued disuse of some other organs leads to their degeneration and ultimate disappearance. Therefore for him, influenced by Goethe, the extinction did not exist (BURKHARDT, 2013). Lamarck told: “*I could prove it is not the form, either of the body or of its parts, that gives rise to habits and way of life of animals, but it is contrary, the habits, the way of life, and all the*

other influential circumstances that have with time constituted the form of the body and the parts of animals. With new forms, new faculties have been acquired, and little by little nature has arrived at the state where we see it at present" (LAMARCK, 1801; BURKHARDT, 2013). The most famous Lamarck's' example was the giraffes stretching their necks to reach leaves high in trees, strengthening and gradually lengthening their necks. These giraffes would have the offspring with slightly longer necks (also known as "soft inheritance"). Although Lamarck's theory was considered speculative, with low impact and acceptance (BURKHARDT, 1977; MARTINS; MARTINS, 1996; MAGNER, 1979), it was important to the understanding of the process of species origin related to environmental influences.

The preparation of these previous theories and the processes of their verification and refutation produced the biggest revolution in biology, determining the current paradigm of Biology. Perhaps no one has influenced our knowledge of life on Earth as much as the English naturalist Charles Darwin (1809-1882). Darwin's principal innovation was the mechanism of **natural selection**, which explained how populations of living forms adapt to changes in their environment by assuming that natural selection operated on occasional variations (GISSIS; JABLONSKA, 2011). This resulted in what Darwin called "*descent with modification*" which gathered a lot of coherent evidences about the transmutation of species (FERREIRA, 2007). During the Beagle journey between 1832-1836, Darwin collected lot of data about the variety of organism forms (livings and fossils). A considerable portion of species examined and described were new to science, especially those collected in South America (DARWIN, 1859). When studying the wildlife from the Galápagos Islands, he noticed that the finches (Figure 2) from the different islands besides to be similar, showed wide variations in their size, beaks and claws from island to island (i.e. their beaks were different depending on the local food source). Returning to England, Darwin began reflecting on his observations and experiences and concluded that, because the islands are so distant from the mainland, the finches that arrived there in the past had changed over time. Over the next two years, Darwin developed the basic outline of his groundbreaking theory of evolution through natural selection (BATESON, 1979).

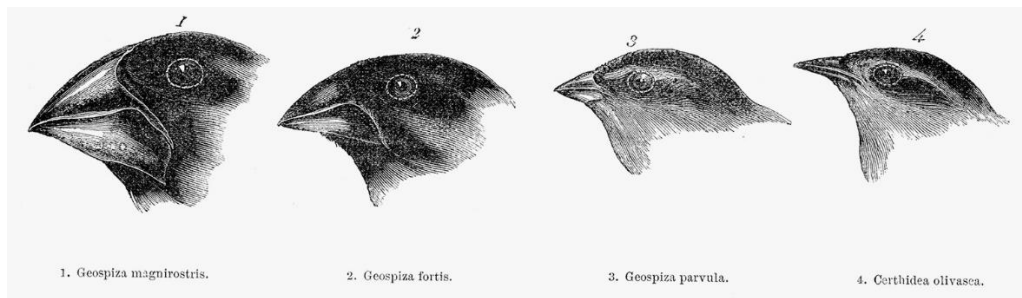


Figure 2. Darwin's drawings of the different heads and beaks he found among the finches on the Galapagos Islands (Source: Darwin Online).

On the Origin of Species may never have been written, let alone published, if it had not been for Alfred Russel Wallace (1823-1913), another British naturalist who independently proposed a strikingly similar theory in 1858 (KUTSCHERA; NIKLAS, 2004; COOPERMAN; MASCI; O'CONNELL, 2009). Together, Darwin and Wallace published in 1858 some manuscripts in the Journal of the Linnaean Society about the hypothesis of descent with modification by means of natural selection (DARWIN, 1859). This hypothesis has five fundamental assertions, *reproduction*: all organisms produce more offspring than their environments can support; *variability*: intraspecific variability of most characters exists in abundance; *struggle for life*: competition for limited resources leads to a struggle for life (Darwin) or existence (Wallace); *inheritance*: descent with heritable modification occurs; and *natural selection*: as a result, new species evolve into being, with its "consequences" divergence of character and the extinction of less improved forms (RAUP, 1994; KUTSCHERA; NIKLAS, 2004). They included evidences of homologies between humans and other mammals, suggesting that men were the transformation from monkeys and God was not involved with the universe and life's creations (FREEMAN, 1977).

In 1859, Darwin published *On the Origin of Species by means of a Natural Selection*, his most important publication which settled the theoretical framework of evolutionary biology and the end of the fixist concept of the species. In this context, the study of comparative anatomy undergoes a substantial change in the concept of the organization of animals since it began to consider the interaction between phenotypic features with the external environmental conditions acting on them (DARWIN, 1859; ALLEN, 1907). The typological concept of anatomy is

abandoned, and the modern concept of **phylogenetic morphology** becomes a key element in the study of evolutionary lines. Therefore, the species transformation through time, as species became modified and diverge to produce multiple descendant species are now referred as evolution (MEYER; KEAS, 2003; LOSOS, 2013). And, how the traits could be inherited through generations was explained from the principles proposed by Gregor Johann Mendel (1822-1884), in 1866 (MIKO, 2008). Mendelian analysis has revealed the further fact, unsuspected by Darwin, that recombination of existing genetic units could both produce as modify new inheritable variations, and this has important evolutionary consequences (HUXLEY, 1942).

It is important to recognize that “natural selection” is not synonymous of “evolution” (FUTUYMA, 2009). Evolution can occur by processes other than natural selection (especially genetic drift), and natural selection can occur without any evolutionary change (as when natural selection maintains the *status quo* by eliminating deviants from the optimal phenotype) (PERETÓ; BADA; LAZCANO, 2009). On the other hand, the natural selection is the only known mechanism to cause adaptive evolutions (FUTUYMA, 2009; PIANKA, 2011; VITT; PIANKA, 2014). **Adaptation** is the important concept that link morphology and ecology, whereby members of a population become better suited to some characteristics of their environment, changing attributes that affects their survival or reproduction (FUTUYMA, 2009). By the way, the **sexual selection** (another of the aspects described by Darwin, in 1859) is the process of choosing morphological and behavioral characteristics that led to the successful crossing, where the features evolution gives reproductive advantages to the organisms (RUNDLE; CHENOWETH; BLOWS, 2006; JONES; RATTERMAN, 2009). At this moment, regarding to studies on environment adaptability, some ecological rules began being formulated.

Joel Asahp Allen (1838-1921) showed that other influences than natural selection operate powerfully in the differentiation of specific forms. He described trends of geographical character variation that became known as Allen's Law, one of the most famous of the so-called "**ecogeographical rules**" (ALLEN, 1877) beside the Bergman's Law, from Carl Georg Lucas Christian Bergmann (1814-1865). Through morphological characters comparison and the assumption of

correlation between the phenotype and the physical habitat, the Allen-Bergmann's rule indicated the existence of a lower surface/volume ratio in homothermous animals of cold waters (NUDDS; OSWALD, 2007).

Another rule of shape transformation was formulated by the naturalist and mathematician D'Arcy Thompson (1860-1948), suggesting that physical forces exert direct and immediate influence in shaping organisms as they grow (GOULD, 1971). This is the guiding concept of 1917 *On Growth and Form*, where Thompson showed that changes on biological form are both modeled and described as mathematical diffeomorphisms (transformations that are smooth and that have smooth inverse), which he called as *cartesian transformations* (BOOKSTEIN, 1991, 1997). D'Arcy Thompson introduced the study of form-comparisons with a latent variable, which have been studied by biologists as homology (BOOKSTEIN et al., 1985; ELEWA, 2010). The Thompson's homology rule refers to parts of different organisms that are correspondents, whereas the Cartesian transformation acts distorting a picture or other specifically geometric representation form (Figure 3) (BOOKSTEIN, 1977, 1991; BOOKSTEIN et al., 1985). This approach, as Thompson pointed out, gives a clearer view of what Darwin (1859) referred to as **correlation of characters** (ARTHUR, 1984).

After the Evolution's theory formulation, there was a stagnation in the appearance of new concepts in morphology. The morphology science lost strength during almost forty years. Just in the middle of the twentieth century, Hans Heinrich Böker (1886-1939) in his 1935 book *Vergleichende biologische Anatomie der Wirbeltiere (Comparative biological anatomy of vertebrates)* incorporated the direct observation of animals under natural conditions to morphological studies, and established that form is derived from function; thus, function always precedes form (DUTTA, 1982). Despite the direct observation importance, Böker's principles were rejected by considering only functional aspects of form and neglecting the influence of genetics and the convergence. In this context, the quality of morphological studies began to be improved, developing essential principles for the **ecomorphology** (or ecological morphology) formulation.

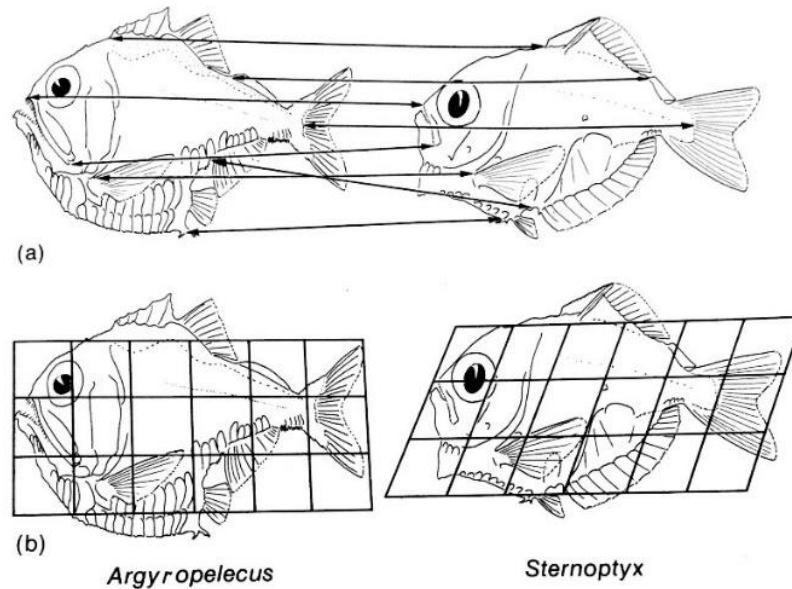


Figure 3. D'Arcy Thompson example of homology as a smooth deformation, displaying the correspondence of homologous points (a) and by a Cartesian grid transformation (b) (Source BOOKSTEIN et al., 1985).

Until Theodosius Grygorovych Dobzhansky (1900-1975) published in 1937 *Genetics and the origin of species*, it was believed that all members of one species had practically identical genes (FORD, 1977). Dobzhansky was the most influent evolutionist at his time and his most significant contribution to science doubtless was the formulation and popularization of the modern synthesis of evolutionary theory (DOBZHANSKY, 1973; KALINOWSKI; LEONARD; ANDREWS, 2010). Evolution was defined as "a change in the frequency of an allele within a gene pool", and according him it was through mutations in genes that natural selection took place, and new species arose (BARAHONA; AYALA, 2005). To Darwin, the difference between species and varieties was that species are delineated by gaps in morphology that persist when they overlap in space, whereas varieties are less definite, and show intermediates (MALLET, 2010). Theodosius Dobzhansky, Ernst Walter Mayr (1904-2005) and Julian Huxley (1887-1975) judged Darwin's species ideas as inadequate and promoted the "Modern Synthesis" view of species (MALLET, 2010; FONSECA, 2006). "Modern Synthesis" was a movement which championed Darwinian natural selection as compatible both with Mendelian genetics and with the data on natural biodiversity, in which species were characterized by 'reproductive isolation' from others

(varieties as geographic subspecies do not) (DOBZHANSKY 1935, 1937; MAYR, 1940, 1942, 1963).

In 1942, with *Systematics and the Origin of Species* (MAYR, 1942) and *Evolution, the modern synthesis* publications (HUXLEY, 1942), the theoretical scope of neoDarwinism (or synthetic theory of evolution) was formulated based on population genetics, ecology, paleontology, biogeography, and morphology in a second plane (FONSECA, 2006). Mayr proposed that the species was a fundamental category of biological organization and was the first taxonomist to introduce the *biological species concept* (BOCK, 2005; QUEIROZ, 2005; MALLET, 2010; POLISELI; OLIVEIRA; CRISTOFFERSEN, 2013). **Species** were defined as groupings of reproductive populations (reproductively isolated from other groups) with the same characteristics that occupies a specific niche in the nature (MAYR, 1982). His work on species and speciation helped scientists to understand the progress and mechanisms of evolution from one species to another, and the importance of the species unit as "the keystone of evolution". *"Without speciation, there would be no diversification of the organic world, no adaptive radiation, and very little evolutionary progress. The species, then, is the keystone of evolution"*, said Mayr (MEYER, 2005). The speciation caused by geographic separation of populations (**allopatry**), such as by rivers or valleys, prohibited homogenizing gene flow between them and accumulated mutations over time. To Mayr this might lead to the divergence of such populations from each other, and reproductive isolation might arise as a simple product of these separate evolutionary histories (LENSKI, 2005; MEYER, 2005).

As significant as the investigations of D'Arcy Thompson, in the 1920's Julian Huxley was pioneer in the quantitative investigation of **allometric growth** (GOULD, 1971; GALL, 2011, PACKARD, 2012). Huxley investigations considered the organism shape as a fundamental feature of its overall design, and an obvious aspect of the individual shape was that it markedly changed many times, and in a continuous manner, throughout its **ontogeny** (STRAUSS, 1993). Huxley's fundamental deduction about body form was his "law" of the constant differential growth ratio (HUXLEY, 1942). In genetics, this mechanism was used to clarify any facts and theoretical constructions in the framework of classical biology, such as morphology and embryology (GALL, 2011). A common point of

view among Huxley and Mayr was that natural selection and mutations were complementary processes.

However, the evolutionary taxonomy school, whose vision was based on the works of Mayr and associates, was completely broken by Emil Hans Willi Hennig (1913-1976) with the proposal of phylogenetic systematics, in 1950 *Fundamentals of a Theory of Phylogenetic Systematics* (HENNIG, 1966). Hennig grounded different classificatory schools of the XX century providing the understanding of the organic diversity at the light of evolution (SANTOS; KLASSA, 2012). In *Phylogenetic Systematics*, the phylogenetic systematic (or cladistic) corresponded to a biological classification reflecting the kinship between the living beings by using the common ancestry concept to identify the monophyletism (HENNIG, 1966). To constitute a natural clade, the kinship relations were established through refined observation on homologous characters, discriminating them among primitives (plesiomorphic) and derivatives (apomorphic). In this sense, the sharing of apomorphies allowed distinguishing homologies from adaptive convergences and thus, monophyletic groups were determined (SANTOS; KLASSA, 2012). Hennig is commonly referred as the father of Phylogenetic Systematics due to his contribution with a great paradigm to the taxonomy history and systematisation of the biological diversity.

In 1943, Robert Gustav Adolf Remane (1898-1976), a morphologist, and Wilhelm Kühnelt (1905-1988), a terrestrial ecologist (SCHALLER, 1990), published separately their concepts of "*Lebensform*" (form of live) based on observations about morphological analogies of organisms distant phylogenetically, produced by adaptive processes to similar environmental factors (MOTTA et al., 1995). Remane (1952) described the criteria by which homologues were to be recognized and his work was very influent (RIEPEL, 2013). The 1952 *Die Grundlagen des natfirlichen Systems, der vergleichenden Anatomic und der Phylogenetik* ("*The foundations of the natural system, of comparative anatomy and phylogenetics*") was explicitly dedicated to the foundations of systematic, phylogenetic and the concept of homology (ZACHOS; HOßFELD, 2006). Six criteria were proposed by him, being the three principles related to: - position: "*Homology can be recognized by similar position in comparable systems of features*"; - structure: "*Similar structures can be*

homologized without reference to similar position, when they agree in numerous special features”; - transition: *“Even dissimilar structures of different position can be regarded as homologous if transitional forms between them can be proved so that in considering two neighboring forms, the first and second conditions are fulfilled. The transitional forms can be taken from ontogeny of the structure or can be true systematically intermediate forms.”* (ZACHOS; HOßFELD, 2006; WHEELER, 2012).

Subsequently, despite environmental constraints, Cornelis Jakob van der Klaauw (1893-1972) connected the morphology to ecology and used it to define the relationship between body structure and environment. Van der Klaauw was able to make the concept of holism operational by introducing the functional component in functional morphology (DUBBELDAM, 2007). In its 1948 *Ecological Morphology* publication, van der Klaauw introduced two new cohering concepts: - the **functional component**: skeletal elements together performing a specific function should be considered as a unit with a certain degree of independence; and, - the **holism**: the various functional components should fit together within the whole of the skull (DUBBELDAM, 2007). Thence, the connection between morphological features of the organism began to be linked with their ecological and functional habits within ecosystems and, on the 1950's, morphology studies focused in functional aspects. That was significant to the establishment of a basis for the development of future studies.

The evolutionary morphology concepts emerged in 1965 with *Adaptation and the form-function complex* by Walter Joseph Bock (1933-) and Gerd von Wahlert (1925-) who presented the **“form and function complex”** and suggested that any component of the life history of the organisms' results of adaptation determined by the interaction of organism with the environmental conditions. They distinguished form, function, faculty and biological role, as follows: - *form*: defined as the material configuration of a feature; - *function*: as its action, or how the feature works; - *faculty*: comprising a form-function complex; and, - *biological role*: defined as the action or the use of the faculty by the organism in the course of its life, with reference to the environment where it lives (BOCK; VON WAHLERT, 1965; BOCK, 1969; BOCK, 1994). The biological adaptation had been interpreted as an interaction between the organism and its environment,

and was used in three different ways in evolutionary studies: - *universal adaptation*: as the bond between living organisms and their environment and was an absolute property of life that can neither increase or decrease; - *physiological adaptation*: as the ability of tissues to modify phenotypically in response to environmental stimuli and a special case of the general principle that the phenotype was an expression of the genotype in a particular environment; and, - *long-term evolutionary adaptation*: as the hereditary adjustment of an organism to a particular set of environmental conditions (BOCK; VON WAHLERT, 1965).

In parallel to the evolutionary morphology development, ecologists perceived that the species morphology was also important to analyze competition, coexistence relationships, habitat differentiation and to elucidate the ecological structure of communities. Thus, the **Ecological** Science introduced new concepts and theories as ecological niches, resource partitioning, habitat differentiation, adaptations and competition within communities (HUTCHINSON, 1959; MACARTHUR; WILSON, 1967; MACARTHUR, 1968; SCHOENNER, 1974). Thereby, studies on morphology, function and ecology of species showed a growing trend in the half century.

In 1959 *Homage to Santa Rosalia or Why Are There So Many Kinds of Animals?* George Evelyn Hutchinson (1903-1991) focused attention on a problem that is central to all ecological theory: what determines the number of species in a particular ecosystem? (HUTCHINSON, 1959; SLOBODKIN; SLACK, 1999; KEARNEY et al., 2010). Among all of his ideas, one received most attention: how species (of similar features) can have their utilization of limiting resources and still avoid interspecific competition sufficiently to coexist in the same community (BROWN, 1981). Hutchinson helped to build the best insights into species **richness** and **community ecology**, which further developed the formal notion of **ecological niche** (LOVEJOY, 2011). Initially, the niche concept was originated on a subjective way in the natural history by Joseph Grinnell (1877-1939) in 1917, and was subsequently employed in quantitative ecology (PATTEN; AUBLE, 1980). In collaboration with his students, in particular with Robert MacArthur (1930-1972), Hutchinson developed the first comprehensive mathematical theory to explain species richness and other mathematical models to depict the various interacting component parts of an ecosystem (BENSON, 2000). The ecological

niche was defined by him as “**hypervolume** in a multidimensional ecological space”, determined by species requirements to reproduce and survive (POLECHOVÁ; STORCH, 2008). The *n-dimensional hypervolume* could be subdivided in two categories: - *fundamental niche*: the full range of conditions (biotic and abiotic) and resources in which one species could survive and reproduce free of interference from other species; and – *realized niche*: a narrower niche resultant of pressure from interactions with other organisms (i.e. inter-specific competition), to which the species would be mostly highly adapted (SCHOENER, 1974, 1986; GRIESEMER, 1992). In other words, ecological niche was the position of an organism within an environmental gradient involving both abiotic conditions exploited by the organisms (e.g. temperature, pH, moisture, solar radiation, humidity, soil texture) as well as biotic interactions (e.g. predators, parasites, competitors), both important for a species persistence (PINTO-COELHO, 2009). For that, adaptations to different ecological conditions and habitat uses require morpho-functional body variations in order to perform relevant behaviors as swimming, habitat choice, prey selection, and anti-predator responses (WAINWRIGTH, 1996; KARPOUZI; STERGIOU, 2003; LANGERHANS; REZNIK, 2010). After Hutchinson’ contribution, the Ecology promised to become a fully mathematized and experimental discipline (BROWN, 1986). This new perspective revitalized Ecology as a science.

Later, MacArthur together with other Hutchinson’ student, Edward Osborne Wilson (1929-), built a general theory to explain how distance and area combine to regulate the balance between immigration of new species to the island and the extinction of species already present (MACARTHUR; WILSON, 1967). MacArthur and Wilson published in 1967 *Theory of Island Biogeography* the first principles of ecology and population genetics used to provide mathematical models which helped to explain the biotic diversity patterns and the species distribution in archipelagos (HAMILTON, 1968; BROWN, 1986). In 1968, MacArthur established a parallelism between niche and phenotype, in the sense that both are intrinsic character reflections of the organisms (PINTO-COELHO, 2009).

When two species differentiate their niches, they tend to compete less strongly, and thus facilitate their coexistence. According to Thomas William

Schoener (1943-), in 1974 *Resource Partitioning in Ecological Communities* the niche overlap between similarly species varies in response to food availability, habitat spatial distribution and time (e.g. feeds at different times of the day), all of them fundamental to community organization (SCHOENER, 1974). He developed resource-partitioning studies, which the major purpose was to analyze the limits placed by the interspecific competition on the number of species that could stably coexist (SCHOENER, 1974).

According to this new scientific trend, ecologists passed to interpret morphological variations among species as different adaptations to the environment, and incorporated the measurements of morphological traits for their analysis in order to clarify evolutionary and ecological questions (HUTCHINSON, 1959; KEAST; WEBB, 1966; MACARTHUR, 1968; SCHOENER, 1974). The term "ecomorphology" was coined by James Richard Karr (1948-) and Francis Crews James (1930-) in his 1975 *Ecomorphological configurations and Convergent Evolution*, where they examined the relationship between morphological features and environmental aspects strictly from the ecological side, in particular related to the structure of communities (KARR; JAMES 1975; Bock, 1994).

The following years finally linked vertebrate morphology and ecology establishing the foundations of the modern ecomorphology. Ecomorphological studies began to focus on the casual consequences of anatomical differences between species and the ecology of the organism (WAINWRIGHT; REILLY, 1994). A series of papers by Walter Joseph Bock (1933-) (BOCK, 1977, 1990) clarified several important points and set a conceptual framework for interpreting the ecological and evolutionary implications of functional morphological observations. The first paper (BOCK, 1977) was important to reinstate the ecomorphology on the perspective of form-function complex and differentiates concepts: - *functional morphology*: deals with the functional properties of the morphological structures; and, - *ecomorphology*: deals with the biological role of structures in the environment and throughout the evolution.

In the 1980's, studies relating the functional design showed how variations in intra and interspecific performance molded the fitness distributions in communities', as Earl Werner and Donald Hall (WERNER; HALL, 1974, 1977, 1979) working on sunfishes, and Peter Raymond Grant (1936-) and his wife

working on Galapagos' finches (GRANT, 1968, 1986; GRANT; GRANT, 1989, 1993, 1996). **Fitness** involves the ability of the organism to survive and reproduce in their environments, having as consequence of success the gene's contribution to the next generation. When no differences in fitness occurs, natural selection cannot act and adaptation cannot occur (ORR 2009), the reason why recent ecomorphologic studies have incorporated phylogenetic hypothesis.

Joseph Felsenstein (1942-) evaluated the species differences and relationships between individuals or populations through **phylogenetic inferences** analyzing heritable traits (such as the DNA sequences) and historical evolution of characters (FELSENSTEIN, 1983). Joe Felsenstein in 1982 *Numerical Methods for Inferring Evolutionary Trees* and in 1983 *Statistical Inference of Phylogenies* used methods of phylogenetic variables to estimate the interspecific correlation among characters noting divergence patterns when sister species evolved independently of their ancestors (FELSENSTEIN, 1982, 1983; WAINWRIGHT; REILLY, 1994). Felsenstein (1983) defined **phylogeny** as a branching tree diagram showing the course of evolution in a group of organisms. However, the phylogeny concept was first introduced by Ernst Haeckel in 1820, when he proposed a link with ontogeny and said: "ontogeny recapitulates phylogeny" (RICHARDSON; KEUCK, 2002).

Even as Felsenstein, George Lauder cautioned the difficulty of determine adaptive processes when historical information is ignored. In this framework, Lauder brought a phylogenetic approach to the study of functional morphology. In 1981 *Form and Function: structural analysis in evolutionary morphology* he stated the relative importance of phylogenetic constraints in the functional morphology evolution (BROOKS; MCLENNAM, 1991). Furthermore, it could be assessed by examining emergent structural or functional traits within a phylogenetic framework and test hypothesis of phylogenetic constraints comparing general properties among clades (BROOKS; MCLENNAM, 1991). In 1990 *Functional Morphology and Systematics*, Lauder contributed with biomechanical studies to define the physical constraints which organisms must work beyond to explain how the phylogenetic analysis on both form and function allows to know the historical pathways taken during transformations of the organismal design (BROOKS; MCLENNAM, 1991).

As exposed, over life, the influence of ecological factors may cause morphological changes and the selection on these characters leads to changes in gene frequencies and extinction or speciation of a taxon (MOTTA et al., 1995). In other words, the speciation is the evolution mechanism of living organism's (DARWIN, 1859; FARKAS et al., 2015). Although speciation process is hard to observe, replicate and manipulate in the wild (GRAS et al., 2015), the last detection was published by Andrew P. Hendry (1968-) and his colleagues, in 2000 *Rapid Evolution of Reproductive Isolation in the Wild: Evidence from Introduced Salmon* describing a fast process of sympatric speciation since an ecological isolation.

3. Quantitative techniques for measuring morphological variability

More than exploring the interactions between intrinsic characteristics of individuals (or taxonomic units) and their environment, the ecomorphology is a developing field of the organismal biology and ecology (NORTON et al., 1995). The addition of phylogenetic components to the ecomorphology studies resolved the statistical dilemma of the nonindependence of characters for those taxa which share a trait due to common ancestry (MOTTA et al., 1995). Species relationships could be ordered as phylogenetic trees using anatomical and molecular traits, according their character differentiation.

Per advent of computing in the 60's many possibilities emerged for the objective classification in quantitative biology (SOKAL, 1966). Robert Rueven Sokal (1926-2012), Peter Sneath (1923-2011) and James Rolhf (1936-) were pioneers in the development of **numerical taxonomy** methods, initially performing their researchs independently (SNEATH, 1995). The numerical taxonomy was the biological classification system where taxonomic units were grouped into taxa by using numerical methods supported by the character states (SNEATH; SOKAL, 1973; HULL, 1988). It used all characters without ignoring any bad character initially rejected by the conventional taxonomy (SOKAL, 1963; SOKAL; SNEATH, 1963). The relationships among characters were inferred without regard to whether character states was derived (apomorphic) or primitive (plesiomorphic) (SOKAL; SNEATH, 1963; HART; REYNOLDS, 2008). The development of numerical taxonomy involved many problems because inevitably

led to a re-examination of the bases of phylogenetic reasoning and to attempts the reconstruction of phylogenetic sequences (SOKAL; CAMIN, 1965).

The 1963 *Principles of Numerical Taxonomy* publication was a preliminary exposition of this new field, when Sokal and Sneath determined as a fundamental principle the strict segregation of phylogenetic speculation from taxonomic procedure. *Taxonomic affinity* was determined as the similarities based on observable characters of taxa, so-called **phenetic** similarities (SOKAL, 1963). To represent the taxa, Sokal and Sneath (1963) used the **Operational Taxonomic Unit (OTU)** as observation of organisms that means species, genus or a group of undetermined evolutionary relationship.

The 1965 *Fundamental problems in numerical taxonomy* published by William Thomas Williams (1913-1995) and M. B. Dale, was the first critic analysis about numerical taxonomy and introduced greater rigor into methodology development (SNEATH, 1995). Williams and Dale (1965) presented viewpoints on monothetic *versus* polythetic classifications, hierarchical *versus* nonhierarchical classifications, and metric (quantitative) *versus* nonmetric (qualitative) resemblance coefficients (ROMESBURG, 2004).

The Numerical Taxonomy progressed quickly, and in sequence Sokal and Rolf (1966) published *Random Scanning of Taxonomic Characters* performing experiments with group identification based on the random sampling of morphology, and introducing image analysis to process electronic data. Sneath, in 1967, published *Trend surface analysis of transformation grids* in order to quantify the D'Arcy Thompson's transformation grids approach to shape analysis through application of trade surface analysis.

Over the years, the measurements and analyses of shape variations were improved and named **morphometrics**, accompanied by the development of rigorous multivariate statistical methods (ROHLF; MARCUS, 1993). Initially, the shape of species was assessed underpinned on linear measurements methods (STRAUSS; BOOKSTEIN, 1982; WINEMILLER, 1991). Although important to the scientific development, the traditional morphometrics studies presented biases by allometry and size effects, the distances between the measurements were difficult to standardize, and mainly, the exact geometric structure of the shape was not preserved (ADAMS et al., 2004). Researchers as Fred Bookstein (1947-

), Richard Arthur Reyment (1926-), Richard E. Strauss (1950-) and Paul Ralph Ehrlich (1932-) pursued applying this numerical approach to quantify organisms shape variation.

In the late 1980's, these approaches were synthesized through efforts of Bookstein and contributions of David George Kendall (1918-2007), Kanti Mardia (1935-) and Ian L. Dryden, Colin Goodall and James Rohlf, resulting in a formulation and subsequent development of the **geometric morphometrics** (GM) (WHEELER, 2012), considered as a 'revolution' in the field (ROHLF; MARCUS, 1993). The geometric morphometrics consists in the analysis of Cartesian geometric coordinates between morphological structures rather than linear, outline or volumetric variables, which enable to describe complex morphological structures in more detail (such as general body shape) (FARRÉ et al., 2016a).

In the 1990's, techniques from mathematical statistics, multivariate biometrics, non-Euclidean geometry and computer graphics were combined in a coherent new system of tools for the complete qualitative and quantitative analysis, the **landmark-based method** (homologous coordinate points in anatomical structures of interest, defining the geometric shape of the object) (BOOKSTEIN, 1996). More formally, a *landmark configuration is a discrete sample from a homology mapping across pairs of specimens* (that literature is summarized in BOOKSTEIN et al., 1985). When important biological information (i.e. the presence of barbel in fish) cannot be defined using landmarks, an additional type of coordinate points can be used to define the shape of boundary curves or of not fixed structures, and are named semilandmarks (BOOKSTEIN, 1991, 1997).

In landmark-based analysis (including the semilandmarks), the non-shape information is removed from the coordinates of landmarks (by scaling or translation) to compare the shapes (KENDALL, 1977). In general, the shapes are scaled to unit centroid size and rotating to minimize the distances between corresponding landmarks (square root of the summed squared distances of each landmark to the centroid). The landmark configuration is rotated to minimize the deviation between it and a reference, typically the mean shape. Because shape space is curved, analyses are done by projecting shapes onto a tangential space. In other words, the Cartesian coordinates of anatomical landmarks are quantified

by the unification of a rigorous statistical theory with analytical procedures for superimposing landmark configurations for all specimens in a common coordinate system (FARRÉ et al., 2016a). Among the superimposition techniques, the Procrustes analysis has been considered the most complete method to provide the uniform components of the shape variation (**partial** or **relative warps**) for each analyzed object (i.e. specimens or species). The resulted warps are utilized as shape variables in the multivariate statistical analysis. The interpretation of the shape patterns is given through graphical representation of the results plotted in a morphological space (**morphospace**). The pattern of clustering the samples in the morphospace represents the similarities and differences of the shapes, which can reflect phylogenetic relationships (WALKER, 2000; ZELDITCH; SHEETS; FINK, 2003; PRICE et al., 2012). Conventional multivariate statistical methods such as multivariate analysis of variance and multivariate regression can be used to test statistical hypotheses about shape (ROHLF; SLICE, 1990; ROHLF; BOOKSTEIN, 1990; BOOKSTEIN, 1991; MARCUS; BELO; GARICA-VALDECASAS, 1993; MARCUS et al., 1996; WALKER, 2000; ELEWA, 2004, 2010). The power of this method lies in the ability to detect and visualize shape differences more clearly than classical approaches (CLABAUT et al., 2007; LOMBARTE et al., 2012; FARRÉ et al., 2013, 2015, 2016).

Because landmark-based GM methods possess more powerful statistical support, they have been considered one of the most appropriate methods to quantify the shape variation between structures (ADAMS; ROHLF; SLICE, 2004; ADAMS; OTAROLA-CASTILLO, 2013). Systematics, phylogeny, paleontology, taxonomy and evolutionary biology are among the main research fields using GM, most of them analyzing differences in bony structures (i.e. skulls, jaws, dentitions, vertebrae, otoliths, etc.) or in overall body shapes in order to answer evolutionary, taxonomic, ecological or biological hypothesis (FARRÉ et al., 2016).

Fishes have been one of the most researched zoological groups by means of GM methods due to the great phenotypic plasticity. The analysis comprises since overall body shape (CLABAUT et al. 2007; COSTA; CATAUDELLA, 2007; ANTONUCCI et al., 2009; YOUNG; SNOEKS; SEEHAUSEN, 2009; PARK et al., 2013; CHAPMAN et al., 2015; FAULKS et al., 2015; PRICE et al., 2015; FARRÉ

et al., 2016; PÉREZ-QUIÑÓNEZ et al., 2017) to specific structures as otoliths (MONTEIRO et al., 2005; PONTON, 2006; LOMBARTE et al., 2010, TUSET et al., 2016, IBAÑEZ; HERNÁNDEZ-FRAGA; ALVAREZ-HERNÁNDEZ, 2017), skulls (WINTZER; MOTTA, 2005; COOPER; MASCI; O'CONNELL, 2009) or fins (WAINWRIGHT; BELLWOOD; WESTNEAT, 2002; STANGE et al., 2016). The purposes cover from taxonomic differentiation among species (VALENTIN; SÉVIGNY, CHANUT, 2002; LANGERHANS et al., 2003; IBAÑEZ; CHOWX; O'HIGGINS, 2007; IBAÑEZ; HERNÁNDEZ-FRAGA; ALVAREZ-HERNÁNDEZ, 2017) to phylogenetic relationships and evolution processes (RÜBER; ADAMS, 2001; CLABAUT et al., 2007; MUSCHICK; INDERMAUR; SALZBURGER, 2012; KLINGENBERG; MARUGÁN-LOBÓN, 2013). Regarding to ecology and biodiversity approaches, the landmark GM method has been successfully employed in studies related to: reconstruction of the trajectory of morphological diversification using fossils (FRIEDMAN, 2010; MARRAMÀ; GARBELLI; CARNEVALE, 2016); complex phenotype–environment associations (WAINWRIGHT; RICHARDS, 1995; KASSAM; SATO; YAMAOKA, 2002; WAINWRIGHT; BELLWOOD; WESTNEAT, 2002; LANGERHANS; CHAPMAN; DEWIT, 2007); resource partitioning (KASSAM et al., 2003); biological invasion success (AZURRO et al., 2014); ontogenetic dynamics (ZELDITCH et al., 2003); diversity measure and communities structure (LAYMAN; LANGERHANS; WINEMILLER, 2005; RECASENS; LOMBARTE; SÁNCHEZ, 2006; LOMBARTE et al., 2012; FARRÉ et al., 2013; TUSET et al., 2014; FARRÉ et al., 2015; 2016b).

Among other zoological groups studied by means of the GM application are dinosaurs (YATES et al., 2010; SERB et al., 2011; BRUSATTE et al., 2012; HEDRICK; DODSON, 2013; KLINGENBERG; MARUGÁN-LOBÓN, 2013); reptiles (CLAUDE et al., 2003, 2004; BONNAN et al., 2008; PIERCE; ANGIELCZYK; RAYFIELD, 2008), amphibians (ADAMS; ROHLF, 2000; BUSKIRK, 2009; KALIONTZOPOULOU, 2011; ORIZAOLA et al., 2013), birds (MARUGÁN-LOBÓN; BUSCALIONI, 2004; KULEMEYER et al., 2009; BHULLAR et al., 2012), and mammals (MARCUS; HYNIGST-ZAHER; ZAHER, 2000; MONTEIRO-FILHO; MONTEIRO; REIS, 2002; PEREZ; BERNAL; GONZALEZ, 2006; DRAKE, 2011; GUNZ et al., 2012; LU et al., 2014).

This above overview gave us a complete overview of the theme, and was useful to situate our study in the context of the area of *Form and Functional* studies.

Final Considerations

Along the Science History, despite many methods to measure or quantify species shape have been developed, the morphology remained as the major player in this field. More possibilities emerged with the advent of computing, and the science passed from traditionally descriptive to measurable and quantitative.

Initially, the shape of species was assessed underpinned on linear measurements methods through morphometrics, and for a while it was sufficient to evaluate the existent morphological variability. Nevertheless, these traditional morphometrics studies presented biases due to allometry and size effects (STRAUSS; BOOKSTEIN, 1982; WINEMILLER, 1991; ROHLF; MARCUS 1993).

In the late 1980's, the geometric morphometry (GM) was created, consisting of the analysis of Cartesian geometric coordinates to describe complex morphological structures in more detail (BOOKSTEIN, 1991; ROHLF; MARCUS, 1993). Currently, the landmarks-based GM method, supported by powerful statistical analysis, is the most appropriate and fast methodology to quantify shape variations between structures (ADAMS et al., 2004; ADAMS; OTAROLA-CASTILLO, 2013), and had been presenting potential to be applied in biodiversity studies. Due to its complexity, biodiversity cannot be explained by simple indexes (MAGURRAN, 2013; LOISEAU; GAERTNER, 2015). As a multidimensional concept, biodiversity includes genetic and phenotypic variability, species richness, their functional properties and phylogenetic relationships (PURVIS; HECTOR, 2000). In this sense, ecological, taxonomical, phylogenetical, morphological and functional measures are recommended (LYASHEVSKA; FARNSWORTH, 2012). Among them, the morpho-functional approach is the most effective in providing the community structure and organization (RECASENS; LOMBARTE; SÁNCHEZ, 2006; LOMBARTE et al., 2012). Especially when the information at the studied area is scarce or absent, even the qualitative application presents good results.

In the beginning of this study, we intended to verify the capacity of the geometric morphology methodology in describing the variability of fish bodies, in a highly diverse ecosystem, the Araçá bay.

The landmarks analysis was able to explain more than 95% of the morphological variability of the fish assemblages present at that area, exceeding

the expectations. The advantage of the method is to be low cost effective only requiring images from which outlines are extracted and analysed with statistical software. The homologue points (landmarks) previously defined in the analysis showed to influence in the species distribution inside the morphospace. Moreover, the semilandmarks were necessary and important to differentiate species concerning their fin adaptations or sensory organs presence, given the ecological value associated to these features.

The qualitative application of geometric morphology allowed defining the best samplers to represent the morphological composition of the fish assemblages, giving an overview of how they were spatially distributed inside the tidal plain. The catch effectiveness was differentiated according to the gear type employed.

Such methodology permitted the acquisition of indices of morphological diversity (MD, MR and EMI) which complemented the information about the shape variability inferring functions, roles and strategies of the fishes inhabiting the bay. It also was useful to predict the habitats of major richness. Indices of morphological diversity are independent of each other, being significantly correlated with other components of biodiversity (MD is linked to taxonomic diversity, EMI defines the structural and taxonomic complexity of the community, and MR is correlated to measures of specific richness and functional diversity) reinforcing their capacity as a complementary tool in biodiversity studies (FARRÉ et al. 2016).

The qualitative perspective will make possible to monitor the evolution of the Araçá fish assemblages along large temporal scales from a list of fish presence/absence. On the other side, the quantitative application of the geometric morphology enriched the knowledge about how fish assemblages use different habitats. The inclusion of fish density data in the morpho and functional spaces demonstrated the structure related to the functioning of the fish assemblages. Differences of abundancies reinforced the hypothesis that fish morphology is related to the complexity of the Araçá habitats: communities that have greater structural complexity (mixture of types of substrates) contain a greater number of body forms since they allow to support a greater variability of ecological strategies.

The habitat complexity affects significantly the ecological composition of the fish assemblages. Fishes living in habitats comprising different substrates, and close to mangrove zones or rocks presented more rich composition and density, whereas simple bottoms were ecologically simpler and less populated. Although the pattern of species distribution in the morphological and functional spaces was similar between the two most diverse habitats (IH and IOS), they presented differences related to dominant species, number of functional groups, functional redundancy and availability of resources.

The functional diversity increased with the habitat complexity, which cause an impoverishment of the functionality at less complex habitats. In the IH, due to the high availability of resources, fish species showed higher degrees of specialization and the differentiation of the niche, thus reducing interspecific competition. In this way, less complex habitats showed enlarged morphological and functional redundancies. Since functional redundancy acts as biological insurance against diversity loss, IH must be a priority protected area, and has to be monitored.

As a multifunctional tool, the landmarks analysis was adequate to quantify the correspondence among otoliths shapes and fish body shapes. Landmarks analysis together with the aspect ratio of the otolith weight were the best methods for species discrimination and for recognizing ecological aspects of the fishes at the Araçá bay. Details of the sulcus acusticus clarified the intraspecific variabilities, rendering the landmarks analysis of otoliths a richer source of information for biological studies, more than the structures contours or outlines.

The results of this thesis reinforce the idea that fish morphology is a valid tool to investigate their ecological and functional roles within ecosystems. The landmarks analysis of fish body shape allows inferring the main aspects of the habitats functioning, such as the species distribution, habitat influences, resources use, coexistence, competition and dominance.

Additionally, landmarks analysis of otoliths emphasized fish ecological patterns, detailing the intraspecific variability embedded in the sulcus acusticus morphology and size. Therefore, the morphology remains an active tool and can help to improve studies on fish assemblages structure, organization and functioning in ecosystems with high diversity.

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